Short Communication: Genotype by Housing Interaction for Conformation and Workability Traits in Danish Holsteins

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ABSTRACT

A total of 30,190 first-parity Danish Holstein cows housed in free stalls or tie stalls were analyzed to quantify to what degree genotype by housing interaction existed for 21 conformation and 2 workability traits. Each trait measured in different housing systems was treated as 2 separate traits in a bivariate animal model. Genetic correlations between the 2 traits as well as differences in genetic and residual variance were used as measurements of whether or not genotype by housing interaction occurred. Genetic correlations were in general close to unity (>0.9), except for body width (0.87 ± 0.06). Genetic variance was greater (22% on average) for all traits except 2, whereas residual variance was greater for feet and leg traits and lower for body and udder traits when measured in tie-stall environments for nearly all traits. In total, this led to a greater heritability for traits measured in tie-stall barns. Conformation and workability traits measured in free stalls and tie stalls should not be considered as different traits when predicting breeding values, but heterogeneous variance could be accounted for.

Key words: heterogeneous variance, genetic interaction, free stall, tie stall

Over the last decades, a considerable structural development has occurred in Danish dairy cattle production, which has resulted in a change in the way cows are housed. A large number of free-stall barns have been built and today most cows are housed this way (an increase from 48 to 75%). The majority of cows entering these new barns are, however, sired by bulls that are selected based on daughter performance in tie stalls. Therefore, the EBV ranking of these bulls could change based on additional offspring in a different environment.

In this study, focus was on conformation and workability traits and their relation to 2 housing environ-

ments. It is of interest to investigate these traits because cows might develop differently in the 2 environments to function and work efficiently. This may be true for all traits but probably more pronounced for feet and leg traits because cows need to be active to function in a free stall.

Dairy cattle are kept in a range of different environments and many examples of genotype by environment interaction have been documented in the scientific literature. Genotype by environment interaction can come either from heterogeneous variances or from heterogeneous genetic correlations between traits across environments (Calus et al., 2002; Kolmodin et al., 2002; Carlén et al., 2005). The genotypes can be measured at different levels; for example, as certain breeds, groups of animals, individual animals, or genes. Likewise, the environment can be defined in many ways such as country, region, herd, cage, climatic descriptor, or housing system. In this study, the additive genetic value of the animal is the considered genotype, and the environment in question is the housing system.

A situation in which genotype by environment interaction occurs but is ignored could lead to biased breeding values and suboptimal selection decisions. One way to account for genotype by environment interaction in terms of heterogeneous variance is to preadjust phenotypically the data (Koots et al., 1994; Weigel and Lawlor, 1994). A way to account for genotype by environment interaction in terms of reranking is to conduct multivariate analyses of data in which the covariance between a trait measured in different environments is taken into account. In international genetic evaluations for bulls, genotype by environment interaction is accounted for by considering data from each country as different but correlated traits (Schaeffer, 1994). Bulls rank differently in each country because of across-country genetic correlations of around 0.6 to 0.9 depending on trait (Mark, 2004). Across-country genetic correlations less than unity are due, in part, to genotype by environment interactions (Mark et al., 2006, 2007).

In an analysis of Canadian Holstein data for 7 feet and leg traits measured in free stalls and tie stalls, genetic correlations significantly different from unity

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Table 1. Number of records before and after data editing

Data edit	Rear udder height and rear teat placement	Body condition score	All other traits
Received	25,878	16,060	51,362
Used for analyses	14,841	9,193	30,190
In free stalls	10,585	6,761	19,347
In tie stalls	4,256	2,432	10,843

were reported on 6 of the traits (Fatehi et al., 2003). The study also reported that heritabilities tended to be greater in tie stalls than in free stalls. Burke and Funk (1993) reported significantly different genetic regression coefficients in American Holsteins for herd life on different conformation traits depending on housing category (tie-stall or free-stall systems). This indicates that genotype by environment interaction exists for conformation traits measured in different housing systems. In a study of longevity in German Holsteins the effect of housing system was included in the model (Buenger et al., 2001). The results showed that risk of culling was lower in free stalls than in tie stalls. The effect of straw bedding, however, was more pronounced.

Genotype by environment interaction in the form of reranking was found for SCC and mastitis across different environments of SCC in Swedish Holstein cows (Carlén et al., 2005). Based on principal component scores for fertility, substantial differences in genetic correlation between 305-d milk production and fertility were found in Dutch Holstein cows (Windig et al., 2006). Genotype by environment interaction for fertility traits was found in 4 Nordic Red breeds using reaction norm models (Kolmodin et al., 2002).

To date no studies have been conducted in terms of genotype by environment interaction in relation to housing systems in Danish Holsteins. Given the latest extreme structural development in dairy cattle production, this study is important to ensure that the genetic parameters used in the population corresponds to the actual production circumstances. The main aim of this study was to investigate the extent of genotype by housing type interaction for conformation and workability traits in Danish Holsteins and to discuss consequences for genetic evaluation and selection.

Information about housing systems for Danish dairy cattle herds from 1997 to 2002 was made available by the Danish Cattle Federation. Several free-stall barns was built during the last 10 yr, and the proportion of cows classified in free-stall barns increased from 48% in 1997 to 75% in 2002 (Figure 1). These numbers reflect the proportion of cows in free-stall barns in the whole population. Conformation and workability records on first-parity Holstein cows obtained in the same period were extracted from the Danish Cattle database. Re-

cords of cows with missing sire information were omitted. Records in herds with <25 classified cows in the period were omitted as well as records made by classifiers with <100 registrations in the period. After this editing of the data, a total of 30,190 cows were available. Of these, 36% were registered in tie stalls (herds = 391) and 64% were registered in free stall barns (herds = 529). Not all cows had observations for all traits. Rear udder height and rear teat placement were only measured since 2000 and body condition since 2001 (Table 1). The pedigree was traced as far back as possible and the pedigree file contained 169,041 animals.

A total of 23 traits were available in this study. Seven of the traits were related to the body of the cow, 5 were feet and leg traits, 9 were udder traits, and 2 were workability traits (i.e., milking speed and temperament). All traits except stature were measured on a scale from 1 to 9 with increments of 1 and with different optima (Table 2). Stature was measured in centimeters and had an optimum between 147 and 150 cm. Conformation traits were objectively measured by professional classifiers, whereas the 2 workability traits were reported by the farmer. The different optima were decided by the national breed associations. Some of the traits are measured today but are not a part of the present breeding goal. Breeding values for the traits are predicted and published.

Figure 1. Trend in distribution of cows in tie and free stalls from 1997 to 2002.

Table 2. Trait optimum, mean, and SD from single-trait analysis¹

Trait ²	Optimum	Mean	SD
Stature	147 to 150	144.3	3.65
Body depth	6	5.89	0.83
Body width	5	4.67	0.98
Dairy character	6.5	5.39	0.85
Rump width	5	5.19	0.94
Rump angle	5	5.02	1.08
Rear leg side view	5	5.31	0.92
Rear legs rear view	8	5.83	1.13
Hock quality	9	5.65	1.18
Bone structure	8	6.69	0.84
Foot angle	6.5	4.92	0.83
Fore udder attachment	9	6.06	1.07
Rear udder width	9	5.82	1.01
Udder support	8	6.66	1.15
Udder depth	8	6.56	1.11
Teat length	5	4.61	1.35
Teat width	4.5	4.89	1.13
Front teat placement	8	6.64	1.22
Rear udder height	—	6.04	0.91
Rear teat placement	—	6.42	1.42
Body condition score	—	4.07	0.97
Milking speed	—	5.19	1.58
Milking temperament	—	5.38	1.51

¹A trait with a (—) indicates that the trait is recorded but is not currently part of the breeding goal, and therefore an optimum has not been suggested.

²All traits except stature were measured on a scale from 1 to 9, with increments of 1. Stature was measured in centimeters.

Variance components were estimated using both a single-trait model (assuming performance in each housing system to be the same trait) and a bivariate model (assuming performance in each housing system to be different traits). The single-trait model was

$$y_{ijkl} = h_i + y_{sj} + b_1(dim) + b_2(age) + cy_k + a_l + e_{ijkl}, [1]$$

where *h* was a fixed effect of the *i*th herd (920 herds); *y_s* was a fixed effect of the *j*th year and season of classification (4 seasons per year); *dim* was the days after calving and *b₁* a fixed regression coefficient (22 ≤ *dim* ≤ 658 d); *age* was the age of the cow when the record was taken and *b₂* a fixed regression coefficient (579 ≤ *age* ≤ 1,379 d); *cy* was a fixed effect of year within each classifier (5 classifiers in 6 yr = 30 *cy* effects; this effect was not included for the 2 workability traits because they were scored by the farmer); and *a* was a random additive genetic effect. The vector of additive genetic effects (**a**) was assumed to be $N(0, A\sigma_a^2)$, where **A** is the additive genetic relationship matrix; *e* was a random residual effect. The vector of residual effects (**e**) was assumed to be $N(0, I\sigma_e^2)$, and $covar(a, e) = 0$.

The bivariate model considered performance in tie stalls and free stalls as different but correlated traits and included the same explanatory variables as model

[1]. The (co)variance structure among vectors of random variables in the bivariate model was

$$var \begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a1}^2 & A\sigma_{a12} & 0 & 0 \\ A\sigma_{a12} & A\sigma_{a2}^2 & 0 & 0 \\ 0 & 0 & I\sigma_{e1}^2 & 0 \\ 0 & 0 & 0 & I\sigma_{e2}^2 \end{bmatrix}.$$

Genetic parameters were estimated using average information (AI)-REML (Jensen et al., 1997) as implemented in the DMU software (Madsen and Jensen, 2008) for both the univariate and bivariate animal models.

Little evidence for genotype by housing interaction was found in this study in terms of reranking caused by genetic correlations different from unity (Table 3). All genetic correlations were greater than 0.90, except for body width (0.87 ± 0.06). Genetic correlations for the 2 workability traits were 0.94 and 0.95 and were a little lower than for most of the conformation traits.

In general, heritabilities were lower (18% on average) in free-stall barns than in tie-stall barns, and estimates from univariate models were intermediate (Table 3). This was more pronounced for body and udder traits than for feet and legs traits. However, the

Table 3. Estimates of heritability (h^2), additive genetic variance (V_a) and residual variance (V_e) for performance in free stall (free), tie stall (tie), and combined performance (all), and genetic correlation (r_g) between performance in free and tie stalls for different traits with relative SE¹

Trait	h^2_{free}	h^2_{tie}	h^2_{all}	$V_{a \text{ free}}$	$V_{a \text{ tie}}$	$V_{a \text{ all}}$	$V_{e \text{ free}}$	$V_{e \text{ tie}}$	$V_{e \text{ all}}$	r_g	SE
Stature	0.55	0.58	0.56	6.43	6.85	6.57	5.16	4.97	5.14	0.99	0.01
Body depth	0.25	0.31	0.27	0.15	0.20	0.17	0.46	0.46	0.46	0.99	0.02
Body width	0.18	0.28	0.20	0.16	0.24	0.17	0.72	0.61	0.70	0.87	0.06
Dairy character	0.16	0.20	0.28	0.10	0.12	0.19	0.52	0.50	0.49	1.00	0.01
Rump width	0.26	0.28	0.27	0.20	0.23	0.22	0.58	0.58	0.58	NC ²	
Rump angle	0.36	0.42	0.38	0.40	0.51	0.43	0.71	0.69	0.71	0.99	0.02
Rear leg side view	0.19	0.26	0.21	0.13	0.25	0.17	0.58	0.70	0.63	0.98	0.03
Rear legs rear view	0.16	0.15	0.15	0.18	0.19	0.18	0.94	1.06	0.99	0.92	0.06
Hock quality	0.19	0.24	0.21	0.22	0.31	0.25	0.96	0.98	0.98	0.99	0.03
Bone structure	0.24	0.30	0.26	0.16	0.21	0.17	0.48	0.49	0.49	0.99	0.02
Foot angle	0.13	0.15	0.14	0.09	0.10	0.09	0.51	0.57	0.55	0.98	0.04
Fore udder attachment	0.24	0.30	0.26	0.29	0.34	0.29	0.83	0.80	0.83	0.97	0.03
Rear udder width	0.18	0.25	0.20	0.16	0.24	0.18	0.73	0.72	0.74	NC	
Udder support	0.22	0.26	0.22	0.28	0.32	0.28	0.97	0.90	0.96	NC	
Udder depth	0.37	0.46	0.40	0.44	0.54	0.46	0.72	0.64	0.71	0.97	0.02
Teat length	0.44	0.46	0.44	0.77	0.86	0.80	1.00	1.00	1.00	0.98	0.02
Teat width	0.28	0.34	0.30	0.32	0.40	0.35	0.78	0.67	0.81	0.98	0.02
Front teat placement	0.40	0.49	0.42	0.63	0.74	0.61	0.85	0.78	0.84	0.98	0.02
Rear udder height	0.17	0.13	0.18	0.13	0.09	0.13	0.62	0.63	0.61	NC	
Rear teat placement	0.33	0.43	0.34	0.62	0.81	0.64	1.26	1.10	1.25	0.91	0.05
Body condition score	0.25	0.18	0.24	0.17	0.10	0.16	0.50	0.47	0.49	NC	
Milking speed	0.29	0.35	0.30	0.71	0.82	0.72	1.66	1.55	1.66	0.94	0.03
Milking temperament	0.17	0.22	0.18	0.34	0.47	0.37	1.68	1.69	1.70	0.95	0.04

¹Standard errors for these genetic parameters were between 0.01 and 0.09 for all traits except for stature where the standard errors were between 0.24 and 0.41.

²NC = no convergence (the algorithm did not converge). Results from last round of iteration showed a correlation of 1.

heritability was greater in free-stall barns than in tie-stall barns for rear leg rear view, rear udder height, and body condition score. For rear leg rear view, one possible explanation could be that classifiers saw some cows walk in the free stalls during classification, and thereby had a better impression of the conformation of the rear legs. The lower heritability in free-stall barns comes both from lower additive genetic variance and greater residual variance in free-stall barns (Table 3). Standard errors for heritability and additive genetic variance were between 0.01 and 0.09 for all traits except for stature, for which the standard errors were between 0.24 and 0.41. Differences in additive genetic variance between free-stall and tie-stall barns may indicate genotype by environment interaction. Another explanation could be that the lower additive genetic variance was due to more cows having a wrong ID or incorrect pedigree information in free stalls compared with tie stalls. However, this has not been investigated further. The greater residual variance indicated that classifiers had more difficulty conducting accurate classification in free stalls than in tie stalls. Free-stall barns are typically larger and cows are not necessarily used to close contact with humans as occurs in a classification situation. There are no guidelines on whether cows should be fixed or not when classified in a free-stall environment, which could lead to inconsistencies

in the classification and thereby greater residual variance.

When editing the data, restrictions on number of observations per classifier (at least 100) and number of classifications per herd in the period (at least 25) were made. The restriction on number of observations per classifier removed very little of the data, so the main reason for data deletion was number of classifications per herd. Tie stalls also tend to be smaller than free stalls, so this restriction meant that the distribution of animals in each housing system was different than in the received data. The main reason for having this restriction was to obtain better estimates of the herd effect by avoiding small groups and thereby obtain lower standard errors on variance components. Using less stringent restrictions on number of classifications per herd to see if genetic parameters were biased was not performed in this study. Also, no restrictions were made on herds that changed from tie stalls to free stalls in the studied period. These herds still contributed with information to the data set according to their housing system code in the specific year.

Burke and Funk (1993) showed that cows with intermediate curvature of rear legs had longer herd life than cows with extreme curvature in both free-stall and tie-stall environments, although the absolute difference between optimum and extreme was greater in

tie stalls than in free stalls. Burke and Funk (1993) also reported greater genetic regressions of herd life on nonlocomotion traits in tie-stall barns than in free-stall barns. The reason for this might be personnel (farmer) preference for different type traits in different environments.

The results in this study will have limited implications for routine evaluations of conformation and workability traits in Danish Holsteins. The traits measured in the 2 different housing systems can be considered the same trait in genetic evaluations because the genetic correlations between traits measured in different housing systems were very high and most were close to unity. Moreover, if the current trend continues, most cows in the future will be in free-stall barns; therefore, splitting the breeding values in 2 will be of decreased interest. However, heterogeneous genetic and residual variances in free and tie stalls were found for conformation and workability traits in Danish Holsteins. Heritabilities were on average 18% greater for traits measured in tie stalls than in free stalls. Therefore, heterogeneous variances could be accounted for in genetic evaluation of these traits. This was also the recommendation from a similar study made in Canadian Holsteins with focus on feet and leg traits (Fatehi et al., 2003). For 6 of 7 feet and legs traits, however, they found genetic correlations between registrations in free-stall and tie-stall environments that were significantly different from 1. A bivariate model to predict breeding values would improve the breeding value estimation if evidence of genetic correlations different from unity between traits measured in 2 environments were found. In this study, difference in terms of heterogeneous variance was found but it was insufficient to justify the implementation of a bivariate model for prediction of breeding values. Moreover, 2 breeding values for the same trait might lead to more confusion for the farmer when choosing bulls for mating.

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