

Genetic parameters for direct and maternal effects on growth traits of sheep

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Abstract

The aim of the present study was to estimate (co)variance components and corresponding genetic parameters for birth weight (BW), weaning weight (WW), 6-month weight (W6), 9-month weight (W9), average daily gain from birth to weaning (WWDG), average daily gain from weaning to 6 months (W6DG) and average daily gain from 6 months to 9 months (W9DG) for a nucleus flock of Iranian Makooei sheep. Genetic parameters were estimated by REML procedure fitting six animal models including various combinations of maternal effects. The Akaike information criterion (AIC) was used to determine the most appropriate model. Estimates of direct heritability (h^2) ranged from 0.13 (W6DG) to 0.32 (BW). Maternal effects were found to be important in the growth performance of the Makooei sheep, indicating the necessity of including maternal effects in the model to obtain accurate estimates of direct heritability. Estimates of maternal heritability (m^2) ranged from 0.05 (W6) to 0.16 (WWDG) and the estimates of proportion of maternal permanent environmental variance to phenotypic variance (c^2) were in the range between 0.05 (BW) and 0.10 (W6). Direct additive genetic correlations were positive in all cases and ranged from 0.00 (BW/W9DG) to 0.99 (WW/WWDG). Phenotypic correlations showed a broad range from -0.27 (WW/W9DG) to 0.99 (WW/WWDG). Estimates of genetic parameters showed that genetic improvement through selection programs is possible. WW would be a suitable selection criterion since it has acceptable direct heritability and relatively high genetic correlation with other traits.

Keywords: sheep, animal model, REML, heritability, body weight

Introduction

Contrary to western countries in which consumers show a great preference for beef and pork, in Middle East countries, mutton has always been preferred to other sources of red meat. Small ruminants, i.e., sheep and goat, are numerically important domesticated animals in Iran and traditionally risen on smallholder farms, utilising the range as the major source of feed. In Iran, the primary aim of the breeding programs in sheep production is increasing the efficiency of meat production because of an increasing demand for animal protein as a direct consequence of population growth and improvement in the level of living.

The improving growth performance through selection programs is an important way to increase meat output in lamb production systems. However, selection for growth is complicated by the fact that in mammal species traits related to growth are determined not only by the animal's own additive genetic merit but also by maternal effects. Ghafouri-Kesbi

& Eskandarinasab (2008) in sheep, Barazandeh *et al.* (2011) in goat and Utrera (2008) in cattle demonstrated that animal models which ignore maternal effects might result in overestimation of direct heritability. A direct consequence of such parameter overestimation will be a similar upward bias in predicted responses to selection measured. Using appropriate models including both direct and maternal effects can result in a more accurate estimation of variance components and provide more accurate predictive ability of selection response than would a model that contains only direct genetic effects (Ghafouri-Kesbi & Eskandarinasab 2008).

The Makooei, numbering about three million heads, is one of the major indigenous sheep breeds of Iran. The animals of this breed are known with medium size, fat tail, carpet wool and white colour. This breed has its origins in the western provinces of Iran which are known as Eastern and Western provinces Azerbaijan. Also, they are reared in Turkey and called White Karaman (Tavakkolian 1999). In the early 1990s, a nucleus flock of Makooei sheep was established at Makoo, Western Azerbaijan, Iran. The aim was to establish a nucleus source for improving other flocks in the region. From the time when first lambs were born, information on growth performance has been recorded and stored in the station. In spite of the presence of this good database, information on genetic parameters for growth traits of Makooei sheep is exceedingly limited. Albeit plenty of genetic information for growth traits has been published in the literature (see for example Safari *et al.* [2005] and references therein), they are not expandable to Makooei sheep because estimation of genetic parameters is affected by several factors such as breed differences, size and structure of data, etc. The present study, therefore, was conducted to estimate (co)variance components due to direct and maternal effects for traits related to growth of Makooei sheep. Results will guide the researchers to carry out correct breeding strategies for further development of the trait of interest.

Material and methods

Data

Data available for analysis were collected on Makooei lambs at the Makooei Sheep Breeding Station at Makoo, Western Azerbaijan, Iran (36°, 35'S and 48°, 22'E). Climatically, this location has temperate summers and cold winters and receives a mean annual rainfall of about 400 mm. Ewes are raised in an annual breeding cycle starting in September. Young ewes are first mated so as to lamb for the first time at approximately 1.5 years of age. In the mating season, initially artificial insemination (AI) is performed, but animals that do not conceive by AI are allocated to natural service. In the latter case, ewes are assigned to ram breeding groups with an average mating ratio of 10-15 ewes per ram. Lambing takes place from mid-January to April. At birth, the relevant information about newborn such as sex, birth type, birth date, birth weight, sire ID and dam ID are recorded. Ewes are supplemented, depending upon ewes' requirements for a few days after lambing. During the suckling period, lambs are fed with ewes' milk and also allowed to access to dry alfalfa after 3 weeks of age. Lambs are weaned on average age of 100 days. After weaning, ewes and young animals are kept on natural pasture as separate flocks. They are kept indoors during winter and received a ration composed of wheat straw, dry alfalfa, minerals and some available concentrates. Ewes are kept in the flock for a maximum of 7 parities and rams for 2 or 3 breeding seasons.

Evaluated traits

The traits studied were: birth weight (BW), weaning weight (WW), 6-month weight (W6), 9-month weight (W9), average daily gain from birth to weaning (WWDG), average daily gain from weaning to 6 months (W6DG) and average daily gain from 6-month to 9 months (W9DG). Weaning weight, 6-month weight and 9-month weight were adjusted to 100, 180 and 270 days of age, using a linear regression calculated for that cohort. The pre- and post-weaning daily gain were calculated as total gain divided by the number of days in the period.

Statistical analysis

Initially, fixed linear models were applied to the data using Proc GLM in SAS 9 (SAS Institute Inc., Cary, NC, USA) for identifying non-genetic factors to be included in the models. Fixed model included effects for year and month of lambing, sex, birth type and age of dam at lambing. All fixed effects were significant ($P < 5\%$) for BW, WW, W6, W9 and WWDG, while final fixed models for W6DG and W9DG included fixed effects of year of birth, month of birth and sex of lambs.

Six uni-variate animal models were fitted for each trait to estimate (co)variance components and corresponding genetic parameters. By ignoring or including maternal genetic effect and maternal permanent environmental effect, the following six different models were used: Model I was a model, with direct additive genetic effect as the only random effect.

$$\text{Model I} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{e} \quad (1)$$

Model II comprised maternal permanent environment effect as an additional random effect.

$$\text{Model II} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{c} + \mathbf{e} \quad (2)$$

Models III and IV included an additive maternal effect fitted as second random effect but allowing a genetic covariance between direct and maternal genetic effects (Cov (**a**, **m**) only for Model IV).

$$\text{Model III} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_3\mathbf{m} + \mathbf{e} \quad \text{Cov}(\mathbf{a}, \mathbf{m}) = 0 \quad (3)$$

$$\text{Model IV} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_3\mathbf{m} + \mathbf{e} \quad \text{Cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{a,m} \quad (4)$$

Models V and VI included maternal permanent environmental and maternal genetic effects, ignoring and fitting, respectively, direct-maternal genetic covariance.

$$\text{Model V} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{c} + \mathbf{Z}_3\mathbf{m} + \mathbf{e} \quad \text{Cov}(\mathbf{a}, \mathbf{m}) = 0 \quad (5)$$

$$\text{Model VI} \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{c} + \mathbf{Z}_3\mathbf{m} + \mathbf{e} \quad \text{Cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{a,m} \quad (6)$$

where **y** is the vector of observations, **b** is the vector of fixed effects, **a**, **m**, **c** and **e** are the vectors of direct additive genetic effect, maternal genetic effect, maternal permanent environmental effect and the residual (temporary environment) effect, respectively. **X**, **Z**₁, **Z**₂ and **Z**₃ are incidence matrices relating individual records to **b**, **a**, **c** and **m**, respectively. The covariance structure for the model was:

$$V(\mathbf{a}) = \mathbf{A}\sigma_a^2, V(\mathbf{m}) = \mathbf{A}\sigma_m^2, V(\mathbf{c}) = \mathbf{I}_n\sigma_c^2, V(\mathbf{e}) = \mathbf{I}_e\sigma_e^2 \text{ and } \text{Cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{a,m} \quad (7)$$

where **I**_n and **I**_e are identity matrices of order equal to the number of dams and number of records, respectively. σ_a^2 , σ_m^2 , σ_c^2 and σ_e^2 are direct additive genetic variance, maternal genetic

variance, maternal permanent environmental variance, and residual variance, respectively, and $\sigma_{a,m}$ is direct-maternal genetic covariance.

DFREML program of Meyer (2000) was used to estimate genetic parameters with a REML algorithm. A variance of 10^{-8} of Simplex function values was chosen as the convergence criterion which gives a good accuracy of estimation.

Traditionally log-likelihood ratio tests (LRT) are used to determine the most appropriate model by comparing the differences between log-likelihoods ($-2\log L$) to a critical value from a chi-square distribution. Using LRT, only models that differ by at least one parameter are comparable, i.e., comparison of model 2 with model 3 is not feasible by LRT because both models include the same number of parameters. For this reason, the Akaike information criterion (AIC) of Akaike (1973) was computed to rank the models. Let p denote the number of random (co)variance parameters to be estimated and $\log L$ is the maximum likelihood, then the information criterion is defined as: $AIC = -2 \log L + 2p$. The model yielding the smallest AIC fits the data best.

The bi-variate animal models which included the same fixed effects as uni-variate models were used to estimate covariances between each pair of traits. The models applied in two-trait analyses were those fitted for each of the underlying traits in the single-trait analyses.

Results and discussion

Characteristics of the data structure are summarised in Table 1. Different growth rates were observed in the various growth phases in a way that average daily gain during pre-weaning period was 2 times as great as that from weaning to 6 months of age and 3 times as great as that observed between 6-month and 9-month. Similarly, Prince *et al.* (2010) in Avikalin sheep and Ghafouri-Kesbi *et al.* (2011) in Zandi sheep observed maximum growth rate in the pre-weaning period. The difference between pre- and post-weaning growth rate might attribute to change in nutritional conditions after weaning caused by terminating of suckling. Among traits studied, BW had the minimum CV. Miraei-Ashtiani *et al.* (2007) in Sangsari sheep and Eskandarinasab *et al.* (2010) in Afshari sheep reported similar findings. The reason of less CV for BW may be due to less variation and effect of outside environment on this trait, as ewes were kept inside and manually fed in the late months of pregnancy period in the winter (Miraei-Ashtiani *et al.* 2007). According to Salako (2006), larger variation within certain measurements suggests absence of selection, or the parts respond more to environment than others.

AIC values for the different models are presented in Table 2. Except for W9DG, on which maternal effects had no significant effect, for other traits studied, considering maternal effects fitted the data substantially better than the simple additive model (Model I). For BW, the considerable increase in likelihood appeared in Model II with the maternal permanent environmental effects fitted as the only additional random effect. For WW and W6, the likelihood values increased even further by partitioning the phenotypic variance into direct additive genetic, maternal genetic, and maternal permanent environmental components (Model V). For W9, by including maternal permanent environmental component the likelihood increased significantly and so Model II was determined as the most appropriate model. The most appropriate model for WWDG and W6DG which described the data best included maternal genetic effect and maternal permanent environmental effect, respectively (Models III and II, respectively). For W9DG, the model including only direct additive effect

(Model I) was sufficient to explain the variation in the data as addition of maternal effects did not improve the likelihood than Model I. Improved fit of analytical models by the inclusion of maternal effects has been reported by other researchers (Abegaz *et al.* 2005, Ghafouri-Kesbi & Eskandarinasab 2008, Kariuki *et al.* 2010, Ghafouri-Kesbi *et al.* 2011). It is notable that data structure has a great impact on the accuracy of maternal effects estimation. With a small data set and shallow pedigree, maternal effects cannot be separated from direct effects very well. For accurately separating maternal genetic components and maternal permanent environmental effects from combined and direct effects, a large dataset and several well-linked generations of records and many relationship between relatives related to the mother are needed. Only after meeting these requirements, accurate estimates of maternal effects would be obtained (Maniatis & Pollott 2003).

Table 1
Characteristics of the data structure

	BW, kg	WW, kg	W6, kg	W9, kg	WWDG, g	W6DG, g	W9DG, g
No. of records	1115	1062	1472	1151	1062	674	570
No. of sires with progeny	68	71	72	71	71	76	61
No. of dams with progeny	444	445	599	514	445	356	315
No. of grandsires with progeny	76	76	66	42	76	59	57
No. of granddams with progeny	271	268	249	210	268	219	210
No. of sires with own record	14	14	19	17	14	11	10
No. of dams with own record	158	155	275	248	155	86	75
Average no. of progeny per sire	12.35	11.99	19.01	15.31	11.52	8.89	7.87
Average no. of progeny per dam	2.49	2.41	2.58	2.30	2.39	1.91	1.71
Mean	4.251	12.283	25.377	27.517	170.146	73.437	49.394
SD	0.587	3.890	4.263	4.760	36.284	48.180	28.126
CV, %	13.81	18.27	16.79	17.29	12.32	65.60	56.94

BW: birth weight, WW: weaning weight (100 days), W6: 6 months weight (180 days), W9: 9 months weight (270 days), WWDG: average daily gain from birth to weaning, W6DG: average daily gain from weaning to 6 months, W9DG: average daily gain from 6 months to 9 months of age, SD: standard deviation, CV: phenotypic coefficient of variation

Table 2
AIC values and direct heritability estimates from six uni-variate analyses for each trait (best model: bold)

Model	BW		WW		W6		W9		WWDG		W6DG		W9DG	
	AIC	h^2	AIC	h^2	AIC	h^2	AIC	h^2	AIC	h^2	AIC	h^2	AIC	h^2
I	-684.66	0.38	3 270.70	0.42	4 815.46	0.38	3 678.22	0.37	7 297.84	0.40	5 221.14	0.18	3 626.78	0.18
II	-675.12	0.32	3 252.30	0.24	4 793.18	0.26	3 676.24	0.28	7 910.28	0.20	5 220.10	0.13	3 627.96	0.18
III	-682.66	0.31	3 248.94	0.22	4 792.34	0.21	3 677.22	0.29	7 909.25	0.17	5 221.18	0.13	3 628.56	0.19
IV	-680.75	0.29	3 250.36	0.28	4 794.30	0.21	3 678.44	0.32	7 910.74	0.22	5 220.30	0.20	3 628.44	0.21
V	-681.22	0.31	3 248.76	0.21	4 787.84	0.22	3 678.98	0.28	7 909.26	0.17	5 222.08	0.12	3 629.09	0.19
VI	-679.60	0.37	3 250.12	0.27	4 789.78	0.24	3 678.20	0.31	7 910.68	0.22	5 221.00	0.20	3 629.14	0.21

BW: birth weight, WW: weaning weight (100 days), W6: 6 months weight (180 days), W9: 9 months weight (270 days), WWDG: average daily gain from birth to weaning, W6DG: average daily gain from weaning to 6 months, W9DG: average daily gain from 6 months to 9 months of age

Results of the uni-variate analyses based on the most appropriate models are shown in Table 3. The estimates of direct heritability (h^2) for traits studied were in the range between 0.13 (W6DG) and 0.32 (BW). These estimates show the presence of heritable variation in the growth traits of Makooei sheep. In spite of increase in direct additive genetic variance with age (from 0.06 at birth to 2.645 at 9 months of age), estimates of direct heritability for WW, W6 and W9 affected by greater contribution of other maternal and environmental components in

the phenotypic variance. Because estimation of heritability is affected by several factors such as genetic structure of the population, management conditions and method of estimation, it appears difficult to compare current results with results from the literature. However, current estimates of h^2 are within the range of reports from other Iranian sheep breeds (Miraei-Ashtiani *et al.* 2007, Bahreini-Behzadi *et al.* 2007, Ghafouri-Kesbi & Eskandarinasab 2008, Eskandarinasab *et al.* 2010, Ghafouri-Kesbi *et al.* 2011). Also they fall within the range reported by Safari *et al.* (2005) for several sheep breeds world wide. In general, moderate estimates of heritability for the growth traits indicate scope for genetic improvement in Makooei sheep through selection for growth traits.

Table 3

Estimates of (co)variance components and genetic parameters (SE) from uni-variate analyses based on the most appropriate models

	Model	σ_a^2	σ_m^2	σ_c^2	σ_e^2	σ_p^2	h^2	m^2	c^2	h_t^2
BW	II	0.060	-	0.009	0.115	0.185	0.32 (0.08)	-	0.05 (0.03)	0.32
WW	V	1.817	0.704	0.726	5.254	8.502	0.21 (0.08)	0.08 (0.06)	0.08 (0.06)	0.25
W6	V	2.277	0.569	1.069	6.292	10.208	0.22 (0.07)	0.05 (0.04)	0.10 (0.04)	0.25
W9	II	2.645	-	0.868	5.975	9.490	0.28 (0.09)	-	0.09 (0.04)	0.28
WWDG	III	140.86	134.49	-	535.476	810.839	0.17 (0.08)	0.16 (0.04)	-	0.27
W6DG	II	134.594	-	65.869	878.108	1076.571	0.13 (0.08)	-	0.06 (0.04)	0.13
W9DG	I	48.437	-	-	220.877	269.315	0.18 (0.09)	-	-	0.18

σ_a^2 : direct additive genetic variance, σ_m^2 : maternal additive genetic variance, σ_c^2 : maternal permanent environmental variance, σ_e^2 : residual variance, σ_p^2 : phenotypic variance, h^2 : direct heritability, m^2 : maternal heritability, c^2 : ratio of maternal permanent environmental variance to phenotypic variance, h_t^2 : total heritability (formula [8]) BW: birth weight, WW: weaning weight (100 days), W6: 6 months weight (180 days), W9: 9 months weight (270 days), WWDG: average daily gain from birth to weaning, W6DG: average daily gain from weaning to 6 months, W9DG: average daily gain from 6 months to 9 months of age

Except for W9DG, other traits influenced by maternal effects. Maternal effects in sheep have been extensively studied in recent years (see e.g. Szwaczkowski *et al.* 2006, Ghafouri-Kesbi & Eskandarinasab 2008, Prince *et al.* 2010). These researchers emphasised on inclusion of maternal effects in the model to obtain accurate estimates of direct heritability. The estimates of maternal heritability (m^2) were in the range between 0.05 (W6) and 0.16 (WWDG) which were close to those reported by Abegaz *et al.* (2005) in Horro sheep. The importance of maternal genetic effects is further evidenced by estimates of total heritability (h_t^2 ; Willham 1972):

$$h_t^2 = \frac{\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{a,m}}{\sigma_p^2} \quad (8)$$

Estimates of h_t^2 are of value to predict phenotypic response to selection. According to the h_t^2 formula, when direct-maternal genetic covariance is positive, presence of maternal genetic effects increases the total heritability, and in consequence, the potential response to selection (Ghafouri-Kesbi & Eskandarinasab 2008). As shown in Table 3, estimates of h_t^2 are higher than estimates of h^2 , indicating that phenotypic response to selection would be higher than that predicted using estimates of h^2 . The estimates of c^2 (the permanent environmental variance due to dam as a proportion of phenotypic variance) ranged from 0.05 (BW) to 0.10 (W6) which are comparable with those in the literature (Ghafouri-Kesbi & Eskandarinasab 2008, Prince *et al.* 2010, Kariuki *et al.* 2010). Estimates of c^2 are not as informative as m^2 , however, in order to

obtain accurate estimates of m^2 , estimation of c^2 is necessary as exclusion of the maternal permanent environmental effects could cause maternal heritability to be overestimated.

Different correlations among traits studied are presented in Table 4. Many of these results are in accord with the findings of other studies (Abegaz *et al.* 2005, Miraei-Ashtiani *et al.* 2007, Eskandarinasab *et al.* 2010, Gowane *et al.* 2011). The additive genetic correlation between growth traits, arising chiefly from pleiotropy, was positive in all cases (0.00 to 0.99), indicating the fact that selection for increased body weight at certain stage would also result in genetic improvement in the subsequent development of body weight, which will be reflected in the average daily weight gain during the pre- and post-weaning stages of development (Gowane *et al.* 2011). The correlations between adjacent measurements were larger than ones between non-adjacent measurements. For example, the additive genetic correlation is 0.60 between BW and WW, falling slightly to 0.31 between BW and W9. This result is expected because an autocorrelation would exist among the genetic and environmental effects associated with the measurements (Shaath *et al.* 2004). A result which has been frequently reported by different researchers (e.g., Abegaz *et al.* 2005, Miraei-Ashtiani *et al.* 2007, Eskandarinasab *et al.* 2010) is the negative phenotypic correlation between pre- and post-weaning daily gain in spite of positive genetic correlation. Compensatory growth of some poorly nursed lambs in post-weaning period may be the reason for this phenomenon (Abegaz *et al.* 2005). The positive genetic and phenotypic correlations between WW and other pre- and post-weaning growth traits, makes this trait to be a suitable selection criterion to improve growth performance of the Makooei sheep. Maternal genetic correlations among WW, WWDG and W6 were highly positive, which indicates that the genes of dams which contribute in milk production could also have some favourable effect on post-weaning growth traits.

Table 4
Correlations between traits yielded from bi-variate analyses

Trait 1	Trait 2	r_a	r_m	r_c	r_p
BW	WW	0.60 (0.16)	-	0.29 (0.27)	0.26
BW	W6	0.42 (0.14)	-	-0.62 (0.37)	0.19
BW	W9	0.31 (0.19)	-	-0.23 (0.16)	0.19
BW	WWDG	0.35 (0.15)	-	-	0.12
BW	W6DG	0.02 (0.02)	-	0.34 (0.53)	0.02
BW	W9DG	0.00 (0.10)	-	-	-0.02
WW	W6	0.87 (0.09)	0.99 (0.18)	0.75 (0.26)	0.62
WW	W9	0.51 (0.12)	-	0.52 (0.22)	0.55
WW	WWDG	0.99 (0.01)	0.99 (0.01)	-	0.98
WW	W6DG	0.46 (0.03)	-	0.08 (0.10)	-0.16
WW	W9DG	0.27 (0.11)	-	-	-0.27
W6	W9	0.44 (0.16)	-	0.32 (0.13)	0.46
W6	WWDG	0.88 (0.10)	0.91 (0.08)	-	0.61
W6	W6DG	0.70 (0.18)	-	0.55 (0.27)	0.58
W6	W9DG	0.17 (0.19)	-	-	0.04
WWDG	W6DG	0.45 (0.21)	-	-	-0.15
WWDG	W9DG	0.08 (0.09)	-	-	-0.22
W6DG	W9DG	0.18 (0.06)	-	-	0.12

r_a : direct additive genetic correlation, r_m : maternal genetic correlation, r_c : maternal permanent environmental correlation, r_p : phenotypic correlation, BW: birth weight, WW: weaning weight (100 days), W6: 6 months weight (180 days), W9: 9 months weight (270 days), WWDG: average daily gain from birth to weaning, W6DG: average daily gain from weaning to 6 months, W9DG: average daily gain from 6 months to 9 months of age

In conclusion, the results of the current study advocate the idea that to obtain accurate estimates of genetic parameters for growth traits and to increase the accuracy of genetic evaluation, both direct and maternal effects need to be included in the model of analysis. Results obtained here could be used by breeders to plan appropriate breeding programs for improving growth performance of the Makooei sheep. Body weight at weaning seems would be a suitable selection criterion, as it is recorded early in life and has acceptable direct heritability and relatively high genetic correlation with other growth traits. However, maternal effects on WW must not be ignored where lambs are selected based on their genetic value for WW because maternal effects can mask true genetic potential of lambs.

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