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Genetic parameters for udder conformation traits derived from Cartesian coordinates generated by robotic milking systems in North American Holstein cattle

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ABSTRACT

Udder conformation is directly related to milk yield, cow health, workability, and welfare. Automatic milking systems (AMS, also known as milking robots) have become popular worldwide, and the number of dairy farms adopting these systems has increased considerably over the past years. In each milking visit, AMS record the location of the 4 teats as Cartesian coordinates in an xyz plan, which can then be used to derive udder conformation traits. Because AMS generate a large amount of data for individual cows per milking visit, they can contribute to an accurate assessment of important traits such as udder conformation without the addition of human classifier errors (in subjective scoring systems). Therefore, the primary objectives of this study were to estimate genomic-based genetic parameters for udder conformation traits derived from AMS records in North American Holstein cattle and to assess the genetic correlation between the derived traits for evaluating the feasibility of multitrait genomic selection for breeding cows that are more suitable for milking in AMS. The Cartesian teat coordinates measured during each milking visit were collected by 36 milking robots in 4,480 Holstein cows from 2017 to 2021, resulting in 5,317,488 records. A total of 4,118 of these Holstein cows were also genotyped for 57,600 SNPs. Five udder conformation traits were derived: udder balance (UB, mm), udder depth (UD, mm), front teat distance (FTD, mm), rear teat distance (RTD, mm), and distance front–rear (DFR, mm). In addition, 2 traits directly related to cow productivity in the system were added to the study: daily milk yield (DY) and milk electroconductivity (EC; as an indicator of mastitis). Variance components and genetic parameters for UB, UD, FTD, RTD, DFR, DY, and EC were estimated based on repeatability animal models. The estimates of heritability (± SE) for UB, UD, FTD, RTD, DFR, DY, and EC were 0.41 ± 0.02, 0.79 ± 0.01, 0.53 ± 0.02, 0.40 ± 0.02, 0.65 ± 0.02, 0.20 ± 0.02, and 0.46 ± 0.02, respectively. The repeatability estimates (± SE) for UB, UD, FTD, RTD, and DFR were 0.82 ± 0.01, 0.93 ± 0.01, 0.87 ± 0.01, 0.83 ± 0.01, and 0.88 ± 0.01, respectively. The strongest genetic correlations were observed between FTD and RTD (0.54 ± 0.03), UD and DFR (−0.47 ± 0.03), DFR and FTD (0.32 ± 0.03), and UD and FTD (−0.31 ± 0.03). These results suggest that udder conformation traits derived from Cartesian coordinates from AMS are moderately to highly heritable. Furthermore, the moderate genetic correlations between these traits should be considered when developing selection subindexes. The most relevant genetic correlations between traits related to cow milk productivity and udder conformation traits were between UD and EC (−0.25 ± 0.03) and between DFR and DY (0.30 ± 0.04), in which both genetic correlations are favorable. These findings will contribute to the design of genomic selection schemes for improving udder conformation in North American Holstein cattle, especially in precision dairy farms.

Key words: genetic correlation, heritability, milking robots, repeatability, udder conformation

INTRODUCTION

Since domestication more than 10,000 years ago (Pitt et al., 2019), cattle populations have been selected for increased milk yield and related traits such as milking temperament. More recently, intensive genetic and ge-

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The list of standard abbreviations for JDS is available at adsa.org/jds-abbreviations-24. Nonstandard abbreviations are available in the Notes.

nomic selection for greater milk yield (Miglior et al., 2017) has indirectly changed udder conformation and udder strength to physically support greater amounts of milk produced per day. However, there is still large genetic and phenotypic variability for udder conformation (Boettcher et al., 1998; Rupp and Boichard, 1999; Poppe et al., 2019), which influences cow health, workability, and welfare.

Teats are the result of mesenchymal proliferation that generates epidermal elevation around the glandular openings (Hyttel et al., 2012). Between birth and puberty, the mammary gland has isometric growth, with complete development occurring during late gestation and parturition (Hyttel et al., 2012). The development and morphogenesis of the mammary gland is dynamically determined by complex biological processes throughout the lives of cows. The udder is suspended by ligaments that attach to the abdominal wall of the body and the pelvis. The lateral ligaments are primarily responsible for maintaining the depth of the udder, and the medial ligament of the udder is responsible for maintaining the positioning centered and perpendicular to the floor of the teats (Jalakas et al., 2000). Udder conformation can be described from 3 dimensions—length, width, and depth—whereas increased milk yield may be associated with increased length and width of the udder but not necessarily depth (Atkins et al., 2008). Genetic evaluations of udder conformation traits have been implemented in dairy cattle breeding schemes around the world (Miglior et al., 2017; Nazar et al., 2021; Omoniwa et al., 2021). Cows with good udder conformation based on scores evaluated by classifiers and well-positioned teats of adequate size have greater chances of remaining productive in the herd for longer periods (Larroque and Ducrocq, 2001; Sewalem et al., 2004).

Traditionally, udder conformation has been measured based on subjective scoring systems or manual measurements (Bharti et al., 2015; Miglior et al., 2017; Beard et al., 2019), both of which are labor-intensive and of lower accuracy due to their subjectivity and low throughput. With the more recent development and availability of automatic milking systems (**AMS**; or robotic milking systems), the interactions between human handlers and cows have reduced substantially (Hansen, 2015; Dechow et al., 2020). Furthermore, AMS record many variables and data describing diverse aspects of the milking process. Especially, teats' Cartesian coordinates can be frequently measured by the AMS, which can be effectively used for describing udder conformation (Poppe et al., 2019). On the contrary, udder conformation can influence the workability of AMS, as the sensor system must be able to identify the position of each teat and attach the teat cup with as few failures as possible (de Koning, 2011; Carlström et al., 2016a).

Cow milking has evolved over time, from manual milking to AMS. The absence of humans at the time of milking modifies the necessary prerequisites for a cow to integrate the production system—in other words, to be able to be milked (Dechow et al., 2020). Requirements related to behavior and udder conformation are among those that can be cited (Jacobs and Siegford, 2012; Poppe et al., 2019) but daily milk yield and absence of mastitis are among the most economically relevant traits in dairy cattle (Szyda et al., 2019; Brito et al., 2021).

The use of data collected by AMS is of great relevance, as the genetic correlation between milk yield in AMS and conventional milking systems (e.g., milking parlor) has been reported to be high (Carlström et al., 2014). The early identification of inflammatory responses of the mammary gland is essential in dairy cattle (Milner et al., 1996), as is the selection of animals more resistant to mastitis (Weigel and Shook, 2018). Among the indicators of mastitis, electrical conductivity (**EC**) has been proposed; AMS are equipped with sensors for measuring EC, which is significantly correlated with mastitis (Martin et al., 2021). Pedrosa et al. (2023) recommended EC as a genetic selection criterion of dairy cattle breeding programs to control mastitis, particularly in AMS herds. The study of the association degree of traits related to udder conformation with daily milk yield and EC is relevant for refining selection programs to improve udder conformation based on phenotypes derived from AMS.

The use of genomic information for estimating genetic parameters and predicting breeding values has become a common practice in animal breeding programs (Misztal et al., 2020), especially when accurate pedigree information is not available. The combination of genomic information with data from AMS poses a great opportunity for developing novel traits to be genomically evaluated and used in selection schemes aiming to improve production efficiency in dairy farms. Therefore, the main objectives of this study were to estimate genomic-based genetic parameters, including heritabilities and genetic correlations, for udder conformation traits derived from Cartesian plan coordinates recorded by AMS in North American Holstein cattle. In addition, we estimated correlations between udder conformation traits and traits related to cow productivity, and interpreted the estimated values from the point of view of multitrait selection schemes in animal breeding programs.

MATERIALS AND METHODS

Ethics Statement

No Animal Care Committee approval was necessary for the purposes of this study, as all information required was obtained from pre-existing databases.

Raw Data

The datasets used were collected by 36 Lely Astronaut A5 AMS robots (Lely, Maassluis, the Netherlands), all purchased at the same time and installed in a commercial farm located in Plymouth, Indiana. Per-visit data were stored in the Lely database and retrieved using the Purdue Animal Sciences Research Data Ecosystem platform (West Lafayette, IN) to be used in the analyses. A total of 5,317,488 phenotypic records from 4,480 cows measured between 2018 and 2021 were available for this study. The variables included in the data ets were the Cartesian coordinates of teats recorded on each milking visit, milking time, milk EC, and milk yield. When the cow does not have a certain teat or an error occurs during the teat cup attachment, the milking robot assigns a predefined position (defined as >100 mm away from the contralateral teat), which was set to missing values before the analyses. Records with missing values for any of the traits were discarded. After this quality control (**QC**) step, 606,749 records from 136 animals were removed from the phenotypic dataset. Records with DIM lower than 5 d and greater than 305 d were also eliminated. Finally, 4,232,026 visit records from 4,280 animals were retained for deriving udder conformation traits. The data editing and QC of the phenotypic database were performed using R software 4.2.1 (R Core Team, 2022).

Trait Definition

Daily milk yield (**DY**) was defined as the total amount of milk produced during a period of 24 h, where milk records from multiple milkings throughout the day were summed up to compute DY (Pedrosa et al., 2023). Electrical conductivity is a measure of the resistance of a specific substance to an electric current. During milking, EC measures the increased blood capillary permeability resulted by mastitis, which affects the ion concentrations in milk, enabling the measurement of EC in milliSiemens (Pedrosa et al., 2023). Electrical conductivity was measured individually in each quarter, and the values were obtained from each visit to the Lely robot; the EC phenotype was defined as the average of the 4 quarters at each visit.

The Cartesian coordinates on AMS are composed of xyz axes for each of the 4 teats. The x-axis refers to the cow's latero-lateral axis; that is, the axis perpendicular to the robot's longest axis. The y-axis refers to the cow's craniocaudal axis, which is the robot's longest axis. The z-axis is perpendicular to the floor, referring to the ventro-dorsal axis of the cow. From the coordinates recorded by AMS, we calculated 5 udder conformation traits (Poppe et al., 2019):

(1) Front teat distance (**FTD**; mm) is defined as the distance between the cow's cranial teats. This trait is obtained by subtracting the x-axis coordinate value of the right cranial teat tip's x-axis coordinate value from the left cranial teat tip's x-axis coordinate value, as the robot is positioned on the cow's right side. This trait expresses the distance between the 2 teat tips to which the robot must attach the teat cup. Extreme values on both sides are undesirable, as they may indicate weakness of the medial udder ligament (when the teats are too far apart), or the robot may have trouble finding the 2 teats (when the distance is too small).

(2) Rear teat distance (**RTD**; mm) is defined as the distance between the caudal teats of the cow. This trait is obtained by subtracting the x-axis coordinate value of the right caudal teat tip's x-axis coordinate value from the left caudal teat tip's x-axis coordinate value. The RTD expresses the distance between the 2 caudal teat tips in which the milking robot must attach the teat cup to. Measures of RTD smaller than FTD values are more common, and animals with close teat tips or close contact with another teat are challenging for the AMS.

(3) Udder depth (**UD**; mm) is the average of the z-axis coordinate values for the 4 teat tips. This trait expresses the average distance between the tips of the cow's teats and the floor. The UD is a good indicator of udder ligament health, and if all cows from the same farm have similar stature, cows with higher values for this trait have stronger ligaments and are less likely to suffer from udder injuries.

(4) Udder balance (**UB**; mm) is the difference between the averages of the z-axis coordinates for the cranial and caudal teat tips. The UB indicates the position of the udder base relative to the floor. A cow with a balanced and desirable udder should have UB values closer to 0.0 mm or slightly positive, indicating a strong attachment of the fore udder in the abdominal wall. High and positive values for UB may indicate problems with udder attachment in the pelvis, indicating that the caudal part of the udder is much closer to the floor than the cranial part. Cows with high and negative values for UB tend to have problems in the AMS, as the milking robot may be unable to identify the rear teats.

(5) Distance front–rear (**DFR**; mm) is defined as the difference between the averages of the coordinates on the y-axis of the cranial and caudal teats. The DFR quantifies the distance between the cranial and caudal teat tips. Higher distances are desirable, reflecting a longer udder (greater milk storage capacity).

Table 1. Descriptive statistics of udder conformation traits in North American Holstein cattle[1]

Trait	Number of animals	Number of records	Mean	SD	Minimum	Maximum	CV (%)
UD (mm)	4,280	4,232,026	608.42	60.94	394.75	812.50	10.01
UB (mm)	4,280	4,230,114	22.33	17.37	−38.50	83.00	77.79
DFR (mm)	4,280	4,229,966	142.27	29.94	37.00	247.5	21.04
FTD (mm)	4,279	4,225,631	153.73	34.72	31.00	277.00	22.59
RTD (mm)	4,278	4,210,533	67.30	23.99	8.00	156.00	35.62
DY (kg)	4,278	1,578,169	41.09	10.42	6.74	78.23	25.37
EC (mS)	4,280	4,209,405	6.94	0.37	5.55	8.32	5.41

[1] UD = udder depth; UB = udder balance; DFR = distance front–rear; FTD = front teat distance; RTD = rear teat distance; DY = daily milk yield; EC = electrical conductivity.

These 5 udder conformation traits were calculated based on the Cartesian coordinates data from the AMS using R software (R Core Team, 2022). The QC for these traits was performed by removing outliers deviating by more than 3.5 SD from the mean. The descriptive statistics of the phenotypic data used in the analyses are shown in Table 1. Figure 1 presents the histograms of the number of records for each cow and lactation.

Genomic Information

The 4,118 cows were genotyped using different SNP panels and imputed to a common set of 72,820 SNPs using the FImpute software (Sargolzaei et al., 2014). Genomic QC was performed using the PREGSf90 package (Aguilar et al., 2014) and required SNPs to be located on autosomal chromosomes and to have known and unique genomic positions, call rate >0.90, minor allelic frequency (**MAF**) >0.05, and no extreme departure from Hardy-Weinberg equilibrium (**HWE**; <0.15, defined by maximum difference between observed and expected frequency of heterozygosity). The initial genomic dataset used for genotype imputation included genotypes from 22,090 cows. The QC steps were performed before (call rate per sample) and after (MAF and HWE) the imputation (Chen et al., 2023). A subset of 14,469 cows and 62,029 SNPs (Chen et al., 2023) was used for this study, and after performing QC on this reduced dataset, 57,600 SNPs and 4,118 animals remained for further analyses.

Statistical Models and Parameter Estimation

Variance components and genetic parameters for all traits were estimated using the AIREMLF90 package from the BLUPF90+ family programs (Misztal et al., 2018). The repeatability model fitted can be described as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wp} + \mathbf{e},$$

where $\mathbf{y}$ is the vector containing repeated phenotypic records for the analyzed trait or traits, $\mathbf{b}$ is a vector containing the fixed effects of DIM, lactation number (1, 2, or 3+), and concatenation of year and season (Mar.–May, Jun.–Aug., Sep.–Nov., Dec.–Feb.) of calving; $\mathbf{u}$ is a vector containing the additive genetic effects of the cows included in $\mathbf{y}$, $\mathbf{u} \sim \mathrm{N}\left(0, \mathbf{G}\sigma_u^2\right)$, where $\mathbf{G}$ is the genomic relationship matrix (VanRaden, 2008) and σ_u^2 is the additive genetic variance; $\mathbf{p}$ is a vector containing the permanent environmental effects of the cows in $\mathbf{y}$, $\mathbf{p} \sim \mathrm{N}\left(0, \mathbf{I}\sigma_{pe}^2\right)$, where $\mathbf{I}$ is an identity matrix and σ_{pe}^2 is the permanent environmental variance; $\mathbf{e}$ is a vector containing the random residual effects, $\mathbf{e} \sim \mathrm{N}\left(0, \mathbf{I}\sigma_e^2\right)$, where $\mathbf{I}$ is an identity matrix and σ_e^2 is the residual variance; and $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are the incidence matrices connecting the phenotypic records to the fixed effects, additive genetic effects, and permanent environmental effects, respectively.

A bivariate linear animal model was used to estimate the genetic, phenotypic, permanent environmental, and residual correlations among all traits. The multiple-trait model included the same fixed and random effects described above. Therefore, the genetic parameters were estimated using the following multiple-trait repeatability model:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{x}_2 & 0 \\ 0 & \mathbf{x}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{z}_1 & 0 \\ 0 & \mathbf{z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{w}_1 & 0 \\ 0 & \mathbf{w}_2 \end{bmatrix} \begin{bmatrix} \mathbf{p}_1 \\ \mathbf{p}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix},$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ contain repeated records of traits 1 and 2; $\mathbf{b}_1$ and $\mathbf{b}_2$ are the vectors containing the fixed effects for both traits, which are the same as described for the single-trait analyses; $\mathbf{u}_1$ and $\mathbf{u}_2$ are the vectors containing the additive genetic effects of the cows included in $\mathbf{y}_1$ and $\mathbf{y}_2$; $\mathbf{p}_1$ and $\mathbf{p}_2$ are the vectors containing the permanent environmental effects of the cows in $\mathbf{y}_1$ and $\mathbf{y}_2$; $\mathbf{e}_1$ and $\mathbf{e}_2$ are the vectors containing the random residual effects; and $\mathbf{X}_1$, $\mathbf{X}_2$, $\mathbf{Z}_1$, $\mathbf{Z}_2$, $\mathbf{W}_1$, and $\mathbf{W}_2$ are the incidence matrices connecting the phenotypic records to the fixed effects, additive genetic effects, and permanent environmental effects for traits 1 and 2, respectively. We assumed that $\mathrm{E}[\mathbf{y}] = \mathbf{Xb}$; $\mathrm{Var}(\mathbf{u}) = \mathbf{G} \times \mathbf{Sa}$; $\mathrm{Var}(\mathbf{p}) = \mathbf{I} \times \mathbf{Sp}$; and $\mathrm{Var}(\mathbf{e}) = \mathbf{I} \times \mathbf{Se}$, where $\mathbf{Sa}$ is the additive

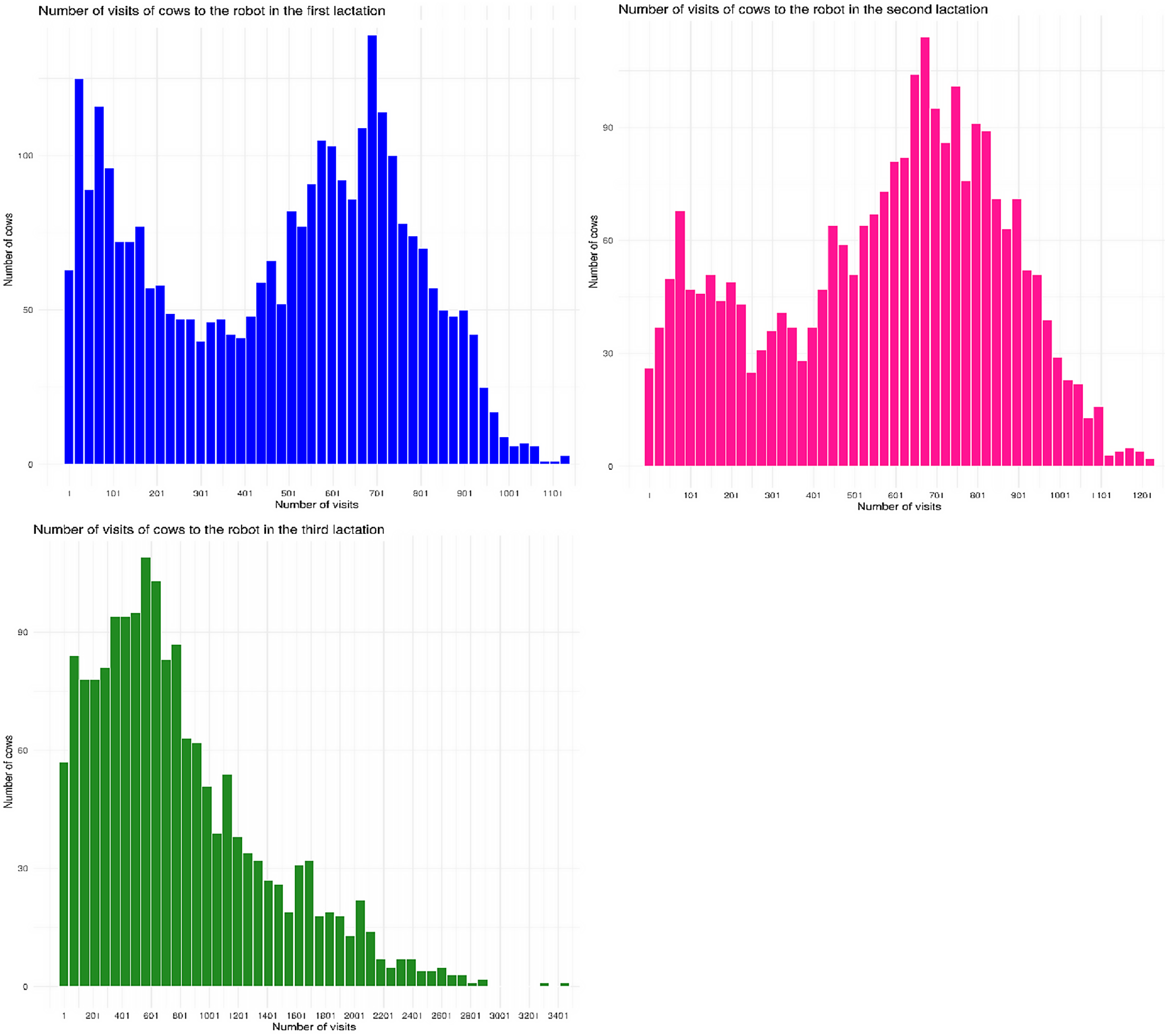

Figure 1. Histograms showing the frequency of the total number of visits to the automatic milking system for each cow in each lactation.

genetic covariance matrix; **Sp** is the permanent environmental covariance matrix; **Se** is the residual covariance matrix; **G** is the genomic relationship matrix; **I** is an identity matrix; and × represents the direct product of the matrices. The vectors **u**, **p**, and **e** were assumed to be uncorrelated.

RESULTS AND DISCUSSION

The numbers of precision dairy farms in Europe and North America are in constant expansion, especially with the adoption of AMS, which enables a large amount of complementary data to be collected and used for deriving many novel traits (Brito et al., 2020; Stygar et al., 2021). In this study, we have used records of the Cartesian coordinates of teats collected on AMS for deriving 5 udder conformation traits and estimated their genetic parameters using genomic information in North American Holstein cattle. This study revealed large genetic variability and precise estimates of genetic parameters for all the traits evaluated. Although the genomic relationship matrix in this study included 4,118 animals, results obtained were similar to those from studies performing pedigree-based analyses with tens of thousands of animals and at least 3 generations of recorded pedigree (Byskov et al., 2012; Carlström et al., 2016b; Poppe et al., 2019).

Udder Conformation Changes Along DIM and Across Lactations

The descriptive statistics of the 5 udder conformation traits are shown in Table 1. The numbers of animals and records are similar for all traits, and the largest and smallest phenotypic means were observed for UD and UB, respectively: UD had the lowest phenotypic variation (CV = 10.01%), and the highest variation was observed for UB (CV = 77.79%). Figure 1 presents histograms with the frequency of the number of available visit records for each cow and lactation, in which the majority of cows had more than 100 measurements per lactation. The large number of records per animal contributes to the calculation of more accurate breeding values, which is a great advantage compared with traditional conformation scoring systems. We further investigated the population trends throughout the lactation periods for the 5 udder conformation traits, as illustrated in Figure 2. Clear differences are apparent in the population average values along DIM and across lactations. The shapes of UD were similar to the shape of lactation curves, although its means decreased from lactation 1 to lactation 3. The UB gradually and considerably increased throughout lactation 1 but changed less within lactations 2 and 3. Both FTD and RTD showed similar changing patterns, gradually decreasing throughout lactation periods across lactations. For DFR, we observed the opposite trends between lactation 1 and the other 2 lactations.

An ideal udder conformation is critical for milk production efficiency, health, workability, and animal welfare (Bhutto et al., 2010). As an alternative to the traditional subjective scoring system implemented by trained technicians, we derived 5 udder conformation traits using the Cartesian coordinates of teats automatically recorded on AMS (Carlström et al., 2016b; Poppe et al., 2019). In this study, we used more than 4 million records for each trait, which produced a comprehensive longitudinal dataset for monitoring udder conformation changes throughout lactation periods. As the cows were raised on a single large farm, we obtained udder conformation traits with smaller standard deviations and ranges, which did not affect the means compared with similar studies (Carlström et al., 2016b; Poppe et al., 2019). This is likely because the studied farm has over 5,000 cows and breeds their cows with semen from various breeding companies, and they also own mothers and other close relatives of AI bulls. Therefore, this farm is a good representation of the North American Holstein population.

We observed clear differences in udder conformation across DIM and lactations. As UD is simultaneously affected by the amount of milk produced and connective tissue in the mammary gland, we observed a similar shape to the traditional lactation curve. At the beginning of lactation, the udder is closer to the floor due to its larger size and edema (Tucker et al., 1992). With the progression of lactation, the udder is held tighter to the body wall, but close to the lactation peak, the udder weight makes the *apparatus suspensorius mammarius* (suspensory apparatus of the udder) sag, getting closer to the floor with increasing DIM. Among lactations, we observed a consistent decreasing of UD, indicating that the udder gets closer to the floor with increasing parities. The UB indicates how the 4 quarters are attached in balance, and a balanced udder is required for a regular milk production and fluent milking (Atkins et al., 2008). We observed considerable changes in UB in lactation 1; at the beginning of the first lactation, the udder is well balanced, but in further lactations, the rear teats approach the floor, due to the weight of the udder acting on the insertion of the ligaments into the pelvis. In the second and later lactations, UB maintained a relatively homogeneous pattern, with increased values only around the lactation peak. After the lactation peak, the decrease in UB might be caused by the approximation of the front teats to the floor, due to the partial loss of attachment to the abdominal wall (Atkins et al., 2008).

The phenotypic patterns of FTD, RTD, and DFR across DIM and lactations are similar, with higher values observed at the beginning of the lactation, followed by decreased values due to edema reduction. This pattern was evident approaching the lactation peak, with a slight increase in the average values, followed by a reduction, which might be caused by a decrease in milk yield and udder size across DIM. Only DFR presented a different pattern in the first lactation, likely because a reduction of edema might have contributed to increased DFR values. This increase in DFR values might be caused by the action of the udder weight on the medial ligament, resulting in an extension of the elastic fibers (Jalakas et al., 2000). The notable decrease in the distance between the front and rear teats throughout lactation is not only due to changes in milk production itself but to changes in udder conformation at different stages of lactation (Blöttner et al., 2011). Minor changes in the distances between the front and rear teats were observed in cows with 3 or more lactations, in which the udder tends to show less pronounced alterations compared with first-parity cows. This could be partially because cows with severe udder issues might have been removed from the AMS pens.

After the lactation period, the mammary gland undergoes intense apoptosis. However, neither the glandular tissue nor the suspensory apparatus of the udder return to their original state. Thus, with each lactation, the mammary gland tends to increase in size, and the tissues of

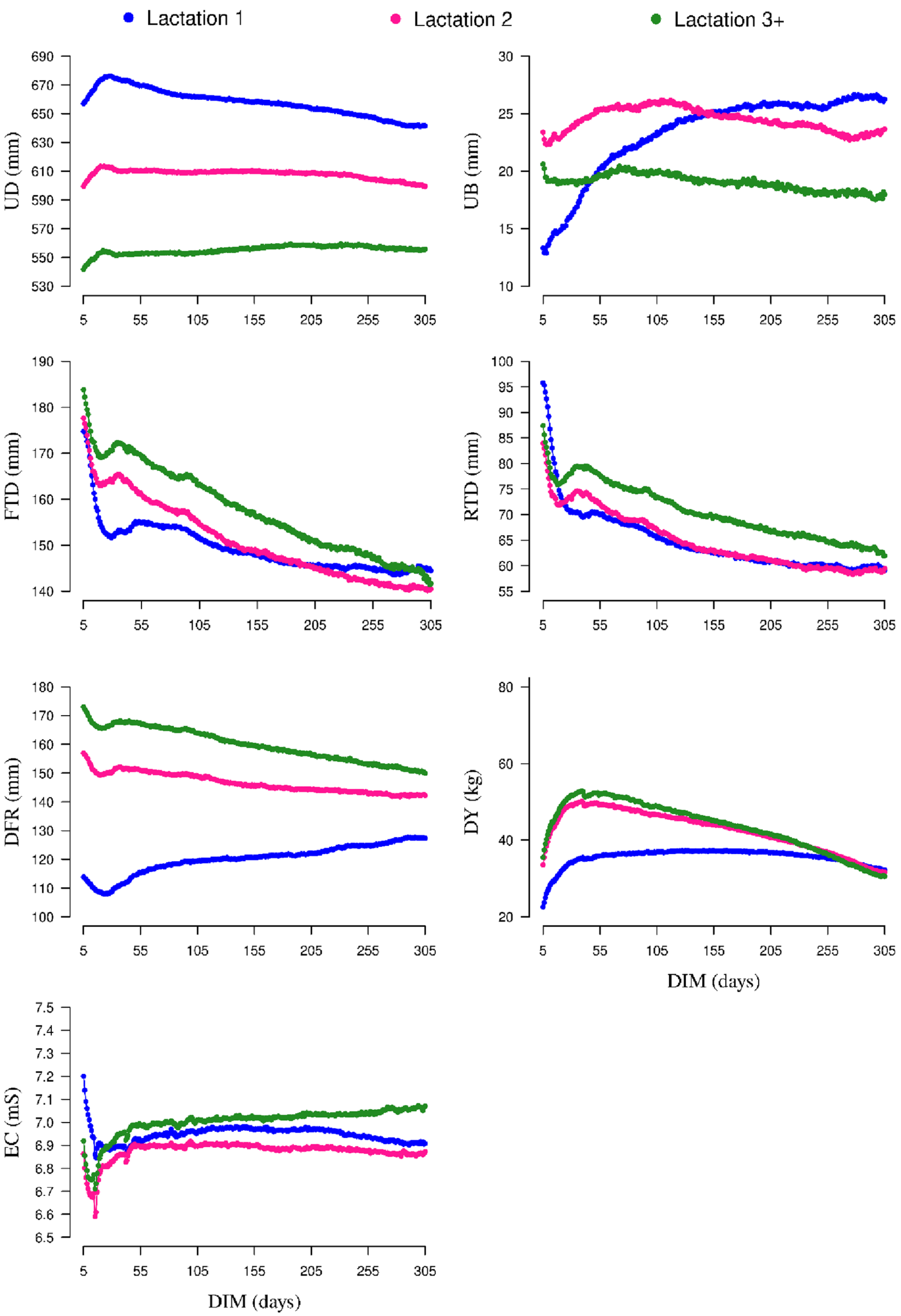

Figure 2. Phenotypic averages estimated in the first, second, and third lactation for udder conformation traits. UD = udder depth; UB = udder balance; DFR = distance front–rear; FTD = front teat distance; RTD = rear teat distance; DY = daily milk yield; EC = electrical conductivity. The values plotted were not pre-adjusted for systematic effects (i.e., they represent observed phenotypic records).

udder support tend to become more flaccid (Junqueira and Carneiro, 1999). This is evidenced by the increase in the phenotypic values of traits over the cow's productive life (Figure 2).

Daily Milk Yield and Electrical Conductivity

Selection for milk yield has been traditionally performed for hundreds of years. It is a fact that the average milk production of a Holstein cow is much higher than the amount needed for calf nutrition (von Keyserlingk et al., 2013). Phenotypic selection has been performed for thousands of years, but the implementation of genetic selection using the animal model and, more recently, genomic selection has provided substantial genetic gains for milk production and milk composition (Guinan et al., 2023), modifying the conformation of Holstein cows (Berry et al., 2022). Losses caused by mastitis have forced producers to also select for udder health indicators and mastitis indicators such as SCS and EC (Barkema et al., 2015). The patterns of the curves presented for DY and EC are consistent with the patterns found in the literature for Holstein cows worldwide (Li et al., 2022; Pedrosa et al., 2023).

In Figure 2, the graph of the average phenotypic pattern of DY during lactation shows that, during the first lactation, the cows have lower milk production, and the peak of lactation is less evident, presenting a substantial increase in production in the first 30 d followed by a plateau, which remains relatively constant up to 305 DIM. These results are consistent with the pattern of the first-lactation curve of modern Holstein cows (Li et al., 2022). The pattern of the DY phenotypic average in the second and third lactations shows a substantial increase up to approximately 40 d, with the peak of lactation occurring at 39 d, followed by a slight decrease in production, approaching the average values of daily production in first lactation after 250 DIM; the values found are similar to those found in the literature for Holstein cows in AMS (Li et al., 2022; Pedrosa et al., 2023).

Observing the phenotypic pattern of EC over the course of lactation, we can see a difference in the pattern of the average values of the first lactation in relation to the following lactations. In the first 2 wk of lactation, EC values in the first lactation differ from the following lactations; this is due to the intense edema and changes in the blood capillarity of the udder, which are being faced for the first time in the animal's life (Morrison et al., 2018). Over the course of lactation, the animal tends to correct the variations that occurred in the peripartum period (Norberg et al., 2004b), and EC values begin to decrease. In the first lactation, the values remain constant, close to 6.9 mS, up to 305 DIM.

In subsequent lactations, the patterns are similar, with a tendency for EC to increase as lactation progresses; increases in the occurrence of mastitis and in SCS over the course of lactation have been reported (Sheldrake et al., 1983; Schutz et al., 1995; Schepers et al., 1997; Norberg et al., 2004a), which may explain the tendency of EC to increase. We also note that the average EC increases when comparing cows from first and second parity with cows of 3 or more parities, as cows of 3 or more parities tend to produce more milk (Li et al., 2022) and present more cases of mastitis (Lean et al., 2023), which changes EC. It is important to highlight that EC has been presented as a controversial indicator of mastitis, and some researchers might disagree with its use as an indicator of clinical mastitis (Hamann and Zecconi, 1998; Hovinen et al., 2006). However, its use in this context is justified, as this information is collected at every visit of the cows, along with the Cartesian coordinates of the teats. Therefore, we can identify changes in milk EC, mainly attributed to alterations in Na^+ and Cl^- levels due to inflammation of the udder (Hamann and Zecconi, 1998), and determine whether these changes are correlated with variations in udder conformation traits. Unfortunately, clinical mastitis records were not available for this study.

Variance Components and Heritabilities

Table 2 presents the variance component estimates, heritability, and repeatabilities for all the udder conformation traits. For interpretation purposes, heritability estimates lower than 0.15 were considered as low, between 0.15 and 0.30 were considered as moderate, and greater than 0.30 were considered as highly heritable traits. Overall, we found significant additive genetic variability for all the traits, with heritability estimates (SE) ranging from 0.40 (0.02) for RTD to 0.79 (0.01) for UD. More importantly, we observed comparable variance components for the permanent environmental effects, especially for UB and RTD.

The heritability estimates observed are higher than reported in the literature (Carlström et al., 2016a; Poppe et al., 2019), possibly due to the reduced nongenetic variance existing in the present herd, as all records were collected in a single large farm. Previous studies used samples from every 20 visits and considered the udder conformation traits as different traits in each lactation (Poppe et al., 2019); however, they reported very high genetic correlations among lactations. Therefore, we analyzed udder conformation records from different lactations together and fitted repeatability models. The repeatability estimates (SE) ranged from 0.82 (0.01) for UB to 0.93 (0.01) for UD (Table 2), which support our analyses considering all the records as the same trait.

Table 2. Estimates (±SE) of variance components, heritabilities, and repeatabilities for udder conformation traits in North American Holstein cattle[1]

Trait	σ^2_a	σ^2_{pe}	σ^2_e	σ^2_p	h^2	t
UD	2,479.6 (105.4)	427.2 (32.9)	231.7 (0.2)	3,139.2 (86.1)	0.79 (0.01)	0.93 (0.01)
UB	126.2 (9.0)	124.9 (5.1)	53.9 (0.0)	305.0 (7.0)	0.41 (0.02)	0.82 (0.01)
DFR	470.7 (23.8)	164.4 (9.3)	86.0 (0.1)	721.2 (18.9)	0.65 (0.02)	0.88 (0.01)
FTD	616.6 (36.7)	387.9 (17.5)	155.2 (0.1)	1,159.7 (28.8)	0.53 (0.02)	0.87 (0.01)
RTD	228.7 (16.6)	244.6 (9.6)	99.8 (0.1)	573.1 (12.9)	0.40 (0.02)	0.83 (0.01)
DY	80.3 (6.9)	131.0 (4.7)	183.6 (0.1)	394.9 (5.5)	0.20 (0.02)	0.54 (0.01)
EC	7.4 (0.4)	3.4 (0.2)	5.2 (0.0)	16.0 (0.3)	0.46 (0.02)	0.68 (0.01)

[1] UD = udder depth; UB = udder balance; DFR = distance front–rear; FTD = front teat distance; RTD = rear teat distance; σ^2_a = additive genetic variance; σ^2_{pe} = permanent environmental variance; σ^2_e = residual variance; σ^2_p = phenotypic variance; h^2: heritability; t: repeatability.

Furthermore, the data from all AMS visits were considered in the analyses to avoid loss of information.

Usually, the heritability estimates of udder conformation traits measured based on traditional and more subjective methods have low to moderate estimates (DeGroot et al., 2002; Wu et al., 2013; Nazar et al., 2022). Therefore, genetic progress for those traits would be slower compared with the traits derived from AMS, as reported in this study. Not all dairy herds have AMS, so the collection of phenotypic data based on traditional type (conformation) for genetic evaluations could be beneficial, as traits from both sources of records (AMS vs. technician scoring systems) are genetically correlated (Poppe et al., 2019). Holstein cattle herds are well connected at the genetic level due to the extensive use of AI, and genomic selection is widely used across the country. Therefore, AMS herds could generate the reference population data for performing genomic predictions in all other herds, as already done for novel traits such as feed efficiency, methane emissions, and robotability traits (Manzanilla-Pech et al., 2021; Pedrosa et al., 2023).

In addition to the additive genetic effects, we must simultaneously estimate the permanent environmental effects when fitting repeated records throughout the lactation period and multiple lactations. We observed that the average repeatability estimates were higher than 0.80 for all 5 traits, Poppe et al. (2019) considered udder conformation traits as different traits across lactations and found high genetic correlations and repeatability estimates greater than 0.90 for all of these traits.

The estimates of the heritabilities and repeatabilities for DY and EC are in accordance with the results presented in the literature (Norberg et al., 2004b; Nixon et al., 2009; Pedrosa et al., 2023). The use of genomic-based genetic parameters is a reality in Holstein herds around the world, mainly for DY (Lee et al., 2020), being usually used for genomic selection in this breed (Wiggans et al., 2017; Guinan et al., 2023). Studies on EC in AMS are relatively recent, but they prove that it is a trait with moderate or high heritability coefficients and that it is associated with SCS and clinical mastitis (Norberg et al., 2004a,b); therefore, genomic selection for EC has the ability to improve mammary gland health in dairy cattle (Pedrosa et al., 2023).

Correlations Among Udder Conformation Traits

Tables 3 and 4 present the genetic, phenotypic, permanent environmental, and residual correlations for all the udder conformation traits evaluated. For interpretation purposes, correlation estimates lower than 0.30 were considered as low, between 0.30 and 0.50 were considered as moderate, and greater than 0.50 were considered as high. Positive genetic correlations were observed between DFR, FTD, and RTD, whereas all of them were negatively correlated with UD and UB at the genetic level. We found weak genetic correlation between UD and UB (0.11 ± 0.04). The strongest positive and negative genetic correlations were found between FTD and RTD (0.54 ± 0.03) and between UD and DFR (−0.47 ± 0.03), respectively. Both phenotypic and permanent environmental correlations showed similar patterns to the genetic correlations. The residual correlations ranged from 0.00 (0.01) between UB and UD to 0.72 (0.01) between FTD and RTD.

Udder conformation is a complex trait that can be described or quantified from different aspects, such as depth, width, and length. Therefore, it is necessary to investigate the genetic and environmental correlations among the derived traits from Cartesian coordinates of teats, which will guide the selection of the most representative traits. In a dairy farm using AMS, the main selection objectives concerning the udder conformation traits are related to the increase of UD, to obtain cows with stronger suspensory apparatus of the udder and, thus, with greater longevity (Morek-Kopeć and Zarnecki, 2012). Adequate UB, FTD, and RTD will allow proper identification of all teats during milking. Greater DFR will contribute to increased milk storage capacity in the udder, because this increase is not the result of sagging

Table 3. Genetic (upper diagonal) and phenotypic (lower diagonal) correlations (SE in parentheses) between udder conformation traits using a repeatability model from North American Holstein cattle[1]

Trait	UD	UB	DFR	FTD	RTD	DY	EC
UD	—	0.11 (0.04)	−0.47 (0.03)	−0.31 (0.03)	−0.27 (0.04)	−0.12 (0.04)	−0.25 (0.03)
UB	0.09 (0.02)	—	0.12 (0.04)	−0.20 (0.04)	−0.11 (0.05)	0.02 (0.06)	−0.13 (0.04)
DFR	−0.40 (0.02)	0.11 (0.02)	—	0.32 (0.03)	0.10 (0.04)	0.30 (0.04)	0.20 (0.04)
FTD	−0.28 (0.02)	−0.15 (0.02)	0.33 (0.02)	—	0.54 (0.03)	0.20 (0.05)	0.11 (0.04)
RTD	−0.22 (0.02)	−0.19 (0.02)	0.15 (0.02)	0.61 (0.01)	—	0.06 (0.06)	0.02 (0.05)
DY	−0.10 (0.01)	0.13 (0.01)	0.24 (0.01)	0.14 (0.01)	0.03 (0.01)	—	0.31 (0.05)
EC	−0.15 (0.02)	−0.09 (0.01)	0.09 (0.02)	0.04 (0.02)	0.02 (0.01)	−0.06 (0.01)	—

[1] UD = udder depth; UB = udder balance; DFR = distance front–rear; FTD = front teat distance; RTD = rear teat distance; DY = daily milk yield; EC = electrical conductivity.

of the medial ligament of the udder (Atkins et al., 2008). The UD has a negative and unfavorable correlation with DFR, FTD, and RTD, indicating that cows with teats farther apart have the udder closer to the floor. This could be a result of either ligamentous sagging or larger udders tending to be closer to the floor and having the teats farther apart. However, as the genetic correlation values are moderate or low, selection can be simultaneously carried out to increase UD without causing a sharp approximation of the teats. In this context, it is possible to find cows with udders far from the floor and well-separated teats, which will result in these cows having longer productive lives and being easier to milk.

The average values of genetic correlation between UB and the FTD and RTD traits were negative and low, indicating that selection for increased FTD and RTD will result in progenies with lower UB values, which is undesirable. Thus, selection for more balanced udders should be prioritized rather than focusing efforts on selecting only for the distance between the teats, since UB exerts a greater influence on milk production and longevity than the latter traits (Blöttner et al., 2011; Tribout et al., 2020). Moreover, the correlation between UB and DFR is positive, favorable, and low; thus, genetic selection for cows with greater distance between the front and rear teats—that is, with greater udder length—will tend to generate animals with udders that are more firmly attached to the abdominal wall.

The udder is suspended on the ventral face of the body by superficial and deep layers of the external fascia of the trunk, which forms the suspensory apparatus of the udder. The udder is composed of lateral and medial laminae, from which thin lamellae extend between the mammary complexes. The medial lamina is largely composed of elastic tissue; the lateral lamina, of dense connective tissue. The left and right portions of the udder are divided by the *sulcus intermammarius* (Dyce et al., 2004; König and Liebich, 2004). The action of the lateral ligaments affects UD and UB, whereas FTD, RTD, and DFR are more affected by the action of the medial lamina. As the lateral and medial ligaments are formed by different tissues, a low or moderate genetic correlation was expected, as different sets of genes likely control both groups of traits.

The genetic correlation found between FTD and RTD was positive, high, and favorable, corroborating with the results reported in the literature (Carlström et al., 2016a; Poppe et al., 2019). The DFR has a positive, moderate, and favorable genetic correlation with FTD and a positive, low, and favorable genetic correlation with RTD, indicating that an increase in udder width will accompany greater udder length. However, because the correlation values are moderate, selection to increase udder milk storage capacity (indirectly built-in concept in higher DFR values) might not necessarily result in animals with weaker medial udder ligaments.

Table 4. Permanent environmental (upper diagonal) and residual (lower diagonal) correlations (SE in parentheses) between udder conformation traits in North American Holstein cattle[1]

Trait	UD	UB	DFR	FTD	RTD	DY	EC
UD	—	0.11 (0.04)	−0.21 (0.04)	−0.21 (0.04)	−0.17 (0.04)	−0.13 (0.04)	0.03 (0.05)
UB	0.00 (0.01)	—	0.10 (0.03)	−0.14 (0.03)	−0.26 (0.03)	0.15 (0.03)	−0.08 (0.03)
DFR	−0.30 (0.01)	0.13 (0.01)	—	0.31 (0.03)	0.15 (0.03)	0.20 (0.03)	−0.05 (0.04)
FTD	−0.34 (0.01)	0.00 (0.01)	0.46 (0.01)	—	0.64 (0.02)	0.06 (0.03)	−0.01 (0.03)
RTD	−0.27 (0.01)	−0.19 (0.01)	0.32 (0.01)	0.72 (0.01)	—	−0.04 (0.03)	0.04 (0.03)
DY	−0.16 (0.01)	0.21 (0.01)	0.31 (0.01)	0.24 (0.01)	0.10 (0.01)	—	−0.35 (0.03)
EC	−0.03 (0.01)	−0.07 (0.01)	−0.04 (0.01)	−0.04 (0.01)	0.00 (0.01)	−0.16 (0.01)	—

[1] UD = udder depth; UB = udder balance; DFR = distance front–rear; FTD = front teat distance; RTD = rear teat distance; DY = daily milk yield; EC = electrical conductivity.

Correlations Between Udder Conformation, Daily Milk Yield, and Electrical Conductivity Traits

Genetic and phenotypic correlations between udder conformation, milk yield, and EC traits are of moderate or low magnitude. One of the most important traits that affect cow longevity in the herd is UD, which has an unfavorable correlation with milk, fat, protein, and lactose production (Tsuruta et al., 2005; Marshall et al., 2023). Our results indicate that selection for udder conformation traits might not influence milk production and mastitis cases, indicated by EC (Norberg et al., 2004a). The genetic correlation between UD and DY is unfavorable and of low magnitude. Therefore, it is possible to select for improvement of UD, aiming to generate cows more suitable for robotic milking (Atkins et al., 2008), without negatively affecting DY; these results are consistent with the results found in other dairy cattle herds (Khan and Khan, 2016; Poppe et al., 2019). In contrast, the correlation between DY and DFR (0.30) was positive, of moderate magnitude, and will respond to selection by the correlated response. Thus, the DFR trait should be an udder conformation trait on which selection should be focused, as it is able to increase the udder storage capacity, by increasing length, and has the ability to increase the cow's daily milk production.

The genetic correlations between the udder conformation traits had average values very close to zero with EC, values indicating that it is possible to select cows with more suitable udders to integrate the AMS without increasing the electroconductivity values and, consequently, the occurrences of clinical mastitis in the herd (Norberg et al., 2004a; Bausewein et al., 2023). The genetic correlation between EC and DY was unfavorable and of moderate magnitude. Therefore, selection for increased DY tends to increase cases of mastitis in AMS farms; the results are consistent with the values found in the literature (Bonestroo et al., 2022; Huang et al., 2023) and are probably related to lower adaptability and resistance to pathogens that enter the mammary gland by ascending route—that is, they penetrate through the teat orifice and multiply in the mammary gland (Rupp and Boichard, 2003; Martin et al., 2018).

Despite udder conformation being less important in dairy herds milked by traditional parlor systems (Cole et al., 2021; VanRaden et al., 2021), proper udder conformation is paramount in AMS herds. With the expansion of AMS systems in North America, genetic selection for udder conformation based on Cartesian coordinates traits could be valuable for herds adopting AMS. We envision that the traits presented in this study might be incorporated in selection subindexes related to cow performance in AMS. The precision in phenotype recording and the large volume of information collected by the AMS largely contribute to obtaining accurate breeding values, which, combined with the fact that these traits have high heritabilities, will enable rapid genetic progress for udder conformation. We expect that cases of cows with teats unidentified by the milking robot could decrease substantially in few generations, depending on the selection pressure adopted in breeding programs. Developing customized selection indexes for AMS producers, which encompass both traditional and AMS-specific traits, holds promise for optimizing cow health and welfare and the profitability of dairy production in AMS systems.

CONCLUSIONS

This study revealed that udder conformation traits derived from Cartesian coordinates from robotic milking systems are highly heritable, indicating that fast genetic progress can be achieved through direct genetic or genomic selection. All traits are highly repeatable, indicating that records from the first parity are sufficient for estimating breeding values for udder conformation traits. Moreover, some udder conformation traits had a low genetic correlation with other relevant traits, which demonstrates that independent selection among those traits and construction of subindexes can be applied. The strongest genetic correlations were found between FTD and RTD (0.54), and UD and DFR (−0.47), suggesting that care is needed when selecting for increased DFR, which could generate cows with udders closer to the floor.

NOTES

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databases. The authors have not stated any conflicts of interest.

Nonstandard abbreviations used: AMS = automatic milking systems; DFR = distance front–rear; DY = daily milk yield; EC = electrical conductivity; FTD = front teat distance; HWE = Hardy-Weinberg equilibrium; MAF = minor allelic frequency; QC = quality control; RTD = rear teat distance; UB = udder balance; UD = udder depth.

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