

Additive and non-additive, direct and maternal genetic effects for growth traits in a multibreed population of beef cattle

Efectos genéticos aditivos y no aditivos, directos y maternos para caracteres de crecimiento en una población multiracial de bovinos productores de carne

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RESUMEN

Registros de pesos de 4319 bovinos, obtenidos entre 1989 y 1997 en un hato en New South Wales, Australia, fueron usados para estimar los efectos genéticos aditivos y no aditivos, directos y maternos para caracteres de crecimiento en una población que involucra animales de raza pura y cruzados de Angus, Gelbvieh, Polled Hereford, Red Angus y Santa Gertrudis. Los pesos ajustados para edad a 200 (W2), 400 (W4) y 600 días (W6), fueron analizados usando un modelo animal multicarácter incluyendo el efecto genético materno para W2. Se incluyeron en el modelo como covariables fijas, los efectos genéticos directos de raza, aditivo materno (Santa Gertrudis vs. otras razas) y los efectos directos de dominancia (heterocigocidad individual del animal) para todos los caracteres estudiados. Los valores intermedios obtenidos para las heredabilidades directas para W2, W4 y W6, son suficientemente altos para obtener progreso genético en la población mediante la selección de los mejores animales usando un modelo animal. Diferentes énfasis para cada característica pueden permitir cambios en la curva de crecimiento de los 200-600 días de edad. La heredabilidad materna para W2 fue cercana a cero, indicando una baja interferencia con el progreso genético de los efectos directos de las características de crecimiento y un valor reducido para la selección de este efecto. El potencial de crecimiento en terneros Gelbvieh y Angus fue mayor que en las otras razas, el potencial de crecimiento de Santa Gertrudis fue el menor. Santa Gertrudis fue superior al promedio de las otras razas para los efectos maternos de raza. El estimado del efecto promedio de dominancia fue positivo para W2 y W6 y negativo para W4 y menor que la diferencia máxima entre los efectos directos de raza.

Key words: heritability, genetic correlation, breed effects, heterosis.

Palabras claves: heredabilidad, correlación genética, efectos de raza, heterosis.

INTRODUCTION

Animal genetic improvement programs involve two main methodologies for increasing the productivity of farm animals; selection of best animals within a breed or population or using the best breeds or breed combination

through crossbreeding systems. Selection within a breed exploits additive genetic variation for selected traits. Selection among populations and crossbreeding systems exploits both additive and non-additive effects (heterosis) and complementarity among breeds (Kinghorn, 1987). Estimation of parameters for additive and non-additive effects in multibreed populations allows the design of efficient genetic improvement strategies to utilize all these types

of variation (Notter and Cundiff, 1991). Growth traits are important for increasing the economic efficiency of beef production in cattle (Koots *et al.*, 1994a). Both additive and non-additive, direct and maternal effects for weaning weight are important to account for the variability of growth traits in cattle (Notter and Cundiff, 1991; Koots *et al.*, 1994a, 1994b; Rodríguez-Almeida *et al.*, 1997).

This preliminary study was undertaken with the aim of estimating direct breed and maternal effects and heterosis and co(variances) for animal and maternal effects for growth traits. Previous studies involved several breed combinations including some, but not all breeds and crosses used in this study (Notter and Cundiff, 1991; Koots *et al.*, 1994a, 1994b; Rodríguez-Almeida *et al.*, 1997).

MATERIALS AND METHODS

The data were generated from 1989 to 1997 on a commercial beef operation at Jemalong, NSW, Australia, latitude: -33.3892 S, longitude: 148.0081 E, elevation: 240.0 m, mean daily maximum temperature: 23.8 C°, mean daily minimum temperature: 10.0 C°, mean annual rainfall: 526.5 mm.

Growth data of 4319 crossbred and purebred cattle were used to estimate additive and non-additive, direct and maternal genetic effects between and within crosses involving Angus, Gelbvieh, Hereford, Poll Hereford, Red Angus and Santa Gertrudis. Birth (BW) and age-adjusted weights to 200 (W2), 400 (W4) and 600-day (W6) by linear interpolation, were analyzed using a mixed, multiple-trait animal model plus the maternal genetic effect for W2. Number of observations by genotype and trait are shown in table 1.

Direct breed and maternal (Santa Gertrudis vs. any other breed) additive genetic effects, direct dominance (individual calf breed heterozygosity) and maternal dominance (dam breed heterozygosity) for BW, were included in the model as fixed covariates (Kinghorn, 1987). The model also included the fixed effects of month-year of birth, sex and the linear and

quadratic effects of dam's age at birth. In previous univariate analysis, permanent maternal environment variances were found close to zero, thus, they were excluded from the final multivariate model. Estimated (co)variances and fixed effects solutions and their standard errors were obtained from the mixed model analysis with the AI-REML algorithm implemented in the program ASREML (Gilmour *et al.*, 1998). In order to avoid singularity, the columns of covariate values for Angus were dropped from the model, thus including the effect of purebred Angus in the intercept. The convergence criterion was attained after 9 iterations.

Estimability of breed and heterosis effects was tested for each trait by finding full rank of $X'X$, where X is the incidence matrix of coefficients with rows for the genotypes and columns for the covariates to be included in the breed genetic model. Maternal dominance from dam heterozygosity was only estimable for BW. Data structure allowed only estimation of average dominance across crosses and average maternal breed effect of Santa Gertrudis vs. any other breed of the dam (table 1). Simplification

TABLE 1. Number of observations by genetic group and trait (in crossbred, sire x dam breeds).

Número de observaciones por grupo genético y carácter (en cruizas, raza del semental x raza de la madre).

Genetic group	Trait			
	BW	W2	W4	W6
Purebred:				
Angus (A)	1185	746	631	475
Gelbvieh (G)	2	2	1	1
Polled Hereford (P)	537	1006	1280	533
Red Angus (R)	236	193	158	149
Santa Gertrudis (S)	325	730	921	286
Crossbred:				
GxP	103	99	89	83
GxR	1	1	1	1
GxS	248	165	115	116
RxP	403	237	162	116
RxS	103	101	97	90
(GxP)x(RxS)	28	—	—	—
(RxS)x(GxP)	17	—	—	—

of the model using average coefficients for groups of genotypes is common in this type of study due to estimability issues (Rodríguez-Almeida *et al.*, 1997; Hikoora *et al.*, 1998). After completion of the analysis, some recording errors were found for birth weight records, thus, results for this variable are not displayed or discussed further in this paper. The inclusion of birth weight in the model would not affect the estimates for parameters of other traits, because correlation estimates of the direct effect for this trait were close to zero with the effects for other traits (results not shown).

RESULTS AND DISCUSSION

Table 2 displays estimated heritabilities and genetic and environmental correlations. The heritability of the direct effect for W2 is within the range of values reviewed by Groeneveld *et al.* (1998) of 0.19 to 0.47 and Koots *et al.* (1994a) of 0.12 to 0.59. The heritability of the maternal effect found in this study was 0.02, lower than the lowest value for the heritability of the maternal effect reported by Koots *et al.* (1994a) of 0.08, Groeneveld *et al.* (1998) of 0.10 and the estimate of 0.13 by Tosh *et al.* (1999). In agreement with most of these studies, the direct effect had a higher heritability than the maternal effect. Heritability values for W4 and W6 were lower than most estimates from the literature (Koots *et al.*, 1994a; Groeneveld *et al.*, 1998).

Correlations are in agreement with the general trend of available estimates (Koots *et al.*, 1994b; Groeneveld *et al.*, 1998), indicating a negative correlation among maternal and direct effects and high and positive genetic correlations among direct effects for weights at different ages. It is surprising to find only moderate standard errors for genetic correlations involving maternal effects for W2 (*viz.* 0.25 to 0.27) given the low heritability estimate for this trait. Previous estimates of correlations between maternal and direct effects for weights obtained using multitrait animal models in multibreed beef populations have ranged from positive (Nuñez-Domínguez *et al.*, 1993), over close to zero (0.07) (Tosh *et al.*, 1999), to negative (Schoeman and Jordaan, 1999).

Figure 1 displays estimates for breed direct effects. Figure 2 displays values for maternal effects and Figure 3 displays direct dominance effects. In agreement with Notter and Cundiff (1991), direct effects in Gelbvieh were higher for all traits than Angus and Polled Hereford. Estimates for Santa Gertrudis and Red Angus were lower than Angus. Additive maternal effect of Santa Gertrudis was positive for all traits ($P < 0.01$). Direct dominance effects were positive for all weights, excepting W4.

This analysis illustrates some of the potentials and limitations of approaches for simultaneous modeling of between and within breed variation. For direct breed genetic effects, Gelbvieh and Angus results were generally

TABLE 2. Heritabilities (diagonal), genetic correlations (above diagonal) and environmental correlations (below diagonal).

Heredabilidades (diagonal), correlaciones genéticas (sobre la diagonal) y correlaciones ambientales (debajo de la diagonal).

Trait	Trait			
	W2 (direct)	W2 (maternal)	W4	W6
W2 (direct)	0.38 (0.06)	-0.65 (0.16)	0.90 (0.06)	0.81 (0.10)
W2 (maternal)	—	0.02 (0.02)	-0.55 (0.25)	-0.41 (0.27)
W4	0.62 (0.03)	—	0.22 (0.04)	0.85 (0.07)
W6	0.48 (0.04)	—	0.76 (0.02)	0.19 (0.05)

Standard error within parentheses.

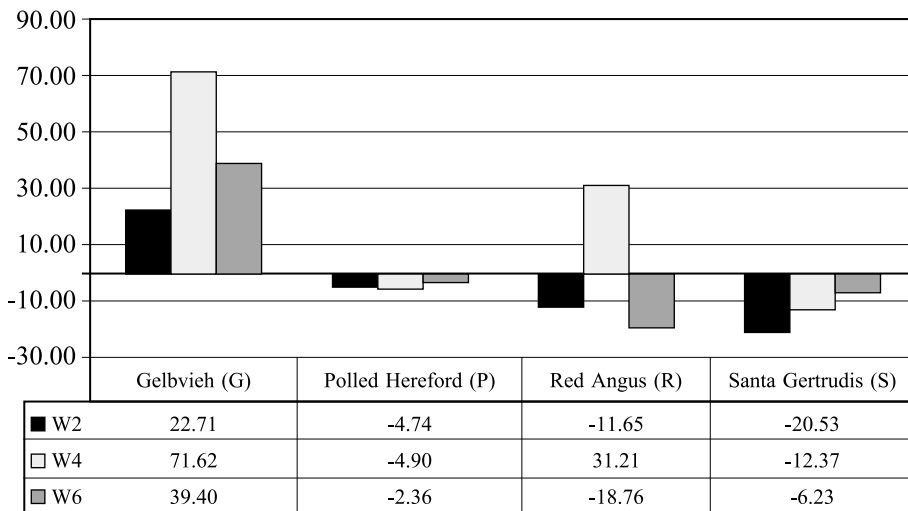


FIGURE 1. Direct breed effects (kg) (Angus=0).
Efectos directos de raza (kg) (Angus=0).

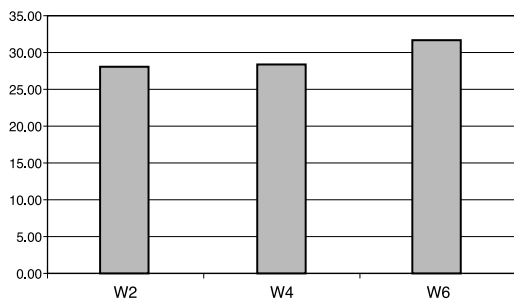


FIGURE 2. Maternal breed effects (Santa Gertrudis vs. any other breed) (kg).
Efectos maternos de raza (Santa Gertrudis vs. otras razas) (kg).

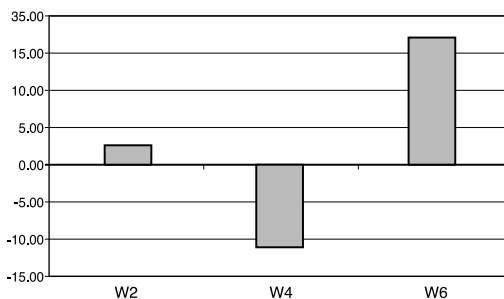


FIGURE 3. Average direct dominance effects (kg).
Efectos promedio de dominancia directa (kg).

higher than those for other breeds, with Santa Gertrudis being the lowest. Superiority of Santa Gertrudis, a composite breed, for maternal genetic effects and inferiority for direct genetic effects, seems to indicate an across-breed negative direct-maternal relationship. However, the positive effect of some retained heterosis by Santa Gertrudis on maternal ability is another possible factor. While these results may be caused by specific characteristics of the traits in the population studied, some inconsistencies are observed for the Red Angus effect (figure 1) and direct dominance for W4 in figure 3. Hence

caution is required when making conclusions about additive and dominance effects among breeds and values of (co)variances from populations with non-designed crosses, even when simplified average parameters for group of breeds are used in certain cases (Rodríguez-Almeida et al., 1997).

The values found in this study for heritabilities and genetic correlations suggest some possibility to make changes to the growth curves, if needed for market requirements. The genetic correlations between direct and maternal effects were all negative, compatible with a

biological negative genetic relationship found by Miller and Wilton (1999) between milk production of the mother and the additive direct value of the calf. However, these values could also be confounded with the negative relationships between cow and calf environments (Meyer, 1997; Schoeman and Jordaan, 1999). The low value found for maternal heritability, together with moderate negative estimates for genetic correlations between maternal and direct effects for all studied traits, may indicate problems for obtaining unbiased estimations for random direct and maternal variances. Models containing both direct and maternal random effects might produce downwards biased estimates and correlations between direct and maternal effects in beef cattle populations by insufficiencies of data (Clément *et al.*, 2001). Most common problems for the estimation of maternal effects are insufficient connection between levels of fixed effect through sires and inadequate familial structures such as the limited number of progeny from each dam. In multibreed studies using an animal model, these problems are probably more serious, because the degree of connection through pedigree of the fixed level of some breed effects would be low – a problem that is not present for a purebred population (Clément *et al.*, 2001). Meyer (1997) and Rodríguez-Almeida *et al.* (1997) mention some of the problems found for the simultaneous estimation of breed and random animal and maternal effects in this type of population. Even with moderately good connection, unfitted effects, such as sire by year interaction, can manifest themselves as direct-maternal correlations (Robinson, 1996ab).

Testing of other models, including models with breed effects and month-year effects considered as random, and with heterogeneous variances by breed (Meyer *et al.*, 1993) may perhaps result in a better understanding of the nature of the genetic (co)variation among and within breeds in this type of study. Further analysis of these data will be done to compare multitrait and longitudinal model approaches (Apiolaza *et al.*, 2000; Meyer, 2001). Ideally, the use of the best model for a particular set of

multibreed data, will allow for a better use of all genetic effects in order to maximize progeny performance.

Medium direct heritability values are high enough to allow genetic progress in the population from selection of best animals for W2, W4 and W6 using an animal model. Different emphasis on each trait could allow changes in the growth curve from 200-600 days of age. Maternal heritability for W2 was close to zero, indicating a low interference with direct effect genetic progress in growth traits and a reduced value for selection for this effect.

The growth potential in Gelbvieh and Angus calves was higher than those for other breeds, with Santa Gertrudis being the lowest. Santa Gertrudis was superior for maternal breed effect to the average of other breeds.

The estimate for the dominance average effect was positive for W2 and W6 and negative for W4 and lower than the maximum difference between direct breed effects.

SUMMARY

Growth data of 4319 calves, obtained from a herd in New South Wales, Australia in 1989-1997, were used to estimate additive and non-additive, direct and maternal genetic effects in a multibreed population on crossbred and purebred Angus, Gelbvieh, Polled Hereford, Red Angus and Santa Gertrudis. Age-adjusted weights to 200 (W2), 400 (W4) and 600-day (W6), were analyzed using a multiple-trait animal model including the maternal genetic effect for W2. Direct breed, maternal additive genetic effects (Santa Gertrudis vs. any other breed) and direct dominance effect (individual calf breed heterozygosity) for all studied traits, were included in the model as fixed covariates. Medium direct heritability values are high enough to allow genetic progress in the population from selection of best animals for W2, W4 and W6 using an animal model. Different emphasis on each trait could allow changes in the growth curve from 200-600 days of age. Maternal heritability for W2 was close to zero, indicating a low interference with direct

effect genetic progress in growth traits and a reduced value for selection for this effect. The growth potential in Gelbvieh and Angus calves was higher than those for other breeds, with Santa Gertrudis being the lowest. Santa Gertrudis was superior for maternal breed effect to the average of other breeds. The estimate for the dominance average effect was positive for W2 and W6 and negative for W4 and lower than the maximum difference between direct breed effects.

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