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Six Different Models for Estimation of Genetic Parameters and Breeding Values for Pre-weaning and Post-weaning Weights in Suckler Cattle

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Abstract: Estimates of (co)variance components and breeding values for pre-weaning (100-day) and post-weaning (300-day) weights were obtained for a commercial herd of Welsh Black cattle recorded from 1976 to 1996. Estimates were obtained from six animal models ranging from a model with only an additive direct effect to a model that also included an additive maternal effect, a maternal permanent environmental effect and a covariance between additive direct and additive maternal effects. The most appropriate model for 100-day weight, based on a likelihood ratio test, was a model with additive direct and additive maternal effects with no covariance between them, yielding estimates of 0.25 (0.053) and 0.07 (0.025) for h^2 and m^2 respectively. For 300-day weight, the model with only an additive direct effect was the most appropriate with an h^2 of 0.27 (0.050). Trends in additive direct breeding values for 100-day and 300-day weights were 0.39 (0.029) and 0.96 (0.077) kg per annum respectively. Additive maternal breeding values for 100-day weight increased by 0.08 (0.008) kg/annum. A correlation of 0.77 (0.066) was estimated between additive direct effects for 100- and 300-day weight.

Key Words: Welsh Black cattle, genetic parameters, maternal effects, genetic trend.

Etci Irk Buzağı ve Danaların Süt Emme Döneminde ve Sütten Kesimden Sonraki Ağırlıklarına Ait Genetik Parametrelerin ve Damızlık Değerlerinin Altı Değişik Modelle Tahmini

Özet: Bu araştırma, Welsh Black buzağıların ve danaların süt emdiği (100 gün) ve sütten kesildikten sonraki (300 gün) dönemlerdeki ağırlıklarına ait genetik parametrelerin, variyans-kovariyans unsurlarının ve damızlık değerlerinin tahmini için yapılmıştır. Araştırmada kullanılan veriler pedigrili kayıt tutan yetiştiricilerden sağlanmış ve 1970-1996 yıllarını kapsamaktadır. Parametrelerin tahmini için, sadece danadan kaynaklanan eklemeli gen etkisini ihtiva eden modelden, eklemeli gen etkisini, ananın kalıcı çevresel etkisini ve bunlar arasındaki kovariyansı da içeren daha komplex modele kadar 6 değişik model kullanılmıştır. Buna göre 100. gün ağırlığı için en uygun model, her bir modelden elde edilen ençok olabilirlik değerleri karşılaştırılarak dananın eklemeli gen etkisiyle beraber ananın da eklemeli gen etkisini içeren fakat bunlar arasındaki kovariyansı hesaba katmayan model olarak belirlenmiş, h^2 0.25 ve m^2 0.07 olarak tahmin edilmiştir. Üçyüzüncü gün ağırlığı için ise sadece dananın eklemeli gen etkisinin hesaba katıldığı model en uygun olarak belirlenmiş, h^2 de 0.27 olarak tahmin edilmiştir. Bireyin eklemeli damızlık değeri 100 ve 300 günlük için ayrı ayrı hesaplanarak yıllara göre regresyon analizi yapılmış ve sırasıyla 0.39 kg/yıl ve 0.077 kg/yıl olarak hesaplanmıştır. Anaya bağlı damızlık değerindeki değişim 100. günlük ağırlık için yılda 0.08 kg'lık bir artış olmuştur. Bireye bağlı 100 ve 300 günlük eklemeli gen etkileri arasındaki genetik korelasyon ise 0.77 olarak tahmin edilmiştir.

Anahtar Sözcükler: Welsh Black Sığırı, genetik parametreler, analık etkisi, genetik yönelim,

Introduction

Weight and growth of suckled calves are related to direct genetic effects, maternal effects and environmental factors. The maternal effects include the genetic and permanent environmental effects of the dam (1). Selection schemes to improve weight in suckler herds have to take into account both direct and maternal genetic effects in order to achieve optimum genetic progress. Several authors have reported estimates of genetic parameters for live weights in beef cattle (2, 3, 4, 5). Estimates for weaning and yearling weight have ranged from 0.10 to 0.34 for h^2, 0.03 to 0.32 for m^2 and 0.05-0.29 for c^2. Estimates of the correlation between additive direct and additive maternal effects for these traits have ranged from -0.7 to zero. The Welsh Black is a traditional breed of the UK, particularly in upland areas of Wales. The objectives of this study were to estimate genetic parameters for pre- and post-weaning weights of Welsh Black cattle by fitting several animal models, attempting to separate additive direct, additive maternal and maternal permanent environmental effects. Breeding values were estimated to determine genetic changes during the years examined.

Materials and Methods

Weight records and pedigree information were obtained from a commercial herd of Welsh Black cattle (Nr. Duns, Berwickshire, UK) recorded by the Meat and Livestock Commission between 1970 and 1996. The herd was predominantly spring calving with calves weaned at the end of December. The cattle grazed outside throughout the year utilising upland pasture at 150-300m above sea level. Traits considered were 100-day weight and 300-day weight. Recorded weights had been pre-adjusted for calf age at weighing (6). There were fewer observations of weights at other times (200 and 400 days) and these were therefore excluded from the analyses. The 200- and 400-day weights are commonly used in UK breeds (6) but in this herd the 100- and 300-day weights were more convenient, coinciding with routine operations and weaning. In addition to weights, animal, sire and dam identities, birth year, birth month, sex, birth type and dam age were also available. Numbers of records together with mean weights and standard deviations (Sd) for the main fixed effects are given in Table 1.

Table 1. Observations, Mean and Standard Deviation for Fixed Effects Classes

	100 day weight (kg)			300 day weight (kg)		
Sex	N	Mean	Sd	N	Mean	Sd
Bull	953	138.6	24.55	878	330.5	50.75
Heifer	1123	129.2	20.89	933	268.7	36.89
Steer	127	136.5	19.65	55	279.9	48.24
Birth Month	N	Mean	Sd	N	Mean	Sd
January	5	102.2	26.60	5	256.4	32.00
February	10	126.3	17.94	9	291.1	60.60
March	259	139.7	20.74	207	284.1	46.71
April	584	144.5	20.33	366	306.2	64.14
May	254	147.6	20.05	145	319.1	61.76
June	65	145.0	18.85	50	318.3	59.58
July	3	129.3	22.80	6	278.7	57.80
August	275	127.1	18.52	308	297.4	53.21
September	374	124.5	18.91	420	296.4	46.04
October	298	117.2	19.48	301	290.9	46.23
November	56	108.0	19.86	37	280.1	42.14
December	20	118.8	21.25	12	305.8	47.20
Birth Type	N	Mean	Sd	N	Mean	Sd
Single	2087	134.6	22.73	1755	299.4	53.69
Twin	116	117.2	20.47	111	278.0	51.96
Total	2203	133.7	22.94	1866	298.1	53.82

Minitab was used for preliminary data analysis with a General Linear Model (7). For each trait the models included birth type, birth year, birth month and sex as fixed effects. Dam age was fitted as a quadratic covariable. (Co)variance components and genetic parameters were estimated for 6 models by ASREML, a restricted maximum likelihood (REML) procedure using a derivative free algorithm (8). All models included an additive direct effect, and this was the only random factor in Model 1. A maternal permanent environment effect was included in Model 2 and an additive maternal effect in Model 3. Model 4 was the same as Model 3, but allowed for a covariance between additive direct and additive maternal effects. Model 5 included additive maternal and maternal permanent environmental effects. Model 6 was the same as Model 5 but with a covariance between additive direct and additive maternal effects. Models for each trait were as follows:

Model 1: $Y_{ijklm} = F_{ijk}+a_l+e_{ijklm}$

Model 2: $Y_{ijklmn} = F_{ijk}+a_l+P_m+e_{ijklmn}$

Model 3: $Y_{ijklmn} = F_{ijk}+a_l+m_m+e_{ijklmn}$ with $\sigma_{AM}A=0$

Model 4: $Y_{ijklmn} = F_{ijk}+a_l+m_m+e_{ijklmn}$ with $\sigma_{AM}A\neq0$

Model 5: $Y_{ijklmn} = F_{ijk}+a_l+m_m+p_m+e_{ijklmn}$ with $\sigma_{AM}A=0$

Model 6: $Y_{ijklmn} = F_{ijk}+a_l+m_m+p_m+e_{ijkmn}$ with $\sigma_{AM}A\neq0$

where

Y_{ijklmn} = adjusted weights with dam and fixed effect combination.

a_l = direct additive genetic effect,

p_m = permanent environmental effect due to the dam,

m_m = maternal additive genetic effect, and

e_{ijklmn} = random error.

F_{ijkl} are fixed effects $bm_i + sj + by_k + bt_l + \theta(X_{ijkl}-\bar{x}) + \theta^2(X_{ijkl}-\bar{x})$

where

bm_i is the effect of the ith birth month,

s_j is the effect of the jth sex of the animal,

by_k is the effect of the kth birth year,

bt_l is the effect of birth type,

θ = linear regression coefficient of observed weights on dam age at weighing,

θ^2 = quadratic regression coefficient of observed weights on dam age at weighing

X_{ijkl} = dam age at weighing, and

$\bar{x}$ = mean dam age at weighing.

The most appropriate model for each trait was determined on the basis of likelihood ratio tests, choosing the model with the fewest parameters in those cases where log likelihoods did not differ significantly (P>0.05). Correlations between the traits were estimated in bivariate analyses using the best model for each trait. The best models were also used to estimate breeding values from univariate analyses, calculating additive direct breeding values for both traits and also a maternal breeding value for 100-day weight. Trends in breeding values were estimated by regressing mean breeding values against calf birth year, with 1970 as year zero.

Results

Results of (co)variance components, genetic parameters and breeding values are presented in Tables 2, 3 and 4.

For 300-day weight, Model 1 with only the additive direct effect was chosen as the best model. Log likelihoods did not improve significantly (P>0.05) by increasing the number of parameters. Model 1 gave an h^2 estimate of 0.27 (0.050), comparable to the h^2 estimates from the other models. The estimates of m^2 and c^2 were small (<0.025) with generally non-significant (P>0.05) estimates of the corresponding maternal direct and maternal permanent environment variance components. Estimates of the correlation between additive direct and additive maternal effects were -0.49 (0.219) and -0.57 (0.270) in Models 4 and 6 respectively (Table 3). The correlations between 100-day and 300-day weights were 0.77 (0.066), 0.55 (0.031) and 0.55 (0.029) for the direct additive, environmental and phenotypic effects respectively. Trends in additive direct breeding values for 100-day and 300-day weights were 0.39 (0.029) kg/annum and 0.96 (0.077) kg/annum respectively. Additive maternal breeding value for 100-day weight increased by 0.08 (0.008) kg/annum (Table 4).

Table 2. Estimates of (Co)variance Components and Genetic Parameters for 100-day Weight (standard errors in parentheses)

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	92.44 (15.154)	76.74 (15.758)	71.95 (16.426)	94.10 (23.350)	71.83 (16.360)	94.19 (15.678)
σ^2_M	-	-	21.62 (7.403)	35.80 (11.974)	15.27 (10.000)	27.55 (14.126)
σ^2_{AM}	-	-	-	-22.94 (14.158)	-	-23.25 (14.353)
σ^2_C	-	18.09 (6.278)	-	-	6.92 (8.440)	8.56 (8.738)
σ^2_E	198.16 (11.910)	194.70 (11.865)	198.28 (11.995)	187.84 (15.346)	196.85 (12.090)	184.84 (15.678)
σ^2_P	290.60	289.53	291.85	294.80	290.87	291.89
h^2	0.32 (0.046)	0.27 (0.050)	0.25 (0.053)	0.32 (0.075)	0.25 (0.053)	0.32 (0.078)
m^2	-	-	0.07 (0.025)	0.12 (0.040)	0.05 (0.034)	0.09 (0.048)
r_{AM}	-	-	-	-0.40 (0.168)	-	-0.46 (0.185)
c^2	-	0.06 (0.021)	-	-	0.02 (0.029)	0.03 (0.029)
-2 Log L	0	-10	-12	-15	-12	-16

σ^2_A direct additive genetic variance; σ^2_M, maternal additive genetic variance; σ^2_{AM}, direct-maternal genetic covariance; σ^2_C, maternal environmental variance; σ^2_E, error variance; σ^2_P, phenotypic variance; h^2, direct heritability; m^2, maternal heritability; r_{AM}, direct-maternal genetic correlation; c^2, permanent environmental variance due to the dam as a proportion of phenotypic variance; -2LogL relative to Model 1

Discussion

The effects were as expected by Pabst et al. (9) for suckler calves with significant effects of sex, birth year, birth month, birth type and dam age. Identification of the most appropriate model for the traits was not straightforward given the similarity in log-likelihoods between the models. In cases where log-likelihoods were not significantly different, the best model was identified as the one with the fewest parameters. The models chosen may be the most appropriate for the dataset, but not necessarily for the breed as a whole. In particular, the best model for 100-day weight excluded maternal permanent environment and a covariance between direct and maternal effects. These have been shown to be important in studies of other breeds (4). The analyses demonstrate the importance of a maternal genetic effect pre-weaning but with additive direct effect being the main contributor to post-weaning weight. The estimates of h^2 and m^2 obtained in this study are within the range of previous estimates of these parameters (4, 5). The estimates of c^2 for 100-day weight were small (<0.025), and lower than the values reported by Meyer (4) for weaning weight of several cattle breeds. The estimate of the direct additive correlation between 100- and 300-day weights was large and positive and comparable to published values for several breeds (1, 4).

The increase in direct and maternal breeding values confirms effective selection for weight in the herd. The gains are within the range reported for other UK beef breeds by Crump et al. (6). Such gains were to be

Table 3. Estimates of (Co) variance Components and Genetic Parameters for 300-day Weight (standard errors in parentheses)

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	355.27 (73.402)	329.93 (76.906)	327.93 (82.394)	403.44 (119.008)	330.58 (82.439)	405.51 (118.917)
σ^2_M	-	-	23.08 (31.613)	84.63 (58.770)	<0.01	56.76 (65.997)
σ^2_{AM}	-	-	-	-89.75 (71.796)	-	-86.00 (69.916)
σ^2_C	-	28.72 (29.305)	-	-	29.67 (41.211)	29.48 (42.112)
σ^2_E	976.19 (61.745)	970.92 (61.568)	979.75 (62.049)	933.19 (79.285)	969.28 (63.435)	924.39 (80.242)
σ^2_P	1331.46	1329.57	1330.76	1331.51	1329.53	1330.14
h^2	0.27 (0.050)	0.25 (0.054)	0.25 (0.058)	0.30 (0.085)	0.25 (0.058)	0.30 (0.085)
m^2	-	-	0.02 (0.024)	0.06 (0.044)	<0.01 (0.031)	0.043 (0.049)
r_{AM}	-	-	-	-0.49 (0.219)	-	-0.57 (0.270)
c^2	-	0.02 (0.022)	-	-	0.02 (0.031)	0.02 (0.032)
-2 Log L	0	-1	-1	-2	-1	-3

σ^2_A direct additive genetic variance; σ^2_M, maternal additive genetic variance; σ^2_{AM}, direct-maternal genetic covariance; σ^2_C, maternal environmental variance; σ^2_E, error variance; σ^2_P, phenotypic variance; h^2, direct heritability; m^2, maternal heritability; r_{AM}, direct-maternal genetic correlation; c^2, permanent environmental variance due to the dam as a proportion of phenotypic variance; -2LogL relative to Model 1

Table 4. Trends in Breeding Values by Birth Year

Trait	Constant	se	Trend Kg/annum	se	R^2
100 day weight direct additive	-1.47	0.421	0.39	0.029	88.8
100 day weight maternal additive	-0.31	0.113	0.08	0.007	82.5
300 day weight direct additive	-4.19	1.135	0.96	0.077	86.7

expected given the emphasis on weight in the selection objectives (10, 11). The current analysis based on EBVs is an independent, objective assessment of genetic trends given that selection over much of the recording period was based on weight contemporary comparisons rather than animal model EBVs, which were first introduced for Welsh Black cattle in 1994 (6,12).

There are few estimates of genetic parameters for Welsh Black cattle, especially calculated using animal models. The estimates presented in this paper will be of value when constructing selection indices for the breed, although attention should be given to re-evaluating which is the “best” model as more data becomes available. It is noteworthy that the genetic parameters are very similar to those used by Crump et al. (6) to evaluate genetic trends for other UK beef breeds. The results therefore reinforce the validity of using the same selection index for recorded herds of Welsh Black cattle as for other UK beef breeds. However, it should be noted that in other UK beef breeds, terminal sire traits are important (13). These traits are not as important, relative to maternal traits, in purebred Welsh Black suckler herds.

In conclusion, the results demonstrate the importance of maternal effects on pre-weaning weights of Welsh Black cattle, and highlight the importance of including such effects in models to analyse early-weight traits in cattle. The analyses also highlight the problem of identifying the most appropriate model when datasets are comparatively small. In these analyses, the choice of the "best" model was based partly on an interpretation of differences between -2LogL values but also on a consideration of the likely importance of maternal effects.

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