Indian Journal of Animal Sciences **87** (9): 1106–1110, September 2017/Article

Estimation of genetic parameters of milk and fat yields using different animal models in Iranian Holstein dairy cattle

MOHAMMAD REZA BAHREINI BEHZADI[1] and ZAHRA MEHRPOOR[2]

Yasouj University, Yasouj 75918–74831 Iran

Received: 26 February 2017; Accepted: 6 April 2017

ABSTRACT

Milk and fat yield records of the first 4 lactations from 58 herds of Holstein cows recorded from 1999 to 2015 were analyzed. Genetic parameters were estimated by using univariate, repeatability and multivariate animal models. The fixed effects of herd-year-season as contemporary group and age at calving as covariate were fitted in the model of analyses. Heritability estimates under univariate model for lactations 1 to 4 were 0.28, 0.20, 0.19 and 0.13 for milk yield and for fat yield were 0.15, 0.12, 0.12 and 0.05, respectively. The repeatability and heritability values under the repeatability model for milk and fat yield were 0.48 and 0.24, and 0.38 and 0.17, respectively. Estimated heritabilities using a bivariate model for lactations 1 to 4 were 0.29, 0.20, 0.20 and 0.15 for milk yield and 0.12, 0.11, 0.13 and 0.05 for fat yield, respectively. Heritability estimates for lactations 1 to 4 by multivariate model were 0.30, 0.23, 0.22 and 0.19 for milk yield, and 0.17, 0.16, 0.17 and 0.12 for fat yield, respectively. Genetic, phenotypic and environmental correlations of milk yield were 0.91, 0.50 and 0.36 for first and second lactation; and 0.87, 0.45 and 0.31 for first and third lactation; and 0.79, 0.39 and 0.26 for first and fourth lactation; and 0.97, 0.53 and 0.41 for second and third lactation; and 0.91, 0.50 and 0.39 for second and fourth lactation; and 0.96, 0.56 and 0.46 for third and fourth lactation, respectively. These parameters for fat yield were 0.87, 0.35, 0.25 and 0.91, 0.29, 0.16 and 0.83, 0.26, 0.17 and 0.96, 0.45, 0.35 and 0.90, 0.40, 0.32 and 0.98, 0.47, 0.38, respectively. Results from this study confirm that multivariate analysis is recommended for estimating the genetic parameter of milk and fat yield, because it considers the effects of selection bias of the first lactation.

Key words: Animal model, Dairy cattle, Fat yield, Genetic parameter, Milk yield

The capacity of milk production depends on the lactation curve trajectory that is influenced by genetic and environmental effects. The environmental effects can alter the genetic potential efficacy of milk production of dairy cows. To estimate the breeding value of animals for selection, variation arising in yield records from systematic environmental effects must be removed. Heritability and genetic correlations are more important genetic parameters for constructing selection indices. From practical viewpoint, basic and simplified assumptions are prepared while predicting genetic parameters and breeding values for large populations using an animal model. Using appropriate method for genetic evaluation of dairy cows is a vital phase in dairy industries. In the last decades, different animal models e.g. univariate, multivariate, and repeatability animal models were used to estimate variance component and genetic parameters for milk yield and its components. Various animal models have previously been studied in several investigations on dairy production traits (Abdallah and McDaniel 2000, Boujenane 2002, Urioste *et al.* 2003, Banik and Gandhi 2006, Banik and Gandhi 2007, Banik and Gandhi 2010, Alijani *et al.* 2012, Bahreini Behzadi *et al.* 2013). When information of some production traits is available, an optimal way to combine all these information to predict genetic parameters is a multivariate analysis. Multivariate models have basic significance in applied and the theoretical quantitative genetics (Gianola and Sorensen 2004). Indeed, using multivariate analysis in national level is computationally difficult. In the past decades for traditionally dairy sire evaluation, mostly two types of records for genetic evaluation are used: first lactation records or, repeated records of more lactation. In repeatability model, assume correlation of unity between traits in different lactations. However, milk, fat and protein yields are usually evaluated separately using a repeatability model (Wiggans *et al.* 1988a, Wiggans *et al.* 1988b, Ducrocq *et al.* 1990, Jones and Goddard 1990). The objectives of this study were to estimate variance component and genetic parameters for milk and fat yield traits by using univariate, bivariate, repeatability and multivariate animal models in Iranian Holstein dairy cattle, and comparing different models for genetic evaluation of animals.

Present address: [1]Assistant Professor (bahreini@yu.ac.ir), [2]MSc Student (zahra.mehrpoor@yahoo.com), Department of Animal Science.

MATERIALS AND METHODS

Milk and fat yield records of Iranian Holstein cows from 58 herds that calved from 1999 to 2015 were used. The data set used in this study consisted of 71,705 records of first four lactations of Holstein cows that were provided by the Animal Breeding Center of Iran. Both traits were adjusted for 305 days and two times milking. Record of first lactation was required and further lactation yields were used only if the previous one was recorded.

Second, third and fourth lactation records were edited to include cows that had calved no earlier than 10 month after their previous calving and no later than 24 month after their previous calving. Descriptive statistics for the final data set are presented in Table 1. Contemporary groups of herd-year-season (HYS) were formed by combining herd, year and season of calving classes, and used as fixed effect. The age at calving as covariate was fitted in the model of analyses. Editing of records for constructing final data set was done by using SAS (SAS Institute 2009) and Microsoft Excel (2007) software. The analyses were carried out using univariate, bivariate, repeatability and multivariate animal models. For univariate analyses, records of four lactations were analyzed separately. The milk and fat production records in four lactations of each animal were considered as repeated measurements and repeatability animal models was applied for both traits. The milk and fat yield records in any lactation were analyzed using bivariate analyses. Records of each trait in different lactations were analyzed together using a four variable model.

In matrix notation, the statistical models can be represented as follows:

$$y = Xb + Za + e \text{ (Model 1)}$$

$$y = Xb + Za + Wpe + e \text{ (Model 2)}$$

where y is the vector of observations measured in Nd animals; b is the vector of fixed effects; a is the vector of additive genetic random coefficients; pe is the vector of animal permanent environmental random coefficients; e is the vector of the N different residuals; X, Z, W are the correspondent incidence matrices for fixed and additive genetic and permanent environmental random effects, respectively. Model 1 was used for univariate, bivariate and multivariate analyses and model 2 was used for repeatability analyses.

Table 1. Descriptive statistics of edited data

Parity	Milk			Fat		
	n	Mean	SD	n	Mean	SD
1	31346	9997.81	1796.33	29792	240.235	86.27
2	20828	9301.97	2077.46	20157	242.977	83.22
3	12579	9219.92	2125.72	12396	237.497	83.54
4	6952	9066.32	2165.75	6933	233.045	83.042

The (co)variance components and genetic parameters of studied traits were estimated with AIREML algorithm of the WOMBAT software (Meyer 2007).

RESULTS AND DISCUSSION

Variance component and heritability estimates of milk and fat yields from univariate animal model analyses are shown in Table 2. The range of heritability in present study was obtained at 0.13 to 0.28 for milk yield and 0.05 to 0.15 for fat yield. Heritability estimations were imperceptibly upper than those from some literature (Alijani *et al.* 2012, Bahreini Behzadi *et al.* 2013) and lower than other literatures (Meyer 1984, Dedkova and Wolf 2001; AL-Seaf *et al.* 2007). Heritability estimates of milk and fat yields had decreasing trend by lactations. The majority of studies reported that heritability estimates for later lactations are lower than estimates for the first lactation (Meyer 1984, Visscher and Thompson 1992, Alijani *et al.* 2012, Bahreini Behzadi *et al.* 2013). This decreasing trend may be consequence of increase in some environmental variance sources such as increasing the effect of days in milk (Barash *et al.* 1996), increasing the effect of days open (Laben *et al.* 1982), and increasing the residual variance by lactations. Adjustments for effect of reproductive traits such as open days in model generate higher heritability estimates for production traits (Urioste *et al.* 2003). Heritability difference between first and second lactations is greater than those between second and third, and third and fourth lactations. This situation probably influenced by the general source of variation such as previous dry period and open days. Also, if studied population was small and has been under selection, the heritability estimates will decrease (Weller *et al.* 1987, Raheja *et al.* 1989). In present study, 2.43% of cows in first lactation had no record in second lactation, 39.61% of cows in second lactation had no record in third lactation, and 46.57% of cows in third lactation had no record in fourth lactation. If culling process occurs in earlier lactations, parameter estimations of later lactations

Table 2. Estimation of residual variance (σ_e^2), additive genetic variance (σ_a^2), phenotypic variance (σ_p^2) and heritability (h^2) from univariate analysis

Parity	Milk				Fat			
	σ_e^2	σ_a^2	σ_p^2	h^2	σ_e^2	σ_a^2	σ_p^2	h^2
1	1402700	534436	1937140	0.28	2351.73	414.157	2765.88	0.15
2	2099160	515850	2615010	0.2	2894.85	411.652	3306.5	0.12
3	2199980	523019	2723000	0.19	3008.38	423.442	3431.82	0.12
4	2414200	370399	2784600	0.13	3058.16	170.255	3228.42	0.05

Table 3. Estimation of residual variance (σ_e^2), additive genetic variance (σ_a^2), permanent environmental variance (σ_{pe}^2), phenotypic variance σ_p^2 , heritability (h^2), permanent environmental variance as a proportion of phenotypic variance (c^2) and repeatability (r) from repeatability model

	σ_e^2	σ_a^2	σ_{pe}^2	σ_p^2	h^2	c^2	r
Milk	1292360	603430	620395	2516190	0.24	0.25	0.48
Fat	1962.65	532.178	679.168	3174	0.17	0.21	0.38

will be bias from univariate analyses (Visscher and Thompson 1992). In general, the heritability of milk and fat yields in first lactations using univariate analyses were larger in comparison with other lactations. This might be created by factors that do not influence the different lactations.

Heritability and repeatability for milk and fat yields are presented in Table 3. In present study, heritability and repeatability for milk yield and fat yield were 0.24 and 0.17; 0.48 and 0.38, respectively. The repeatability of milk yield trait was higher than fat yield trait. Dematawewa and Berger (1998) applied a repeatability model and reported heritabilities of 0.20, 0.18 and repeatabilities of 0.42 and 0.41 for first 3 lactation records of milk yield and fat yield traits, respectively. The heritability values of both traits obtained by repeatability model were comparatively higher than those calculated by univariate model. These higher heritability values are probably due to permanent environmental effects. This result was in agreement with the results obtained by other researchers (Palacios *et al.* 2007, Alijani *et al.* 2012). The result confirms that the genetic correlations between lactations were not equal to unity. Coefficient of variation (CV) for milk and fat yields were 22% and 16%, respectively. These CV values show that phenotypic variances were high and resulted in lower heritability estimates. Heritability estimation of milk yield was in the range of estimates reported in literature but heritability of fat yield was lower than literature reports. The results of present study show that repeatability of milk and fat yields was high, because of high ratio of the permanent environmental to the phenotypic variance (c^2). These repeatability values were higher than estimates from literature (Alijani *et al.* 2012, Bahreini Behzadi *et al.* 2013). Pertaining to repeatability, it should be noted that this genetic parameter is correlation between consecutive records of a trait. Thus, selection on the first lactation eventuate increasing production mean in subsequent lactations. Differences between heritability and repeatability of present study were high and revealed that non-additive genetic and permanent environment had more influence on these traits. Ratio of the residual variance to phenotypic variance ($\frac{\sigma_e^2}{\sigma_P^2}$) for milk and fat yields were 0.51 and 0.62, respectively. These high ratios showed that there are unknown effects that had high consequence on production such as accuracy of recording system, and dissimilarity in different feeding systems that had high effect on production. The weak structure of pedigree information can result in low heritability (Urioste *et al.* 2003). Dong *et al.* (1988) reported that heritability estimates from REML were lower if the relationships in pedigree were from sires only, compared with more complete pedigrees. They also found that complete relationships from ancestors of about two generations resulted in slightly higher heritability estimates comparing to one generation. Also, if a selection criterion is just based on phenotype, it is possible to remain high production cows in later lactations in herds because of their gene combination value. This phenomenon can decrease heritability of traits under selection over years.

Co (variance) components, heritabilities and correlations between milk and fat yields of all four lactations obtained from bivariate analysis are shown in Table 4. Heritability estimates of milk yield were slightly greater than those estimated from univariate analyses, and for fat yield were slightly fewer. Additive genetic variance was about 3.6% greater than those from univariate analysis for milk yield and was about 16.11% fewer for fat yield. Multivariate predictions are fundamentally equivalent to those from univariate analysis when parameter estimations of two traits are equal. In a multivariate analysis, traits with smaller heritability gain more when analyzed with traits with upper heritability. Besides, better connections in the data due to residual covariance between traits in multivariate analysis make a further raise in accuracy (Mrode 2005). Differences

Table 4. Estimation of residual, additive genetic, phenotypic variance (on diagonal), covariance (lower diagonal) and correlations (upper diagonal) between milk and fat yields of first four lactations from bivariate analysis

	Phenotypic		Additive genetic		Residual		h^2
	F	M	F	M	F	M	
M_1	1380910	0.5	554405	0.52	1935320	0.49	0.29
F_1	29520.2	2554.78	7255.2	347.431	36775.4	2902.21	0.12
M_2	2107330	0.56	515559	0.56	2622890	0.56	0.2
F_2	46125.9	3169.47	7872.42	378.652	53998.3	3548.12	0.11
M_3	2184250	0.57	551836	0.59	2736090	0.57	0.2
F_3	48151.2	3249.72	9549.88	476.585	57701	3726.31	0.13
M_4	2375040	0.62	426041	0.4	2801080	0.6	0.15
F_4	54820.2	3249.69	3516.15	179.746	58336.4	3429.43	0.05

between genetic and environmental correlations was small that resulted in slight alteration in heritability of both traits. There was a large positive genetic correlation of 0.52, 0.56, 0.59, and 0.40 between milk and fat yields for lactations 1 to 4, respectively. These large positive genetic correlations suggested that the same genes employ a common influence on the both traits and selection for one trait would increase another. Also, there was a large positive residual correlation of 0.50, 0.56, 0.57, and 0.62 between milk and fat yields for lactations 1 to 4, respectively. High positive residual correlations indicated that both traits were affected by the same environmental effects. In general, estimated correlations were in the range of estimates from literature.

Co (variance) components, heritabilities and correlations between lactations from multivariate analyses are shown in Table 5 for milk yield and fat yield. All genetic correlations among milk yield of four lactations and fat yields obtained in the present study were high and positive. Heritabilities of both traits had decreasing trends across four lactations. Visscher and Thompson (1992) reported decrease in heritability of production traits across lactations. Correlations of both traits and heritability for milk yields were in the range of estimates from literature but heritability for fat yields were lower. On comparing variance components of univariate and multivariate analyses, it can be concluded that the first lactation records were without culling bias, but other lactations were influenced by this phenomenon. Assessment of estimated variance components from univariate and multivariate analyses confirmed that there were small going up (almost 7.3%) in additive genetic variances in first lactation for both traits but these rising were about 15.7%, 18.77% and 56.33% for milk yield of second to fourth lactations and about 29.32%, 39.80% and 58% for fat yield of second to fourth lactations. Heritability estimates of milk and fat yield from multivariate analyses were greater than heritabilities estimated from univariate analyses, probably because of selection bias correction through multivariate analysis. If the management of cow industry is weak, high producing heifers are not capable to recover itself after first lactation and cannot realize their full potential during second lactation. So the genetic variance of multiparous cows will reduce in herds with weak management (Weller *et al.* 1987). Genetic and residual correlation estimations between successive lactations (first and second; second and third; third and fourth) were higher than correlations between nonconsecutive lactations. This conclusion was in agreement with the results of Visscher and Thompson (1992), and Bahreini Behzadi *et al.* (2013). The differences between genetic and residual correlations among lactations in present study varied from 0.50 to 0.75, consequently using multivariate analyses is convincing. Schaeffer (1999) recommended the possibility of multivariate analysis for traits where there are high differences between the genetic and residual correlations, preferably larger than 0.50. Also, using these analyses without consideration to their individual description will consequence in unexpected result in genetic trend.

Comparing various animal model analyses revealed that univariate analyses are unproblematic but the results were only unbiased for the first lactation because of inexistence of culling bias. Indeed, only result of first lactation was in agreement with multivariate analyses. Thus selection based on univariate analysis's breeding values of second or later lactations will be biased because inattention to earlier selection process. Main hypothesis for using repeatability models is that all lactations are genetically the same trait and records have high genetic correlations (Tong *et al.* 1979, Meyer 1984, Meyer 1985, Mrode 2005). Conversely, several study proposed that lactations should be considered as separate traits and suggested use of multivariate analysis (Alburqueque *et al.* 1996). However, differences between genetic and residual correlations of each trait for lactations in present study showed that we must envisage different lactations as separate traits and the same set of genes aren't influencing them. Repeatability of successive lactations increased gradually as the cows got older whereas repeatability of no successive lactations decreased gradually as the lactations became more separated in time (Butcher and Freeman 1968). Using repeatability model account to

Table 5. Estimation of residual, additive genetic variance (on diagonal), covariance (lower diagonal), and correlations (upper diagonal) between milk yield and fat yield of the first four lactations from multivariate analysis

	Milk yield								
	`Residual				Additive genetic				
	M_1	M_2	M_3	M_4	M_1	M_2	M_3	M_4	h^2
M_1	1371360	0.36	0.31	0.26	576668	0.91	0.87	0.79	0.30
M_2	599069	2035830	0.41	0.39	533506	596868	0.97	0.91	0.23
M_3	529503	855803	2179530	0.46	518994	590786	621210	0.96	0.22
M_4	478579	863608	1046990	2406720	456249	535478	575009	579066	0.19
	Fat yield								
	F_1	F_2	F_3	F_4	F_1	F_2	F_3	F_4	h^2
F_1	2310.62	0.25	0.16	0.17	471.67	0.87	0.91	0.83	0.17
F_2	640.76	2810.94	0.35	0.32	437.00	532.36	0.96	0.90	0.16
F_3	424.12	985.51	2910.19	0.38	482.48	540.47	592.01	0.98	0.17
F_4	434.96	919.10	1114.40	2921.46	364.33	416.18	477.86	405.38	0.12

select older animals and this increase generation interval and decrease genetic progress (De Varies *et al.* 1998).

In general, our results showed that by using multivariate analysis, the heritabilities were higher than those estimated by univariate analyses, because it considers the effects of selection bias according to the first lactation. However, it could be concluded that multivariate analysis is the best model for estimating the genetic parameters of milk and fat yield. Also, the genetic and residual correlation differences between lactations validate use of multivariate analyses instead of univariate and repeatability models.

REFERENCES

Abdallah J M and McDaniel B T. 2000. Genetic parameters and trends of milk, fat, days open, and body weight after calving in North Carolina experimental herds. *Journal of Dairy Science* **83**: 1364–70.

Albuquerque L G, Keown J F and Van Vleck L D. 1996. Genetic parameters of milk, fat, and protein yield in the three lactations, using an animal model and restricted maximum likelihood. *Brazilian Journal of Genetics* **191**: 79–86.

Alijani S, Jasouri M, Pirany N and Kia H D. 2012. Estimation of variance components for some production traits of Iranian Holstein dairy cattle using Bayesian and AI-REML methods. *Pakistan Veterinary Journal* **32**: 562–66.

Al-Seaf A, Keown J F and Van Vleck L D. 2007. Genetic parameters for yield traits of cows treated or not treated with bovine somatotropin. *Journal of Dairy Science* **90**: 501–06.

Bahreini Behzadi M R, Amini A, Aslaminejad A A and Tahmoorespour M. 2013. Estimation of genetic parameters for production traits of Iranian Holstein dairy cattle. *Livestock Research for Rural Development* **25**(9): 1–7.

Banik S and Gandhi R S. 2006. Animal model versus conventional methods of sire evaluation in Sahiwal cattle. *Asian Australasian Journal of Animal Science* **19**(9): 1225–28.

Banik S and Gandhi R S. 2007. Effectiveness of DFREML versus conventional methods of Sahiwal sire evaluation. *Indian Journal of Animal Sciences* **77**(11): 1143–47.

Banik S and Gandhi R S. 2010. Estimation of genetic parameters in Sahiwal cattle using single and multi-trait restricted maximum likelihood method. *Indian Journal of Animal Sciences* **80**(3): 266 – 68.

Barash H, Silanikove N and Weller J I. 1996. Effect of season of birth on milk, fat, and protein production of Israeli Holsteins. *Journal of Dairy Science* **79**: 1016–20.

Boujenane I. 2002. Estimates of genetic and phenotypic parameters for milk production in Moroccan Holstein-Friesian cows. *Revue D'Elevage Et De Medecine Veterinaire Des Pays Tropicaux* **55**: 63–67.

Butcher D F and Freeman A E. 1968. Heritabilities and repeatabilities of milk and milk fat production by lactations. *Journal of Dairy Science* **51**: 1387–91.

Dedkova L and Wolf J. 2001. Estimation of genetic parameters for milk production traits in Czech dairy cattle population. *Czech Journal of Animal Science* **46**: 298–307.

Dematawewa C M B and Berger P J. 1998. Genetic and phenotypic parameters for 305–day yield, fertility and survival in Holsteins. *Journal of Dairy Science* **81**: 2700–09.

De Vries M J, Van der Waaij E H and Van Arendonk J A M. 1998. Estimation of genetic parameters for litter size in sheep: A comparison of repeatability and a multivariate model. *Animal Science* **66**: 685–88.

Dong M C, Van Vleck L D and Wiggans G R. 1988. Effect of relationships on estimation of variance components with an animal model and restricted maximum likelihood. *Journal of Dairy Science* **71**: 3047–52.

Ducrocq V, Boichard D, Bonaiti B, Barbat A and Briend M. 1990. A pseudo-absorption strategy for solving animal model equations for large data files. *Journal of Dairy Science* **73**: 1945–55.

Gianola D and Sorensen D. 2004. Quantitative genetic models for describing simultaneous and recursive relationships between phenotypes. *Genetics* **167**: 1407–24.

Jones L P and Goddard M E. 1990. Five years experience with the animal model for dairy cattle evaluations in Australia. 4th World Congress on Genetics Applied to Livestock Production, Edinburgh, Scotland, July 27, **13**: 382–85.

Laben R C, Shanks R D, Berger P J and Preemaa A E. 1982. Factors affecting milk yield and reproductive performance. *Journal of Dairy Science* **65**: 1005–15.

Meyer K. 1984. Estimates of genetic parameters for milk and fat yield for the first three lactations in British Friesian cows. *Animal Production* **38**: 313–32.

Meyer K. 1985. Genetic parameters for dairy production of Australian black and white cows. *Livestock Production Science* **12**: 205–19.

Meyer K. 2007. WOMBAT – A tool for mixed model analyses in quantitative genetics by REML. *Journal of Zhejiang University Science B* **8**: 815–21.

Mrode R A. 2005. Linear models for the prediction of animal breeding values (2nd ed). CAB International, Wallingford, UK.

Palacios A, Espinoza L J, Pena G D, Iglesias G D, Rafael L P and Almeida R F. 2007. Estimation of covariance components for the first four lactations in Holstein cattle according to different models. *Zootecnia Tropical* **25**: 9–18.

Raheja K L, Burnside E B and Schaeffer L R. 1989. Relationships between fertility and production in Holstein dairy cattle in different lactations. *Journal of Dairy Science* **72**: 2670–78.

SAS, 2009. User's guide, Release 9.2. SAS Institute Inc., Cary, NC, USA.

Schaeffer L R. 1999. Multiple traits animal models. Guelph University. http://www.aps.uoguelph.ca/~lrs/Animalz/lesson15.

Tong A K W, Kennedy B W and Moxley J E. 1979. Heritabilities and genetic correlations for the first three lactations from records subject to culling. *Journal of Dairy Science* **62**: 1784–90.

Urioste J I, Rekaya R, Gianola D, Fikse W F and Weigel K A. 2003. Model comparison for genetic evaluation of milk yield in Uruguayan Holsteins. *Livestock Production Science* **84**: 63–73.

Visscher P M and Thompson R. 1992. Univariate and multivariate parameter estimates for milk production traits using an animal model. I: Description and result of REML analyses. *Genetic Selection Evolution* **24**: 415–30.

Weller J I, Ron M and Bar-Anan R. 1987. Effects of persistency and production on the genetic parameters of milk and fat yield in Israeli-Holsteins. *Journal of Dairy Science* **70**: 672–80.

Wiggans G R, Misztal I and Van Vleck L D. 1988a. Implementation of an animal model for genetic evaluation of dairy cattle in the United States. *Journal of Dairy Science* **71**: (suppl 2): 54–69.

Wiggans G R, Misztal I and Van Vleck L D. 1988b. Animal model evaluation of Ayrshire milk yield with all lactations, herd-sire interaction, and groups based on unknown parents. *Journal of Dairy Science* **71**: 1319–29.