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Genetic parameters of linear conformation type traits and their relationship with milk yield throughout lactation in mixed-breed dairy goats

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1 LINEAR CONFORMATION TRAITS IN MIXED-BREED DAIRY GOATS

2 Interpretive summary: Genetic parameters of linear conformation type traits and their 3 relationship with milk yield throughout lactation in mixed-breed dairy goats. By 4 McLaren et al. Whilst striving to improve profitability, dairy goat breeders should also 5 consider traits relating to body conformation. In this study, the majority of genetic correlations estimated between milk yield and both udder and teat traits were negative. 6 7 Farmers should therefore consider these traits when making animal selection decisions to 8 ensure that selection for increased productivity is not accompanied by any potential unwanted 9 deterioration of fitness.

10

11 Genetic parameters of linear conformation type traits and their relationship with milk

12 yield throughout lactation in mixed-breed dairy goats.

13

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24 Abstract

Conformation traits are of interest to many dairy goat breeders not only as descriptive traits in their own right, but also because of their influence on production, longevity and profitability. If these traits are to be considered for inclusion in future dairy goat breeding programmes, relationships between them and production traits such as milk yield, must be considered. With the increased use of regression models to estimate genetic parameters, there is now an opportunity to investigate correlations between conformation traits and milk yield throughout lactation in more detail. The aims of this study were therefore to a) estimate genetic 32 parameters for conformation traits in a population of crossbred dairy goats, b) estimate 33 correlations between all conformation traits and c) assess the relationship between 34 conformation traits and milk yield throughout lactation. No milk composition information 35 was available. Data were collected from goats based on 2 commercial goat farms, during 36 August and September in 2013 and 2014. Ten conformation traits, relating to udder, teat, leg 37 and feet characteristics, were scored on a linear scale (1-9). The overall dataset comprised of 38 data available for 4,229 goats, all in their first lactation. The population of goats used in the 39 study was created using random crossings between 3 breeds: British Alpine, Saanen and 40 Toggenburg. In each generation, the best performing animals were selected for breeding 41 therefore leading to the formation of a synthetic breed. The pedigree file used in the analyses 42 contained sire and dam information for a total of 30,139 individuals. The models used fitted 43 relevant fixed and random effects. Heritability estimates for the conformation traits were low 44 to moderate, ranging from 0.02 to 0.38. A range of positive and negative phenotypic and 45 genetic correlations between the traits were observed, with the highest correlations found 46 between udder depth and udder attachment (0.78), teat angle and teat placement (0.70), and back legs and back feet (0.64). The genetic correlations estimated between the conformation 47 48 traits and milk yield, across the first lactation, demonstrated changes during this time period. 49 The majority of correlations estimated between milk yield and both the udder and teat traits 50 were negative. Therefore, future breeding programmes would benefit from including these 51 traits in order to ensure that selection for increased productivity is not accompanied by any 52 unwanted change in functional fitness.

53 Key Words: dairy goat, conformation, milk yield, random regression

54

INTRODUCTION

55 Conformation traits are of interest to many animal breeders not only as descriptive traits in 56 their own right, but also because of their influence on production, longevity and profitability 57 (Brotherstone 1994). In dairy cattle, linear type traits were first recorded in the early 1980's (Meyer et al., 1987; Short and Lawlor, 1992; Brotherstone, 1994). In terms of small 58 59 ruminants, one of the earliest scales developed was by the American Dairy Goat Association 60 (ADGA), which has been used to score goats across a range of different breeds since 1988 (Luo et al., 1997). The linear traits included in this scale are scored from 1 to 50, with an 61 62 additional score, based on overall appearance according to a number of weighted criteria, scored between 50 and 99. However, several other scales, which have also been used to 63 64 assess conformation traits, have been developed based on 9-point linear type scoring systems. One of the earliest proposed for dairy sheep was by de la Fuente et al. (1996) during the evaluation of Churra ewes, from which a number of other scales, adapted for different breeds, have emerged (Carta et al., 2009). In terms of dairy goats, a 9-point scale has also been developed and is currently used by French dairy goat breeders, as described by Manfredi et al. (2001).

Initially, the most commonly recorded traits were udder and teat type traits, mainly due to their influence on the milking ability, udder health and longevity of animals. More recently a number of studies have also considered additional traits, such as those relating to the legs and feet of the animals (Manfredi et al., 2001; de la Fuente et al., 2011). By improving aspects such as animal mobility and structural correctness, there is the prospect that the productivity and profitability of dairy goat herds could further improve particularly when coincidentally exposed to intense selection pressure for yield traits.

77 If conformation traits were to be considered for inclusion in future dairy goat breeding 78 programmes, relationships between the conformation traits themselves, as well as with 79 production traits such as milk yield, must be considered. Fernandez et al. (1997) as well as 80 Legarra and Ugarte (2005), while estimating genetic correlations between conformation traits 81 and milk yield in Churra and Laxta sheep respectively, calculated correlations that indicated 82 that selection for improved milk yield could have implications on udder morphology. The 83 depth of the udder and the placement of the teats were particularly affected, leading to a 84 possible decline in the milking ability of animals in machine milking environments. Similar 85 findings were also observed by Manfredi et al. (2001), indicating that to reduce the decline of 86 milking ability, whilst attempting to improve milk yield, the inclusion of conformation traits in breeding programmes would be valuable. 87

However, while examining the links between conformation traits and milk yield, many of these studies have used cumulated milk yields, produced during lactations of different length, for example 120-day milk yield in sheep (Fernandez et al., 1997; Legarra and Ugarte, 2005) or 250-day milk yield in goats (Manfredi et al., 2001; Rupp et al., 2011). With the increased use of random regression models to estimate genetic parameters in goats (Menendez-Buxadera et al., 2010; Mucha et al., 2014), there is now the opportunity to investigate correlations between conformation traits and milk yield throughout lactation in more detail.

The aims of this study were therefore to a) estimate genetic parameters for conformation traits in a population of crossbred dairy goats, b) estimate correlations between all conformation traits and c) assess the relationship between conformation traits and milk yield throughout lactation.

99

MATERIALS AND METHODS

100 Conformation Traits

101 Conformation trait data were collected from goats based on 2 farms, owned by the same 102 farming business and consisting of related animals, during August and September in 2013 and 2014. The dataset comprised of data available for 4,220 goats all in their first lactation. 103 104 The traits recorded for each animal, scored by the same recorder, were linear in form and 105 scored using a 9-point scale which had many similarities to that developed by the French 106 dairy goat breeders' association CAPGENES and used by Manfredi et al. (2001) and Rupp et 107 al. (2011). The data contained information for three udder traits, three teat traits and four 108 traits relating to legs and feet.

109 The udder traits, as shown in Figure 1 were: Udder furrow (UF), viewed from the rear view 110 of the udder, indicating the prominence of the medial suspensory ligament. A score of 1 111 indicates that the ligament is highly prominent, with an extreme cleft in the base of the udder, 112 whereas a score of 9 indicates the ligament is not prominent and there is little/no cleft visible. 113 Udder depth (UD) is the depth of the udder is measured in comparison to the hocks of the 114 animal. Udders scored 1 are close to the ground whereas those scored 9 are well above the 115 hocks. A score of 5 indicates that the cleft of the udder is at the hocks level; Udder 116 attachment (UA) represents the strength of attachment, based on the perimeter of the insertion 117 to the abdominal wall. A score of 1 represents udders with a weak and narrow level of attachment whereas those scored 9 are udders with a large and strong perimeter of 118 119 attachment.



120

121 Figure 1. Scoring criteria used for the udder and teat traits.

The teat traits, also shown in Figure 1 were: Teat shape (TS) indicating the diameter and shape of the teat ranging from wide and conical for score 1 to small and cylindrical for score 9; Teat angle (TA) describes whether the teat, when looking from the side of the animal, is pointing forwards (score 1) or towards the rear (score 9). The score of 5 represents teats pointing straight downwards. Teat placement (TP) is scored using a rear view of the udder and gives an indication as to placement of the teats in relation to the medial ligament. Teats pointing outwards, away from each other, would be scored as 1, whereas those pointing inwards, towards each other, would be scored 9. A score of 5 would be given for teatspointing straight down.

131 The leg and feet traits are shown in Figure 2. The scoring for the front legs was similar to that 132 shown for the back legs. A score for both the Front legs (FL) and Back legs (BL) of 5 represented legs that were completely straight. Animals with legs that pointed inwards at a 133 134 severe angle, resulting in the hocks (BL) or knees (FL) nearly touching, would be given a 135 score of 1 where as those completely the opposite, with the hocks/knees a large distance apart 136 and forming bowed legs, would be scored as a 9. The Front feet (FF) and Back feet (BF) 137 scores describe the direction that the hooves were facing when the animal was standing 138 (Figure 2). A score of 1, considered to be the worst score for both FF and BF, represented 139 hooves that were facing away from each other. A score of 5 represented hooves pointing 140 outwards, but at a less severe angle. The best score for both FF and BF was 9 and was given 141 to animals with both hooves pointing straight forward. In addition to the conformation traits, 142 test day milk yield and cumulative milk yield data, up to day 305, were also available.



143

144 Figure 2. Scoring criteria used for the leg and feet traits.

145 Genetic analysis

The population of goats used in the study, as described by Mucha et al. (2014), was created using random crossings between 3 breeds: British Alpine, Saanen and Toggenburg. In each generation, the best performing animals were selected for breeding therefore leading to the formation of a synthetic breed. No information was available in terms of the breed composition of the animals in the population therefore this could not be included in the 151 analyses. The pedigree file used in the analyses contained sire and dam information for a total 152 of 30,139 individuals. Estimates of (co)variance components were obtained by the average 153 information-REML algorithm in the DMU package (Madsen and Jensen, 2008). The model 154 fitted for the conformation traits was:

155
$$y = Xb + Za + e$$
, [1]

156 where \mathbf{v} is a vector of observations for the analysed conformation score; \mathbf{b} is a vector of fixed 157 effects: farm, lactation stage, year of scoring and birth year; a is the vector of random 158 additive animal effects; e is the vector of random residual effects, and X and Z are incidence 159 matrices relating records to their respective effects. Lactation stage, defined as the number of 160 days between kidding date and scoring date, was grouped into 7 different levels in order to 161 achieve an appropriate distribution; i) 100 days or less (939 records), ii) between 101-200 days (2123 records), iii) 201-300 days (536 records), iv) 301-400 days (276 records), v) 401-162 163 500 days (129 records), vi) 501-600 days (114 records) and vii) 601 days and above (103 164 records). Year of scoring had 2 levels; 2013 (1662 records) and 2014 (2558 records) and birth 165 year had 5 levels; 2009 (49 records), 2010 (162 records), 2011 (661 records), 2012 (1810 166 records) and 2013 (1538 records). Only the direct genetic effect (animal) was fitted in each 167 model due to the fact that the conformation scores were recorded only once on each 168 individual animal.

169 Genetic and phenotypic correlations between each individual conformation trait were 170 estimated using a multivariate analysis including all traits. The covariance structure for the 171 multivariate analyses was:

Where indices 1 and 2 (and so on) indicate the two conformation traits, **A** is the additive genetic relationship matrix **I** are identity matrices, σ_g^2 and σ_e^2 are the genetic and residual variances, respectively.

176 Milk yield was modelled with a random regression animal model developed in a previous177 study (Mucha et al., 2014):

178
$$y = Xb + Za + Wp + e$$
, [2]

172

where \mathbf{y} is the vector of test-day observations; \mathbf{b} the vector of fixed effects, consisting of age 179 180 at kidding, herd test day, year-season, and fixed lactation curves modeled by fitting Legendre polynomials (Kirkpatrick et al., 1990) of fourth order; **a** is a 1×3 vector of random 181 182 regression coefficients (Legendre polynomials of second order) for the animal effect; **p** is the 183 1×3 vector of random regression coefficients (Legendre polynomials of second order) for 184 the permanent environment effect; and \mathbf{e} is the vector of random residual effect. The matrix \mathbf{X} 185 is the incidence matrix for fixed effects; Z and W are matrices of Legendre polynomials of 186 DIM of second order for random animal and permanent environment effect, respectively.

187 Random effects were assumed to be normally distributed with zero means and the following188 covariance structure:

189
$$\operatorname{Var}\begin{bmatrix}\mathbf{a}\\\mathbf{p}\\\mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A} \otimes \mathbf{G} & 0 & 0\\ \mathbf{I} \otimes \mathbf{P} & 0\\ symm & \mathbf{I}\sigma_e^2\end{bmatrix}$$

where **G** and **P** are 3×3 (co)variance matrices of the random regression coefficients for the animal and permanent environment effects, respectively.

192 The variance-covariance structures for the bivariate analyses of milk yield and conformation193 traits were as follows:

194
$$\operatorname{Var}\begin{bmatrix}\mathbf{a}_{1}\\\mathbf{a}_{2}\\\mathbf{p}_{2}\\\mathbf{e}_{1}\\\mathbf{e}_{2}\end{bmatrix} = \begin{bmatrix}\mathbf{AG}_{1} & \mathbf{AG}_{12} & 0 & 0 & 0\\ & \mathbf{AG}_{2} & 0 & 0 & 0\\ & & \mathbf{IP}_{2} & 0 & 0\\ & & & \mathbf{I}\sigma_{e1}^{2} & \mathbf{I}\sigma_{e12}^{2}\\ symm & & & & \mathbf{I}\sigma_{e2}^{2}\end{bmatrix}$$

Where indices 1 and 2 indicate the two traits. The first trait was one of the conformation traits (following model 1), and the second trait was milk yield (following model 2). G_1 contained only one value, G_{12} contained one row (1x3), whereas G_2 and P_2 were 3x3 (co)variance matrices as defined for model 2. Because the first trait was modelled with model 1 it had no permanent environment, thus P_1 and P_{12} do not exist.

The genetic covariances between milk yield and conformation traits on the *i*th DIM were calculated as $\hat{\sigma}_{gi12} = \mathbf{L}'(\text{DIM}_i)\hat{\mathbf{G}}_{12}$ where $\mathbf{L}(\text{DIM}_i)$ is the row vector of Legendre polynomials for DIM_i (Kirkpatrick et al., 1990), of size 3. The phenotypic covariance was the sum of genetic and residual covariance. An additional analysis with cumulative 305 day milk yield was also performed, using the following model:

205 y = Xb + Za + e, [3]

where **y** is a vector of observations for the 305 day milk yield; **b** is a vector of fixed effects: age at kidding, farm, year-season; **a** is the vector of random additive animal effects; **e** is the vector of random residual effects, and **X** and **Z** are incidence matrices relating records to their respective effects. Subsequently bivariate analyses of milk and conformation were performed where conformation traits were modelled using model 1 and 305 day milk yield with model 3. The covariance structure for the bivariate analyses was:

212
$$\operatorname{Var}\begin{bmatrix}\mathbf{a}_{1}\\\mathbf{a}_{2}\\\mathbf{e}_{1}\\\mathbf{e}_{2}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_{g1}^{2} & \mathbf{A}\sigma_{g12} & \mathbf{0} & \mathbf{0}\\ & \mathbf{A}\sigma_{g2}^{2} & \mathbf{0} & \mathbf{0}\\ & & \mathbf{I}\sigma_{e1}^{2} & \mathbf{I}\sigma_{e12}\\ symm & & & \mathbf{I}\sigma_{e2}^{2}\end{bmatrix}$$

213 Where indices 1 and 2 indicate the two traits. The first trait was one of the conformation 214 traits, and the second trait was 305d milk yield, **A** is the additive genetic relationship matrix, 215 **I** are identity matrices, σ_g^2 and σ_e^2 are the genetic and residual variances, respectively.

The standard errors for heritability and genetic and phenotypic correlations were calculated using the methodology proposed by Fischer et al. (2004), with the interpretation proposed by Frigo et al. (2010). Fat and protein content was not included in the analysis as no data was available from either of the farms contributing data to the study.

220

RESULTS & DISCUSSION

A summary of traits included in the analyses are shown in Table 1. The average scores recorded on both farms were similar for all traits. The front legs trait had the lowest overall standard deviation (0.37) which was a reflection that 88% of records were a score of 5. The average daily milk yield, during the first lactation, was 3.32 +0.003 kg. The additional summary statistics for this trait are provided by Mucha et al. (2014).

Table 1. Summary of conformation traits included in the analyses.

Trait	Count	Minimum	Maximum	Average	S. Dev.
Udder Furrow (UF)	4153	2	9	6.42	<u>+</u> 0.99
Udder Depth (UD)	4220	2	9	5.93	<u>+</u> 0.94
Udder Attachment (UA)	4220	3	9	7.69	<u>+</u> 0.68
Teat Shape (TS)	4198	1	8	4.17	<u>+</u> 1.00
Teat Angle (TA)	4216	1	6	4.24	<u>+</u> 0.81
Teat Placement (TP)	4216	1	8	3.37	<u>+</u> 0.81
Front Legs (FL)	4216	2	9	4.88	<u>+</u> 0.37
Back Legs (BL)	4219	2	9	4.60	<u>+</u> 0.62
Front Feet Set (FF)	4213	3	9	8.23	<u>+</u> 0.74
Back Feet Set (BF)	4217	4	9	7.78	<u>+</u> 0.77
305 day milk yield (kg)	4170	157.05	3002.50	1151.75	<u>+</u> 325.88

226

227 Genetic Parameters

228 The univariate heritability estimates for each trait, across both farms, ranged from 0.02 to 229 0.38 (Table 2). The highest estimates were generally associated with the udder and teat 230 related traits, where as those estimated for the legs and feet were lower. The individual traits 231 with the overall highest and lowest heritability estimates were UD (0.38) and FL (0.02)232 respectively. Manfredi et al. (2001) also observed generally higher estimates for the udder 233 and teat traits when compared with the legs and feet. However, although a similar scale and 234 scoring system was used, some of the traits considered by Manfredi et al. (2001), differed 235 from those in the present study. The leg and feet traits similar between both studies were 236 those relating to hock distance (similar to BL in the present study) and feet angle, although no 237 indication was given as to whether this was relating to the angle of all feet, or just the 238 front/back ones. Nonetheless, heritability estimates for the hock distance (0.16 and 0.12 for the Alpine and Saanen breeds respectively), were reasonably similar to the present study 239 240 (0.13). In dairy sheep, de la Fuente et al. (2011) estimated a heritability of 0.18 for rear legs, 241 scored in the same manner but with a slight difference in score definitions. The very low 242 heritability estimate observed for FL is likely due to the lack of variation in the scores given for this trait, perhaps influenced by previous selection criteria on the farms which may have only selected animals with straight front legs to remain in the herd. The heritability of milk yield in this population was 0.56, as estimated by Mucha et al. (2015). The authors suggest that this relatively high estimate could be influenced by the reduction in "noise" due to the automated recording equipment used and the fact that the data originates from just two farms.

248 Considering the udder and teat traits in more detail, the estimates observed in the present 249 study for UD, UF, TS, were in close agreement to those observed by both Manfredi et al. 250 (2001) and Rupp et al. (2011), despite some differences between the individual breeds. 251 However, estimates observed for UA (0.15) and TP (0.23) were lower than the values 252 estimated by Manfredi et al. (2001) and Rupp et al. (2011), who both referred to these traits as the rear udder and teat placement respectively. The estimates given by these two authors 253 254 ranged from 0.23-0.29 for UA and 0.25-0.38 for TP. Additionally, the heritability of 0.36 255 observed for TA was higher than previous estimates, which ranged from 0.15-0.22 (Manfredi 256 et al., 2001; Rupp et al., 2011). When compared to the estimates given by Luo et al. (1997) 257 for TP and UD, all of the estimates observed in the current study were low, although some 258 similarities were seen between the UF and TS estimates (referred to as suspensory ligament 259 and teat diameter respectively).

Many of these differences may be related to the number of data records available (n=4,220) and the breed composition of animals used in this study. The three studies discussed above all had data available from just less than 19,000 up to just over 43,000 animals recorded over a number of different years. It is likely that as more data becomes available future estimates may become more accurate, particularly in terms of the standard errors associated with the estimates observed. The lower estimates observed for the feet and leg traits in general could be influenced by farm selection policies already in place as individuals with undesirable 267 conformation for these traits can become visible from an early age and therefore can be 268 removed before becoming established in the herd. The synthetic nature of the population 269 structure in the current study, based on a history of crossbreeding, also differed from the 270 pure-bred populations previously referred to. This could also influence the heritability values 271 estimated due to the expected increase in the additive genetic variance in mixed populations 272 when compared to pure-bred populations. Luo et al. (1997) mention data available from crossbred goats, which they refer to as 'experimentals', but unfortunately data from these 273 274 animals was not used in their final analyses to keep consistency with additional data they 275 were using in the study.

276 Relationships between Conformation Traits

The genetic and phenotypic correlations estimated between all of the conformation traits are shown in Table 2. A range of positive and negative genetic correlations were observed, with the highest estimated between UD and UA (0.77) and the lowest between FL and TS and between BF and TP (both -0.01). The standard errors associated with the genetic correlations were relatively high, with the highest generally associated with the leg and feet traits. The phenotypic correlations were low to medium, ranging from 0.003 to 0.38 with standard errors between 0.01 and 0.02.

Among the udder traits, the genetic correlations ranged from 0.12 - 0.77, with the highest observed between UD and UA. The relationships between the teat traits were similar to those observed among the udder traits, ranging from -0.10 - 0.69, with negative values estimated between TS and both TA and TP. The moderately high positive correlation between TA and TP (0.69) indicated that selection for improved teat placement would also result in the improved angle of the teats. The relationships between the udder and teat traits followed a similar pattern to those observed by Manfredi et al. (2001), in both Alpine and Saanen breeds, in terms of direction of the relationships. All were positive, with the exceptions of those observed between UF and both TA and TP, indicating that as the strength of the medial ligament changed, there was a negative knock-on effect on the angle and placement of the teats.

Genetic correlations estimated between the leg and feet traits ranged from 0.05 to 0.64. The highest estimate, estimated between BL and BF (0.64), suggests that improvements made in back leg conformation would also have a positive effect on the conformation of the back feet. In general, relatively high standard errors were also observed between these traits and the other conformation traits which, in part, are most likely influenced by the low heritability estimates associated with these traits, particularly those relating to FL.

conformation traits, during first factation only. Standard errors in parentilesis.											
Trait	UF	UD	UA	TS	TA	TP	FL	BL	FF	BF	
Udder Furrow (UF)	0.28 (0.04)	0.24 (0.02)	0.09 (0.02)	0.32 (0.02)	-0.13 (0.02)	-0.20 (0.02)	0.02 (0.02)	0.01 (0.02)	-0.03 (0.02)	-0.01 (0.02)	
Udder Depth (UD)	0.23 (0.10)	0.38 (0.05)	0.38 (0.01)	0.23 (0.02)	0.23 (0.02)	0.17 (0.02)	-0.06 (0.02)	0.05 (0.02)	-0.06 (0.02)	-0.02 (0.02)	
Udder Attachment (UA)	0.12 (0.13)	0.77 (0.08)	0.15 (0.04)	0.07 (0.02)	0.15 (0.02)	0.19 (0.02)	-0.04 (0.02)	0.03 (0.02)	-0.04 (0.02)	-0.01 (0.02)	
Teat Shape (TS)	0.41 (0.10)	0.30 (0.10)	0.25 (0.13)	0.32 (0.05)	-0.10 (0.02)	-0.07 (0.02)	-0.01 (0.02)	0.01 (0.02)	-0.02 (0.02)	-0.01 (0.02)	
Teat Angle (TA)	-0.25 (0.11)	0.29 (0.10)	0.35 (0.13)	-0.14 (0.11)	0.36 (0.05)	0.38 (0.01)	-0.07 (0.02)	0.08 (0.02)	0.04 (0.02)	0.04 (0.02)	
Teat Placement (TP)	-0.25 (0.11)	0.25 (0.11)	0.57 (0.11)	-0.10 (0.12)	0.69 (0.08)	0.23 (0.04)	-0.05 (0.02)	0.04 (0.02)	0.02 (0.02)	0.003 (0.02)	
Front Legs (FL)	0.14 (0.25)	-0.33 (0.24)	-0.30 (0.28)	-0.01 (0.26)	-0.55 (0.24)	-0.26 (0.26)	0.02 (0.02)	0.02 (0.02)	0.16 (0.02)	0.01 (0.02)	
Back Legs (BL)	-0.10 (0.15)	0.02 (0.14)	0.24 (0.17)	0.12 (0.15)	0.11 (0.15)	0.13 (0.15)	0.19 (0.30)	0.13 (0.04)	0.04 (0.02)	0.40 (0.01)	
Front Feet Set (FF)	-0.08 (0.15)	-0.07 (0.14)	-0.02 (0.18)	-0.09 (0.15)	0.26 (0.15)	0.02 (0.16)	-0.37 (0.31)	-0.18 (0.19)	0.13 (0.04)	0.22 (0.02)	

0.17 (0.12)

-0.01 (0.13)

0.05 (0.27)

0.64 (0.11)

0.25 (0.05)

0.08 (0.16)

Table 2. Univariate heritabilities (on diagonal in bold), genetic (below diagonal) and phenotypic (above diagonal) correlations between conformation traits, during first lactation only. Standard errors in parenthesis.

-0.08 (0.12)

Back Feet Set (BF)

-0.07 (0.12)

-0.16 (0.11)

-0.09 (0.15)

303 Relationships between Conformation Traits and Milk Yield throughout lactation

To our knowledge, this is the first time that correlations between conformation traits and milk yield have been estimated throughout lactation in this manner. As many dairy goats herds strive to make improvements in milk yields, it is important to consider the relationship and effects that this may have on other traits such as those associated with conformation. The genetic correlations observed between each conformation trait and milk yield during the first lactation are shown in Figure 3. Phenotypic correlations estimated were all close to zero, with the exception of UD, which ranged from -0.35 to -0.07.



311

Figure 3. Genetic correlations (r_g) between milk yield and conformation traits; Udder traits (3a) of Udder Furrow (UF), Udder Depth (UD), Udder Attachment (US); Teat traits (3b) of Teat Shape (TS), Teat Angle (TA), Teat Placement (TP); Feet and leg traits (3c) of Back Legs (BL), Front Feet (FF) and Back Feet (BF); during 500 days of lactation, based on a random regression model.

Genetic correlations associated with the udder traits (UF, UD and UA) are shown in Figure318 3a. The correlations estimated between milk yield and UF ranged from -0.42 and 0.18.

319 Positive values were found up to approximately 50 DIM after which the values became 320 negative and remained negative throughout the remainder of the lactation. The size of the 321 correlations increased up to around 300 DIM (-0.42) after which they began to steadily fall 322 back towards zero. Standard errors ranged from 0.05 to 0.07. The correlations observed 323 between milk yield and UD followed a similar pattern, however unlike UF, all values were 324 negative ranging from -0.24 and -0.83. The absolute correlation values increased sharply 325 during the first 100 DIM before continuing to increase, at a slower rate, between 100 DIM 326 and 350 DIM. From 350 DIM onwards the correlations fell back to around -0.27 at 500 DIM. 327 Standard errors were between 0.03 and 0.06 with the lowest occurring mid-lactation between 328 approximately 200 and 300 DIM. Correlation values observed for UA were also all negative 329 ranging from -0.07 to -0.32. There was a gradual increase in the strength of the correlation 330 during the first 70 DIM from a value of -0.21 to -0.32, after which values remained 331 approximately -0.32 until 350 DIM. Standard errors were between 0.06 and 0.09 with the 332 lowest found during mid-lactation. When compared with the genetic correlations estimated 333 with the cumulative milk yield at 305 days, the udder traits all behaved consistently in the 334 fact that all correlations observed were negative (-0.25 + 0.13, -0.71 + 0.08 and -0.28 + 0.17)335 for UF, UD and UA respectively). Manfredi et al. (2001), when estimating correlations 336 between udder traits and milk yield at 250-days also observed negative correlations ranging 337 from -0.51 to -0.19 whereas Barillet (2000) comments that, across a number of different 338 studies in both dairy goats and sheep, correlations between milk yield and UD, although to 339 varying degrees, were always antagonistic. Similar relationships between UD and milk yield 340 have also been observed in dairy cattle (Brotherstone, 1994). The correlations that we have 341 observed in the current study therefore seem to be in agreement with those estimated 342 previously. Another method of udder scoring, relating to UD, was investigated by Casu et al. (2006) using the degree of suspension of the udder, calculated using the ratio between the 343

344 udder attachment width and udder height. They suggested this trait as a possible alternative 345 due to the fact that in their study it had a similar heritability as UD, it was highly correlated 346 with UD (0.82) and it had a low and unfavourable genetic correlation with milk yield. In 347 addition, although not investigated in the present study, results reported by Marie-Entacelin et 348 al. (2005) and Rupp et al. (2011) suggest the possibility that selection for improved udder 349 conformation can reduce lactation somatic cell counts in both sheep and goats respectively. 350 Overall, the results found in the present study, particularly the highly negative correlations 351 observed between milk yield and UD, suggest that future breeding programmes would benefit 352 by taking into account udder traits so that selection for productivity is not accompanied by 353 the possible deterioration in udder conformation, especially in the absence of detailed 354 measures of mastitis.

355 The genetic correlations associated with the teat traits (TS, TA and TP) varied throughout the 356 first lactation (Figure 3b). Correlations between milk yield and TS had a similar pattern as the 357 udder traits in that the values became increasingly negative in the early stage of lactation and 358 began to decrease and approach zero towards the end. The values ranged from -0.36 to 0.23 359 and followed a similar pattern to those observed for UF. Standard errors ranged from 0.05 to 360 0.07. The correlations estimated between milk yield and both TA and TP followed a different 361 pattern, when compared with TS, with all estimates remaining negative throughout the 362 lactation. During the first 50 days in milk, the correlations associated with TA changed from -363 0.40 to -0.45. From this point onwards, the correlation values began to decrease again 364 steadily, levelling off at -0.35 for a period after 250 DIM before falling again after 350 DIM 365 to -0.05. The standard errors ranged from 0.04 to 0.07. The correlation values observed for 366 TP ranged from -0.15 and -0.25 and were therefore relatively more stable across lactation 367 when compared to the other teat traits. The overall standard errors ranged from 0.05 to 0.08. 368 The relationship with the cumulative milk yield at 305 days were in general agreement,

particularly for TS and TP with genetic correlations of -0.35 (0.13) and -0.05 (0.15) 369 370 respectively observed. However, the magnitude of the correlation associated with TA (0.03 371 ± 0.13), which is essentially zero given the standard error, is different to the estimate from the 372 random regression analyses in early lactation but not very different to the very low, negative, 373 estimates towards the end of lactation. The relationship between TP and milk yield, as 374 reported by Manfredi et al. (2001) was low, with absolute values below 0.2, similar to the 375 values observed in the present study between 100 and 300 DIM. Correlations of a similar 376 magnitude between these two traits were also observed by Fernandez et al. (1997) and 377 Legarra and Ugarte (2005) in different breeds of dairy sheep. Manfredi et al. (2001) reports 378 that there was an extremely small relationship between TS and milk yield with a correlation 379 of just 0.03 in the Saanen breed, which is very different to the values observed in the present 380 study which went to -0.36. Although moderate, the size of the correlations observed for both 381 TS and TA indicate that increased milk yield will affect the size and angle of the teats which, 382 depending on the milking equipment used, may prove problematic. Rupp et al. (2011), also 383 observed favourable correlations between some teat conformation characteristics and somatic 384 cell count, although this was much more evident in the Saanen breed than the Alpine, 385 suggesting that individual breed differences would need to be taken into consideration. The 386 inclusion therefore of teat conformation information, in addition to the udder traits mentioned 387 previously, would further benefit future breeding programmes, particularly in terms of 388 milking ability but possibly also, after further investigation, milk quality and udder health.

The correlations estimated for BL, FF and BF are shown in Figure 3c. The values estimated between milk yield and FL are not shown due to the unreliable nature of the results from the low heritability of FL and the lack of variation in the scores associated with this trait. The correlations associated with BL were associated with high standard errors (0.06-0.10) and not significantly different to zero (p<0.05). The correlations with the feet traits both became 394 increasingly positive, at different rates, during the early stages of lactation before beginning 395 to fall again towards 500 DIM. Both were also associated with standard errors ranging from 396 0.05 to 0.08. The FF correlations became more positive during early lactation, moving from -397 0.31 at the beginning to 0.11 at 250 DIM. The values then fell again to -0.16 at 500 DIM. 398 Although following a similar pattern to FF, the strength of the correlations observed for BF 399 were higher. Positive correlations were observed between approximately 20 DIM and 480 DIM. The highest correlation was 0.24 at 250. Like the previous correlations estimated 400 401 between the conformation traits and milk yield at 305 days, the standard errors were 402 relatively high. The relationship with FF (0.08 ± 0.18) and BF (-0.09 ± 0.15), were again both 403 essentially zero. This was similar to the majority of correlations observed throughout mid-404 lactation in the random regression analyses for FF but only for the correlations associated 405 with BF during early and late lactation. The correlation observed with 305 day milk yield for 406 BL was 0.33 (+0.17) which was quite different to the low correlations estimated in the 407 random regression analyses (close to zero). This can be interpreted as a reflection of the 408 product of the relative contribution of each daily milk yield to the 305 yield and the genetic 409 correlations of the trait with daily milk. However, as mentioned previously, the addition of 410 more data records for these traits may improve the reliability of results in the future. In terms 411 of other estimates available in the literature, which are comparable with the ones presented 412 here, there are very few, due to the investigation of differently defined traits relating to the 413 legs and feet or the fact that many focus on udder and teat related traits. De la Fuente et al. 414 (2011), estimated a small genetic correlation of -0.09 between the back legs and milk yield of 415 Churra ewes which was markedly different to when compared with our estimate of 0.33 with 416 milk yield at 305 days.

417 The results presented have improved our knowledge of this population in terms of both the 418 conformation traits themselves and their relationship with milk yield. It is unfortunate that no 419 information was available with regards to the milk composition such as fat, protein and 420 somatic cell counts as these are also economically important traits to consider. Future studies 421 would therefore benefit from recording this data as well. Additionally, further investigation 422 into the economic values of these traits and the effects of any changes in conformation on 423 aspects such as udder health and the longevity of the animals in the herd would be also 424 worthwhile. The impact of the different scores will depend on aspects such as the 425 environments in which goats such as these are being milked. For example the milking 426 machines used may influence which teat and udder scores are the most (and least) desirable. 427 Nonetheless, the heritability and correlation estimates observed for the majority of traits in 428 our study, indicate that genetic change can be achieved using conventional quantitative 429 selection methods. In addition however, the development over recent years in genomic 430 selection provides further opportunities for this population and indeed dairy goats worldwide. 431 Although becoming increasingly popular in species such as dairy and beef cattle, genomic selection in dairy goats is still relatively new. A recent study by Mucha et al. (2015), using 432 433 the same sample population as this study, found that genomic breeding values could be 434 estimated using a single-step approach. Using such methodology offers potential to identify 435 animals, at a very early age, with favourable conformation characteristics and milk yield, thus 436 improving the efficiency and production of the herd further.

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CONCLUSIONS

Conformation traits investigated in the present study had a low to moderate range of heritabilities, with those relating to the udders and teats providing the highest estimates. The traits relating to the feet and legs were less heritable and less reliable, although this could potentially be improved in the future with the collection of more data records from the population studied. The genetic correlations estimated between the conformation traits and

443 milk yield, across the first lactation, demonstrate the changes that occur during this time 444 period. The majority of the correlations estimated between milk yield and both the udder and 445 teat traits were negative, therefore future breeding programmes would benefit from including 446 these traits in order to ensure that selection for increased productivity is not accompanied by 447 the unwanted deterioration of functional fitness.

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