

Sources of sire-specific genetic variance for birth and weaning weight in *Bruna dels Pirineus* beef calves

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This research investigated two sources of sire-specific genetic effects on the birth weight (BWT) and weaning weight (WWT) of Brunna dels Pirineus beef calves. More specifically, we focused on the influence of genes located in the non-autosomal region of the Y chromosome and the contribution of paternal imprinting. Our analyses were performed on 8130 BWT and 1245 WWT records from 12 and 2 purebred herds, respectively, they being collected between years 1986 and 2010. All animals included in the study were registered in the Yield Recording Scheme of the Brunna dels Pirineus breed. Both BWT and WWT were analyzed using a univariate linear animal model, and the relevance of paternal imprinting and Y chromosome-linked effects were checked by the deviance information criterion (DIC). In addition to sire-specific and direct genetic effects, our model accounted for random permanent effects (dam and herd-year-season) and three systematic sources of variation, that is, sex of the calf (male or female), age of the dam at calving (six levels) and birth type (single or twin). Both weight traits evidenced remarkable effects from the Y chromosome, whereas paternal imprinting was only revealed in WWT. Note that differences in DIC between the preferred model and the remaining ones exceed 39 000 and 2 800 000 DIC units for BWT and WWT, respectively. It is important to highlight that Y chromosome accounted for ~2% and ~6% of the total phenotypic variance for BWT and WWT, respectively, and paternal imprinting accounted for ~13% of the phenotypic variance for WWT. These results revealed two relevant sources of sire-specific genetic variability with potential contributions to the current breeding scheme of the Brunna dels Pirineus beef cattle breed; moreover, these sire-specific effects could be included in other beef cattle breeding programs or, at least, they must be considered and appropriately analyzed.

Keywords: *Brunna dels Pirineus*, sire-specific genetic variance, birth weight, weaning weight

Implications

Despite the fact that sire-specific genetic effects are typically ignored in genetic evaluation models, their real impact remains almost unknown in livestock species. Both Y chromosome-related effects and paternal imprinting effects were evaluated on birth and weaning weight (WWT) in the *Brunna dels Pirineus* beef cattle breed. Whereas Y chromosome effects influenced both traits and accounted for ~2% and 6% of the phenotypic variance, respectively, paternal imprinting effects restricted to WWT (~13% of the phenotypic variability). Our results highlighted the relevance of these sire-specific sources of variation in beef cattle, and provided relevant information to optimize genetic evaluation models for weight traits.

Introduction

Quantitative genetic studies in beef cattle typically rely on the direct infinitesimal polygenetic effect (Henderson, 1973)

and sometimes on maternal genetic effects (Quintanilla *et al.*, 1999). These additive genetic effects derive from the contribution of both parents on the offspring's genome, although parent-of-origin-specific effects have been previously suggested in beef cattle (Bünger *et al.*, 1995; Goodall and Schmutz, 2007). Focusing on sire-specific variability, both the influence of genes from the non-autosomal region of the Y chromosome and the effect of paternal imprinting must be anticipated as potential sources of non-Mendelian inheritance. Nevertheless, little is known about the impact of these genetic mechanisms on productive traits in beef cattle.

Contradictory results about the impact of the Y chromosome on carcass traits in Simmental cattle were provided by Reinsch *et al.* (1999) and Neugebauer *et al.* (2010), although large effects were discarded. However, in mice, Schwenker and Maxon (1986) and Bünger *et al.* (1995) reported significant influences from the Y chromosome on growth, BW and testis weight. A similar scenario was found for the imprinting phenomenon in beef cattle where available

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results restricted to original researches conducted on German Gelbvieh (Engellandt and Tier, 2002) and Simmental cattle (Neugebauer *et al.*, 2010); imprinting variability was revealed on several carcass traits. Furthermore, some imprinted quantitative trait loci have been detected in livestock species for growth and fatness traits (De Koning *et al.*, 2001a and 2011b).

Given the shortage of results on the contribution of paternal genetic effects in beef cattle, this manuscript focused on the Bayesian modeling of two sire-specific additive genetic variances on birth weight (BWT) and weaning weight (WWT) traits in the *Bruna dels Pirineus* beef cattle breed.

Material and methods

Animal Care and Use Committee approval was not obtained for this study because analyses were performed on existing data obtained under standard management from commercial farms. Both productive and reproductive data were collected by the stockbreeders themselves and managed by the *Bruna dels Pirineus* Breed Society (FEBRUPI; <http://www.brunadelspirineus.org>) within the context of its Yield Recording Scheme.

Population and data source

This study was performed on field data from the *Bruna dels Pirineus* breed, an autochthonous beef cattle breed located in the mountainous areas of Catalonia (Northeastern Spain). The *Bruna dels Pirineus* is a medium-sized cattle breed (bulls, 950 to 1400 kg of live BW; cows, 550 to 950 kg of live BW) with an approximate census of 30 000 cows (FEBRUPI, personal communication). This breed is reared under extensive conditions for the production of beef calves; they reach an average carcass weight at slaughter of 330 kg (~12.5 months; Serra *et al.*, 2004).

Raw data from purebred calves were recorded between 1985 and 2010 in 12 herds participating in the Yield Recording Scheme of the *Bruna dels Pirineus* breed. This study focused on BWT and 185 day-standardized WWT, following the guidelines from the Beef Improvement Federation (1986). Herds were chosen on the basis of their genetic connectedness following Tarrés *et al.* (2010). Calves lighter than 20 kg or heavier than 70 kg at birth were removed from the final data set, as well as those calves with WWT smaller than 120 kg or larger than 400 kg. Moreover, calves with unknown paternity were discarded in order to prevent disturbances in the analysis of the effect of sire lineage (see below). After editing, only those herds contributing a minimum of 100 calves with BWT or WWT data were included in the analyses. Final data sets consisted of 8130 BWT records and 1245 WWT records from 12 and 2 herds, respectively. Note that these two herds contributing WWT data were also involved in the analysis of BWT.

Pedigree file for BWT included 10 266 animals with 230 sires and 2671 dams, whereas WWT pedigree had 1799 individuals, 97 and 565 of them being bulls and cows with registered offspring, respectively. As Y chromosome effects

are inherited from father to sons without changes, it was important to identify every sire lineage where this effect was shared. For each male offspring, the origin of its Y chromosome was traced back to the oldest male ancestor in the pedigree. This study included 47 sire lineages for BWT and 34 for WWT.

Statistical analyses

Operational model. For both weight traits, data (y) were analyzed under four different models. Nevertheless, only the most complex model (i.e. full model) will be described in detail in order to avoid redundancies in the manuscript. In addition to the systematic (\mathbf{b}), permanent and genetic effects outlined below, the full model (model **YI**) accounted for the Y chromosome permanent genetic effect (\mathbf{s}) and the paternal imprinting additive genetic effect (\mathbf{i}). The three remaining models assumed the same structure of model **YI**; however, they excluded Y chromosome effects (model **IN**), paternal imprinting effects (model **YN**) or both Y chromosome and paternal imprinting effects (model **NN**). Focusing on model **YI**, it was stated as

$$y = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{i} + \mathbf{Z}_3\mathbf{d} + \mathbf{Z}_4\mathbf{h} + \mathbf{Z}_5\mathbf{s} + \mathbf{e}$$

where \mathbf{a} was the vector of direct additive infinitesimal genetic effects, \mathbf{d} was the vector of dam-specific permanent environmental effects, \mathbf{h} was the vector of herd-year-season permanent environmental effects, \mathbf{e} was the vector of residual terms and \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , \mathbf{Z}_3 , \mathbf{Z}_4 and \mathbf{Z}_5 were appropriate incidence matrices. Systematic effects accounted for the age of the dam at calving with six categories as defined by Casellas and Piedrafita (2002), birth type (single or twins), and sex of the calf (male or female).

Bayesian inference. All models were analyzed under a Bayesian approach. The joint posterior distribution of all unknown parameters in model **YI** was proportional to

$$\begin{aligned} p(\mathbf{b}, \mathbf{a}, \mathbf{i}, \mathbf{d}, \mathbf{h}, \mathbf{s}, \sigma_e^2, \sigma_a^2, \sigma_h^2, \sigma_s^2, \mathbf{G} | \mathbf{y}) &\propto p(\mathbf{y} | \mathbf{b}, \mathbf{a}, \mathbf{i}, \mathbf{d}, \mathbf{h}, \mathbf{s}, \sigma_e^2) \\ p(\mathbf{b})p(\mathbf{a}, \mathbf{i} | \mathbf{A}, \mathbf{G})p(\mathbf{G}) &\times p(\mathbf{d} | \sigma_d^2)p(\sigma_d^2)p(\mathbf{h} | \sigma_h^2)p(\sigma_h^2) \\ p(\mathbf{s} | \sigma_s^2)p(\sigma_s^2)p(\sigma_e^2) \end{aligned}$$

where \mathbf{A} was the numerator relationship matrix (Wright, 1922) with genetic groups (Westell *et al.*, 1988). Following Casellas *et al.* (2007), BWT analyses accounted for 28 genetic groups, 25 for unknown sires and 3 for unknown dams, whereas WWT analyses accounted for 6 genetic groups, 5 for unknown sires and 1 for unknown dams. In a Bayesian setting, the joint *a priori* distribution of \mathbf{a} and \mathbf{i} effects was assumed multivariate normal,

$$p(\mathbf{a}, \mathbf{i} | \mathbf{A}, \mathbf{G}) = \text{MVN}(0, \mathbf{G} \otimes \mathbf{A})$$

where \mathbf{G} was the additive genetic (co)variance matrix with structure $\mathbf{G} = \begin{bmatrix} \sigma_a^2 & \sigma_{aj} \\ \sigma_{aj} & \sigma_j^2 \end{bmatrix}$, and σ_a^2 , σ_j^2 and σ_{aj} were the direct additive genetic variance, paternal imprinting variance and the genetic covariance, respectively. *A priori* distributions for

random permanent effects were also assumed multivariate normal,

$$p(\mathbf{d}|\sigma_d^2) = MVN(0, \mathbf{I}_d\sigma_d^2)$$

$$p(\mathbf{h}|\sigma_h^2) = MVN(0, \mathbf{I}_h\sigma_h^2)$$

$$p(\mathbf{s}|\sigma_s^2) = MVN(0, \mathbf{I}_s\sigma_s^2)$$

$$p(\mathbf{e}|\sigma_e^2) = MVN(0, \mathbf{I}_e\sigma_e^2)$$

where \mathbf{I}_d , \mathbf{I}_h , \mathbf{I}_s and \mathbf{I}_e were identity matrices with dimensions as the number of elements stored in \mathbf{d} , \mathbf{h} , \mathbf{s} and \mathbf{e} , respectively. Note that σ_d^2 was the permanent environmental variance, σ_h^2 was the herd-year-season variance, σ_s^2 was the Y chromosome genetic variance and σ_e^2 was the residual variance. Flat priors were assumed for $p(b)$, $p(\sigma_d^2)$, $p(\sigma_h^2)$, $p(\sigma_s^2)$ and $p(\sigma_e^2)$.

Markov chain Monte Carlo (MCMC) sampling. Marginal posterior distributions of all unknowns were estimated by using the Gibbs sampling algorithm (Geman and Geman, 1984). After exploratory analyses, we launched three independent chains with 5 050 000 iterations for each analysis (i.e. model within phenotypic trait) and the first 50 000 were discarded as burn-in (Raftery and Lewis, 1992). A total of 100 000 samples of model parameters were saved from each chain with a lag interval of 50 iterations; samples from all three chains were used to characterize the posterior distribution of each model parameter invoking the ergodic property of the chains (Gilks *et al.*, 1996). The effective chain length of the MCMC process was calculated by Geyer (1992).

Model comparison. The within-trait statistical performance of models YI, NI, YN and NN was compared by the deviance information criterion (DIC; Spiegelhalter *et al.*, 1998 and 2002). This statistic measures model performance in two different ways, the posterior expectation of the Bayesian deviance (i.e. model fit) and the effective number of parameters (i.e. model complexity). A smaller value of DIC indicates a better fit of the model and a lesser degree of complexity. Note that reductions of three or more DIC units are typically considered as statistically relevant (Spiegelhalter *et al.*, 2002).

Results

Phenotypic and genealogic summary

A phenotypic summary of BWT and WWT in the *Bruna dels Pirineus* beef cattle breed is shown in Table 1. Calves contributing to our analyses averaged 45.6 ± 0.1 kg at birth and reached 235.5 ± 0.6 kg at weaning, although there were remarkable phenotypic differences linked to sex, birth type and age of the dam. Focusing on genealogical data, all individuals derived from 47 founder bulls which became the origin of the 47 sire lineages included in our analyses for BWT. In order to characterize the persistence and contribution of the different sire lineages in current generations, we focused on male calves born during the last 5 years (i.e. 2006 to 2010). Only 30 sire lineages contributed male calves since

Table 1 Number of records (*n*), mean and standard error (*s.e.*) of BWT and WWT for sex, type of birth and age of the dam at calving in the *Bruna dels Pirineus* beef cattle breed

	BWT (kg)			WWT (kg)		
	<i>n</i>	Mean ¹	<i>s.e.</i>	<i>n</i>	Mean ¹	<i>s.e.</i>
Sex of the calf						
Male	4083	47.0	0.1	635	242.2	0.9
Female	4047	44.3	0.1	610	228.5	0.7
Type of birth						
Single	7788	46.0	0.1	1209	235.7	0.6
Twin	342	37.3	0.3	36	227.5	3.4
Age at calving						
2	193	42.4	0.4	4	218.7	3.0
3	885	43.5	0.2	86	229.9	1.9
4	987	45.3	0.2	144	232.1	1.7
5	1017	45.7	0.2	159	232.5	1.5
6	980	46.1	0.2	156	234.7	1.6
>6	4068	46.2	0.1	696	237.9	0.8
Overall	8130	45.6	0.1	1245	235.5	0.6

BWT = birth weight; WWT = weaning weight.

¹Raw means from phenotypic data.

2006 (Figure 1a), whereas there were no offspring from 17 sire lineages, which could be extinct from our beef cattle population (36.2%). It is important to highlight that the contribution of the different sire lineages was highly heterogeneous. A unique sire lineage contributed 18% of male calves born during the last 5 years (lineage SL_B12), whereas there were 15 minority lineages with a joint contribution of 18% too (each one contributed <3% of male calves; Figure 1a). The remaining sire lineages generated between 3% and 7% of male calves.

In a similar way, the pedigree for WWT included 97 sires, 49 of them contributing calves with phenotypic data. Given that the analyses was restricted to two herds, only 34 sire lineages were identified and 18 of them (52.9%) contributed offspring during the last 5 years (52.9%). Four lineages individually contributed more than one-tenth of male calves (SL_W5, SL_W6, SL_W10 and SL_W13) and 50% of the lineages had residual contributions smaller than 3% of the individuals (Figure 1b).

Model comparison

Models were compared by the DIC statistic (Table 2). It is important to highlight that despite launching very long MCMC chains with 5 million iterations there were substantial departures across chains from the same model and phenotypic trait. Nevertheless, this variability did not contradict the final conclusions derived from average DIC estimates. This statistic clearly favored model YN for BWT and left model NN in the second position, with a DIC penalization exceeding 39 000 units. These results suggested that only Y chromosome-related effects could be reported for BWT, whereas there were no statistical evidences of paternal imprinting. On the other hand, model YI was clearly preferred for WWT, suggesting the influence of both sire-related sources of additive genetic variability, Y chromosome effects

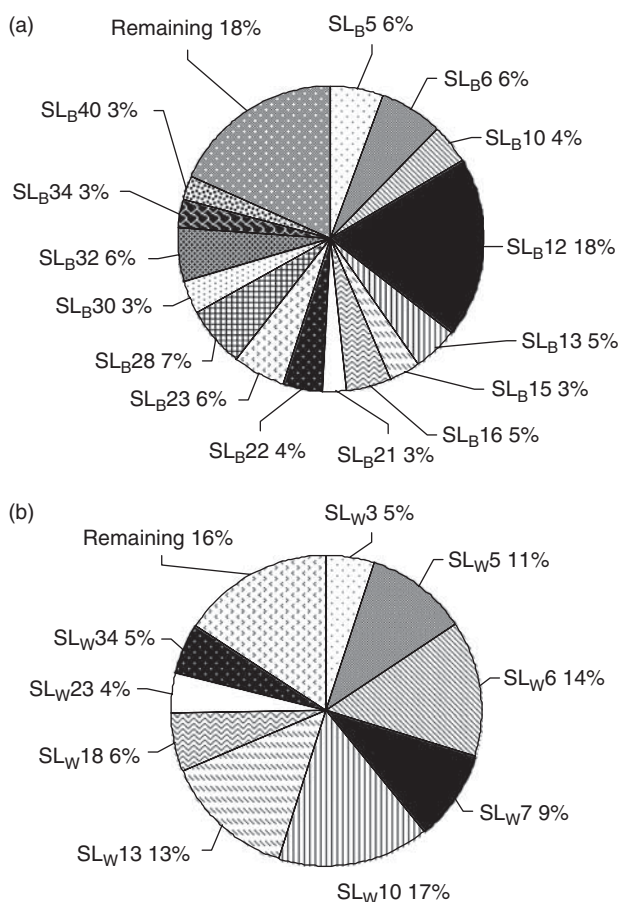


Figure 1 Sire lineages contributing offspring during the last 5 years (2006 to 2010) and percentage of male calves with phenotypic data for birth weight (a) and weaning weight (b).

and paternal imprinting effects. The average DIC estimate for the model YI in the WWT analysis was more than 2.8 million DIC units smaller than any other model implemented for this trait in the current manuscript (Table 2). From now on, estimates from the analysis of BWT and WWT will refer to the ones obtained under models YN and YI, respectively. The effective length of MCMC for genetic and residual variances is shown in Table 3.

Genetic variance components and sire lineage estimates

Additive genetic variance components and heritabilities for BWT and WWT were presented in Table 4. Direct heritabilities for BWT and WWT were 0.29 and 0.34, respectively, and paternal imprinting for WWT accounted for ~13% of the phenotypic variance; note that paternal imprinting was discarded for BWT. Although restricted to WWT, it is important to highlight that the genetic covariance between direct and paternal imprinting effects was -97.8, with a credibility interval (CI; percentiles 2.5% and 97.5%) ranging from -198.9 to -16.1. Note that this covariance led to a negative genetic correlation between direct and parental imprinted effects of -0.89. Moreover, these estimates were statistically relevant, with their CI excluding the null estimate in all cases. Focusing on Y chromosome effects, their variance

Table 2 DIC for BWT and WWT traits under the four competing models including effects from the Y chromosome (models YI and YN) and paternal imprinting (models YI and IN) or excluding both effects (model NN)

	Analytical model			
	NN	IN	YN	YI
BWT				
Chain 1	2 709 082	3 046 437	2 669 669	3 018 774
Chain 2	2 707 984	3 044 791	2 667 828	3 015 607
Chain 3	2 710 699	3 050 242	2 671 033	3 004 168
Mean	2 709 255	3 047 157	2 669 510	3 012 850
s.e.	789	1614	929	4436
WWT				
Chain 1	129 038 421	84 552 917	135 761 164	81 552 108
Chain 2	128 267 943	85 499 427	136 417 250	81 912 458
Chain 3	128 307 293	84 534 316	137 051 514	81 844 916
Mean	128 537 886	84 862 220	136 409 976	81 769 828
s.e.	250 525	317 116	372 510	110 592

DIC = deviance information criterion; BWT = birth weight; WWT = weaning weight.

Note that three independent Monte Carlo Markov chains were launched for the Bayesian analysis of each analytical model.

Table 3 Effective chain size for the Bayesian analysis of BWT and WWT under models YN and YI, respectively

	Variance component ¹				
	σ_a^2	σ_i^2	σ_{ai}	σ_s^2	σ_e^2
BWT					
Chain 1	132 999	- ²	-	898 046	179 697
Chain 2	143 507	-	-	901 889	214 320
Chain 3	137 416	-	-	913 034	182 266
Mean	137 974	-	-	904 323	192 094
s.e.	3046	-	-	4495	11, 137
WWT					
Chain 1	9455	2020	3953	101 477	10 965
Chain 2	9009	3029	4143	98 094	10 564
Chain 3	8807	2895	3656	93 434	10 082
Mean	9090	2648	3917	97 668	10 537
s.e.	191	316	142	2331	255

BWT = birth weight; WWT = weaning weight.

Note that three independent Monte Carlo Markov chains were launched for the Bayesian analysis of each analytical model.

¹ σ_a^2 = additive genetic variance; σ_i^2 = paternal imprinting variance; σ_{ai} = covariance between direct and paternal imprinting effects; σ_s^2 = Y chromosome variance; σ_e^2 = residual variance.

²Note that the model for WWT included both paternal imprinting and the effect of the Y chromosome, whereas the model for BWT did not account for paternal imprinting.

for BWT was 0.5 kg², with the CI ranging between 0.2 and 0.8 kg². These effects generated a variance of 32.4 kg² in WWT (CI: 2.5 to 92.3 kg²). It is important to highlight that Y chromosome effects accounted for ~2% of the total phenotypic variance of BWT and ~6% of WWT. The average estimates for the different sire lineages are shown in Figure 2. There was an important degree of heterogeneity for both traits,

Table 4 Variance components for BWT and WWT in the Bruna dels Pirineus beef cattle

Parameter ¹	BWT (kg)		WWT (kg)	
	Mean	Percentiles 2.5% to 97.5%	Mean	Percentiles 2.5% to 97.5%
σ_a^2	6.8	5.2 to 8.6	175.3	52.2 to 300.4
σ_i^2	– ²	–	68.6	8.4 to 169.1
σ_{ai}	–	–	–97.8	–198.9 to –16.1
σ_d^2	1.6	1.0 to 2.2	27.7	3.6 to 60.6
σ_h^2	1.6	1.1 to 2.1	34.4	11.2 to 82.8
σ_s^2	0.5	0.2 to 0.8	32.4	2.5 to 92.3
σ_e^2	13.0	12.0 to 14.2	180.14	113.6 to 244.9
h^2	0.29		0.34	
h_i^2	–		0.13	
h_s^2	0.02		0.06	

BWT = birth weight; WWT = weaning weight.

¹ σ_a^2 = additive genetic variance; σ_i^2 = paternal imprinting variance; σ_{ai} = covariance between direct and paternal imprinting effects; σ_d^2 = maternal permanent environmental variance; σ_h^2 = herd-year-season permanent environmental variance; σ_s^2 = Y chromosome variance; σ_e^2 = residual variance; h^2 = heritability of the trait; h_i^2 = imprinting effect heritability; h_s^2 = Y chromosome effect heritability.

² Note that the model for WWT included both paternal imprinting and the effect of the Y chromosome, whereas the model for BWT did not account for paternal imprinting.

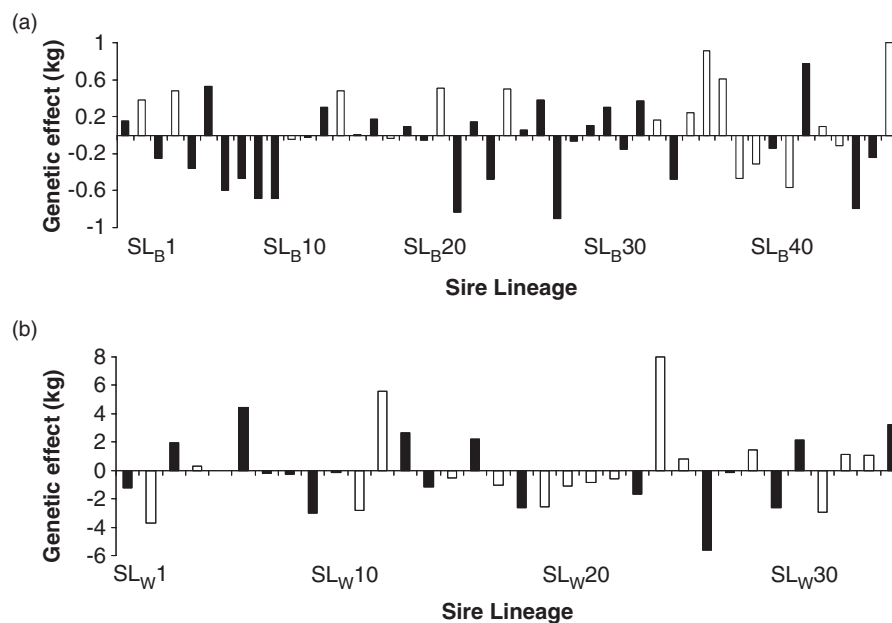


Figure 2 Average of the posterior distribution of the sire lineage effect for birth weight (a) and weaning weight (b). Black bars highlight sire lineages contributing calves during the last 5 years (2006 to 2010) and white bars are for the remaining sire lineages.

with maximum absolute contributions of ~ 1 kg for BWT and up to 8 kg for WWT.

Discussion

Bruna dels Pirineus data set

Analyses were performed on the *Bruna dels Pirineus* beef cattle breed, which is a representative example of meat-producing cattle population under a Mediterranean extensive production system. This is an autochthonous beef cattle breed reared under a traditional valley-mountain grazing in the Pyrenees Mountains of Catalonia (Northeastern Spain).

In order to put into context the *Bruna dels Pirineus* and to highlight the relevance for the beef cattle industry of the analyses performed in this breed, it is important to link its phenotypic performances with other beef cattle breeds. Average BWT (45.6 kg) and WWT (235.5 kg) were close to ones reported by Casellas and Piedrafita (2002) and Quintanilla *et al.* (1999) in the same breed and similar to the performances reported in other Spanish beef cattle breeds such as Asturiana de los Valles (Menéndez-Buxadera *et al.*, 2008) and Pirenaica (Villalba *et al.*, 2000). Focusing on international and worldwide distributed beef breeds, our weight phenotypes were comparable with the averages

reported in Charolais (Mujibi and Crews, 2009), Limousin (Tinker *et al.*, 1988) and Hereford (Eriksson *et al.*, 2004). It is well known that pedigree losses are usual in extensive beef cattle populations where paternity information can be difficult to register and the acquisition of foreign animals, mainly bulls, becomes common. Nevertheless, our percentage of missing data in the pedigree file was moderate (14.3% for BWT and 16.1% for WWT) and close to the one reported by Golden *et al.* (1994) in the Angus breed.

Several sire lineages were identified to study the impact of the non-autosomal region of the Y chromosome on beef traits. Although 47 sire lineages contributed data to BWT analyses, only 30 of them were present during the last 5 years. In a similar way, only 18 of the 34 original sire lineages for WWT contributed offspring during the last 5-year period (Figure 1). These values suggested the loss of multiple sire lineages, as well as their specific genetic background on BWT and WWT. Both the reduced number of breeding bulls and current selection program for these two weight traits could be the main reasons for this loss of genetic variability in the *Bruna dels Pirineus* breed. Note that these losses could be of special relevance if they had a substantial and positive effect on the different weight production traits.

Model comparison

Given the potential impact of the model on predicted breeding values and other parameters, making comparisons between candidate models becomes a topic of major interest in research oriented to animal breeding programs. Within this context, the DIC was calculated to elucidate the most appropriate model for BWT and WWT when accounting for sire-specific genetic variances. Average DIC values favored model YN for BWT, suggesting the incidence of Y chromosome effects while discarding paternal imprinting. On the other hand, both Y chromosome and paternal imprinting effects were postulated for WWT given the DIC outcome provided by model YI and competing models (Table 2). Although the inclusion of additive genetic terms (*a* and *i*) in the model implied a relevant increase in model parameterization, DIC suggested a sufficient compensation in terms of model fit for WWT data. Note that DIC estimates evidenced substantial departures when comparing independent chains from the same analysis (Table 2), although this variability did not contradict the final conclusions derived from average DIC estimate, and its standard error was smaller than 1% of the average DIC in all cases (Table 2). Moreover, the smallest effective chain lengths for genetic and residual variances were comparables to the values provided by other studies on sire-specific genetic variability in beef cattle (Reinsch *et al.*, 1999).

In contrast to other studies focusing on traits at adult ages (e.g. Neugebauer *et al.*, 2010) where the influence of the maternal environment must be almost null, we focused our analyses on weight traits that were clearly influenced by the permanent environment provided by the cow (Quintanilla *et al.*, 1999). Within this context, the current parameterization for paternal imprinting could not be generalized to the

maternal component because maternal imprinting and direct maternal effects were confounded and the final model was not identifiable. Indeed, we preferred to accumulate all maternal contributions into the *d* vector assuming that, if existed, maternal effect through milk and both maternal imprinting and effects from the mitochondrial DNA would accumulate there (Neugebauer *et al.*, 2010).

Variance components and sire lineage estimates

The analysis of BWT revealed that ~2% of the phenotypic variance was accounted for by σ_s^2 , whereas this percentage increased up to ~6% for WWT. These results partially agreed with those reported by Engellandt and Tier (2002) and Neugebauer *et al.* (2010) in Gelbvieh and Simmental cattle, respectively, although contradictory results were also available (Reinsch *et al.*, 1999). The influence of the Y chromosome was previously highlighted by Kieffer and Cartwright (1968) and Schoeman (1989), who reported that even the morphology of this chromosome (i.e. acrocentric *v.* submetacentric) was associated with variations in the BWT of Brahman, Angus and Tuli calves. Note that *Bos taurus* and *Bos indicus* trunks differed in the Y chromosome, which is submetacentric and acrocentric, respectively (Potter and Upton, 1979). Nevertheless, *Bruna dels Pirineus* breed must be free from genetic influences from the *B. indicus* bovine trunk. As a consequence, σ_s^2 should not be related to the shape of the Y chromosome but to polymorphisms located on the non-pseudo-autosomal region of the Y chromosome, as suggested by Maxon (1990) and Bünger *et al.* (1995) in other mammalian species. In laboratory species, Maxon (1990) and Sluyter *et al.* (1996) found influences due to the Y chromosome on the aggressive behavior and Bünger *et al.* (1995) described influences on growth.

The effect of each sire lineage in the *Bruna dels Pirineus* population was shown in Figure 2. Note that black bars characterized sire lineages contributing offspring during the last 5 years, whereas white bars showed probably extinct sire lineages. While discarding these non-contributing sire lineages, it is important to highlight the heterogeneity inherent to the different sire lineage effects (Figure 2). These estimates must be viewed as a direct contribution for the *Bruna dels Pirineus* breeding scheme in which higher BWT is prevented because the incidence of dystocia and sires contributing average and smaller BWTs becomes preferable (VanRaden and Klaaskate, 1993), mainly for heifers. In a similar way, sire lineages for WWT also revealed a substantial degree of heterogeneity, providing a new and relevant source of genetic variability for the selection program.

Paternal imprinting effects were discarded for BWT, whereas they accounted for ~13% of the phenotypic variance for WWT. Note that we lack comparable results about the possibility of imprinting at early ages, whereas results from the WWT analysis would be comparable to the significant imprinting variances reported by Engellandt and Tier (2002) and Neugebauer *et al.* (2010) on fatness and carcass traits at older ages. Indeed, one of the main examples of paternally imprinted genes in livestock is the *Igf2*, which is systematically linked to

muscle mass and fat deposition (Jeon *et al.*, 1999; Nezer *et al.*, 1999); note that fat is scarce at birth and the deposition of both tissues increases with age during the growing period, with *Igf2* being typically associated with carcass traits at older ages (Goodall and Schmutz, 2007). Although there are no evidences of segregating *Igf2* polymorphisms in the *Bruna dels Pirineus* breed, this kind of biological backgrounds could be a suitable example for the differential contribution of paternal imprinting at birth and at weaning.

Conclusions and final remarks

In order to assess the relevance of sire-specific genetic variability on productive traits of interest for the beef industry, the contribution of both paternal imprinting and the Y chromosome was analyzed on weight traits in the *Bruna dels Pirineus* breed. Both sources of genetic variability contributed relevant genetic variability with the only exception of paternal imprinting on BWT. Indeed, ~19% of the phenotypic variance for WWT was accounted for by these sire-specific effects that must be addressed in further genetic evaluations. These results allow for a better characterization of the genetic background of weight traits in beef cattle and must be viewed as an appealing starting point to decipher the genetic architecture of these imprinting and Y chromosome effects. Moreover, they must be accounted for in the current breeding scheme of the *Bruna dels Pirineus* beef cattle breed.

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