Using geometric morphometrics for the genetics analysis of shape and size of lactation curves in Israeli first-parity Holstein cattle

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ABSTRACT

Our objective was to combine the methods of geometric morphometrics and multivariate quantitative genetics to genetic evaluation of the size and shape of lactation curves of milk of 3,492 Israeli first-parity Holstein cattle. Lactation records were treated as morphological data, for which 2 different lactation shape functions were evaluated, one depicted by a line graph and the other by an orbital graph. The lactation curves from both shape functions were represented by 2-dimensional Cartesian landmark coordinates. The 2 sets of landmarks were then analyzed individually for each shape function with geometric morphometrics to separate variation into components of size and shape. The analysis yielded 2 size measures and 2 sets of shape variables, and they were the inputs to estimate variance components using the MTC REML individual animal model program. Variance components were also estimated for the 305-d lactation production as a reference. Shape variables showed negligible correlation with 305-d production, providing evidence of size and shape of lactation curve as separate characters. The size measure derived from the orbital-depicted lactation curve had equal heritability (0.39 ± 0.01 ; $\pm$ standard error) and complete genetic and environmental correlations with 305-d production, whereas the size measure derived from the line-depicted lactation curve showed low heritability (0.09 ± 0.01) and environmental correlation (0.02 ± 0.004) and relative high genetic correlation with 305-d production (0.48 ± 0.04). This may validate both the orbital graph to depict lactation records and the use of geometric morphometrics to split variation of lactation curve into size and shape components. The maximal heritability for shape of lactation curve was 0.55 for orbital- and 0.56 for line-depicted lactation

curves. The respective patterns of variations were visualized as shape changes from the mean shape in the data set. Geometric morphometrics are well grounded within the theory of shape analysis and can be paired with conventional methods in the field to characterize the patterns of phenotypic and genetic variation of shape and size of lactation curve in dairy cattle.

Key words: geometric morphometrics, shape heritability, lactation curve, genetic analysis

INTRODUCTION

Many advanced dairy enterprises currently record daily milk production. In addition, methods are being developed for accurate on-farm daily recording of milk components (Weller and Ezra, 2016). Data sets of this type are increasingly available by recording systems, making its study an important and growing challenge (Rauw et al., 2015).

In genetic evaluation of the lactation curve shape, proposed methods have used single values (Sanders, 1930; Gengler, 1996; Cole and Vanraden, 2006), parameters defining the lactation curve (Shanks et al., 1981; De Boer et al., 1989; van Der Linde et al., 2000; Rekik et al., 2006), direct analysis of test-day (TD) records (Meyer et al., 1989; Swalve, 1995; Savegnago et al., 2013), and eigenvectors of the additive genetic matrix (Druet et al., 2005; Macciotta et al., 2006; Togashi and Lin, 2006). In TD analyses (e.g., random regression models), most heritabilities and genetic correlations for shape are provided as a range of single values derived from the TD records defining the lactation curve, which do not consider the shape as a whole and as a separate character from yield (size). First, these analyses cannot consider how different parts of the shape may be related to each other; the univariate heritabilities values correspond to the magnitude of the single TD of shape variation and ignore the direction of variation in all dimensions of shape space. Second, as genetic correlations are computed directly from the TD records defining lactation curve, the estimations correspond to yield (size), and no strict distinction is made between

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the size of lactation curve and the shape, an inherently multidimensional feature.

Historically, Bonnier (1935) not only considered the size and shape of lactation curve as separate features, but also concluded that the shape was an inherited character. Other studies have reached similar conclusions (e.g., Sanders, 1923; Becker and McGilliard, 1929), but unavailability of sufficient records and the lack of suitable analysis methods precluded accurate estimation of the heritability of the shape of lactation curves (Bonnier, 1935). Thus, the methods for the genetic evaluation have been size-dependent (first on cumulative 305-d and then on TD productions). A method that could characterized the size and shape of lactation curves into separate components and study shape as a whole might be useful for both genetic selections and management decisions. For instance, it would be possible to select based on shape as a whole and as a separate trait.

In this context, the pattern of variation in the spatial geometry of the shape of lactation curve can be studied using geometric morphometrics methods (**GMM**). Geometric morphometrics methods are powerful tools that have been developed in biology to quantify shape variation and its covariation with biotic and abiotic variables (Webster and Sheets, 2010); GMM has been successfully applied in medicine and engineering (Viscosi and Cardini, 2011; Cooke and Terhune, 2015). Individual shapes are represented by a collection of Cartesian coordinates of anatomical landmarks or semilandmarks on corresponding outlines and surfaces (Gunz and Mitteroecker, 2013; Weaver and Gunz, 2018). Geometric morphometrics methods analysis separates the morphological variation of biological forms (e.g., human skull, insect wing, or leaf) into components of size and shape, and it has been developed in the context of quantitative genetic studies of different species' shapes (Klingenberg and Leamy, 2001; Monteiro et al., 2002; Klingenberg et al., 2010).

To adopt GMM, we can view the geometric shape of lactation curve as a biological form and analyze the production records as morphological data. We can then treat all the records (daily, weekly, or monthly) defining a lactation curve as a single collection of traits. The configuration of traits corresponds to the form and structure of the lactation curve, and that configuration is a single datum. With this new definition of the data, we should be able to use GMM to split variation of the lactation curve into components of size and shape. Here, we demonstrate the use of geometric morphometrics and multivariate quantitative genetics for genetic evaluation of size and shape of lactation curve of milk in first-parity Israeli Holstein cattle.

MATERIALS AND METHODS

Data and Definition of Lactation Curve

To define the shape of lactation curve, we used as a reference the mean 305-d lactation curve of first-parity Israeli Holsteins. Data were daily milk production from December 2013 through April 2015 of 43 large kibbutz (communal) farms from Israel. First-parity lactation of milk production up to 305 DIM were included based on the following criteria: (1) first record in lactation ≤ 10 d after parturition, (2) last record ≥ 276 d after parturition, and (3) period between consecutive records ≤ 29 d. The data were further filtered to include only lactations with a minimum of 271 valid daily records. A total of 3,492 lactations were included in the analysis, of which 2,080 were complete and 1,412 had 1 to 29 missing records. Missing daily records were replaced by the mean of the 2 closest valid records, both for embedded missing values and missing values at the beginning and end of the lactation. To construct the lactation curve of 10 mo, we averaged the 30 daily records of every month.

The ascending phase of the first-parity lactation curve corresponds to approximately 0 to 3 mo in milk (**MIM**; Weller et al., 2006) and the descending phase to 4 to 10 MIM (Figure 1). The ascending phase is produced by the increased secretory activity per cell and the descending phase is produced by the loss of mammary epithelial cells by apoptosis (Capuco et al., 2001).

Depiction of Lactation Records

We present 2 types of graphs: line and orbital. The line graph is the traditional depiction of lactation records on milk production traits, in which the daily production corresponds to the y-axis and DIM to the x-axis (Figure 1, line). Orbital graphs depict production traits in a circular form corresponding to lactation as cycle (Figure 1, orbital). The production system of 305 DIM comprised 10 monthly records, but the number of axes was adjusted to the 12-mo yearly cycle. The 10 monthly records were plotted, starting with mo 1 on the first axis, following a counterclockwise rotation that ended with mo 10 on the tenth axis and left the 2 axes of the dry period empty. Regardless of the calving month, all lactation curve shapes were aligned to start and end on the same axes.

Landmark Acquisition

The 10 monthly records corresponded to the 10 landmarks defining the contour of the shape of lacta-

tion curve. A set of x and y Cartesian coordinates were estimated for each of the 10 landmarks. We estimated 2 different sets of Cartesian coordinates, one for the line-depicted lactation curves and one for the orbital-depicted lactation curves. For the line-depicted lactation curve, the x values were the MIM, 1 to 10, and the y values were the daily production in the MIM. For the orbital-depicted lactation curve, we used Pythagorean Theorem to estimate the value of the x and y coordinate for each landmark according to its position on the Cartesian plane. More details of this procedure and the application of GMM to milk production data can be found in Durón-Benítez and Huang (2016a).

Procrustes Superimposition

The GMM analysis separates the morphological variation from the coordinates data into components of size and shape (Klingenberg and Leamy, 2001). The configurations of x and y coordinates contain information on location, size, and orientation, which is irrelevant for the comparison of the geometrical structure of shape; shape is defined as all the geometrical information that remains after removing these 3 effects from an object (Kendall, 1977). We implemented the Procrustes superimposition with semilandmarks to extract the shape variables. The centroid size is a single trait derived from a set of landmarks representing the shape of lactation curve, and it is measured in units of distance. The centroid size was computed as the square root of the sum of the squared distances of the landmarks from the centroid (center) of a configuration (Zelditch et al., 2012). Details of the mathematical notations of the different operations can be found in Claude (2008) and Zelditch et al. (2012).

Semilandmarks were implemented because they are specific for geometrical feature, such as curves, edges, and surfaces, and our subjects are curves. Semilandmarks provide information about curvature and are used alongside fixed landmarks. An additional step for sliding semilandmarks was added to the Procrustes superimposition analysis to minimize variation tangential to the curve. We implemented the Procrustes distance method for sliding the semilandmarks. For more information about the pros and cons of implementing the algorithms see Perez et al. (2006) and Gunz and Mitteroecker (2013). We treated landmarks 1 and 10 as fixed landmarks and 2 to 9 as semilandmarks (sliding semilandmarks). We conducted 2 individual analyses, one for every shape type. The data containing the raw landmarks were imported to R using the geomorph package (Adams et al., 2017) for superimposition with semilandmarks.

Figure 1. Form and structure of lactation curve. The ascending phase is shown with dark shading and the descending phase with light shading.

We computed ANOVA for the fixed effects of herd, calving month, pregnancy, calving age, and days open for the 2 centroid sizes, 305-d lactation production, and the 2 types of shapes variables (20 x and y coordinates) yielded by the Procrustes superimposition analysis with semilandmarks. We ran 5 Procrustes ANOVA, one for each trait, as implemented for centroid size and shape variables in the GMM using geomorph package in R (Adams et al., 2017).

Quantitative Genetic Analysis

Computation of Variance and Covariance for Size and Shape Components. The genetic evaluation of the first-parity Holstein cows was based on the individual animal model (AM), and was implemented

as in previous evaluations of the Israeli Holstein population by Weller and Ezra (2004, 2016). The size measures (derived from the line- and orbital-depicted shapes), 305-d production, and the shapes variables (20 x and y Procrustes coordinates) were the inputs. We conducted separate analyses for size and shape.

The 2 centroid sizes and 305-d production were single traits and the genetic evaluations can be computed as routinely done for milk traits. Before estimation of variance components, these variables were corrected for the effects of calving month, calving age, pregnancy status, and days open. Variance components were estimated by the multitrait AM by the MTC program that uses a REML algorithm (Misztal, 1994). The model included a fixed herd-year-season effect and a random additive genetic effect. Two seasons were defined for each herd-year beginning in April and October. A herd-year-season effect was included in the model because the number of herd-year-season effects was greater than the other effects described previously, and distribution of cows across herds was not random. The relationship matrix included all known parents and grandparents of the 3,492 cows with valid first-parity records; thus, the total number of animals included in the analysis was 10,755. Two genetic groups were defined for animals with unknown parents, one for males and one for females. All animals with records had known parents; only ancestors of these animals had unknown parents. There were 3,648 animals with both parents missing and 86 animals with 1 parent missing; thus, it would probably not be possible to accurately estimate more than 2 group effects. The 2 centroid sizes of lactation curve and 305-d lactation production were analyzed jointly. Heritability was estimated as the ratio of the additive genetic variance and the phenotypic variance, computed as the sum of the additive genetic and environmental variance components.

Approximate standard errors of the variance components were estimated by application of a modified jackknife algorithm. Twenty samples were drawn from the actual data with a random 5% of the cows deleted, and variance components were estimated for each sample. Standard errors were computed as the standard deviations of the 20 jackknife samples.

In the REML analysis for shape, the dependent variables were the 20 x and y Procrustes coordinates; that is, each of the landmark coordinates was a trait. Thus, the dimensionality of the shape tangent space was preserved in the analysis (Klingenberg et al., 2010). The genetic model for the shape variables were corrected for the same effects and included the same relationship matrix as for size. A separate analysis was run for each shape type of lactation curve (line and orbital). The

covariance matrices obtained from the REML were imported to MorphoJ (Klingenberg, 2011) for estimating heritabilities of shape.

Genetic correlations between the 305-d production and principal component scores computed from the Procrustes coordinates (from both shapes types) were estimated by the MTC REML program using the same factors as for size. Principal component analysis (**PC**) was conducted in R using the geomorph package (Adams et al., 2017). In addition, phenotypic correlation between 305-d production and Procrustes coordinates from each shape function (line and orbital) were also calculated in R 3.3.2 (R Core Team, 2013).

Estimation of Heritability of Shape. In GMM, although heritability of shape variables can be calculated as a single ratio (see Monteiro et al., 2002), we computed it as a range of values (see Klingenberg and Leamy, 2001) to avoid the limitation of ignoring directionality of variation in the phenotypic (**P**) and additive genetic (**G**) covariance matrices. For details on the shortcomings of the single ratio estimation of heritability for shape see Klingenberg (2003) and Klingenberg and Monteiro (2005).

The eigenvalues and eigenvectors were computed from the $\mathbf{GP}^{-1}$ matrix. The procedure implements a generalized inverse of the **P** matrix because it is not of a full rank due to the degrees of freedom lost in the Procrustes superimposition (translation, scaling, and rotation). The largest and smallest eigenvalues of the $\mathbf{GP}^{-1}$ matrix were interpreted as the maximal and minimal heritabilities for the set of the shape variables (Klingenberg and Leamy, 2001; Klingenberg et al., 2010). The eigenvectors were visualized as changes from the mean landmark configuration in the data set and scaled to an arbitrary magnitude of +0.1 and -0.1 units of Procrustes distance.

RESULTS AND DISCUSSION

Phenotypic and Genetic Variation of Size

The average 305-d lactation production ($\pm$ SD) was $10,586 \pm 1,262$ kg, the average centroid size for line-depicted and orbital-depicted lactation curves were 14.3 ± 2.9 and 105.7 ± 12.5 Procrustes units, respectively. The type I sum of squares coefficients of determination for the effects included in the fixed model analyses of centroid size of orbital, line graphs, and 305-d lactation production are presented in Table 1. All effects included in the model were significant except for the effect of pregnancy status on centroid size-line. All factors combined explained 23.4, 23.3, and 16.4% of the total variance in the 305-d production, centroid size-

Table 1. Type I sum of squares coefficients of determination for the different effects for variation of 2 centroid sizes of the lactation curve and 305-d lactation production (n = 3,492)

Variable source	305-d production	Centroid size	
		Orbital	Line
Herd (43) ¹	0.16	0.16	0.06
Calving month (12)	0.01	0.009	0.06
Pregnancy (2)	0.006	0.005	0.0004 ^{NS}
Calving age ²	0.02	0.02	0.004
Days open ²	0.04	0.04	0.04
Total	0.236	0.234	0.164

¹Number of levels in parentheses for the class effects.²Regression effects.^{NS}Not significant, $P > 0.05$; all other effects were significant at $P < 0.001$.

orbital, and centroid size-line models, respectively. The percentage of variance explained by each factor in the model for centroid size of orbital graph are very close to that in the model for 305-d lactation. Conversely, the percentage of variance explained by the model of centroid size of line graph show less similarity with the reference model, and pregnancy status was not significant.

The heritabilities and genetic and environmental correlations for the 3 traits using 3,492 first-parity lactations are presented in Table 2. The centroid size of orbital-depicted lactation curve demonstrated equal heritability and complete genetic and environmental correlations with 305-d lactation production. Centroid size of line-depicted lactation curve, conversely, showed the lowest heritability and genetic and environmental correlations with the other traits among the 3 measures of size of lactation curve. These results may serve to validate the depiction of lactation records by orbital graph, and the use of GMM to split the variation of lactation curve into size and shape components.

The heritability of 0.39 ± 0.01 of centroid size from the orbital-depicted lactation curve equals the estimate obtained for the 305-d lactation, and is consistent with previous estimates in the Israeli Holstein population. Weller and Ezra (2004, 2016) reported heritabilities of

0.39 (n = 6,244) and 0.35 (n = 7,866), respectively. Selecting for this trait could be done as implemented for cumulated 305-d production, in which the desirable size measure of lactation curve would depend on the breeding goals. However, there would be no difference in selecting for centroid size from the orbital-depicted lactation curve because it is the same trait as 305-d production.

Phenotypic and Genetic Variation of Shape

The type I sum of squares coefficients of determination from the fixed model analyses for orbital- and line-depicted shapes of lactation curves superimposed with semilandmarks are presented in Table 3. All factors were significant ($P < 0.001$), with the exception of age at calving for both shapes. All factors combined explained about 14 and 16% of the total variance in the orbital- and line-depicted shape models, which was about the same with the centroid size-line model, but lower than the 305-d production and centroid size-orbital ones.

Genetic correlations among the different multivariate measures included principal component 1 from line-depicted shapes (LPC1), principal component 2 from line-depicted shapes (LPC2), principal component 1

Table 2. Heritabilities for 2 centroid sizes of milk production and 305-d lactation production (bold, on the diagonal) and genetic (above diagonal) and environmental (below diagonal) correlations among 3,492 first-parity lactations¹

Variable	305-d production	Centroid size	
		Orbital	Line
305-d production	0.39 ± 0.01	1.00 ± 0.00	0.48 ± 0.04
Centroid size, orbital	1.00 ± 0.00	0.39 ± 0.01	0.49 ± 0.04
Centroid size, line	0.02 ± 0.004	0.02 ± 0.004	0.09 ± 0.01

¹Standard errors are given after the estimates based on a modified jackknife algorithm. All jackknife samples gave correlations of unity between 305-d production and size-orbital. Thus the estimated standard error was zero.

Table 3. Type I sum of squares coefficients of determination for the different effects for variation of shape of the lactation curve depicted by orbital and line graph (n = 3,492)

Variable	Orbital-depicted	Line-depicted
Herd (43) ¹	0.06	0.06
Calving month (12)	0.05	0.05
Pregnancy (2)	0.003	0.005
Calving age ²	0.0003 ^{NS}	0.0003 ^{NS}
Days open ²	0.03	0.04
Total	0.14	0.16

¹Number of levels in parentheses for the class effects.²Regression effects.^{NS}Not significant, $P > 0.05$; all other effects were significant at $P < 0.001$.

from orbital-depicted shapes (OPC1), principal component 2 from orbital-depicted shapes (OPC2), and 305-d production and are presented in Table 4. Phenotypic correlations between 305-d production and Procrustes coordinates for orbital-depicted shapes (PCOS) and Procrustes coordinates for line-depicted shapes (PCLS) are also presented in Table 4. All PC scores from orbital- and line-shape coordinates demonstrated low and negative relationship with the 305-d production except for LPC2, which was positive. The absolute values of the correlations between 305-d production and PC were lower for shape coordinates by orbital than line graph. The correlation with LPC1 (-0.31) was much lower than the value of 0.78 reported by Macciotta et al. (2006) using TD records. The phenotypic correlations between 305-d production and Procrustes coordinates of both shape functions were negligible (0.03 and -0.01 for orbital- and line-depicted shapes, respectively). Thus, the proposed method produced shape variables (Procrustes coordinates) that are uncorrelated with 305-d production. Overall, the weak relationship (phenotypical and genetic) between shape variables (Procrustes coordinates and PC) and 305-d production provide evidence of the independence between size and shape of lactation curve.

Heritability of Lactation Curve Shape

The analysis of the $\mathbf{GP}^-$ matrix yielded a range of eigenvalues from 0.55 to 0.00009 for orbital- and 0.56 to 0.0005 for line-depicted lactation curves (Figure 2). Eigenvalues for PC2, PC3, and PC4 were higher for the line-depicted shape. The eigenvalues correspond to the range of possible heritabilities of the shape variables that can be computed as a linear combinations of the landmark coordinates (Klingenberg and Leamy, 2001; Klingenberg et al., 2010). The PC1 identified the shape features that would most readily respond to selection for both shapes functions.

The heritability values of the first 2 PC (either the orbital- or line-depicted shapes) were higher than those presented by Macciotta et al. (2006; 0.19 and 0.07) calculated with the univariate model and TD records of multiple-parity Simmental cows. The first 4 PC corresponding to the 4 maximal eigenvalues are presented in Figures 3 and 4 for orbital- and line-depicted shapes, respectively; they are shown as shape changes from the mean shape in the data set. The shape changes associated with the 2 eigenvalues with the highest heritabilities corresponded to an increase in the ascending phase, a slightly decrease in mid lactation mo 5 and 6, and a decrease in the last 2 mo. Similar pattern of variation described by the first PC of the $\mathbf{P}$ matrix was also found by previous analysis across parities 1 to 3 (Durón-Benítez et al., 2017) and between Holstein and Jersey breeds (Durón-Benítez and Huang, 2016b) using GMM. On average, cows in our study became pregnant at 4.6 ± 2.2 mo of lactation. Previous studies assessing the effect of pregnancy stage on milk yield have reported a significant decrease beginning in either the 4 or the fifth month of lactation (Olori et al., 1997; Loker et al., 2009; Lainé et al., 2017).

The main advantages of the proposed approach are that heritability estimates for shape correspond to shape as a whole, including the magnitude and direc-

Table 4. Genetic and phenotypic correlations among 305-d production and different multivariate measures¹

Correlation type	Trait	r	Minimum	Maximum
Genetic	LPC1	-0.31 ± 0.03		
	LPC2	0.13 ± 0.03		
	OPC1	-0.21 ± 0.03		
	OPC2	-0.03 ± 0.05		
Phenotypic	PCOS ²	0.03 ± 0.08	-0.06	0.2
	PCLS ²	-0.01 ± 0.09	-0.2	0.1

¹LPC1 = principal component 1 from line-depicted shapes; LPC2 = principal component 2 from line-depicted shapes; OPC1 = principal component 1 from orbital-depicted shapes; OPC2 = principal component 2 from orbital-depicted shapes; PCOS = Procrustes coordinates for orbital-depicted shapes; PCLS = Procrustes coordinates for line-depicted shapes. Standard errors are given after the estimates based on a modified jackknife algorithm.

²Mean correlation was taken from the 20 estimates.

tionality of variation, and as a separate character (low or negligible correlation with 305-d production, Table 4). The eigenvalues of the $\mathbf{GP}^-$ matrix represent the magnitude of shape variation (Figure 2) and the eigenvector the direction of variation in all dimensions of shape tangent space (Figures 3 and 4). In contrast, the univariate heritability estimated as a range of single values derived from each TD records defining the lactation curve (e.g., TD models) ignore the directionality of shape variation and do not consider shape as a whole and as a separate character from yield (size). Shape is an inherently multidimensional feature, and quantitative genetics of shape as a whole, rather than single-shape TD records, require an explicitly multivariate approach (Klingenberg and Monteiro, 2005).

Commercial breeding programs can implement TD models (e.g., random regression with algorithms B-

splines and Legendre polynomials) and other breeding designs to extract the covariance components from the Procrustes coordinates and then use PC analysis on the matrix $\mathbf{GP}^-$ to compute heritability (eigenvalues) and shape variation (eigenvectors). The PC analysis can also be used to describe the pattern of variation on the $\mathbf{G}$ and $\mathbf{P}$ covariance matrices (which consider the shape as whole). For selection purposes, the eigenvectors of the matrix $\mathbf{GP}^-$ can be used following the procedure presented by Togashi and Lin (2006, 2007). Alternatively, selection based on shape can be developed, classifying animals based on shape using the Procrustes coordinates. For this purpose, it would be best to only translate and scale coordinates, which can be done in R. Moreover, the response to selection on shape can be simulated using the multivariate breeders' equation, $\Delta\mu = \mathbf{GP}^-s = \mathbf{G}\beta$, where $\Delta\mu$ is the response to selection, $\mathbf{G}$ and $\mathbf{P}$ are as defined previously, s is the selection differential, and β is the selection gradient (e.g., Klingenberg and Leamy, 2001; Klingenberg et al., 2010).

It is possible to use traditional lactation records as morphological data to analyze shape of lactation curve as a biological form, having shape and size. The set of landmarks representing a lactation curve shape were demonstrated to be suitable for the GMM description and quantitative genetics evaluation. With this new view of the data and the protocol of analysis, we were able to extract shape variables from lactation records and present measure of heritability for shape as a whole and as a separate character from yield (size).

CONCLUSIONS

We combined the methods of geometric morphometrics and multivariate quantitative genetics to evaluate the heritability and genetic correlations of size and shape of lactation curves for milk in first-parity Israeli Holstein cattle. The lactation curve demonstrated a relatively high heritable genetic variation for shape, 0.55 for orbital versus 0.56 for line for the first eigenvalue. The centroid size derived from orbital-depicted shape and 305-d lactations both had heritability of 0.39 ± 0.01 and complete genetic and environmental correlations. The use of GMM allowed us to separate the morphological variation of lactation curves into components of size and shape, and provide genetic estimates for each of these 2 intrinsic features.

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Figure 2. Eigenvalues of the additive genetic and phenotypic matrices ($\mathbf{GP}^-$) for shape of lactation curve. These can be interpreted as the heritability of the shape variables associated with each of the eigenvalues. Eigenvalues are shown for orbital- and line-depicted lactation shapes.

Figure 3. Principal component (PC) of the additive genetic and phenotypic matrixes (GP^-) for orbital-depicted lactation curve. The first 4 PC present the shape features of the lactation curve with the maximal eigenvalue heritability (PC1 = 55.4, PC2 = 27.8, PC3 = 22.1, PC4 = 18.1). The outlines are presented as shape changes (black and closed circle) with a +0.1 (right figures) and -0.1 (left figures) Procrustes unit from the mean shape (gray and open circle) in the data set.

Figure 4. Principal component (PC) of the additive genetic and phenotypic matrixes (GP^{-}) for line-depicted lactation curve. The first 4 PC present the shape features of lactation curve with the maximal eigenvalue heritability (PC1 = 56.0, PC2 = 38.5, PC3 = 27.5, PC4 = 20.1). The outlines are presented as shape changes (black and closed circle) with a +0.1 (right figures) and -0.1 (left figures) Procrustes unit from the mean shape (gray and open circle) in the data set.

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