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The effect of model structure on the model performance to fit milk production data in Isfahan Holstein cows

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Abstract The structure of the fixed and random parts of the genetic evaluation model plays a significant role in fitting data and the estimation of genetic parameters for economic traits in livestock. The present study was conducted to investigate the effect of different fixed and random effects combinations in an animal model framework on the general properties of the model and estimates of the genetic parameters for milk production traits. Traits studied were 305-day milk production (305-MY, 15920 records), fat percentage (FP, 27954 records), protein percentage (PP, 26183 records), average daily milk production (ADM, 30954 records) and milk somatic cell score (SCS, 25408 records) in Isfahan Holstein cows. In general, 54 scenarios were studied which differed in fixed and random parts of the model. Variance components were estimated using the animal model fitting restricted maximum likelihood (REML) procedure. The best model for each trait was selected based on the Bayesian Information Criterion (BIC). Results showed that for all traits studied, models in which the effect of contemporary groups Herd-Year-Season (HYS) or Herd-Year-Month (HYM) were fitted as the random or fixed effect together with age at the first calving and inbreeding as a classified fixed effect or covariate lead to a significantly better data fit instead of fitting herd, year, season and month of calving separately. For each trait, a wide range of heritability was obtained by fitting 54 models. Based on the best models, the estimates of heritability for 305-MY, ADM, FP, PP and SCS were 0.33, 0.28, 0.21, 0.16 and 0.61, respectively. It was concluded that a single model should not be used for analyzing all milk production traits and that for each trait a series of models which differ in random and fixed parts should be tested to find the most suitable model which describes the data best. Fitting the effects of herd and year, season and month of calving as contemporary groups HYS or HYM was recommended for genetic evaluation of milk production traits as resulted in better data fit. Depending on the trait, inbreeding and age at first calving can be fitted as a classified fixed effect or as a covariate.

Keywords: Holstein cow, variance components, contemporary groups, inbreeding, heritability

Introduction

The domestication of cattle (*Bos taurus* and *Bos indicus*) took place about 8000–10,000 years ago in two separate events: one in the region of the Fertile Crescent (the origin of taurine cattle) and the other in the Indus Valley (the origin of indicine or zebu cattle) (Qanbari et al., 2011). Since that time, a wide range of natural and artificial selection events have greatly changed important characteristics

such as their adaptation to different environments, reproduction, body conformation, behavior, resistance to diseases and parasites, and the desirable economic traits (Alinaghizadeh et al., 2007). In this regard, selection of the livestock with superior production traits has greatly improved livestock production (Hill, 2008). The most important economic traits in dairy cows are quantitative traits influenced by multiple genetic and environmental factors. Selection of animals for these traits in breeding programs is performed based on breeding values obtained when they reach a certain age using phenotypes from the animals themselves and their relatives (Nassiry et al., 2005).

There are about seven million cattle in Iran, of which some 700,000 are Holstein distributed in more than 2000 herds. The herd sizes vary from 20 to 3000 dairy cows with a mean 305-day milk production of 7200 kg (Atashi and Hostens, 2021). In Iran, for dairy cattle breeders, milk yield and its fat and protein content are the main sources of income and are considered the most important traits in selection purposes. They are interested in milk production traits due to the possibility of genetic improvement and high economic value (Mehrpoor and Bahreini-Behzadi, 2016) and, therefore, focus has been on increasing the genetic potential of dairy cows for milk production traits. To design breeding programs, we need accurate estimates of variance components and genetic parameters (Lasley, 1978). Different models have been used to estimate the variance components and genetic parameters for milk production traits. Univariate, multivariate, repeatability and test-day models have been used to genetic analysis of milk yield and its components (Bahreini Behzadi et al., 2013). These models have fixed and random parts. The effects of herd, year and season of calving are the most important fixed effects (known environmental factors) affecting milk production traits. In most of studies, a combination of herd, year and season of calving was fitted in the fixed part of the model along with the effect of the age at first calving as covariate (Ojango et al, 2001; Nilforooshan et al., 2004; Shadparvar et al., 2005; Bahreini Behzadi et al., 2013; Cho et al., 2016; Mehrpoor and Bahreini-Behzadi., 2016). Designing appropriate statistical model that includes appropriate combination of fixed and random effects is pre-requisite for accurate genetic evaluation. For estimating genetic parameters for growth traits in Mehraban sheep, Pezhman (2009) used a model that contained the effects of herd, year and season of birth as separate fixed effects and compared it with models containing their combination as contemporary groups Herd-Year-Season (HYS) fitted as fixed or random effects and reported that each model provided different estimates of variance components and breeding values. Goli (2020) analyzed body weight traits of Moghani lambs with 108 models in which HYS was fitted either random or fixed along with dam age and inbreeding as covariate. In terms of overall fit, models in which HYS was considered as the random or fixed effect were superior to models in which herd, year and season

of birth were fitted separately. The framework of statistical model also played a significant role on data fit (Pezhman, 2009). It is more important in analyzing milk production traits where production records originate from many herds with different genetic structures and from cows calving in different years and seasons. This can result in many levels for HYS contemporary groups which allow it to be fitted in the model as a random effect. In addition, inbreeding coefficient and age at first calving can be fitted in the model as a fixed effect with several classes or as an auxiliary variable (covariate). Although, the effect of model structure on the general properties of the model and estimation of genetic parameters has been studied in sheep (Pezhman, 2009; Goli, 2020), so far, no effort has been made to study the effect of model structure on the performance of the model for genetic evaluation of milk production traits and, therefore, a comprehensive study was needed to address this issue. Hence, the aim of this study was to evaluate the effects of different structures of fixed and random parts of the model on the general properties of the model and accuracy of genetic evaluation of the milk production traits in Holstein cows in Isfahan province.

Materials and methods

Data file

Information on production traits including 305 days milk production (305-MY), average daily milk production (ADM), fat percentage (FP), protein percentage (PP), number of milk somatic cell (cells.mL) related to the first lactation of Holstein cows belonging to 62 dairy herds collected by the Vahdat Cooperative in Isfahan Province in a 20 years period was used. The data were edited in a way that all production records were corrected based on 305 lactation days and two milking per day. Moreover, erroneous records and records out of mean±3 standard deviation were eliminated from the data files. In addition, herds that had less than 5 records were eliminated. Furthermore, cows with age at first calving below 540 days and above 1200 days were also removed from the data file. The number of somatic cells count was converted to somatic cell score (SCS) based on the following equation.

$$\text{SCS} = log_2(\text{SCC}/100,000) + 3$$

After editing the data, 125,789 records, related to the first lactation, remained for analyses.

To calculate the inbreeding coefficients, the whole pedigree which included 86481 animals was analyzed with CFC program (Sargolzaei et al., 2006).

Statistical analysis

Variance components and genetic parameters were estimated using the following model:

$$\text{y= X}\beta \text{ +Zu+e}$$

where **y** is the vector of observations, **β** is the vector of fixed effects fitted with design matrix **X**. **u** is the vector of animal random effects fitted with design matrix **Z** and **e** is the vector of residual effects. The structure of fixed and random parts of the model is described in Table 1. In some models the effect of heard, year, season, and month of calving were fitted separately as the fixed effects. In some models, the combination of herd, year, season and month of calving was fitted as contemporary group either as a fixed or random effect. The age at first calving in these models was fitted as either an auxiliary variable (covariate) or a fixed effect with two subclasses,

class 1 (543 to 912 days) and class 2 (913 to 1247 days). To fit the inbreeding coefficients in the models, two scenarios were used. In the first scenario it was fitted as a covariate and, in the second scenario it was fitted as a classified fixed effect with four classes: class 1 (animals with inbreeding coefficient equal to zero), class 2 (animals with inbreeding coefficient between zero and 3.99%), class 3 (animals with inbreeding coefficient between 3.99 and 7.99%) and class 4 (animals with inbreeding coefficient higher than 7.99%). In general, each trait was analyzed using 54 different models.

Table 1. Fixed and random components of different models

Models	Herd	Year	Season	Month	HYS_{Fix}	HYS_{Random}	HYM_{FIX}	HYM_{Random}	AFC_{COV}	AFC_{Class}	F_{Cov}	F_{Class}
1	✓	✓	✓									
2					✓							
3						✓						
4	✓	✓		✓								
5							✓					
6								✓				
7	✓	✓	✓							✓		
8					✓					✓		
9						✓				✓		
10	✓	✓		✓						✓		
11							✓			✓		
12								✓		✓		
13	✓	✓	✓						✓			
14					✓				✓			
15						✓			✓			
16	✓	✓		✓					✓			
17							✓		✓			
18								✓	✓			
19	✓	✓	✓									✓
20					✓							✓
21						✓						✓
22	✓	✓		✓								✓
23							✓					✓
24								✓				✓
25	✓	✓	✓							✓		✓
26					✓					✓		✓
27						✓				✓		✓
28	✓	✓		✓						✓		✓
29							✓			✓		✓
30								✓		✓		✓
31	✓	✓	✓						✓			✓
32					✓				✓			✓
33						✓			✓			✓
34	✓	✓		✓					✓			✓
35							✓		✓			✓
36								✓	✓			✓
37	✓	✓	✓								✓	
38					✓						✓	
39						✓					✓	
40	✓	✓		✓							✓	
41							✓				✓	
42								✓			✓	
43	✓	✓	✓						✓		✓	
44					✓					✓	✓	
45						✓				✓	✓	
46	✓	✓		✓						✓	✓	
47							✓			✓	✓	
48								✓		✓	✓	
49	✓	✓	✓						✓		✓	
50					✓				✓		✓	
51						✓			✓		✓	
52	✓	✓		✓					✓		✓	
53							✓		✓		✓	
54								✓	✓		✓	

The WOMBAT program of Meyer (2007) was used to estimate the variance components and genetic parameters. The Bayesian information criterion (BIC) was computed (Schwarz et al., 1978) was computed to rank the models according to their power to fit the data.

$$BIC= -2 \, Log(L)+P \, Log(N-r)$$

where Log (L) is the maximum likelihood, P denotes number of parameters in the model, N denotes number of records and r denotes the rank of matrix. The model with the lowest value of BIC was selected as the best model.

Results

Statistical description of production traits is given in Table 2. The 305-MY and SCS were, respectively, the least and most variable traits. Their phenotypic coefficients of variations were 19.82% and 46.59%, respectively.

Table 2. Summary Statistics of the studied traits

Trait	Number	Mean	SD	CV(%)
305-MY (Kg)	15290	9377.84	1859.09	**19.82**
FP (%)	27954	2.82	0.738	**26.18**
PP (%)	26183	2.63	0.641	**24.37**
ADM (Kg)	30954	31.25	6.63	**21.32**
SCS (Cell.ml)	25408	1.99	0.927	**46.59**

305-MY: 305 days milk yield; FP: Fat percentage; PP: Protein percentage; ADM: Average daily milk production; SCS: Somatic cell score; CV: Coefficient of variation; SD: Standard deviation.

Pedigree structure is shown in Table 3. The pedigree, including 86481 animals, was distributed over 46 generations. The base population (generation 0) consisted of 11.61% of pedigreed animals and remained 88.39% were non-base animals (generation 1-46). In general, the pedigree was deep enough to allow accurate estimates of variance components and genetic parameters.

Table 3. Pedigree structure of the studied population

Parameter	Number	% of total animals
Total animals	86481	100
Base animals	10045	11.61
Females	78425	90.68
Males	8056	9.32
Animals with known father	73781	85.31
Animals with known mother	73258	84.71
Animals with known father and mother	70603	81.64
Animals with unknown father and mother	3177	3.68
Animals with F=0.00	29247	33.8
Animals with F between 0.00 and 3.99%	36609	42.3
Animals with F between 3.99 and 7.99%	18654	21.5
Animals with F higher than 7.99%	1971	2.3
Average F in the population	2.33%	
Average F in inbred animals	3.52%	

For each trait, LogL and BIC values for 54 different models are listed in Tables 4 and 5. Models in which the effect of herd and year, season and month of calving were fitted separately, had less power to fit the data and provided highest BIC value. In all models studied, inclusion of the contemporary groups Herd-Year-Season (HYS) and/or Herd-Year-Month (HYM) either random or fixed led to a better data fit according to BIC criterion.

For 305-MY, model 29 which included HYM as a random effect and age at first calving and inbreeding as a classified fixed effect provided the best fit of the data. For ADM, model 51 in which HYS was fitted as a random effect along with age at first calving and inbreeding as covariate was the best model. For FP and PP, model 5 in which HYM was fitted as a fixed effect provided the best fit of data. For SCS, model 9 in which the effect of HYS was random and the age at first calving was fitted as a classified fixed effect with two classes had less BIC and, therefore, was selected as the best model.

The estimates of variance components and heritability (h^2) for each trait obtained from 54 fitted models are presented in Tables 6 and 7. Each model resulted in a different estimate of h^2. For 305-MY, the h^2 estimates ranged between 0.3 to 0.46. For ADM, h^2 ranged from 0.18 to 0.24. For FP, h^2 estimates were between 0.05 to 0.28. For PP and SCS, the h^2 estimates ranges were 0.07 to 0.21 and 0.05 to 0.18, respectively. Based on the best models, the estimates of heritability for DMY-305, ADM, FP, PP and SCS were 0.33, 0.21, 0.28, 0.16 and 0.06, respectively.

Discussion

Model selection

Different models have been used to estimate the variance components of milk production traits in Holstein cows. These included the Bayesian and REML methods in Tunisian Holstein cows (Zaabza et al., 2016), random regression models in South Korean Holstein cows (Cho et al., 2016), test day model based on spline functions in Portuguese Holstein cows (Silvestre et al., 2005) and univariate and multivariate animal models in Iranian Holstein cows (Bahreini Behzadi et al, 2013). However, no effort has been made to study the structure of the fixed and random parts of the model on general properties of the model and estimation of variance components for milk production traits which makes comparison difficult. Usually a model in which HYS was fitted as the fixed part of the model and age at first calving as the covariate has been used to analysis milk production traits (Zink et al., 2012; Bahreini Behzadi et al., 2013; Mehrpoor and Bahreini-Behzadi, 2016; Buaban et al., 2020). However, as different traits have different genetic architecture and are affected differently by environmental noises, this model may not fit the data best and, therefore, doesn't guarantee accurate estimation of the variance components and genetic parameters. Pezhman et al. (2009) reported that fitting the effect of herd, year and season of birth as the fixed -

effect of HYS for analyzing production and reproduction traits in Mehraban sheep, provided better fit of data instead of using these effects separately. Our data in cattle support their findings. Goli (2020) analyzed growth-related traits of Moghani sheep and reported that models in which the effects of herd, year and season of calving were fitted separately had less power to fit the data, and fitting their combination as the random HYS in addition to inbreeding effect as the covariate improved the general properties of the model. Our data are in line with these findings. These published data and the current results showed that fitting the effect of herd, year, season

and month of calving as contemporary group is preferred to fitting these effects separately. The inclusion of the effect of the age at first calving as either a covariate or a classified fixed effect improved the fit of the model, probably because the age at first calving is a managerial and non-genetic factor influencing milk production and milk composition (Pirlo et al., 2000). Improving the general properties of the model by including the effect of inbreeding either as a covariate or a classified effect is because it contains the pedigree and inbreeding information of each individual in the model, leading to more accurate estimation of the genetic variance and heritability (Dong et al., 1998).

Table 4. LogL and BIC values for different models

Trait	305-MY		FP		PP		SCS		ADM	
Models	LogL	BIC	Log(L)	BIC	Log(L)	BIC	Log(L)	BIC	Log(L)	BIC
1	-118475.67	236970.6	4929.7	-9838.9	9773.2	-19526.1	3952.8	-7885.4	-68223.4	136467.5
2	-115004.55	230028.1	8108.5	-16196.7	15179.2	-30338.1	7375.5	-14730.9	-66622.7	133266.1
3	-118328.63	236686.1	8081.2	-16131.8	-21796.3	NC*	7418.2	-14806.0	-68156.0	136343.0
4	-118428.07	236875.4	4994.3	-9968.1	9900.6	-19781.5	3943.7	-7867.1	-68232.2	136485.2
5	-110686.22	221391.5	**8177.2**	**16334.1**	**16251.6**	**-33023.0**	6483.0	-12945.9	-64626.0	129272.7
6	-118735.41	237499.7	8073.3	-16115.9	16466.8	-32903.1	6468.6	-12906.8	-68619.6	137270.2
7	-118471.37	236962.0	4929.6	-9838.7	9772.6	-19524.9	3956.1	-7891.9	-68209.9	136440.5
8	-115000.32	230019.8	8107.5	-16194.6	15177.2	-30334.2	7380.3	-14740.4	-66611.6	133243.8
9	-118247.01	236576.9	8077.7	-16124.7	15179.1	-30327.8	**7422.7**	**-14815.0**	-68070.4	136171.8
10	-118423.78	236866.8	4994.0	-9967.6	9900.0	-19779.6	3947.0	-7873.8	-68218.7	136458.2
11	-110681.94	221383	8174.9	-16329.5	16519.4	-33018.6	6486.4	-12952.6	-64616.6	129253.7
12	-118653.28	237335.4	8069.6	-16108.6	16471.9	-32913.3	6472.9	-12915.3	-68484.3	136999.6
13	-118482.55	236984.3	4915.5	-9810.5	9760.8	-19501.2	3938.3	-7856.3	-68205.8	136432.3
14	-115012.67	230044.5	8086.7	-16153.1	15158.8	-30297.4	7365.4	-14710.7	-66605.2	133231.1
15	-118336.90	236702.7	8060.1	-16089.6	-21321.2	NC	7404.8	-14785.1	-68064.8	136160.6
16	-118434.97	236889.2	4980.7	-9940.9	9889.7	-19759.2	3929.2	-7838.2	-68214.4	136449.5
17	-110694.26	221407.6	8154.2	-16288.1	16504.0	-32987.9	6471.9	-12923.6	-64611.1	129242.9
18	-118743.09	237515.0	8051.7	-1672.8	16449.0	-32867.4	6457.1	-12883.9	-68610.9	137252.9
19	-118460.29	236940.0	4919.1	-9817.8	9769.9	-19513.5	3941.6	-7868.9	-68224.3	136469.3
20	-114989.54	229998.2	8069.6	-16172.8	15167.3	-30314.3	7366.3	-14712.5	-66625.9	133272.6
21	-118262.25	236553.4	8065.9	-16101.2	15168.5	-30307.0	7408.3	-14786.2	-68085.7	136202.4
22	-118412.7	236844.6	4983.8	-9947.1	9897.3	-19774.4	3932.4	-7844.5	-68233.0	136486.8
23	-110671.26	221361.6	8166.7	-16313.1	16512.2	-33004.3	6473.5	-12927	-64628.1	129276.8
24	-118636.92	237308.7	8059.5	-16088.3	16463.5	-32896.4	6459.0	-12887.5	-68499.0	137029.1
25	-118456.09	236931.4	4919.0	-9817.6	9796.4	-19518.4	3944.8	-7869.4	-68210.6	136441.9
26	-114985.3	229989.8	8095.6	-16170.8	15165.3	-30310.4	7371.0	-14721.8	-66614.7	133250.1
27	-118257.99	236544.8	8029.0	-16027.4	15166.8	-30303.1	7412.8	-14795.2	-68073.2	136177.6
28	-118408.41	236836.0	4983.5	-9946.6	9896.7	-19773.2	3935.7	-7851.2	-68219.4	136459.4
29	**-110666.97**	**221353.0**	8164.5	-16308.7	16510.0	-32999.9	6476.8	-12933.5	-64618.5	129257.6
30	-118635.61	237300.1	8021.4	-16012.2	16461.7	-32893.0	6462.2	-12894.0	-68485.9	137003
31	-118467.31	236953.8	4904.9	-9789.5	9757.5	-19494.8	3927.0	-7833.8	-68206.6	136433.9
32	-114997.64	230014.5	8074.8	-16129.3	15146.9	-30273.6	7356.2	-14692.6	-66608.4	133221.5
33	-118270.41	236569.7	8045.0	-16059.3	15148.2	-30265.8	7398.3	-14766.2	-68070.6	136147.2
34	-118419.64	236858.5	4970.2	-9920.0	9886.5	-19752.7	3917.9	-7815.6	-68228.2	136477.2
35	-110679.29	221377.7	8143.7	-16267.2	16494.7	-32969.3	6462.3	-12904.6	-64613.2	129246.9
36	-118647.22	237323.3	8038.1	-16045.6	16446.0	-32861.5	6448.1	-12865.9	-68489.6	137010.2
37	-118471.9	236963.0	4929.7	-9838.9	9761.8	-19503.3	3938.6	-7857.0	-68227.2	136475.1
38	-115001.49	230022.2	8095.8	-16171.3	15164.1	-30307.9	7361.8	-14703.5	-66630.5	133281.6
39	-118305.12	236639.1	8067.1	-16103.6	-21620.6	NC	7406.3	-14782.1	-68139.6	136310.2
40	-118424.15	236867.5	4979.9	-9939.4	9889.7	-19759.0	3929.5	-7838.7	-68236.0	136492.6
41	-110683.16	221385.4	8163.7	-16307.2	16507.2	-32994.2	6496.6	-12919.0	-64633.4	129278.2
42	-118690.74	237410.3	8058.4	-16086.2	16454.5	-32878.6	6457.5	-12884.6	-68619.6	137270.2
43	-118467.59	236954.4	4915.2	-9810.0	9761.3	-19502.3	3941.9	-7863.5	-68213.5	136467.6
44	-114997.25	230013.7	8094.8	-16169.2	15162.2	-30304.1	7366.6	-14713.0	-66619.3	133209.2

305-MY: 305 days milk yield; ADM: Average daily milk production; FP: Fat percentage; PP: Protein percentage; SCS: Somatic cell score; LogL: Log likelihood; BIC: Bayesian Information Criterion. NC: not converged.

Table 5. The LogL and BIC values for different models (continuation of Table 4)

Trait	305-MY		FP		PP		SCS		ADM	
Models	LogL	BIC	Log(L)	BIC	Log(L)	BIC	Log(L)	BIC	Log(L)	BIC
45	-118270.51	236596.9	8064.7	-16098.8	15164.0	-30297.6	7408.8	-14787.2	-68078.0	136187.1
46	-118419.86	236858.9	4979.7	-9338.9	9889.1	-19758.0	3932.8	-7845.3	-68222.3	136465.2
47	-110678.87	221376.8	8161.4	-16302.6	16505.0	-32989.8	6472.9	-12925.8	-64623.9	129268.3
48	-118648.74	237326.3	8055.7	-16080.8	16457.5	-32884.4	6458.9	-12887.4	-68491.6	137014.3
49	-118478.81	236976.8	4915.3	-9810.2	9749.4	-19478.5	3924.1	-7827.9	-68209.5	136439.7
50	-115009.60	230038.4	8074.0	-16127.7	15143.7	-30267.2	7351.8	-14683.3	-66612.9	133246.6
51	-118313.38	236655.6	8045.9	-16061.2	15143.8	-30257.2	7396.1	-14761.7	**-64120.5**	**128502.4**
52	-118431.09	236881.4	4966.3	-9912.2	9878.8	-19734.4	3915.0	-7809.8	-68218.0	136456.7
53	-110691.19	221401.5	8140.7	-16261.1	16489.7	-32959.2	6458.5	-12896.8	-64618.5	129257.6
54	-118743.09	237515.0	8036.8	-16043.0	16436.9	-32843.3	6446.5	-12862.5	-68562.6	137156.4

Heritability estimates

The narrow-sense heritability of a trait (h^2), defined as the proportion of the phenotypic variance accounted for by the additive genetic effects, is an important indicator of the extent to which a trait can be improved by selection. Information on heritability is crucial in the formulation of optimum breeding objectives and an effective genetic improvement program. In agreement with Shahdadi et al. (2017), we obtained a relatively wide variation in heritability estimates from 0.06 (SCS) to 0.33 (305-MY). Except for SCS, the estimates of heritability for other traits were large enough for selection to be effective for improving any of the studied traits. The estimates of heritability for studied traits were affected by fitted model which was in agreement with Goli (2020). It means that models with different structure provide different estimates of heritability, and the model which fit the data best, most probably provides most accurate estimate of h^2. Comparing to other reports, the current estimates of heritability for milk production traits were intermediate among other estimates. For example, in Brazilian Holstein cows, Bignardi et al. (2011) using a random regression model estimated the heritability of the MY in a range from 0.09 to 0.14. Sneddon et al. (2015) who worked on New Zealand multi-breed dairy cows, estimated h^2 for MY, FP, PP and SCS as 0.19, 0.35, 0.32 and 0.08, respectively. Shahdadi et al. (2017) estimated the heritability for milk production traits for Iranian Holstein dairy cow in 5 different climate regions. For 305-MY, they reported h^2 for arid, semi-arid, Mediterranean, semi-humid and humid regions as 0.29, 0.24, 0.11, 0.16 and 0.13, respectively. For FP, the estimates of h^2 were 0.28, 0.22, 0.10, 0.12 and 0.15 for arid, semi-arid, Mediterranean, semi-humid and humid regions, respectively. Weller et al. (2004) estimated the heritability for 305-MY and SCS in five parities. Their estimates of heritability for 305-MY were in the range from 0.12 in the 5th parity to 0.39 in 1st parity. For SCS, the estimates of heritability ranged from 0.18 in 5th parity to 0.25 in 1st parity. Moreover, in Chinese Holstein dairy cows (Xue et al., 2022) the estimates of h^2 for 305-MY, ADM, FP, PP and SCS were 0.50, 0.47, 0.45, 0.3 and 0.23, respectively. Atashi and Hostens (2021) estimated the heritability value for SCS in Iranian Holstein dairy

cows to be 0.18, 0.15 and 0.15 for the first, second and third parities, respectively. The difference between the reported heritability for the same trait could be because of different pedigree and data-set, genetic structure of the populations, different environmental conditions and the model used (Hanford et al., 2002).

Conclusions

Our results showed significant effect of the model structure on general properties of the model and estimation of genetic parameters for milk production traits. In general, for all traits studied, models with contemporary groups (HYS or HYM) were superior to models in which the effects of herd and year, season and month of calving were fitted separately. These models showed better performance in fitting the data. In addition, including the effect of age at first calving and inbreeding as the covariate or a classified fixed effect improved the general properties of the model. Our results also showed that a single model should not be used for analyzing all milk production-related traits, whereas a series of models, differing in the random and fixed parts, should be tested to find the most suitable model. The heritability estimates were close to other reports and were large enough for selection to be effective.

Acknowledgements

Table 6. The estimates of variance components and genetic parameters for the studied traits

Trait	305-MY				FP				PP				SCS				ADM			
Model	σ_a^2	σ_p^2	σ_e^2	h^2	σ_a^2	σ_p^2	σ_e^2	$h^2\pm SE$	σ_a^2	σ_p^2	σ_e^2	$h^2\pm SE$	σ_a^2	σ_p^2	σ_e^2	$h^2\pm SE$	σ_a^2	σ_p^2	σ_e^2	$h^2\pm SE$
1	69637	223399.0	153762.0	0.31	0.076	0.27	0.19	0.28±0.01	0.037	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.18±0.01	6.67	31.68	25.0	0.21±0.01
2	66204	195365.0	129161.0	0.33	0.053	0.20	0.14	0.26±0.01	0.014	0.10	0.92	0.13±0.01	0.013	0.19	0.17	0.06±0.01	5.58	29.69	24.1	0.18±0.01
3	17183	368755.0	685175.5	0.43	0.036	0.56	0.54	0.06±0.01	0.054	0.56	0.14	0.09±0.02	0.030	0.49	0.13	0.06±0.01	10.3	40.3	6.2	0.25±0.01
4	68713	223803.0	154090.0	0.30	0.075	0.27	0.19	0.27±0.01	0.036	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.63	31.6	25.0	0.21±0.01
5	64983	192775.0	127799.0	0.33	0.051	0.18	0.13	0.28±0.01	0.014	0.85	0.71	0.16±0.01	0.011	0.18	0.17	0.06±0.01	5.37	29.2	23.9	0.18±0.01
6	13304	330994.0	748299.0	0.40	0.036	0.54	0.53	0.06±0.09	0.036	0.44	0.14	0.80±0.06	0.034	0.52	0.12	0.05±0.01	9.15	39.3	7.85	0.23±0.09
7	69660	223419.0	153758.0	0.31	0.077	0.27	0.19	0.28±0.01	0.037	0.18	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.72	31.6	24.9	0.21±0.01
8	66220	195382.0	129161.0	0.33	0.053	0.20	0.14	0.26±0.01	0.014	0.10	0.92	0.13±0.01	0.012	0.19	0.17	0.06±0.01	5.58	29.6	24.0	0.18±0.01
9	14679	343442.0	689220.0	0.42	0.036	0.56	0.54	0.06±0.01	0.034	0.44	0.14	0.08±0.01	0.030	0.49	0.13	0.06±0.01	8.77	38.7	6.35	0.22±0.01
10	68729	222821.0	154091.0	0.30	0.075	0.27	0.19	0.27±0.01	0.036	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.69	31.6	24.9	0.21±0.01
11	65008	192795.0	1277860	0.33	0.051	0.18	0.13	0.28±0.01	0.014	0.85	0.71	0.16±0.01	0.011	0.18	0.17	0.06±0.01	5.39	29.2	23.8	0.18±0.01
12	11804	315489.0	751274.0	0.37	0.036	0.54	0.53	0.05±0.09	0.035	0.44	0.15	0.07±0.01	0.034	0.52	0.12	0.05±0.01	7.73	37.9	7.99	0.20±0.08
13	75127	223331.0	153889.0	0.31	0.077	0.27	0.19	0.28±0.01	0.037	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.09	6.83	31.6	24.8	0.21±0.01
14	66311	195419.0	129108.0	0.33	0.053	0.20	0.14	0.26±0.01	0.014	0.10	0.92	0.13±0.01	0.012	0.19	0.17	0.06±0.01	5.72	29.6	23.9	0.19±0.01
15	171835	368805.0	685216.0	0.46	0.036	0.56	0.54	0.05±0.01	0.054	0.56	0.14	0.08±0.01	0.030	0.49	0.13	0.17±0.01	8.88	38.8	6.49	0.22±0.01
16	68502	222730.0	154228.0	0.30	0.076	0.27	0.19	0.28±0.01	0.036	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.80	31.6	24.8	0.21±0.01
17	65087	192828.0	127741.0	0.33	0.051	0.18	0.13	0.28±0.01	0.014	0.85	0.71	0.16±0.01	0.011	0.18	0.17	0.06±0.01	5.52	29.2	23.7	0.18±0.01
18	13242	330366.0	746278.0	0.40	0.036	0.54	0.53	0.05±0.09	0.036	0.44	0.15	0.07±0.01	0.034	0.52	0.12	0.05±0.01	9.27	39.4	8.02	0.23±0.08
19	69605	223347.0	153742.0	0.31	0.077	0.27	0.19	0.28±0.01	0.037	0.18	0.14	0.21±0.01	0.049	0.27	0.22	0.18±0.09	6.71	31.6	24.9	0.21±0.01
20	66057	195284.0	129227.0	0.33	0.053	0.20	0.14	0.26±0.01	0.014	0.10	0.92	0.13±0.01	0.013	0.19	0.17	0.06±0.01	5.56	29.7	24.1	0.18±0.01
21	14581	342345.0	686681.0	0.42	0.036	0.56	0.54	0.05±0.01	0.034	0.44	0.14	0.76±0.01	0.030	0.49	0.13	0.06±0.01	8.79	38.7	6.32	0.22±0.01
22	68670	222745.0	154075.0	0.30	0.075	0.27	0.19	0.27±0.01	0.036	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.67	31.6	24.9	0.21±0.01
23	64799	192684.0	127885.0	0.33	0.051	0.18	0.13	0.28±0.01	0.014	0.85	0.71	0.16±0.01	0.011	0.18	0.17	0.06±0.01	5.38	29.2	23.9	0.18±0.01
24	11714	314412.0	746761.0	0.37	0.036	0.54	0.53	0.05±0.09	0.035	0.44	0.15	0.08±0.02	0.034	0.52	0.12	0.06±0.01	7.77	38.0	7.94	0.20±0.01
25	69629	223367.0	153737.0	0.31	0.077	0.27	0.19	0.28±0.01	0.038	0.18	0.14	0.21±0.01	0.049	0.27	0.22	0.17±0.09	6.76	31.6	24.9	0.21±0.01
26	66074	195301.0	129227.0	0.33	0.053	0.20	0.14	0.26±0.01	0.014	0.10	0.92	0.13±0.01	0.013	0.19	0.17	0.06±0.01	5.61	29.6	24.0	0.18±0.01
27	14579	342343.0	687026.0	0.42	0.036	0.56	0.54	0.06±0.01	0.034	0.44	0.14	0.08±0.01	0.030	0.49	0.13	0.06±0.01	8.76	38.7	6.38	0.22±0.01
28	68688	222763.0	154075.0	0.30	0.076	0.27	0.19	0.28±0.01	0.037	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.73	31.6	24.9	0.21±0.01
29	64825	192704.0	127878.0	0.33	0.051	0.18	0.13	0.28±0.01	0.014	0.85	0.71	0.16±0.01	0.011	0.18	0.17	0.06±0.01	5.43	29.2	23.8	0.18±0.01
30	11712	314418.0	747236.0	0.37	0.036	0.54	0.53	0.06±0.09	0.035	0.44	0.15	0.07±0.06	0.034	0.52	0.12	0.05±0.01	7.73	37.9	8.02	0.20±0.08

Table 7. The estimates of variance components and genetic parameters for the studied traits (continuation of Table 6)

31	69418	223282.0	153864.0	0.31	0.078	0.27	0.19	0.28±0.01	0.038	0.18	0.14	0.21±0.01	0.049	0.27	0.22	0.18±0.09	6.87	31.6	24.7	0.21±0.01
32	66167	195339.0	129171.0	0.33	0.053	0.20	0.14	0.26±0.01	0.014	0.10	0.92	0.13±0.01	0.013	0.19	0.17	0.06±0.01	5.75	29.6	23.9	0.19±0.01
33	14574	342297.0	686944.0	0.42	0.036	0.56	0.54	0.06±0.01	0.034	0.44	0.14	0.08±0.01	0.030	0.49	0.13	0.61±0.01	8.90	38.8	6.53	0.22±0.01
34	68468	222676.0	154208.0	0.30	0.076	0.27	0.19	0.28±0.01	0.037	0.17	0.14	0.21±0.01	0.049	0.27	0.22	0.17±0.01	6.98	31.7	24.7	0.22±0.01
35	64906	192738.0	127831.0	0.33	0.051	0.18	0.13	0.28±0.01	0.014	0.85	0.71	0.16±0.01	0.011	0.18	0.17	0.06±0.01	5.56	29.2	23.7	0.19±0.01
36	11646	313719.0	744766.0	0.37	0.036	0.54	0.53	0.06±0.09	0.035	0.44	0.15	0.07±0.01	0.034	0.52	0.12	0.07±0.01	7.86	38.0	8.16	0.20±0.01
37	69494	223340.0	153845.0	0.31	0.076	0.27	0.19	0.28±0.01	0.037	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.18±0.09	6.73	31.6	24.9	0.21±0.01
38	66098	195332.0	129234.0	0.33	0.053	0.20	0.14	0.26±0.01	0.014	0.10	0.92	0.13±0.01	0.013	0.19	0.17	0.06±0.01	5.58	29.7	24.1	0.18±0.01
39	15395	350385.0	676939.0	0.43	0.036	0.56	0.54	0.05±0.01	0.054	0.56	0.14	0.09±0.04	0.030	0.49	0.13	0.06±0.01	9.45	39.4	6.18	0.24±0.01
40	68557	222736.0	154178.0	0.30	0.075	0.27	0.19	0.27±0.01	0.036	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.69	31.6	24.9	0.21±0.01
41	64840	192732.0	127891.0	0.33	0.051	0.18	0.13	0.28±0.01	0.014	0.85	0.71	0.16±0.01	0.011	0.18	0.17	0.06±0.01	5.40	29.3	23.9	0.18±0.01
42	12174	318867.0	727421.0	0.38	0.036	0.54	0.53	0.05±0.09	0.035	0.44	0.14	0.08±0.01	0.034	0.52	0.12	0.05±0.09	9.15	39.3	7.85	0.23±0.01
43	96519	223360.0	153840.0	0.31	0.077	0.27	0.19	0.28±0.01	0.037	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.78	31.6	24.8	0.21±0.01
44	66116	195349.0	129233.0	0.33	0.054	0.20	0.14	0.26±0.01	0.014	0.10	0.92	0.13±0.01	0.012	0.19	0.17	0.06±0.01	5.63	29.6	24.0	0.19±0.01
45	14634	342922.0	687029.0	0.42	0.036	0.56	0.54	0.05±0.01	0.034	0.44	0.14	0.76±0.01	0.030	0.49	0.13	0.06±0.01	8.77	38.7	6.40	0.22±0.01
46	68575	222754.0	154179.0	0.30	0.075	0.27	0.19	0.27±0.01	0.036	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.75	31.6	24.9	0.21±0.01
47	64867	192751.0	127884.0	0.33	0.051	0.18	0.13	0.28±0.01	0.014	0.85	0.71	0.16±0.01	0.011	0.18	0.17	0.06±0.01	5.45	29.2	23.8	0.18±0.01
48	11749	314806.0	746817.0	0.37	0.036	0.54	0.53	0.06±0.09	0.035	0.44	0.15	0.07±0.01	0.034	0.52	0.12	0.05±0.01	7.73	37.9	8.03	0.20±0.01
49	69303	223274.0	153970.0	0.31	0.077	0.27	0.19	0.28±0.01	0.037	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.89	31.6	24.7	0.21±0.01
50	66208	195387.0	129179.0	0.33	0.054	0.20	0.14	0.26±0.01	0.014	0.10	0.92	0.13±0.01	0.012	0.19	0.17	0.06±0.01	5.77	29.6	23.9	0.19±0.01
51	15396	350625.0	677121.0	0.43	0.036	0.56	0.54	0.06±0.01	0.034	0.45	0.14	0.08±0.01	0.030	0.49	0.13	0.06±0.01	6.87	36.2	24.9	0.21±0.01
52	68349	222665.0	154316.0	0.30	0.076	0.27	0.19	0.28±0.01	0.036	0.17	0.14	0.20±0.01	0.049	0.27	0.22	0.17±0.01	6.86	31.6	24.7	0.21±0.01
53	64946	192785.0	127839.0	0.33	0.051	0.18	0.13	0.28±0.01	0.014	0.85	0.71	0.16±0.01	0.011	0.18	0.17	0.06±0.01	5.58	29.2	23.7	0.19±0.01
54	74627	197936.0	123309.0	0.40	0.036	0.54	0.53	0.06±0.09	0.035	0.44	0.15	0.09±0.02	0.034	0.52	0.12	0.05±0.09	8.35	38.5	7.89	0.21±0.01

305-MY: 305 days milk yield; ADM: Average daily milk production; FP: Fat percentage; PP: Protein percentage; SCS: Somatic cell score; σ_a^2: additive genetic variance; σ_e^2: residual variance; σ_p^2: phenotypic variance; h^2: heritability.

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