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Modeling Extended Lactations of Holsteins

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ABSTRACT

Modeling extended lactations for the US Holsteins is useful because a majority (>55%) of the cows in the present population produce lactations longer than 305 d. In this study, 9 empirical and mechanistic models were compared for their suitability for modeling 305-d and 999-d lactations of US Holsteins. A pooled data set of 4,266,597 test-day yields from 427,657 (305-d complete) lactation records from the AIPL-USDA database was used for model fitting. The empirical models included Wood (WD), Wilmink (WIL), Rook (RK), monophasic (MONO), diphasic (DIPH), and lactation persistency (LPM) functions; Dijkstra (DJ), Pollott (POL), and new-multiphasic (MULT) models comprised the mechanistic counterparts. Each model was separately tested on 305-d (>280 days in milk) and 999-d (>800 days in milk) lactations for cows in first parity and those in third and greater parities. All models were found to produce a significant fit for all 4 scenarios (2 parity groups and 2 lactation lengths). However, the resulting parameter estimates for the 4 scenarios were different. All models except MONO, DIPH, and LPM yielded residuals with absolute values smaller than 2 kg for the entire period of the 305-d lactations. For the extended lactations, the prediction errors were larger. However, the RK, DJ, POL, and MULT models were able to predict daily yield within a ±3 kg range for the entire 999-d period. The POL and MULT models (having 6 and 12 parameters, respectively) produced the lowest mean square error and Bayesian information criteria values, although the differences from the other models were small. Conversely, POL and MULT were often associated with poor convergence and highly correlated, unreliable, or biologically atypical parameter estimates. Considering the computational problems of large mechanistic models and the relative predictive ability of the other models, smaller models such as RK, DJ, and WD were recommended as sufficient for modeling extended lactations unless mechanistic details on the extended curves are needed. The recommended models were also satisfactory in describing fat and protein yields of 305-d and 999-d lactations of all parities.

Key words: dairy cow, Holsteins, lactation curve, modeling

INTRODUCTION

Lactation curves are a valuable tool in designing suitable breeding and management strategies for cattle (Papajcsik and Bodero, 1988; Beever et al., 1991; Pietersma et al., 2001) as well as other species (Gipson and Grossman, 1990; Ruiz et al., 2000). Population- and time-specific lactation models help genetic selection (Dekkers et al., 1996; VanRaden et al., 2006), predict yield from incomplete data, analyze yield responses to management and environmental changes, diagnose problems, and identify opportunities for increased net merit effectively (Scott et al., 1996; Pietersma et al., 2001; Val-Arreola et al., 2004).

Presently in a number of countries, many cows have lactations extended beyond 305 d (Vargas et al., 2000). Lactation length has increased by about 30 d over the last decade in some populations (Gonzalez-Recio et al., 2004). Recent studies show that over 55% of US Holstein cows record lactations longer than 305 d (Tsuruta et al., 2005; VanRaden et al., 2006). The undesirable trend that exists with loss of fertility and reproductive failures in dairy cattle (Butler, 1998; Silvia, 2003) is a well-known contributor to extended lactations. However, extended lactations could be a part of management strategy (Tarazon-Herrera et al., 2000; Gonzalez-Recio et al., 2006). Almost all validations and uses of the lactation models reported in literature have been for 305-d or shorter lactations, with rare exceptions (Vargas et al., 2000; Grossman and Koops, 2003) in which lactations extending up to 18 mo have been examined. Papajcsik and Bodero (1988) cited a list of 20 different empirical formulas developed since 1923. The incomplete gamma function (**WD**) proposed by Wood (1967) was the earliest popular model conceived for the whole lactation, although inverse polynomial (**IP**; Nelder, 1966) is still a favorite choice for modeling (Batra, 1986; Scott et al., 1996). Subsequent attempts to

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Table 1. Number of records, average 15th day and peak milk yields (kg), and peak day in milk for 305-d (>280 DIM) and 999-d (>800 DIM) lactations for first and third and greater parities

Parity	Lactation length (d)	Lactation records, n	Test-day records, n	d 15 yield	Peak yield	Peak DIM
First	305	235,241	2,128,015	26.4	33.1	94
	999	1,692	38,495	25.4	35.0	98
Third and greater	305	237,416	2,138,582	38.0	44.3	51
	999	1,012	22,487	35.2	45.6	70

improve WD with respect to its functional form, mathematical properties, and forecasting ability were reviewed by Beever et al. (1991). Wilmink's exponential (**WIL**) function (Wilmink, 1987) has an advantage over WD and IP because the initial yield is not forced to zero. Rook et al. (1993) showed that their Mitscherich × exponential and Michaelis-Menten × exponential functions, which described the lactation curve as a product of growth and death processes of mammary cells, fit better than the WD model. Val-Arreola et al. (2004) found that the Michaelis-Menten × exponential function (**RK**) is the most superior model of Rook et al. (1993). Grossman and Koops (1988) showed that both WD and IP overpredict yield during early lactation and underpredict the peak, and produce autocorrelated residuals. Alternatively, they proposed a multiphasic curve using sums of logistic functions to overcome those problems. Their monophasic (**MONO**) and diphasic (**DIPH**) variants (with 3 and 6 parameters, respectively) were supposed to be the optimal versions (Gipson and Grossman, 1990). However, many have criticized the multiphasic model for its lack of a biological basis (Beever et al., 1991; Rook et al., 1993). Grossman et al. (1999) also proposed a model to measure persistency of lactation. The proposed lactation persistency model (**LPM**) assumes a constant yield in mid lactation, and the length of this period is the measure of lactation persistency.

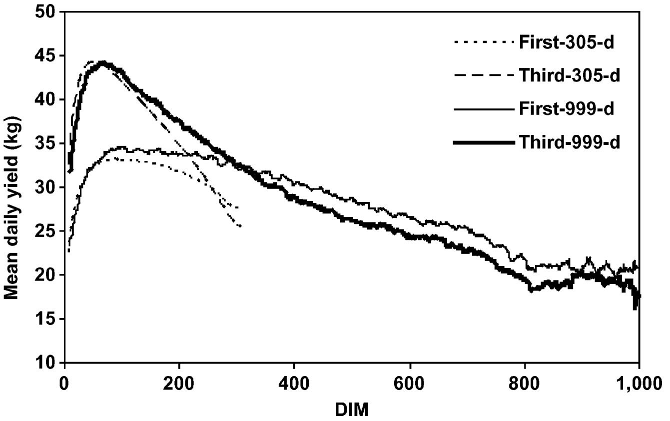

Figure 1. Observed daily mean yields from 305-d and 999-d lactations of cows in the 2 parity groups. First-305-d and first-999-d = first-parity cows with >280 DIM and >800 DIM, respectively; third-305-d and third-999-d = cows in third and greater parities with >280 DIM and >800 DIM, respectively.

Alternatively, several mechanistic models have been developed to simulate the metabolic response of the whole animal with each term of the model having a biological interpretation (Beever et al., 1991). The initial mechanistic model of Neal and Thornley (1983) was based on mammary cell differentiation and programmed cell death (apoptosis), but had limited practical use due to nonavailability of information on inputs required. Subsequently, Dijkstra et al. (1997) developed a 4-parameter model that describes the mammary growth pattern (cell proliferation and apoptosis) of mammals during pregnancy and lactation. The Dijkstra model (**DJ**) was found to fit well for lactations of dairy cows (Dijkstra et al., 1997; Val-Arreola et al., 2004). Pollott (2000) proposed a model that mimics 3 processes including mammary cell differentiation, apoptosis, and milk secretion rate per cell. The basic Pollott model (**POL**) contained 6 parameters, with an additional parameter for each new factor (secondary growth, pregnancy, etc.). An alternative mechanistic version of the multiphasic model was proposed by Grossman and Koops (2003). This new multiphasic model (**MULT**) contained 13 parameters that could be interpreted with respect to the shape of the curve. Such large models are expected to have better predictive ability but could be computationally demanding.

Alternative models have been compared with respect to their ability to fit individual lactation curves of various shapes (Macciotta et al., 2005; Silvestre et al., 2006). Alternatively, the models have been used to describe average lactation curves of various groups such as parities and lactation lengths (Tozer and Huffaker, 1999; Vargas et al., 2000; VanRaden et al., 2006). Group-average lactation curves are useful in design of optimization models, simulations, reproductive and management strategies (Freeze and Richards, 1992; Vargas et al., 2000; Pietersma et al., 2001), and breeding (VanRaden et al., 2006).

Until recently, lack of sufficiently large datasets on extended lactations has been a hindrance to modeling

Table 2. Lactation formulas used to model 305-d and extended lactations

Lactation model	Code	Functional form[1]	Reference
Wood	WD	$Y_t = a\ t^b e^{-ct}$	Wood (1967)
Wilmink	WIL	$Y_t = a - bt - ce^{-dt}$	Wilmink (1987)
Rook	RK	$Y_t = a\{1/[1 + b/(c + t)]\}e^{-dt}$	Rook et al. (1993)
Dijkstra	DJ	$Y_t = a\ \exp[b(1 - e^{-ct})/c - dt]$	Dijkstra et al. (1997)
Pollott	POL	$Y_t = a\{1/[1 + ((1 - b)/b)\ e^{-ct}]$ $- 1/[1 + ((1 - d)/d)\ e^{-gt}]\}(1 - e^{-ht})$	Pollott (2000)
Grossman models			
Monophasic	MONO	$Y_t = ab[1 - \tanh^2(b(t - c))]$	Grossman and Koops (1988)
Diphasic	DIPH	$Y_t = ab[1 - \tanh^2(b(t - c))]$ $+ dg[1 - \tanh^2(g(t - h))]$	Grossman and Koops (1988)
New multiphasic	MULT	$Y_t = a\{1/[1 + e^{-(t - c)/b}]$ $- p/[1 + (0.5e^{-(t - g)/d})^2] - q/[1 + e^{-(t - i)/h}]$ $- (1 - p - q)/[1 + (0.5e^{-(t - k)/j})^2]\}$	Grossman and Koops (2003)
Persistency	LPM	$Y_t = (a/b)(t - \mathrm{Ln}[(e^t + e^b)/(1 + e^b)])$ $- c\ \mathrm{Ln}[(e^t + e^{(b + d)})/(1 + e^{(b + d)})]$	Grossman et al. (1999)

[1] Y_t is milk yield (kg/d), t is the time of lactation (d), and a, b, c, d, g, h, i, j and k are parameters that define the individual curves.

extended lactations. The expansions made in 1997 in the AIPL-USDA database to store lactation records up to 999 d in length now allow extensive examination of the characteristics of lactation curves of US Holsteins and other breeds beyond 305 DIM. Subsequently, the productive life trait has been redefined in the US genetic evaluations to give credit to lactations extending up to 999 d (VanRaden et al., 2006). At present, the credits are based on a modified version of the DJ model fitted to average 999-d/extended lactation curves of first, second, and greater parity groups.

The objective of this study was to compare the widely used empirical and mechanistic formulas with respect to their suitability for modeling the average (305-d) and extended (999-d) lactation curves of different parities of the present US Holstein population. The average lactation curves, representing the 305-d and 999-d lactations of first vs. third and greater parities, were separately modeled.

MATERIALS AND METHODS

Data Sources

Test-day data of 152,734 Holstein cows with calvings between 1997 and 2003 were obtained from the AIPL-USDA database. Test days varied from 7 to 999 d in lactation with about 0.1% of cows having 999 DIM (maximum 35 test-days per cow). The first test day was required to be ≤60 DIM. Only cows that had at least 280 and 800 DIM in a lactation were considered for the 305-d and 999-d subsets (lactation length groups), respectively. After edits there were 4,266,597 test-day records of 427,657 complete 305-d lactations (Table 1). Records of first parity and third and greater parities were used separately to fit the alternative models because those 2 parity groups showed 2 very different shapes of lactation curve (Figure 1). The second-parity curve had an intermediate shape. Thus, comparisons of models of second-parity data were not included in this article. Each lactation model was fitted once to test-day data of all cows within a parity–lactation length subgroup to obtain a single set of parameter estimates for the average lactation curve of each of the 4 subgroups.

Selection of Lactation Models

A wide range of empirical and mechanistic models available in literature were initially tested on mean yields (kg/d) of each 30-d interval of the lactations, and 9 of the best-fit models (WD, WIL, RK, DJ, POL, MONO, DIPH, MULT, and LPM) were selected for further analysis (Table 2), based on lowest mean square error (**MSE**). The IP and Cobby and Le Du (1978) functions did not provide low MSE values consistently for all subgroups and were excluded from further consideration. Legendre polynomials are often used in random regression models to model individual lactation curves (Schaeffer, 2004). However, the orthogonal Legendre polynomials of degree 2, 3, and 4, when tested in this study, did not fit the extended lactations as closely as the nonlinear functions. Individual test-day yields of the 305-d and 999-d subsets were fitted for the selected models within parity using a nonlinear regression procedure (PROC NLIN; SAS Institute, 2000). Initial search grid was specified covering the parameter bounds of each model. Convergence criterion was defined as the error sum of squares between successive iterations and was set to 10^{-6}. The Marquardt method was used as the primary iteration method, but other available methods were also used with various step sizes (SSIZE = halve, golden, and cubic) when models failed to converge. Sum of squares of error (**SSE**), square root of MSE (root MSE), adjusted R-square (**ADJRSQ**), and asymptotic standard errors of the parameters were recorded. Some authors have used mean square prediction error (= SSE/no. of observations) to measure error variation because MSE is influenced by the number of parameters (Val-Arreola et al., 2004). However, in this study both prediction error variance and MSE were very similar due to the large number of observations present. The Durbin-Watson test (Durbin, 1970) was conducted on the residuals of each model and parity group (using mean daily yields of each day of lactation) to test for possible first-order autocorrelations among residuals. The autoregressive procedure in SAS (PROC AUTOREG with *dw=1* and *dwprob* options) provided the Durbin-Watson statistic, autocorrelation coefficient, and the associated probabilities. Model selection criteria included SSE, root MSE, ADJRSQ, convergence properties, standard errors of estimates, positive autocorrelation of errors, and Bayesian information criteria (**BIC**; Leonard and Hsu, 2001). The BIC are parsimony based model-order selection criteria that penalize the model for inclusion of additional parameters while rewarding for improved fit, as follows:

$$\mathrm{BIC} = -2 \log (\boldsymbol{L}) + \boldsymbol{K} \log (\boldsymbol{N}),$$

where $\boldsymbol{L}$, $\boldsymbol{K}$, and $\boldsymbol{N}$ represent the maximum likelihood, number of independent parameters in the model, and sample size, respectively (Leonard and Hsu, 2001; Val-Arreola et al., 2004). Consequently, the best model was selected based on the smallest numerical value of BIC. The nonlinear mixed procedure (PROC NLMIXED; SAS Institute, 2000) was used to obtain BIC for each model.

The preliminary analysis also included fitting the selected models on test-day fat and protein yields within parity–lactation sub groups. All 9 models satisfactorily described the fat and protein yields of extended lactations. Wood's model, having the fewest parameters and wide applicability, was chosen to report the respective parameter estimates for fat and protein lactation curves of all 3 parity groups.

RESULTS AND DISCUSSION

Observed Lactation Curves

The average 15th day and peak yields of each parity–lactation length subgroup are given in Table 1. Peak day was considered as the DIM on which daily average milk yield of the subgroup was highest. Table 1 shows that the long lactating cows (>800 DIM) in the data (999-d group) tended to reach a higher peak (on average) at a later DIM although they started slower than the entire group of cows that reached 280 DIM (305-d group). Clear differences can also be seen between the lactation curves of first parity and the 3+ parity group, with the mature cows (3+ group) reaching a higher peak earlier than the maturing heifers. Generally, there can be many reasons for cows to be allowed to continue for extended lactations. However, in this study, the 999-d group was more persistent than the 305-d group (Figure 1). Because of the differences in shapes of lactation curves, the parameter estimates were expected to differ depending on parity or lactation length.

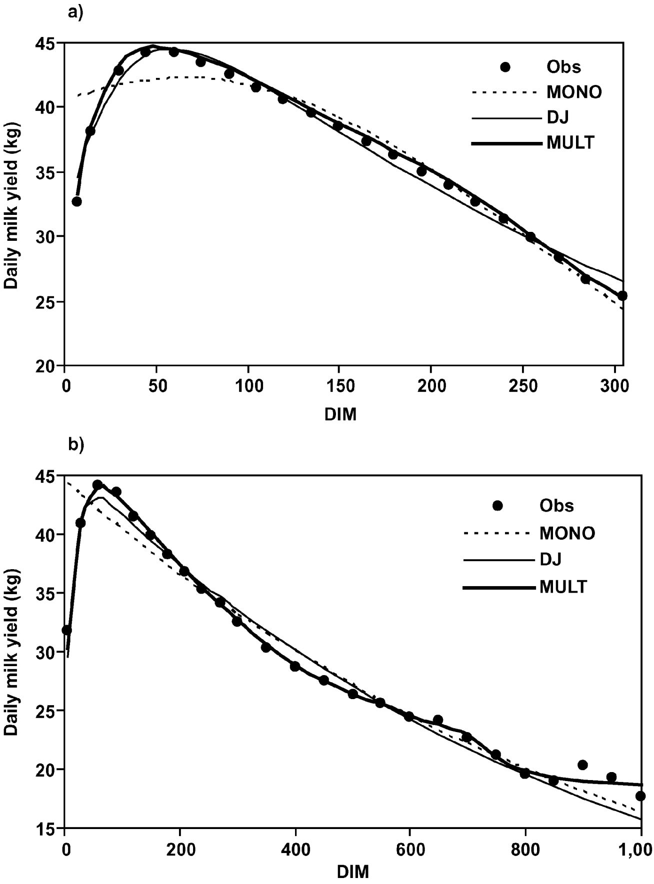

Figure 2. Mean milk yield of a given DIM (Obs), and 3 example curves [MONO = Grossman monophasic (poor fit); DJ = Dijkstra (average fit); and MULT = Grossman new multiphasic (better fit)] fitted to all test-day yields of third and greater parities; a) 305-d and b) 999-d lactations.

Fits of Lactation Models

The F-values associated with the model sum of squares showed that all 9 models in general provided highly significant fits ($P < 0.01$) for all 4 parity–lactation length subgroups. Most models provided similar lactation curves that described the data accurately. The

Table 3. Comparison of lactation models fitted on test-day yields of 305-d complete lactations of first-parity cows[1]

	Lactation model[2]								
Parameter	WD	WIL	RK	DJ	POL	MONO	DIPH	MULT[3]	LPM
a	15.6862	37.348	43.799	21.764	33.6398	11,223.9	819.1	192.4	32.1985
	(0.0311)	(0.030)	(0.089)	(0.042)	(0.022)	(15.303)	(47.1)	(216.8)	(0.006)
b	0.2081	0.030	17.16	0.0176	0.5876	0.003	0.0128	16.6364	13.564
	(0.0006)	(0.0001)	(0.206)	(0.0001)	(0.0016)	(4.5E–6)	(0.0002)	(0.994)	(0.022)
c	0.002	16.433	12.459	0.032	0.0639	140.6	50.461	–40.954	0.043
	(5.1E–6)	(0.044)	(0.204)	(0.0002)	(0.0004)	(0.122)	(0.472)	(22.148)	(0.0003)
d		0.030	0.0013	0.00095	0.0045		7,736.6	–180.8	180.0
		(0.0002)	(5.9E–6)	(4.1E–6)	(0.0002)		(117.1)	(91.16)	(0.42)
g					0.0132		0.004	733.0	
					(1.2E–4)		(5.1E–5)	(315.5)	
h					0.99		204.7	13.7831	
					(0.0)		(1.793)	(3.7875)	
Peak yield	33.35	33.55	33.41	33.59	33.08	33.11	33.49	33.08	32.20
Peak day	102	93	95	91	86	140	83	96	27–184
Selection criteria[4]									
SSE ($\times 10^8$)	1.096	1.097	1.096	1.098	1.094	1.115	1.098	1.094	1.125
Root MSE	7.175	7.181	7.177	7.184	7.171	7.239	7.184	7.170	7.264
ADJRSQ	0.076	0.074	0.075	0.073	0.077	0.059	0.074	0.077	0.053
BIC $\times 10^7$	1.44	1.44	1.44	1.44	1.44	1.45	1.44	1.44	1.45
DW	0.474	0.185	0.327	0.135	0.8966	0.023	0.087	2.0838	0.0618
P < DW	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.7502	0.0001
ρ	0.60	0.92	0.82	0.92	0.085	0.95	0.92	0.085	–0.844
H_s	P	P	NP	P	P	NP	NP	NP	P

[1] Standard errors of estimates are within parentheses.

[2] WD = Wood; WIL = Wilmink; RK = Rook; DJ = Dijkstra; POL = Pollott; MONO = monophasic; DIPH = diphasic; MULT = multiphasic; LPM = persistency model. MONO, DIPH, MULT, and LPM are Grossman models.

[3] Other estimates of multiphasic model: i = 273.3 (5.12); j = 103.6 (12.337); and k = 272.3 (26.428); P = 0.8414 (0.1719); q = 0.0124 (0.0165).

[4] SSE = error sum of squares; root MSE = square root of mean square error; ADJRSQ = adjusted R^2; BIC = Bayesian information criterion; DW = Durbin-Watson statistic; P < DW = P-value for testing positive autocorrelation; ρ = autocorrelation of errors; H_s = singularity of Hessian matrix (P = positive definite and NP = nonpositive definite).

MONO and LPM models were exceptions for some subgroups. Figure 2 (a and b) was included to provide a visual representation of the fits of several curves. The curves produced by the MONO, DJ, and MULT models for 305-d and 999-d lactations of cows in third and greater parities exemplify poor, average, and better fits, respectively. For a 999-d lactation of the third and greater parity group, MONO produced a monotonically decreasing curve (Figure 2b).

305-d Lactations

Table 3 shows the parameter estimates and selection criteria for the various models fitted on 305-d (>280 DIM) lactations of first-parity cows. Figure 3 shows that, for the US Holsteins considered, all models predicted the average yield with respect to each DIM of 305-d first lactations with an absolute error margin of <2 kg, except the MONO, DIPH, and LPM models, which had relatively larger prediction errors at early stages of lactations. The WIL and RK models predicted the peak day most accurately (±1 d margin) although DJ and MULT were very close. The widely used WD model had its peak 8 d later than the actual peak. The LPM model predicted a plateau of peak yield persisting for about 180 d starting from wk 4 of lactation, which is unrealistic, and resulted in the poorest fit. Having more than 5 parameters, the POL and MULT models recorded the lowest SSE and the highest ADJRSQ values, with the WD and RK models also providing very close estimates. The ADJRSQ was less than 8% for all models. In this study, the models were fitted to the parity–lactation length subgroups instead of on lactations of individual cows. The substantial variation in the test-day yields of cows at each DIM caused the very low ADJRSQ values. The Durbin-Watson statistic showed that all models except MULT had significantly positive autocorrelation of residuals. Positive autocorrelations occur when adjacent values of residuals tend to share the same sign (positive or negative) more than randomly possible. Figure 3a clearly shows a typical positively autocorrelated pattern of residuals in WD, WIL, RK, and DJ models. The above results were comparable with those reported by Pollott (2000) and Grossman and Koops (2003). The MULT model was slightly superior to POL with respect to root MSE. However, MULT resulted in highly correlated parameter estimates that made the respective Hessian matrix nonpositive definite. This has also caused some parameter estimates to have large standard errors, making them

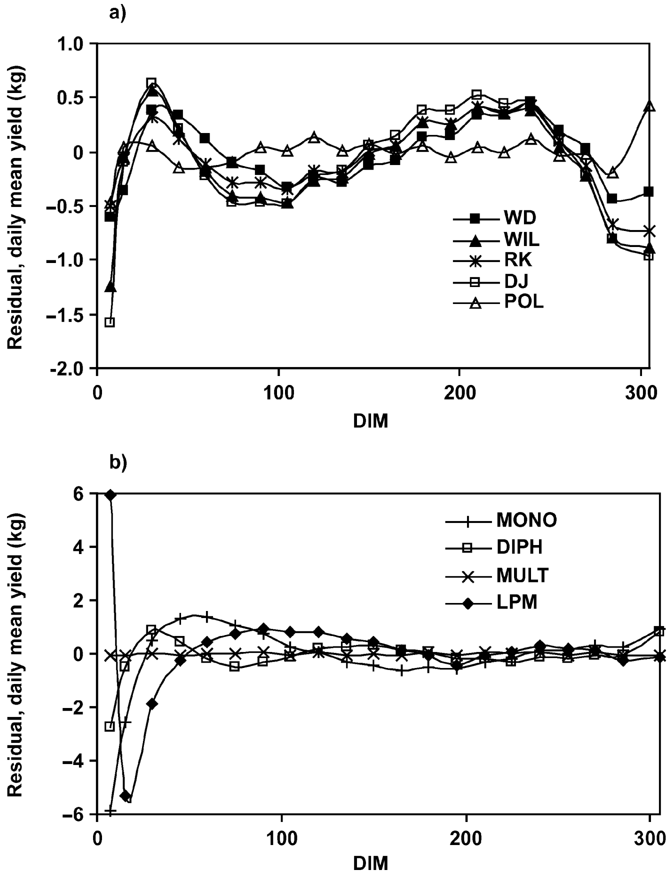

Figure 3. Residuals for first-parity 305-d complete lactation. a) Wood (WD), Wilmink (WIL), Rook (RK), Dijkstra (DJ), and Pollott (POL) models; b) Grossman monophasic (MONO), diphasic (DIPH), multiphasic (MULT), and lactation persistency (LPM) models.

nonsignificant or unreliable. Although the parameters of MULT are claimed to be biologically meaningful (Grossman and Koops, 2003), estimates falling beyond the reasonable bounds (with large standard errors) have made them less useful in explaining the underlying biology. Among the models with <5 parameters, WD was the best with respect to root MSE and ADJRSQ.

Similar performance of the models can be seen in the 305-d lactations of cows in third and greater parities, with POL and MULT recording the lowest SSE and the highest ADJRSQ values (Table 4). The BIC values of POL and MULT were also comparable with the estimates of the models with fewer parameters, implying that those 2 models produce likelihood estimates large enough to overcome the penalty assigned by the BIC for having more parameters. However, MULT was marginally better than POL with respect to root MSE, as experienced by Pollott (2000). The MULT model also predicted the peak day exactly whereas WIL, RK, DJ, and POL had predictions within a 7-d absolute error margin. However, MULT again resulted in a singular Hessian matrix with strong correlations among parameter estimates indicating a possible overparameterization of the model. The estimates of MULT such as a (asymptotic value of milk secretion potential, kg/d) and h (relative rate of change in secretion rate) are clearly out of the expected range, and some parameters are nonsignificant ($P > 0.05$). However, the estimates of POL were within the bounds imposed by the mechanics of the model and were readily interpretable. For example, parameter a represents the maximum potential daily milk production of the udder if all parenchyma cells were differentiated at the same time and were operating at the highest secretion rate (Pollott, 2000). Because it is almost unlikely that all parenchyma cells become differentiated and operate at the highest rate at exactly the same time, observed peak yields are almost always less than the maximum potential production (a). The model estimates show that the maximum potential daily milk production was 33.6 kg for heifers and 53.5 kg for the older parity group. These average estimates for the population seem reasonable given that the observed peaks were 33 and 44 kg, respectively (Table 1). Among the simpler models, WIL showed the best fit although the differences among them were marginal. The DIPH model (with 6 parameters) performed better than the MONO model (as expected) although its performance relative to the models with fewer parameters was not satisfactory (contrary to the findings of Vargas et al., 2000). Figure 4 shows that the residual distribution of the models for cows in third and greater parities was somewhat similar to those of the heifers, except that the overprediction by several models during the first few weeks of lactation was higher for older cows. Autocorrelations of residuals were also significant for all models. The root MSE values in Table 4 are higher than the respective values in Table 3, indicating the higher yield variability within older cows compared with within first-parity cows. However, the respective ADJRSQ values were also higher in Table 4 due to the higher model sum of squares generated by the shape of lactation curve of older cows with higher peak.

Extended Lactations

Figure 4 shows that all models described the extended lactations of first parity reasonably well up to 999 d, except MONO, DIPH, and LPM, which had large absolute prediction errors (>4 kg) at early stages of lactation (contrary to the findings of Grossman and Koops, 1988). For extended lactations of first-parity cows, the MULT, POL, and RK models produced the lowest prediction errors, with MULT being marginally the best (Table 5). The BIC values showed that the RK

Table 4. Comparison of lactation models fitted on test-day yields of 305-d complete lactations of cows in third and greater parities[1]

	Lactation model[2]								
Parameter	WD	WIL	RK	DJ	POL	MONO	DIPH	MULT[3]	LPM
a	23.0892	50.4670	62.9955	30.7791	53.5278	12999	911.9	153,606	42.8484
	(0.0439)	(0.0247)	(0.1204)	(0.0636)	(0.1568)	(18.545)	(43.177)	(80,685)	(0.012)
b	0.2094	0.0811	14.6000	0.0215	0.6251	0.0033	0.0152	16.7972	10.476
	(0.0005)	(0.0001)	(0.1684)	(0.0002)	(0.007)	(4.6E–6)	(0.0002)	(0.4571)	(0.021)
c	0.00357	23.1904	10.0377	0.0378	0.0796	65.1667	43.63	–147.8	0.082
	(5.5E–9)	(0.0885)	(0.1718)	(0.0002)	(0.0007)	(0.2421)	(0.4371)	(12.169)	(0.0001)
d		0.0487	0.0027	0.0023	0.1217		8660.4	173.0	84.5845
		(0.0003)	(6.1E–6)	(4.2E–6)	(0.0018)		(114.5)	(105.4)	(0.2472)
g					0.0069		0.00417	137.4	
					(4.7E–5)		(3.8E–5)	(20.695)	
h					0.99		148.8	20764.9	
					(0.0)		(2.1035)	(3583)	
Peak yield	43.93	44.42	44.28	44.49	44.19	42.25	44.62	44.68	42.85
Peak day	59	54	56	58	49	65	59	51	27–82
Selection criteria[4]									
SSE ($\times 10^6$)	1.882	1.880	1.882	1.886	1.878	1.917	1.884	1.878	1.905
Root MSE	9.380	9.376	9.381	9.390	9.372	9.467	9.386	9.371	9.438
ADJRSQ	0.270	0.271	0.270	0.268	0.271	0.256	0.269	0.271	0.261
BIC ($\times 10^7$)	1.56	1.56	1.56	1.56	1.56	1.57	1.56	1.56	1.63
DW	0.250	0.264	0.183	0.091	0.903	0.022	0.069	1.226	0.142
P < DW	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
ρ	0.860	0.826	0.896	0.910	0.217	0.910	0.852	0.33	0.851
H_s	P	P	P	P	P	NP	NP	NP	NP

[1] Standard errors of estimates are within parentheses.

[2] WD = Wood; WIL = Wilmink; RK = Rook; DJ = Dijkstra; POL = Pollott; MONO = monophasic; DIPH = diphasic; MULT = multiphasic; LPM = persistency model. MONO, DIPH, MULT, and LPM are Grossman models.

[3] Other estimates of multiphasic model: i = –195606 (6.579); j = 26.0595 (6.579); and k = 260.5 (6.203); P = 0.000274 (2.5E–5); q = 0.9997 (0.00).

[4] SSE = error sum of squares; root MSE = square root of mean square error; ADJRSQ = adjusted R^2; BIC = Bayesian information criterion; DW = Durbin-Watson statistic; P < DW = P-value for testing positive autocorrelation; ρ = autocorrelation of errors; H_s = singularity of Hessian matrix (P = positive definite and NP = nonpositive definite).

model (having fewer parameters) was superior to the other 2 models. All models (except LPM with a plateau of peak yield) predicted peak day to be later than actual, with POL having the lowest error. Again, the Grossman models (except LPM) had singular Hessian matrices and atypical values for some parameters. The LPM model, although computationally less problematic (due to few parameters), did not provide a satisfactory fit for any stage of lactation contrary to the results on extended lactations by Vargas et al. (2000). The plateau of yield expected by the LPM model during mid lactation (the duration of which is the intended measure of persistency) seems unrealistic for 305-d as well as 999-d lactations of US Holsteins.

For the third and greater parities, the MULT model again had the lowest root MSE and BIC values, followed by DJ and POL (Table 6). The MULT model also had the closest prediction of peak day. The MONO model produced a continuously decreasing curve atypically peaking at the onset of lactation. Here, POL resulted in a singular Hessian matrix with an inexplicably large estimate for the highest potential yield (a). Attempts to lower the upper bound for parameter a to reasonable values resulted in lack of convergence. Val-Arreola et al. (2004) experienced the same problem when POL was used on lactations of less than 400 DIM. The LPM model, with its long plateau of yield, once again produced the poorest fit.

Residual variation was higher in mature cows (Figure 6) than in heifers (Figure 5) for all models. This is also related to the larger root MSE values in Table 6 compared with those in Table 5. This is partly because the higher parity group included records from the third to ninth lactation. However, all models were able to predict daily yield within an error margin of ±2 kg for over 90% of the extended lactations. Because the prediction errors are less than 10% of the magnitude of daily yield (which includes measurement errors), it is evident that even the 3-parameter models can be used to model extended lactations with reasonable accuracy.

Fat and Protein Yields

The performances of alternative models with respect to describing fat and protein yields of extended lactations were similar to those for milk yield. Because all

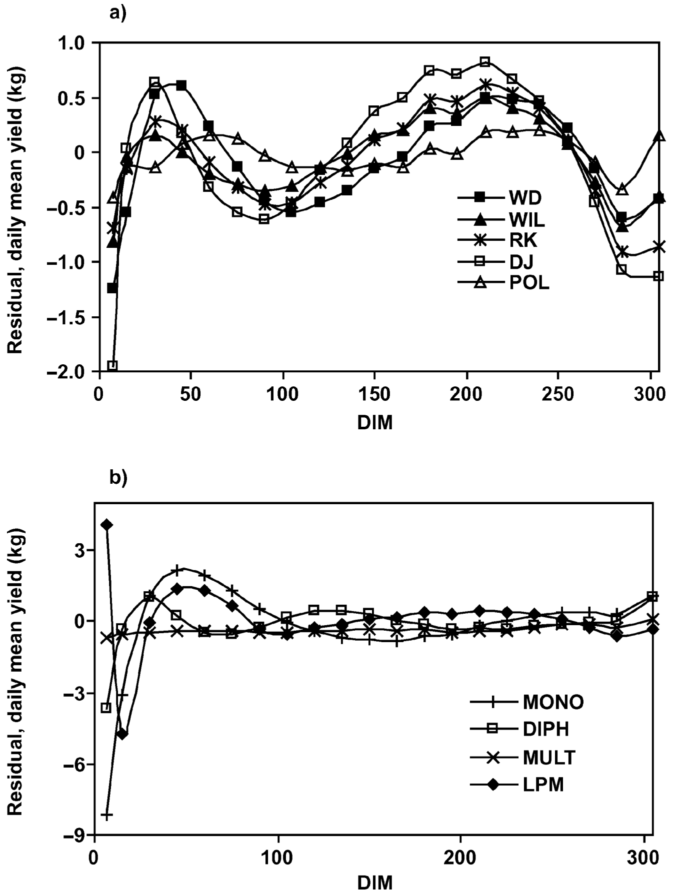

Figure 4. Residuals for 305-d complete lactation of third and greater parities. a) Wood (WD), Wilmink (WIL), Rook (RK), Dijkstra (DJ), and Pollott (POL) models; b) Grossman monophasic (MONO), diphasic (DIPH), multiphasic (MULT), and lactation persistency (LPM) models.

models provided highly significant fits ($P < 0.001$), only the parameter estimates of WD model (having the fewest parameters) are given in Table 7. The measure of persistency [$c^{-(b+1)}$] of the WD model (Wood, 1967) in Table 7 showed that the older cows were less persistent than the heifers with respect to producing fat and protein. In addition, the cows with extended lactations showed high persistency compared with their 305-d counterparts with respect to fat and protein yields, in spite of changes taking place in milk composition during lactation.

Biological Implications

The physiological processes of extended lactations seem somewhat different from those of 305-d lactations. Longer lactating cows enjoy longer periods of days open without the effects of pregnancy and associated physiological changes taking place. Thus, lactation phases of extended lactations are less affected by pregnancy. Mechanistic models help analyze possible underlying reasons for the differences in lactation curves of various genetic or nongenetic groups. For example, in the DJ model, parameters a and b represent theoretical initial milk production and specific rate of parenchyma cell proliferation, respectively. Consequently, the higher estimates of a and b for the ≥ 3 parities (Tables 3 vs. 4, and 5 vs. 6) are comparable with their initial higher daily yields than heifers. On the other hand, within-parity comparisons (Tables 3 vs. 5, and 4 vs. 6) show that parameters c (decay parameter) and d (specific rate of cell death) were smaller for extended lactations, indicating their higher persistency compared with their shorter counterparts. Accordingly for POL model, parameters a (asymptotic value of milk secretion potential) and b (proportion of parenchyma cells differentiated at parturition) were higher for the older group (≥ 3 parities) following their high yield. Moreover, the smaller within-parity estimates for g (relative death rate of cells) for the long lactating cows again partially explained their higher persistency than those with shorter lactations. Alternatively, persistency measures of the empirical models (e.g., $c^{-(b+1)}$ of WD, parameter d of LPM) also show higher values for long lactating cows, although they do not provide a causative explanation.

The parameter estimates reported in the present study describe the current situation of the US Holstein population. However, use of those estimates for extrapolation to the future yield of cows that are in their mid lactations could be misleading. One reason is that not every cow in the present population (or the data set) was given an equal opportunity to produce extended lactations. The present findings allow accurate modeling of milk yield only of cows that had the opportunity for extended lactations. However, parameter estimates of this study document the sustained yields of a substantial part of the present US Holstein population.

Convergence Properties

The models with fewer parameters (WD, WIL, RK, DJ, MONO, and LPM) reached convergence consistently and quickly regardless of the prior estimates or the iterative method used in NLIN and NLMIXED procedures, similar to the findings reported by Vargas et al. (2000) and Val-Arreola et al. (2004). When the NLIN procedure (least squares approach) was used, the steepest descent iterative method had a slower rate of convergence compared with Gauss-Newton, Newton, or Marquardt methods, but was sometimes useful when priors were poor. The Marquardt method, which follows an intermediate path between Gauss-Newton (Taylor

Table 5. Comparison of lactation models fitted on test-day yields of 999-d complete lactations of first-parity cows[1]

	Lactation model[2]								
Parameter	WD	WIL	RK	DJ	POL	MONO	DIPH	MULT[3]	LPM
a	17.8808	37.9287	43.4057	23.5033	44.0935	32,092.9	2,878.8	55.3079	33.3707
	(0.2721)	(0.1161)	(0.3688)	(0.3699)	(1.259)	(418.2)	(1,364.1)	(0.3310)	(0.072)
b	0.1616	0.0191	19.2666	0.0106	0.6501	0.00103	0.0043	21.2208	16.904
	(0.0035)	(0.0002)	(1.4130)	(0.0007)	(0.014)	(1.3E–5)	(0.0006)	(1.5653)	(0.277)
c	0.00107	16.7479	14.8437	0.0203	0.0374	158.0	117.4	–19.9970	0.0199
	(1.4E–5)	(0.4889)	(1.9398)	(0.0007)	(0.0021)	(6.6569)	(14.456)	(2.5189)	(0.0004)
d		0.0249	0.00078	0.0006	0.1731		20,569.3	–38.354	237.8
		(0.0011)	(1.2E–5)	(8.9E–6)	(0.0196)		(3,283.7)	(5.873)	(6.7082)
g					0.0019		0.0013	–645.5	
					(1.1E–5)		(1.4E–4)	(9.9546)	
h					0.9536		474.7	114.0	
					(0.9020)		(80.15)	(30.993)	
Peak yield	34.22	34.80	34.62	34.93	34.67	33.06	34.62	34.27	33.37
Peak day	151	124	133	135	111	158	171	113	30–246
Selection criteria[4]									
SSE ($\times 10^6$)	2.349	2.348	2.347	2.353	2.347	2.409	2.369	2.341	2.383
Root MSE	7.811	7.810	7.809	7.819	7.808	7.911	7.844	7.799	7.868
ADJRSQ	0.210	0.211	0.211	0.209	0.211	0.190	0.204	0.213	0.199
BIC	267,548	267,541	267,527	267,632	267,543	268,519	267,958	267,556	268,120
DW	1.854	1.865	1.903	1.802	1.878	1.114	1.495	2.068	1.293
$P <$ DW	0.0095	0.015	0.059	0.0008	0.025	0.0001	0.0001	0.8496	0.0001
ρ	0.065	0.059	0.042	0.090	0.054	0.420	0.234	–0.039	0.342
H_s	P	P	P	P	P	NP	NP	NP	P

[1] Standard errors of estimates are within parentheses.

[2] WD = Wood; WIL = Wilmink; RK = Rook; DJ = Dijkstra; POL = Pollott; MONO = monophasic; DIPH = diphasic; MULT = multiphasic; LPM = persistency model. MONO, DIPH, MULT, and LPM are Grossman models.

[3] Other estimates of multiphasic model: i = 438.4 (57.647); j = 48.8359 (8.443); and k = 642.7 (9.821); P = 0.368 (0.00619); q = 0.1929 (0.0593).

[4] SSE = error sum of squares; root MSE = square root of mean square error; ADJRSQ = adjusted R^2; BIC = Bayesian information criterion; DW = Durbin-Watson statistic; $P <$ DW = P-value for testing positive autocorrelation; ρ = autocorrelation of errors; H_s = singularity of Hessian matrix (P = positive definite and NP = nonpositive definite).

Table 6. Comparison of lactation models fitted on test-day yields of 999-d complete lactations of cows in third and greater parities[1]

	Lactation model[2]								
Parameter	WD	WIL	RK	DJ	POL	MONO	DIPH	MULT[3]	LPM
a	34.5682	43.1760	47.9555	21.9930	702,712	764,532	2,467.5	80.7882	41.2243
	(0.6446)	(0.1361)	(0.2413)	(1.5174)	(1.40E9)	(1.4E6)	(744.6)	(11.471)	(0.242)
b	0.0625	0.0304	3.7556	0.0554	0.99996	0.0005	0.0062	17.4219	12.2094
	(0.0044)	(0.0003)	(0.2243)	(0.0092)	(7.627)	(3.9E–5)	(0.0007)	(2.1478)	(0.347)
c	0.00126	27.251	1.0E–8	0.0742	0.0678	–3,382.3	86.06	–15.324	0.030
	(2.0E–5)	(3.2970)	(0.0)	(0.0061)	(0.0072)	(2,024.5)	(9.7604)	(4.733)	(0.0004)
d		0.0981	0.0011	0.0011	0.99993		26,951.5	–33.866	45.4377
		(0.0103)	(1.2E–5)	(1.1E–5)	(0.132)		(4,950.4)	(8.450)	(8.363)
g					0.0011		0.00105	644.1	
					(9.4E–5)		(1.3E–4)	(16.792)	
h					0.9999		245.3	182.9	
					(0.0)		(122.6)	(47.422)	
Peak yield	41.45	41.48	42.19	43.18	43.04	44.46	42.74	44.02	41.22
Peak day	50	46	56	53	54	1	94	62	27–47
Selection criteria[4]									
SSE ($\times 10^6$)	2.083	2.100	2.059	2.048	2.049	2.103	2.054	2.033	2.108
Root MSE	9.623	9.657	9.568	91.098	91.125	93.534	9.559	9.502	9.683
ADJRSQ	0.367	0.362	0.374	0.377	0.377	0.361	0.375	0.383	0.359
BIC	165,687	165,849	165,437	165,321	165,347	165,906	165,495	165,222	165,871
DW	1.329	1.183	1.494	1.602	1.575	1.228	1.561	1.898	1.106
P < DW	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0506	0.0001
ρ	0.329	0.408	0.252	0.199	0.208	0.366	0.207	0.051	0.431
H_s	P	P	P	P	NP	NP	NP	NP	P

[1] Standard errors of estimates are within parentheses.

[2] WD = Wood; WIL = Wilmink; RK = Rook; DJ = Dijkstra; POL = Pollott; MONO = monophasic; DIPH = diphasic; MULT = multiphasic; LPM = persistency model. MONO, DIPH, MULT, and LPM are Grossman models.

[3] Other estimates of multiphasic model: i = 114.3 (91.99); j = 41.7966 (9.433); and k = 640.5 (16.212); P = 0.2279 (0.0387); q = 0.5023 (0.0982).

[4] SSE = error sum of squares; root MSE = square root of mean square error; ADJRSQ = adjusted R^2; BIC = Bayesian information criterion; DW = Durbin-Watson statistic; P < DW = P-value for testing positive autocorrelation; ρ = autocorrelation of errors; H_s = singularity of Hessian matrix (P = positive definite and NP = nonpositive definite).

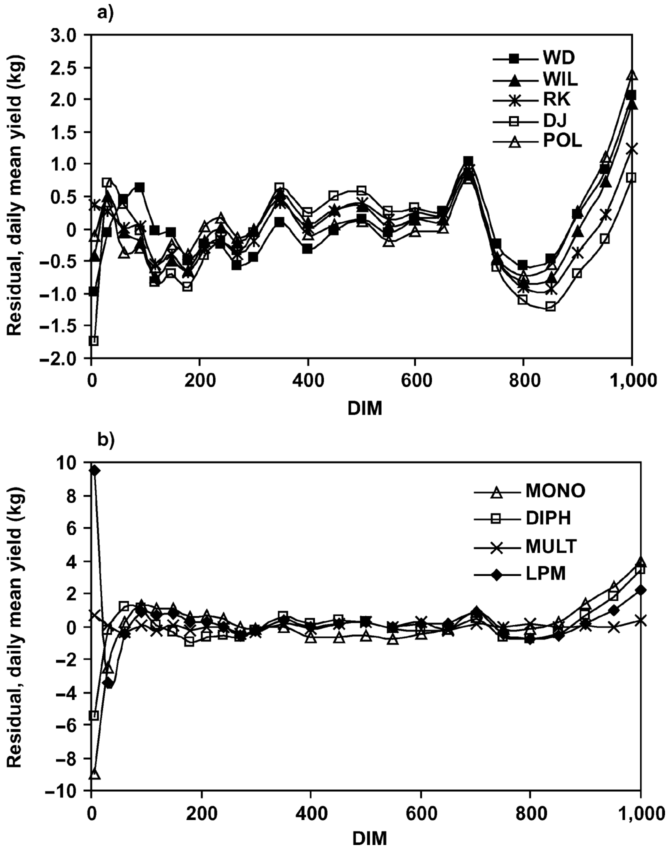

Figure 5. Residuals for first-parity 999-d complete lactation. a) Wood (WD), Wilmink (WIL), Rook (RK), Dijkstra (DJ), and Pollott (POL) models; b) Grossman monophasic (MONO), diphasic (DIPH), multiphasic (MULT), and lactation persistency (LPM) models.

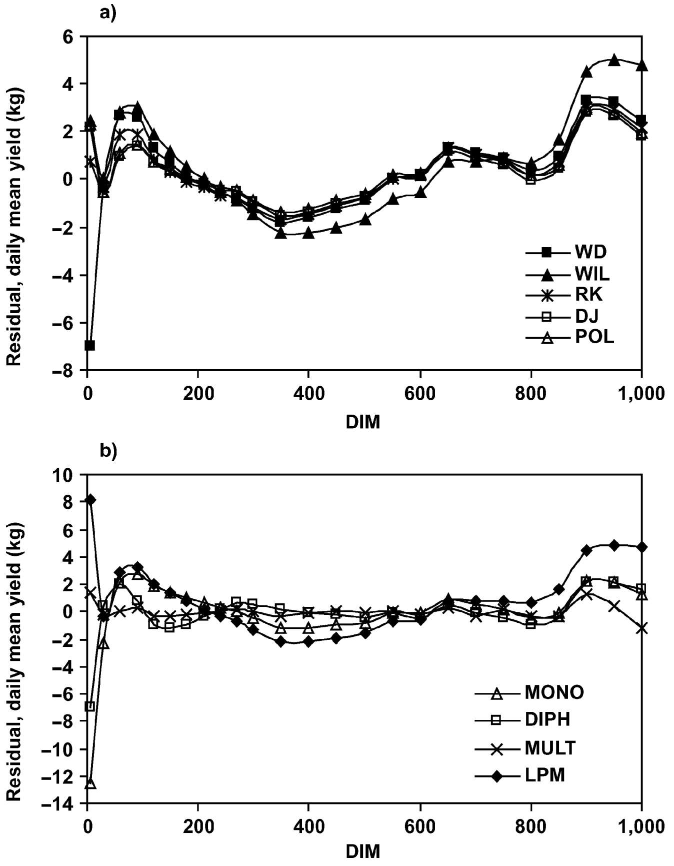

Figure 6. Residuals for 999-d complete lactation of third and greater parities. a) Wood (WD), Wilmink (WIL), Rook (RK), Dijkstra (DJ), and Pollott (POL) models; b) Grossman monophasic (MONO), diphasic (DIPH), multiphasic (MULT), and lactation persistency (LPM) models.

series-based) and Newton (second-derivative based) methods (SAS Institute, 2000), was often found to be better in reaching convergence when the parameter estimates were highly correlated. The Marquardt method also provided estimates with smaller MSE than PROC NLMIXED, which uses a maximum likelihood approach and dual quasi-Newton algorithm by default. The models with more than 5 parameters were very sensitive to the priors because unsuitable priors often resulted in lack of convergence or reached a local minimum. In some cases, lack of convergence could be avoided by changing the iterative procedure or step-size option (halve, golden, or cubic). Occasionally, a better convergence (lowest SSE and MSE) could be reached with parameter estimates falling beyond the acceptable bounds that were initially specified by the large models; however, this made the parameters uninterpretable. When the possible computational problems associated with larger mechanistic models are weighed against the satisfactory predictive ability of smaller empirical models, the smaller models (such as WD, RK, and DJ) can be favored for modeling extended lactations, unless investigation of underlying lactation physiology is intended. Being a smaller mechanistic model, the DJ model seemed to be a good choice if biological interpretation of parameters is required.

CONCLUSIONS

Longer lactating cows on average are also high producers with greater peaks and persistency. Consequently, within-parity parameter estimates of 305-d lactation curves were different from those of extended lactations. Parameter estimates of lactation models used for designing management and breeding strategies and developing software packages for any other purpose based on 305-d lactations may not be entirely appropriate for the cows with longer lactations. Although complicated mechanistic models with 6 parameters or more, if converged properly, could reveal the details underlying extended lactations more precisely,

Table 7. Parameter estimates of the Wood's function for fat and protein components of 305-d and 999-d lactations of various parity groups[1]

		Parameters							
		305-d				999-d			
Parity	Yield trait (kg)	*a*	*b*	*c*	Pers[2]	*a*	*b*	*c*	Pers
First	Fat	0.7131	0.1743	0.00183	1,639.5	0.7632	0.1473	0.00103	2,674.1
	Protein	0.5209	0.1818	0.00190	1,644.3	0.5538	0.1493	0.00104	2,681.2
Second	Milk	24.1895	0.1783	0.00308	910.4	33.4298	0.0624	0.00113	1,351.5
	Fat	1.0558	0.1456	0.00283	830.3	1.3613	0.0517	0.00110	1,292.9
	Protein	0.8257	0.1464	0.00283	834.2	1.0696	0.0487	0.00108	1,291.4
Third or greater	Fat	1.0503	0.1728	0.00329	816.3	1.4489	0.0516	0.00125	1,129.5
	Protein	0.7918	0.1724	0.00329	814.4	1.0863	0.0497	0.00124	1,124.7

[1] Parameter estimates for milk yield of first and third or greater parities are given in Tables 3, 4, 5 and 6.

[2] Pers = Wood's measure of persistency = $c^{-(b+1)}$.

their computational complexities often make their use infeasible or impractical. Simpler models such as Rook or Wood can be recommended for most instances in which precise information on underlying mammary mechanisms are not of primary interest. The Dijkstra model can be recommended if a mechanistic interpretation is required.

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