NON-LINEAR GENETIC RELATIONSHIPS BETWEEN MILK YIELD AND TYPE TRAITS IN HOLSTEIN CATTLE

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SUMMARY
Non-linear genetic relationships between 305-day milk yield and 18 type traits in first lactating US Holstein cattle were estimated on the basis of a polynomial offspring-parent regression model of order 2. In total, 24,470 dam-daughter records were used. Significant offspring-parent regression coefficients for the quadratic term were found between milk yield and the type traits front teat placement, fore udder attachment, udder depth and final score. For these relationships the genetic regression coefficients were calculated from the phenotypic regression coefficients according to formulae derived elsewhere. The transformation from the phenotypic offspring-parent regression to the genetic level resulted in rather strong non-linear relationships between milk yield and the respective type traits.
Keywords: milk yield, type, Holstein cattle, non-linear relationship

INTRODUCTION
The estimation of genetic parameters including heritabilities and genetic correlations is usually based on the assumption of linear relationships between the traits involved. However, a model with non-linear relationships should better match the true state of biology, especially for the relationships between quantitative and fitness-related traits since intermediate expressions of quantitative traits may often be optimal with respect to fitness (Falconer 1989). A genetic model producing non-linearity in the relationship between two traits competing for resources was presented by Sölkner and James (1994). The model was based on pleiotropy of loci responsible for acquisition and allocation of resources. Fitting a polynomial regression appeared to produce good results under this type of nonlinear genetic relationship. Following this concept, formulae for evaluating non-linear genetic relationships were derived on the basis of a polynomial offspring-parent regression model of order 2 (Fürst-Waltl *et al.* 1996) and were applied on the relationship between milk yield and protein percentage (Fürst-Waltl *et al.* 1996) and milk yield and type traits (Sölkner and Fürst-Waltl 1996) in Austrian Simmental (dual purpose) cattle. In both cases, significant non-linearity was found in the offspring-parent regression. The objective of this study was to investigate the genetic relationship between 305-day milk yield and various linear type traits in first lactating US Holstein cattle.

MATERIALS AND METHODS
First lactation milk records of US Holstein cows and type trait classifications of their first lactating daughters were used. In addition to the usual data edits, pairs of dams and daughters

were required to be in different herds. In total, 24,470 dam-daughter records were used to evaluate the relationship between 305-day milk yield and 16 linear type traits, final score, and feet and leg score. Because of missing values only 23,854, 24,362 and 9837 records were available for analyzing the relationship between milk yield and teat length, rear legs rear view, and feet and leg score, respectively.

To adjust for systematic environmental effects, residuals for 305-day milk yield were predicted for dams by treating calving year (1982-94), calving month and herd (731, 721 for teat length, 729 for rear legs rear view, 477 for feet and leg score) as fixed effects, and age at first calving and days open (linear and quadratic) as covariates. Residuals for type traits were predicted for daughters by treating year of classification (1985-96, 1988-96 for teat length, 1987-96 for rear legs rear view, 1993-96 for feet and leg score), month of classification, classifier (55, 43 for feet and leg score) and herd (826, 812 for teat length, 825 for rear legs rear view, 475 for feet and leg score) as fixed effects, and age at first calving and stage of lactation (linear and quadratic) as covariates. Using the standardised residuals (mean = 0, standard deviation = 1) a quadratic regression analysis was conducted to compute estimates of the phenotypic regression coefficients (b_1 and b_2) and their standard deviations (s_{b_1} and s_{b_2}), with milk yield as the independent (=X), and the respective type trait as the dependent (=Y) variable. If phenotypic regression coefficients were significant, estimates of genetic regression coefficients (a_1 and a_2) and their standard deviations (s_{a_1} and s_{a_2}) were computed following Fürst-Waltl *et al.* (1996) as:

$$\hat{a}_1 = \frac{\hat{b}_1}{0.5 \cdot h^2(x)} \quad \text{and} \quad s_{\hat{a}_1} = \frac{s_{\hat{b}_1}}{0.5 \cdot h^2(x)}; \qquad \hat{a}_2 = \frac{\hat{b}_2}{0.25 \cdot h^4(x)} \quad \text{and} \quad s_{\hat{a}_2} = \frac{s_{\hat{b}_2}}{0.25 \cdot h^4(x)}$$

RESULTS AND DISCUSSION

The estimated heritability for milk yield ($h^2 = 0.34$) lies within the range reported by other authors (e.g., Short and Lawlor 1992; Albuquerque *et al.* 1995). Heritabilities for type traits ranged from 0.09 (foot angle, rear legs rear view) to 0.39 (stature) and were also similar to literature estimates (e.g., Short and Lawlor 1992) (Table 1). Significant phenotypic regression coefficients for the quadratic term were found between milk yield and final score, front teat placement, fore udder attachment and udder depth. For these traits, genetic regression coefficients were calculated as described above. Phenotypic and genetic regression coefficients are shown in Table 1. As expected from the formula, the transformation from the phenotypic to the genetic level produced a rather extreme curvilinearity, as depicted in Figure 1. When describing the relationship between milk yield and linear type traits, phenotypic and genetic correlations are usually used (e.g., Short and Lawlor 1992; Brotherstone 1994). However, Norman *et al.* (1988) showed that the phenotypic relationship between linear type traits and milk yield is often non-linear and consistent across different dairy breeds and traits. By means of offspring-parent regression, Sölkner and Fürst-Waltl (1996) found significant phenotypic quadratic regression coefficients between milk yield and the linear type traits fore udder, teat placement, udder attachment and aggregate score for udder in Austrian Simmental (dual purpose) cattle.

Table 1. Heritabilities for type traits and phenotypic ($\hat{b}_1, \hat{b}_2$) and genetic ($\hat{a}_1, \hat{a}_2$) regression coefficients of type traits on 305-day milk yield

Type traits[1]		Milk yield (h^2 = 0.34)					
Trait	h^2	$\hat{b}_1$	P[2,3]	$\hat{b}_2$	P	$\hat{a}_1$	$\hat{a}_2$
Body depth	0.29	0.050	***	-0.003659	>0.1		
Dairy form	0.29	0.115	***	0.003063	>0.1		
Foot angle	0.09	0.003	>0.1	0.003066	>0.1		
Feet and leg score		0.058	***	0.008615	>0.1		
Final score	0.36	0.069	***	-0.010661	**	0.404	-0.368912
Front teat placement	0.24	0.008	>0.1	-0.009115	*	0.047	-0.315405
Fore udder attachm.	0.26	0.002	>0.1	-0.010989	**	0.009	-0.380238
Rump angle	0.26	0.029	+	0.003589	>0.1		
Rear legs rear view	0.09	0.041	***	0.003066	>0.1		
Rear leg set	0.10	0.004	>0.1	-0.000706	>0.1		
Rump width	0.23	0.046	***	-0.000863	>0.1		
Rear udder height	0.25	0.041	***	-0.005186	>0.1		
Rear udder width	0.23	0.076	***	-0.002987	>0.1		
Stature	0.39	0.056	***	-0.006759	+		
Strength	0.24	0.048	***	-0.005666	>0.1		
Teat length	0.23	0.027	***	0.001384	>0.1		
Udder cleft	0.15	0.006	>0.1	-0.006749	+		
Udder depth	0.25	-0.054	***	-0.012567	**	-0.316	-0.434840

[1]only 590 dam-daughter pairs for feet and leg score; [2] *** = P≤0.001, ** = P≤0.01, * = P≤0.05, + = P≤0.10; [3]$s_{b_1} \approx 0.006$, $s_{b_2} \approx 0.004$, $s_{a_1} \approx 0.035$, $s_{a_2} \approx 0.138$

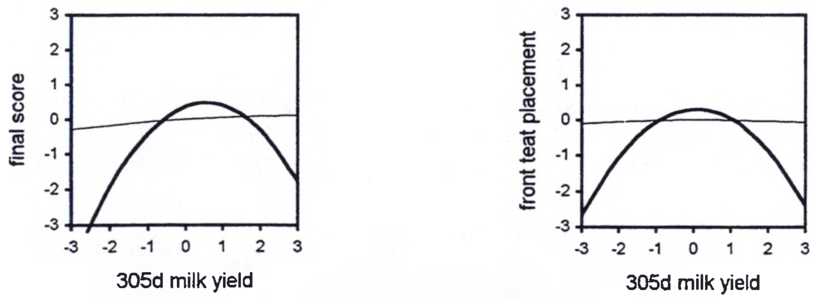

Figure 1. Phenotypic (fine line) and genetic (bold line) regression curves of final score and front teat placement and on milk yield (traits standardised).

Since intermediate expressions of quantitative traits are likely to be optimal with respect to fitness, the results for the three linear type traits are not unexpected. The non-linearity between final score and milk yield is somewhat surprising, though. It seems that cows with highest yields do not represent the „ideal standard“ on the genetic level with regard to type.

CONCLUSIONS

Non-linear relationships between traits will certainly have consequences for multivariate selection strategies applied in breeding programs. The conclusions drawn from non-linear relationships will differ markedly from what may be predicted from a linear relationship. Due to their genetic nature, non-linear relationships to other traits may especially be expected for fitness-related traits. One of the problems associated with the offspring-parent regression is that a strong genetic non-linearity leads to a rather small deviation from linearity at the phenotypic level. Such findings can be misinterpreted when the observed phenotypic non-linearity is caused by other than genetic factors. Additional research is clearly needed in the area of developing alternative estimation methods to the parent-offspring regression. Besides, possibilities for including such non-linear genetic parameters in selection decisions in a formalised way need to be found. However, knowledge of curvi-linear rather than of linear relationships between traits should improve our understanding of the true nature of the physiological basis of genetic relationships.

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