Canalization analysis of birth weight in Bruna dels Pirineus beef cattle[1]

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ABSTRACT: Although heteroskedasticity has been a main topic of interest in beef cattle during recent decades, the current availability of canalization models provided new insights for animal breeding programs. Within this context, birth BW (BWT) was analyzed in the Bruna dels Pirineus beef cattle breed by implementing canalization models that accounted for heterogeneous residual variances due to systematic, permanent environmental effects and additive genetic effects. Analyses were performed on BWT data from 8,130 calves born in 12 commercial breeding herds contributing to the yield recording scheme of the Bruna dels Pirineus breed. Analytical models accounted for direct additive genetic, permanent environmental, and 4 systematic effects (i.e., age of the dam, sex of the calf, birth type, and herd-year-season), and the same effects were evaluated as potential sources of variation in the residual term. Their relevance was checked by the deviance information criterion (DIC), and only residual additive genetic, permanent environmental, birth type, and herd-year-season remained in the operational model, all of them originating relevant reductions in the DIC parameter. Bruna dels Pirineus calves showed a moderate heritability of 0.30 (95% high posterior density, 0.19 to 0.40) for BWT; additional additive genetic variability was revealed in the residual term, this being positively correlated with the direct additive genetic component (0.44; 95% high posterior density, 0.37 to 0.54). Genetic trends were evaluated on both sources of additive genetic variance, and relevant patterns were identified in several herds. Although this breed did not evidence a homogeneous genetic trend for the whole population, herd-specific positive and negative trends were revealed, suggesting the plausibility of genetic selection for canalization on BWT in beef cattle breeds. These results must be viewed as a contribution to the canalization research field, providing relevant information for the breeding scheme of the Bruna dels Pirineus breed, as well as important insights about the genetic background of BWT for the beef industry worldwide.

Key words: Bayesian analysis, birth weight, Bruna dels Pirineus, canalization, heterogeneous variance

INTRODUCTION

Currently, the performance of the livestock industry in developed countries is high, and this tends to focus its concern on offering homogeneous-quality products. The reduction of heterogeneity at the production level is receiving special attention from all animal production research fields, as this is a new challenge for animal breeding as well. Current genetic evaluation models typically include the unaccounted variability into a common residual variance term, although it is well known that heterogeneous residual variances were reported in almost all livestock species, e.g., litter size and slaughter weight in pigs (Sorensen and Waage-petersen, 2003; Ibáñez-Escriche et al., 2007), BW in poultry (Rowe et al., 2006), litter size in sheep (San-Cristobal-Gaudy et al., 2001), and weight and dairy traits in beef and dairy cattle (Rodríguez-Almeida et al., 1995; Robert-Granié et al., 1999). These studies and other evidence reported in laboratory species (Gutiér-

rez et al., 2006; Ibáñez-Escriche et al., 2008a) suggested the possibility of modifying the additive genetic background of the residual variation by selection. It is important to highlight that specific hierarchical models accounting for genetic variability on both the trait itself and its residual variance (i.e., canalization models) were released by SanCristobal-Gaudy et al. (1998) and Sorensen and Waagepetersen (2003).

Birth BW (**BWT**) is a major breeding objective in the Bruna dels Pirineus beef cattle breed, where extreme BWT are discouraged to prevent dystocia (i.e., too heavy calves) and low neonatal vitality (i.e., too light calves) and their subsequent penalization of cow and calf survival (Tarrés et al., 2004, 2005). Within this context, the implementation of canalization models to account for the variability pattern of BWT would be of special interest in this breed, providing a reliable example for worldwide beef cattle populations under extensive production systems. Our main objectives were to investigate the presence of additive genetic effects influencing residual variation of BWT in the Bruna dels Pirineus beef cattle and to explore genetic trends after several years of stabilizing selection on BWT.

MATERIALS AND METHODS

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

Population and Field Data Source

Analyses were performed on BWT data from the Bruna dels Pirineus cattle, an autochthonous beef breed located in the mountainous areas of Catalonia (northeastern Spain) and with an approximate census of 30,000 cows (FEBRUPI, personal communication). This breed originated from the cross of native cattle with imported old-type Brown Swiss individuals during the first decades of the 20th century. After that, animals were empirically selected for meat production purposes. This breed is typically reared under extensive conditions for the production of beef calves with an average carcass weight at slaughter of 330 kg (~12.5 mo of age; Serra et al., 2004). Its herd book was founded in 1990 and anticipated the implementation of a genetic selection program including BWT as selection objective, among others. Note that BWT was under stabilizing selection to prevent too high and low weights at birth and the sub-

Table 1. Phenotypic summary of birth BW in the Bruna dels Pirineus beef cattle breed

Factor	n	Phenotypic mean, kg		Phenotypic variance, kg²	
		Estimate	95% Confidence interval	Estimate	95% Confidence interval
Sex of the calf					
Male	4,083	46.98[a]	46.81 to 47.15	31.02[a]	29.72 to 32.41
Female	4,047	44.27[b]	44.11 to 44.43	26.13[b]	25.03 to 27.31
Type of birth					
Single	7,788	46.00[a]	45.88 to 46.11	27.47[a]	26.63 to 28.36
Twin	342	37.26[b]	36.73 to 37.78	24.43[a]	21.14 to 28.55
Age at calving					
2 yr	193	42.42[c]	41.60 to 43.23	33.12[a]	27.37 to 40.88
3 yr	885	43.54[c]	43.20 to 43.88	26.86[a]	24.52 to 29.55
4 yr	987	45.36[b]	45.01 to 45.70	30.22[a]	27.72 to 33.08
5 yr	1,017	45.72[a,b]	45.39 to 46.06	29.54[a]	27.13 to 32.29
6 yr	980	46.12[a,b]	45.77 to 46.47	31.01[a]	28.44 to 33.95
>6 yr	4,068	46.16[a]	46.00 to 46.33	29.43[a]	28.19 to 30.75
Herd					
1	1,726	45.44[c]	45.22 to 45.67	22.8[c]	21.36 to 24.41
2	701	45.22[c]	44.91 to 45.53	17.56[d]	15.86 to 19.56
3	170	41.29[e]	40.83 to 41.74	8.98[e]	7.34 to 11.26
4	315	46.35[b]	45.81 to 46.88	23.12[c]	19.89 to 27.21
5	384	46.55[b]	46.05 to 47.05	24.71[c]	21.56 to 28.63
6	387	45.77[b,c]	45.28 to 46.25	23.39[c]	20.41 to 27.07
7	2,088	47.32[a]	47.08 to 47.56	32.11[b]	30.24 to 34.15
8	385	42.10[d,e]	41.71 to 42.50	15.63[d]	13.64 to 18.11
9	154	42.94[d]	42.15 to 43.72	24.48[b,c]	19.80 to 31.04
10	184	41.66[d,e]	40.79 to 42.54	36.19[a,b]	29.79 to 44.92
11	1365	46.07[b]	45.74 to 46.10	39.20[a]	36.42 to 42.32
12	271	42.29[d,e]	41.58 to 43.00	35.59[a,b]	30.27 to 42.45
Overall	8,130	45.63	45.51 to 45.75	30.42	29.51 to 31.38

[a–e]Estimates with the same superscript did not differ significantly ($P < 0.05$).

sequent increase in calf mortality due to dystocia and neonatal weakness, respectively (Tarrés et al., 2005).

Data from 8,130 calves were recorded between 1986 and 2010 in 12 commercial breeding herds contributing to the yield recording scheme of the Bruna dels Pirineus breed (Table 1). Note that calves with too extreme BWT (i.e., <20 kg or >70 kg) were previously removed from the data set, and only those herds with pedigree connection (Tarrés et al., 2010) and contributing a minimum of 100 calves with recorded BWT were considered. This restriction was applied to ensure a proper characterization of within-herd genetic trends for BWT. The pedigree file contained 10,266 individuals, including 230 sires and 2,671 dams; both sire and dam were known for all calves contributing phenotypic data.

Analytical Model

On the basis of the model developed by Sorensen and Waagepetersen (2003), the following hierarchical structure was assumed for the analysis of BWT data:

$$y_i = \mathbf{x}_i'\mathbf{b} + \mathbf{w}_i'\mathbf{p} + \mathbf{z}_i'\mathbf{a} + \exp\left(\frac{\chi_i'\beta + \omega_i'\pi + \zeta_i'\alpha}{2}\right)\varepsilon_i,$$

where y_i is the BWT phenotype of the ith individual, $\mathbf{b}$ and β are vectors of systematic effects, $\mathbf{p}$ and π are vectors of permanent environmental effects, $\mathbf{a}$ and α are vectors of infinitesimal additive genetic effects, and ε_i is a random variable from a standard Gaussian distribution. Note that $\mathbf{x}_i$, $\mathbf{w}_i$, $\mathbf{z}_i$, χ_i, ω_i, and ζ_i are appropriate incidence vectors.

Under a standard Bayesian approach, the a priori distribution for additive genetic effects (i.e., $\mathbf{a}$ and α) was assumed to be multivariate Gaussian:

$$\begin{pmatrix}\mathbf{a}\\\alpha\end{pmatrix}\bigg|\sigma_a^2,\sigma_\alpha^2,\mathbf{A},\rho = N\left(\begin{bmatrix}\mathbf{0}\\\mathbf{0}\end{bmatrix},\begin{bmatrix}\sigma_a^2 & \rho\sigma_a\sigma_\alpha\\\rho\sigma_a\sigma_\alpha & \sigma_\alpha^2\end{bmatrix}\otimes\mathbf{A}\right),$$

where $\mathbf{0}$ is a zeroing vector with dimensions equal to the number of individuals in the pedigree file, $\mathbf{A}$ is the additive genetic relationship matrix (Wright, 1922), σ_a^2 is the direct additive genetic variance of the trait, σ_α^2 is the residual additive genetic variance of the residual variability, ρ is the coefficient of genetic correlation, and $\otimes$ is the Kronecker product. Vectors $\mathbf{p}$ and π were assumed to be independent, with a priori probabilities

$$\mathbf{p}\big|\sigma_p^2 = N\left(0,\mathbf{I}_p\sigma_p^2\right)$$

and

$$\pi\big|\sigma_\pi^2 = N\left(0,\mathbf{I}_\pi\sigma_\pi^2\right),$$

where $\mathbf{I}_p$ and $\mathbf{I}_\pi$ are identity matrices with dimensions equal to the number of elements in vectors $\mathbf{p}$ and π, respectively, and σ_p^2 and σ_π^2 are permanent environmental variances affecting the trait and its log variance, respectively. The variance parameters σ_a^2, σ_α^2, σ_p^2, and σ_π^2 were assigned to scale-inverted χ^2 a priori distributions, ρ was assigned to a uniform prior bounded between -1 and 1, and systematic effects (i.e., $\mathbf{b}$ and β) were assigned to unbounded uniform priors. Note that all models tested in subsequent sections derived from this parameterization and, in some cases, simplified its structure by removing appropriate parameters.

It is important to highlight that h^2 cannot be reduced to a unique value because residual variance changed among levels of the systematic effects (Ros et al., 2004; Ibáñez-Escriche et al., 2008a). Within this context, h^2 can be approximated as follows:

$$h_i^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_p^2 + \exp\left(\chi_i'\beta + \sigma_\alpha^2\big/2 + \sigma_\pi^2\big/2\right)},$$

where the resulting value accounts for a given combination of systematic effects (see Sorensen and Waagepetersen, 2003, for additional details).

Comparison of Model Fit

On the basis of the model developed above, all analyses were performed by assuming $\mathbf{b}$, $\mathbf{p}$, and $\mathbf{a}$ as defined in previous analyses of the same data set (Casellas and Piedrafita, 2002). More specifically, $\mathbf{b}$ accounted for the population mean, sex of the calf (male or female), age of the dam at calving with 6 levels (2, 3, 4, 5, 6, and >6 yr), birth type (single or twins), and herd-year-season with 135 levels. Vector $\mathbf{p}$ contained permanent maternal effects with 2,317 levels. Given the parametric complexity of the analytical model and the moderate size of the Bruna dels Pirineus data set, both genetic and environmental maternal effects were summarized into $\mathbf{p}$. This simplification partially agreed with Beef Improvement Federation (2010) recommendations and provided a less parameterized framework that must be viewed as a reasonable compromise between biological plausibility and computational robustness.

All model comparisons were performed by using the deviance information criterion (**DIC**) proposed by Spiegelhalter et al. (2002). This statistic combines a measure of model fit and a measure of model complexity where models with smaller DIC are favored. In general, differences between models larger than 3 to 5 DIC units are assumed as statistically relevant (Spiegelhalter et al., 2002). To evaluate the contribution to heteroskedasticity of the

elements in the expression $\chi_i'\beta + \omega_i'\pi + \zeta_i'\alpha$, we took as a starting point a base model where β was restricted to the population mean ($\chi_i'\beta = \mathbf{1}'\beta$; $\mathbf{1}' = \begin{bmatrix}1 & 0 & 0 & \dots & 0\end{bmatrix}$) and the terms $\omega_i'\pi$ and $\zeta_i'\alpha$ were removed (model HO; see the Results section). The relevance of the different sources of heteroskedasticity (i.e., random and systematic effects) was evaluated by a 2-step approach. The first step evaluated random effects π and α by comparing 3 models with $\mathbf{1}\beta + \omega_i'\pi$, $\mathbf{1}\beta + \zeta_i'\alpha$, and $\mathbf{1}\beta + \omega_i'\pi + \zeta_i'\alpha$, respectively. After that, the second step used a stepwise-like approach with forward selection (Hocking 1976; Casellas et al., 2010) to define the appropriate structure for the term $\chi_i'\beta$. As previously included in vector $\mathbf{b}$, candidate effects

for β were sex of the calf, age of the dam at calving, birth type, and herd-year-season. This stepwise approach took place through different rounds that started with the base model defined in the previous step. At each round, the base model was compared with several competing models generated by the independent inclusion of each systematic effect. The competing model with the lowest DIC was assumed as the base model for the next round. The stepwise selection procedure finished when the base model obtained a DIC smaller than any competing model.

All analyses were performed with the GSEVM software package (http://www.bdporc.irta.es/estudis.jsp) developed by Ibáñez-Escriche et al. (2010). The results for each model were computed by averaging estimates obtained from 3 independent Monte Carlo Markov chains (**MCMC**) with 500,000 iterations. The first 5,000 iterations were discarded as burn-in (Raftery and Lewis, 1992), and only 1 sample of each 10 was saved to avoid the high correlation between consecutives samples.

Genetic Trends

Within-flock, across-year genetic trends were computed to reveal genetic changes on BWT as well as its dispersion pattern. The posterior distribution of within-year average breeding values (i.e., a and α) was characterized within herd at the end of the MCMC process. Although 12 herds contributed phenotypic data to this study, 2 pairs of them were grouped for genetic trend purposes given their geographic proximity and to avoid too small samples when averaging breeding values. The first group was composed of herds 1 and 3, and the second group was composed of herds 10 and 12.

RESULTS

Phenotypic Performances

The phenotypic summary of BWT in the Bruna dels Pirineus beef cattle breed is shown in Table 1. Calves averaged 45.63 kg at birth, with a phenotypic variance of 30.42 kg^2. Phenotypic means showed significant ($P < 0.05$) departures across levels of birth type, sex of the calf, age of the dam, and herd, whereas significant differences ($P < 0.05$) for phenotypic variability were restricted to herd and sex (Table 1). More specifically, male calves showed larger variability (31.02 kg^2) when compared with females (26.13 kg^2), and within-herd phenotypic variances fluctuated between 8.98 and 39.20 kg^2. Although sex-specific differences in the mean and variance showed a similar trend (i.e., the largest mean was linked to larger variance), this did not generalize to herds; herds 10 and 12 showed small averages and

Table 2. Stepwise rounds for model selection[1]

Item	Stepwise rounds		
	1	2	3
Base model[2]			
Effects	0	HYS	HYS + BT
DIC	2,920,305	2,603,536	2,482,593
Tested effect			
Age of the dam	2,912,759	2,671,208	2,500,636
Sex of the calf	2,884,956	2,524,370	2,616,098
Birth type (BT)	2,921,794	2,482,593	
Herd-year-season (HYS)	2,603,536		
Selected effect[3]	HYS	BT	none
DIC difference[4]	−316,769	−120,943	

[1] Models were compared in terms of deviance information criterion (DIC; Spiegelhalter et al. 2002).

[2] Reference model obtained from the previous stepwise iteration. This model accounted for 2 random sources of variation (permanent environmental and additive genetic effects) and the systematic effects selected during the previous stepwise rounds in the heteroskedasticity term.

[3] Systematic effect from the model with the smallest DIC value.

[4] DIC difference between the base model and the competing model with the smallest DIC value.

large variances, whereas herd 1 had small variance and a moderate to large mean for BWT (Table 1).

Model Comparison

We took as a starting point the homoscedastic mixed linear model (**model HO**) defined by Casellas and Piedrafita (2002) in the Bruna dels Pirineus breed; this model accounted for systematic (i.e., age of dam at calving, sex of the calf, birth type, and herd-year-season effects), permanent environmental, and additive genetic effects and assumed the same common residual variance for all BWT data. This model provided the poorest goodness of fit, with a DIC value of 3,156,557 units. A first round of evaluations focused on the random sources of variation for the variance term (i.e., π and α). The independent inclusion of π and α reduced DIC to 2,979,213 and 2,925,557, respectively; a joint model with both π and α provided a DIC value of 2,920,305. Within this context, this last model accounting for both random sources of variation in the variance term was used as the base model for evaluating the relevance of the different systematic effects (Table 2). The first 2 stepwise rounds sequentially picked herd-year-season and birth type, with DIC values of 2,603,536 and 2,482,593, respectively. This stepwise process ended in the third round, where neither age of the dam nor sex of the calf reduced the DIC (Table 2). Within this context, the heteroscedastic model accounting for herd-year-season, birth type, π and α was used to estimate model parameters and genetic trends (**model HE**).

Table 3. Posterior mean and 95% credibility interval of variance components for birth BW in the Bruna dels Pirineus beef cattle breed

Variance component[1]	Model HO[2]		Model HE[3]	
	Mean	95% Credibility interval	Mean	95% Credibility interval
σ_a^2	6.42	4.72 to 8.23	5.88	5.00 to 6.23
σ_p^2	1.58	1.07 to 2.12	0.70	0.56 to 1.10
σ_e^2	13.22	12.14 to 14.28	—	—
σ_α^2	—	—	0.55	0.36 to 0.69
σ_π^2	—	—	0.20	0.12 to 0.30
ρ	—	—	0.44	0.37 to 0.54
h^2	0.30	0.23 to 0.38	0.30	0.19 to 0.40

[1]Components: σ_a^2 (σ_α^2) = direct (residual) additive genetic variance of the trait; σ_p^2 (σ_π^2) = direct (residual) permanent environmental variance of the trait; σ_e^2 = residual variance; ρ = genetic correlation. Heritability refers to single-birth calves from average herd-year-season effect.

[2]Homoscedastic mixed linear model. A dash indicates not estimable.

[3]Heteroscedastic mixed linear model accounting for herd-year-season, birth type, permanent environment and additive genetic effects in the variance term. A dash indicates not estimable.

Systematic Effects

Model HE identified 2 systematic sources of heteroskedasticity on BWT in the Bruna dels Pirineus breed, birth type and herd-year-season. Whereas the contribution of single-birth calves in vector **β** was fixed to zero as a reference, twins reached an average estimate of 1.78, with a 95% credibility interval ranging from 0.76 to 2.90. Herd-year-season had 135 independent levels, and their posterior averages spanned from −0.60 to 1.92; the average herd-year-season effect was 0.77.

Variance Components

Table 3 reported posterior means and 95% credibility intervals for the variance components derived from models HO and HE. Although model HO was clearly discarded by the DIC, its variance component estimates were provided to compare the performance of both heteroscedastic and homoscedastic parameterizations. Although σ_a^2 did not differ at a statistically relevant level between models HO and HE (i.e., 95% credibility intervals overlapped), σ_α^2 reached a moderate estimate, and its 95% credibility intervals did not include the zero value, thus supporting the evidence of additive genetic control for residual variation. Focusing on model HE, the posterior mean for ρ was 0.44, and its 95% credibility interval ranged between 0.37 and 0.54. This parameter showed a positive and relevant relationship between σ_a^2 and σ_α^2 for BWT in the Bruna dels Pirineus breed, as evidenced
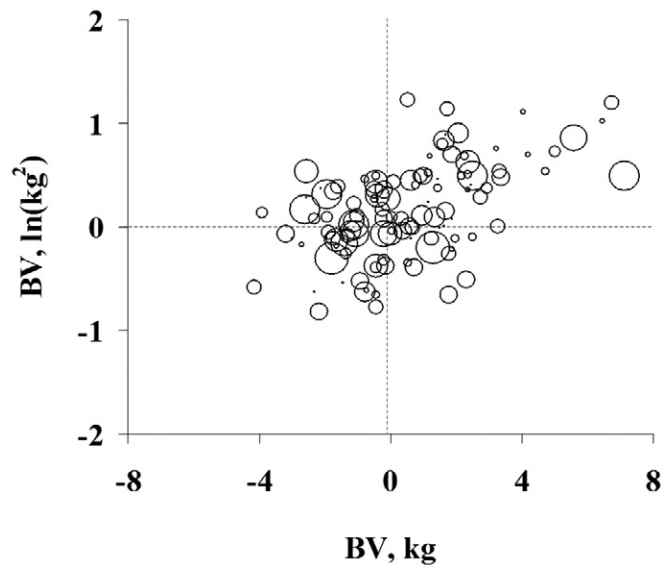

Figure 1. Plot of direct breeding value (BV; x axis) against residual BV (y axis) for breeding sires. The diameter of each circle characterizes the number of offspring (this parameter ranged from 1 to 283 calves).

in Fig. 1 for breeding sires. Estimates of σ_p^2 suggested remarkable departures between models HO and HE; this variance component decreased when heteroskedasticity was accounted for properly (Table 3). Indeed, this source of permanent environmental variability influenced the residual term in model HE by providing a σ_π^2 of 0.20.

Although both models suggested remarkable departures in terms of h^2 for BWT (Table 3), we must be conscious that h^2 under model HE depended on the combination of systematic effects. In this case, single-birth calves with an average contribution of the herd-year-season effect were assumed and provided an h^2 estimate of 0.30, which agrees with the h^2 under model HO (Table 3). Nevertheless, the h^2 under model HE decreased for twin-birth calves (0.27) and fluctuated from 0.12 and 0.85 for extreme herd-year-season effects.

Genetic Trends

Figure 2 shows the herd-by-herd genetic trend (i.e., average predicted breeding value of the calves born each year) for both **a** and **α** effects. All plots indicate relevant departures from zero when focusing on **a** (i.e., 80% credibility intervals excluded the null estimate), although a consistent general trend could not be suggested. Whereas herds 1 and 3, 9, and 11 reported positive trends, at least during the last years, the remaining herds showed inconsistent paths that suggested null trends or, in extreme cases like herd 8, even negative trends. Focusing on the variance term, 80% credibility intervals included the null estimate for most of the year-by-year averages, although relevant departures were reported in herds 1 and 3, 5, 7, and 8. It is important to highlight
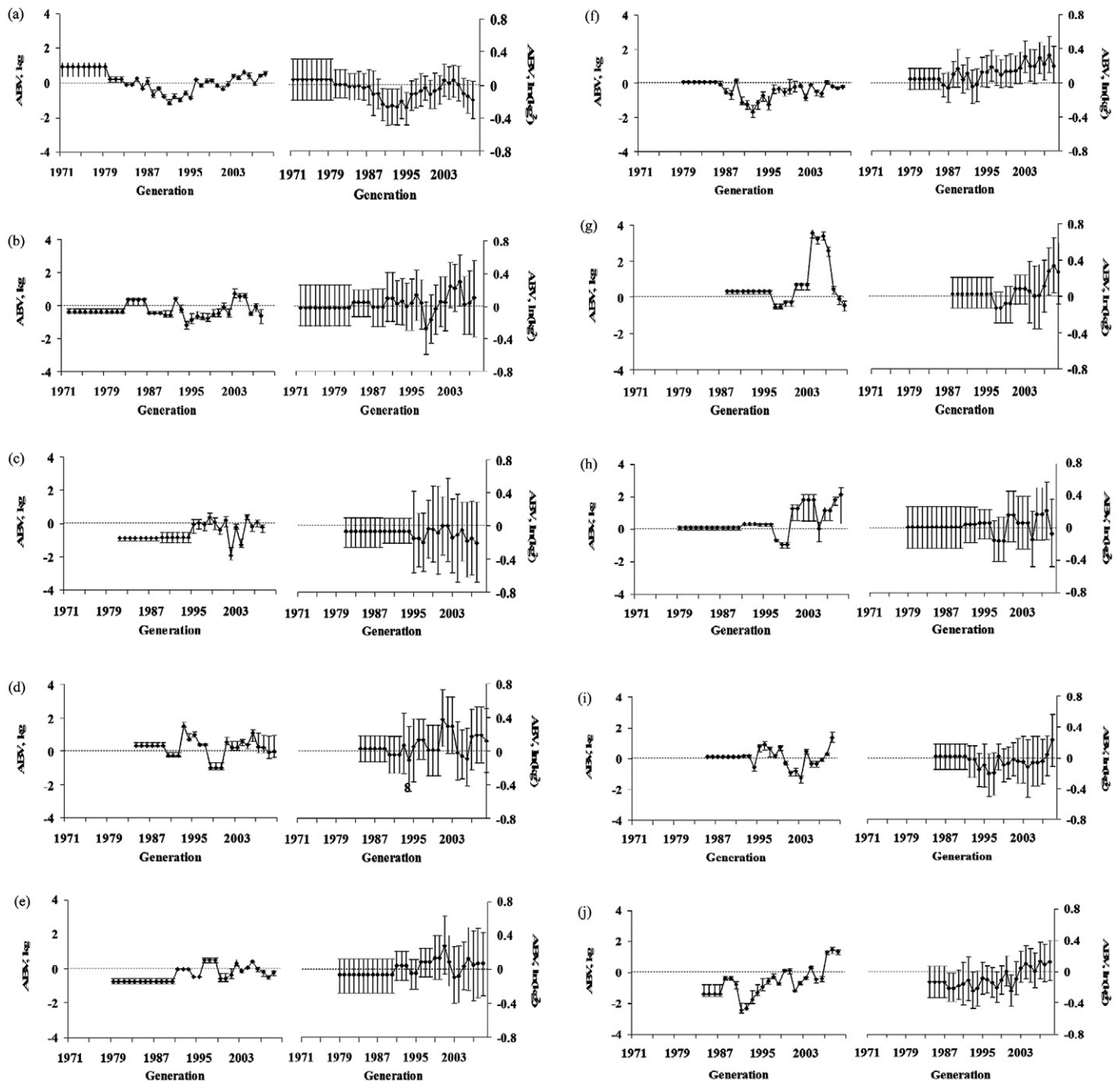
Figure 2. Genetic trends of the direct additive genetic effect (left plot) and the residual additive genetic effect (right plot) for birth BW in Bruna dels Pirineus herds (a) 1 and 3, (b) 2, (c) 4, (d) 5, (e) 6, (f) 7, (g) 8, (h) 9, (i) 10 and 12, and (j) 11. Note that the black point characterizes the posterior mean of average within-year breeding value (ABV), whereas whiskers show the 80% high posterior density. Note that averages for years that were grouped for calculation purposes were independently plotted.

the results provided by herd 7 because this was the only herd showing a statistically relevant and consistent positive genetic trend for **α**.

DISCUSSION

Phenotypic Summary

These analyses of BWT in the Bruna dels Pirineus breed must be viewed as a relevant implementation of

the heteroscedastic model released by SanCristobal-Gaudy et al. (1998) and Sorensen and Waagepetersen (2003), providing new insights into this topic in beef cattle. To the best of our knowledge, available results on beef cattle are restricted to Neves et al. (2011, 2012). Although Bruna dels Pirineus must be viewed as a representative example of extensive beef cattle production in the Mediterranean Basin, its BWT should be put into context to highlight the relevance of the analyses performed in this breed for beef cattle worldwide. Average BWT in the

Bruna dels Pirineus (45.63 kg) was slightly larger than in other Spanish beef cattle breeds, such as Asturiana de los Valles (Goyache et al., 2000; ~44 kg), Pirenaica (~42 kg; Blasco et al., 1992; Altarriba et al., 1996), and Brown Swiss (~45 kg; Villalba et al., 2000). From an international point of view, BWT in the Bruna dels Pirineus was lower than in the Charolais beef cattle breed (47.3 kg; Mujibi and Crews, 2009), although greater than in Hereford (39.5 kg; Eriksson et al., 2004) and Angus breeds (36.5 kg; Berger et al., 1992). In terms of phenotypic variability, Bruna dels Pirineus averaged 30.42 kg^2 and suggested significant departures among sexes and herds. This degree of phenotypic variability fell within the range of values previously reported in other beef cattle breeds. Whereas Belgian Blue had larger estimates (50.41 kg^2; Kolkman et al., 2010) and the neighbor *Pirenaica* breed showed vaguely greater phenotypic variability (37.7 kg^2; Blasco et al., 1992), Phocas and Laloë (2004) reported 30.2 kg^2 in the Charolais breed, and some other worldwide distributed beef cattle breeds, such as Hereford (18.6 kg^2; Eriksson et al., 2004), Charolais (22.94 kg^2; Mujibi and Crews, 2009), and Angus (25 kg^2; Berger et al., 1992), illustrated the lower boundary for this dispersion parameter.

Model Comparison and Systematic Sources of Heteroscedacity

Heteroskedasticity has been previously suggested in beef cattle for weight and growth traits (Varona, 1994; Cardoso et al., 2005, 2007; Kizilkaya and Tempelman, 2005), and current results in the Bruna dels Pirineus breed corroborated this hypothesis on BWT. Model HO was completely discarded by the DIC parameter, and sources of heteroskedasticity were characterized from both systematic and random effects. Although these were the first results in beef cattle derived from the model of Sorensen and Waagepetersen (2003), similar conclusions were obtained in other species, such as rabbits (Ibáñez-Escriche et al., 2008b), mice (Gutiérrez et al., 2006), and pigs (Ibáñez-Escriche et al., 2007). Genetic, permanent, and systematic effects contributed statistically relevant departures in the residual variability of BWT, improving the goodness of fit of the model for genetic evaluation in the Bruna dels Pirineus beef cattle breed. Although these results cannot be directly extrapolated to all beef cattle breeds worldwide, current animal breeding programs must be aware of the relevance of canalization models for genetic evaluation purposes, even more when production homogeneity is considered as an important factor of economic efficiency in animal breeding (SanCristobal-Gaudy et al., 1998).

Focusing on systematic effects, birth type, and herd-year-season revealed relevant contributions to het-eroscedacity, whereas sex of the calf and age of the dam at calving were discarded during the stepwise selection process. These results partially agreed with raw averages from our data set (e.g., herd-year-season and sex) and highlighted the remarkable impact of herd on residual variability as suggested by Kizilkaya and Tempelman (2005) in Italian Piedmontese calves. On the other hand, it is important to note that the sex of the calf and age of the dam at calving were not included, contrary to the results previously reported for BW traits in cattle (Garrick et al., 1989; Kizilkaya and Tempelman, 2005), pigs (Ibáñez-Escriche et al., 2007), and broiler chickens (Rowe et al., 2006). Although our results suggested greater phenotypic variability in males than in females, the DIC statistic discarded sex as a relevant source of heteroskedasticity in Bruna dels Pirineus calves. Note that the exponential parameterization assumed for the residual term of our analytical model mitigates scale effects influencing residual variability (Ibáñez-Escriche et al., 2010). Within this context, a scale effect linked to the larger BWT of male calves could be the origin of the sex-specific differences in our results, which are mainly accommodated by the paramaterization of the model without requiring the inclusion of additional effects.

Variance Components

Both models HO and HE showed similar σ_a^2, which was slightly smaller for model HE (5.88 vs. 6.42 kg^2, respectively), although with overlapping 95% credibility intervals. On the other hand, relevant departures were reported for σ_p^2, which was 0.70 kg^2 for model HE and 1.58 kg^2 for model HO; note that 95% credibility intervals did not overlap. These differences had a close similarity to results reported by Garreau et al. (2008) in canalizing selection for rabbit BWT. Both models matched heritability ($h^2 = 0.30$), although this estimate under model HE was restricted to single-birth calves from an average herd-year-season effect; heritability was slightly lower when accounting for twins ($h^2 = 0.27$) and ranged from 0.14 to 0.42 under extreme herd-year-season effects. Nevertheless, it is important to highlight that model HE captured σ_α^2 as an additional and relevant source of genetic variability with a magnitude of 0.55. The first evidence for residual additive genetic variability in beef cattle was provided by Neves et al. (2011, 2012), and current heritability estimates agree with previous values reported in the scientific literature. Phocas and Laloë (2004) obtained heritabilities for BWT ranging from 0.28 to 0.38 in 4 French beef cattle breeds, Koots et al. (1994) reported a mean heritability of 0.31, and Varona et al. (1999) provided heritabilities of ~0.26 in American Gelbvieh, although with some departures on the basis of the analytical model. Greater heritabili-

ties for BWT in calves were provided by other authors, such as Gutiérrez et al. (2007) in the Asturiana de los Valles beef cattle breed (0.39), Mujibi and Crews (2009) in the Charolais breed (0.46), and Eriksson et al. (2004) in Charolais and Hereford breeds (0.44).

The genetic correlation between σ_a^2 and σ_α^2 was moderate and positive (0.44; Table 3), agreeing with the results reported by Damgaard et al. (2001) and Huby et al. (2003) for weight traits in pigs and Gutiérrez et al. (2006) for individual weight at birth in mice and Neves et al. (2011, 2012) in beef cattle. This estimate suggested that although BWT in Bruna dels Pirineus calves could be homogenized by selection, breeders must be cautious of indirect selection responses reducing the average BWT. A wide range of genetic correlations for canalization studies in adult BW were reported in the literature. Ros et al. (2004) found an extremely high positive correlation for adult BW in snails, whereas Ibáñez-Escriche et al. (2007) found no correlation for slaughter BW at 175 d in pigs, and Ibáñez-Escriche et al. (2008a) found moderate negative correlations for BW at 21 and 42 d and BW gain between 21 and 42 d of age. The positive genetic correlation between direct and residual breeding values was corroborated by plotting estimates from breeding sires. Moreover, a slight overrepresentation of positive breeding values may be suggested for both direct and residual additive genetic effects, although this departure could be viewed as the indirect consequence of selection for larger weaning weights in this breed; note that BWT and weaning weight are positively correlated traits in beef cattle (Phocas and Laloë, 2004). The current results are highly relevant for the breeding scheme of this breed because those sires providing a more homogeneous progeny with an intermediate direct genetic effect are clearly identified, and they must be used as preferential sires for further generations of calves.

Genetic Trends

Average across-year **a** and **α** effects were calculated to characterize the selection success of the breeder over all generations. There were not consistent genetic trends when comparing herds for **a** and **α** plots. Positive, negative, and null trends were observed for **a**, highlighting the heterogeneous selection criteria applied in the different Bruna dels Pirineus herds during recent decades. Although selection objectives suggested stabilizing selection on BWT to prevent extreme BW and their subsequent consequences, some successful trends were revealed. In a similar way, changes in average within-generation **α** were also reported in several herds, highlighting the feasibility of canalization selection programs for weight traits in beef cattle. Although the magnitude of the response on BWT under selection is still poorly understood, our re-

sults suggest that further studies are required to appreciate the relationship between mean and variance and their influence on this trait. However, the genetic-trend estimates allow the possibility of improving growth traits in the Bruna dels Pirineus beef cattle and the possibility for selection. Herd genetic trend lines could be used by the breeder as a tool to increase the merchandising and the price of their animals.

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