

Genetic relationship of functional longevity with female fertility and milk production traits in Czech Holsteins

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ABSTRACT: The objectives of this study were to estimate heritabilities of and genetic correlations among longevity, milk production, and female fertility traits of Holstein cows. Fertility traits were days open, interval from parturition to first service, and days between the first and last insemination in the first and second lactation, respectively. Production traits were first lactation milk, fat, and protein yield. Functional longevity was defined as the number of days between the first calving and culling, i.e. the length of the productive life. The linear animal model included fixed effects of month-year of first calving, regression on age at first calving, regression on milk yield (only for longevity), and random effects of herd-year, animal, and residual. Heritability estimates for fertility traits ranged from 0.02 ± 0.009 to 0.06 ± 0.004 . Heritability of longevity was 0.09. Heritability estimates for production traits ranged from 0.29 ± 0.009 (fat and protein yield) to 0.34 ± 0.009 (milk yield). Genetic correlations of longevity with fertility were moderate and favourable, ranging from -0.37 ± 0.068 to -0.44 ± 0.055 , except the days between the first and last insemination in the second lactation. Genetic correlations of fertility with production traits were moderate to high and unfavourable, ranging from 0.48 ± 0.042 to 0.65 ± 0.034 . Substantial herd-year correlations were found between fertility traits. Residual correlations were small except for those between production traits (> 0.85) and between days open and days between the first and last insemination (0.87). Month-year of first calving effects for longevity declined between 1994 and 2002, while those for production traits and for fertility increased slightly or remained stable during this period. Between 1991 and 2003, genetic trend for longevity declined and increased for production. Estimated genetic changes for fertility were unfavourable.

Keywords: Holstein cattle; genetic parameters; milk yield; functional traits

In most countries, milk production has been the primary selection objective in dairy cattle breeding. During the 1980's and into the 1990's, selection was focused almost entirely on protein production, with substantial genetic improvement taking place for this trait. An undesirable result has been the reduced ability of Holstein cows to produce and survive in their prevailing environments. As a consequence, functional traits such as reproduction and health are receiving increased

focus, not only for economical reasons but also for welfare concerns (Miglior et al., 2005).

Several investigations have reported antagonistic genetic correlations between fertility and milk production (e.g. Dematawewa and Berger, 1998; Kadarmideen et al., 2000; Royal et al., 2002). Selection for increased milk yield is expected to result in genetic decline of female fertility (Pryce et al., 2004), implying that selection is necessary to genetically stabilize or improve female fertility.

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High producing cows tend to be less fertile, and this prolongs the length of calving interval and it increases the rate of involuntary culling. In addition, less fertile cows have decreased longevity (Sewalem et al., 2008), and their lifetime production can be less than that of cows with adequate fertility (González-Recio et al., 2004). Hence, a balance between production and functional traits must be pursued, and proper economic weights must be applied to every trait.

Female fertility is a complex trait that can be characterized by at least 2 components: time interval between events and success vs. failure of a particular event. One of the most widely used interval traits is the number of days from calving to first insemination, which describes the ability of a cow to express postpartum estrus. The advantage of the interval from calving to first insemination is that it is available earlier than alternative measures and is less biased because of selection of data compared with other fertility traits. The disadvantages of interval traits are that they may be influenced by farmer decision. For example, the interval from calving to first insemination for high-yielding cows may be lengthened compared to their less productive herd-mates for economic reasons (Andersen-Ranberg et al., 2005).

Longevity expressed as length of productive life is measured as the number of days from first calving until removal of a cow from the herd by death or culling (Ducrocq et al., 1988). It quantifies the propensity of a cow to avoid both voluntary and involuntary culling by farmers. Functional

longevity is an appropriate measure for involuntary culling. Low milk yield has been described as the major reason for voluntary disposal of a cow. Hence, a statistical adjustment of longevity for milk production should reveal differences among animals for reasons of disposal other than production, e.g. differences in voluntary culling due to type, old age, or general health and, above all, due to infertility, illness, or chronic mastitis (Ducrocq et al., 1988).

The objective of this study was to assess relationships among functional longevity, first lactation production traits, and female fertility traits during first and second lactation of Holstein cows, and to describe the environmental effects and genetic trends for these traits. Such results are prerequisite to define selection indices with the inclusion of LPL and fertility.

MATERIAL AND METHODS

Data

The dataset included Holstein cows with calving dates for first, second, and third calving where available, and date of culling. Fertility traits were days open (DO1 and DO2), interval from parturition to first service (CFI1 and CFI2), and days between the first and last insemination (FLI1 and FLI2) in the first and second lactation, respectively. Production traits were first 305-day lactation milk (MY1), fat (FY1), and protein (PY1) yield.

Table 1. Descriptive statistics (mean, SD, minimum, and maximum) for longevity (LPL), milk (MY1), fat (FY1), protein yield (PY1), days from calving to first insemination (CFI1), days open (DO1), and days between first and last insemination (FLI1) in first lactation and days from calving to first insemination (CFI2), days open (DO2), and days between first and last insemination (FLI2) in second lactation of Holstein cows expressed as the range for four analyzed data subsets

Trait	Mean	SD	Min	Max
LPL (days)	1 248–1 283	602–621	308–314	4 835–5 234
MY1 (kg)	5 870–6 702	1 546–1 712	2 001–2 028	13 136–16 560
FY1 (kg)	236.4–259.8	60–63.7	49–70	530–661
PY1 (kg)	194.1–221.6	51.4–56.0	50–57	442–530
DO1 (days)	127.4–130.4	67.6–69.6	31–31	400–400
DO2 (days)	127.4–131.4	67.2–69.0	31–31	400–400
CFI1 (days)	80.29–83.43	31.72–35.28	21–21	230–230
CFI2 (days)	77.70–80.19	29.75–33.08	21–21	230–230
FLI1 (days)	43.95–50.13	60.59–63.64	0–0	349–365
FLI2 (days)	47.20–53.66	61.19–64.03	0–0	350–356

All data were extracted from the Czech national milk-recording database. First calving of all cows was between 1994 and 2004. Only lactations with milk yield equal to or exceeding 2000 kg and with minimal length of 240 days were considered. Cows were required to have valid sire identification and age at first calving between 16 and 46 months. Days open had to be 30–400 days, interval between calving and first insemination 20–230 days, and interval between first and last insemination either zero or 20–120 days.

A minimum of three contemporaries per herd-year-season class was required. Cows from sires with fewer than 40 daughters in the data set before editing were excluded. Herds with fewer than 60 records per dataset were also excluded from the analysis.

Longevity (LPL) was expressed as the number of days between first calving and culling, i.e. as length of productive life. All cows included in the present study died or were culled so the actual length of life was known.

The final dataset included 364 705 cows from 1690 sires. Pedigree included 563 155 animals. This dataset was used for estimation of breeding values. Because of computational limitations for genetic parameters estimation, four data subsets were randomly formed based upon herd identification. The subsets contained 103 499, 75 541, 92 211, and 91 261 first lactation observations and 59 937, 53 024, 53 466, and 41 291 observations in the second lactation. Corresponding pedigree files included 267 363, 238 820, 230 343, and 267 363 animals, respectively. Descriptive statistics for analyzed traits and four data subsets are presented in Table 1.

Model

(Co)variance components were calculated using a bivariate linear animal model or a trivariate linear animal model. The bivariate animal model was used to estimate the genetic parameters between production and fertility traits in first lactation and LPL. The trivariate model was used for joint analysis of fertility traits in first and second lactation and LPL.

The model equation was:

$$Y_{ijklmn} = MY_i + \beta_1 \text{age}_j + \beta_2 \text{age}_k + \gamma_1 \text{milk}_l + hy_m + \text{animal}_n + e_{ijklmn}$$

where:

- Y_{ijklmn} = observation of the trait
- MY_i = fixed effect of month-year of calving i (January, February, March, April, May, June, July, August, September, October, November, December; 1994–2004)
- $\beta_1 \text{age}_j$ = linear regression on age j at first calving
- $\beta_2 \text{age}_k$ = quadratic regression on age k at first calving
- $\gamma_1 \text{milk}_l$ = linear regression on milk production l in the first lactation (only for LPL)
- hy_m = random effect of herd-year of calving m (herd; 1994–2004)
- animal_n = random effect of animal n connected with pedigree
- e_{ijklmn} = random residual effect

Longevity was adjusted for milk production by including the effect of first lactation milk yield in the model employed for genetic parameters estimation. After this correction, the longevity trait included in the analysis was considered to be “functional” as opposed to overall observed longevity.

The breeding values for assessment of genetic trends in cows were estimated using an univariate animal model. The model equation was:

$$Y_{ijklm} = HYS_i + \beta_1 \text{age}_j + \beta_2 \text{age}_k + \gamma_1 \text{milk}_l + \text{animal}_n + e_{ijklm}$$

where:

- Y_{ijklm} = observation of the trait
- HYS_i = fixed effect of herd-year-season of calving i (herd; 1994–2004; January to March, April to June, July to September, October to December)
- $\beta_1 \text{age}_j$ = linear regression on age j at first calving
- $\beta_2 \text{age}_k$ = quadratic regression on age k at first calving
- $\gamma_1 \text{milk}_l$ = linear regressions on milk production l in the first lactation (only for LPL)
- animal_m = random effect of animal m connected with pedigree
- e_{ijklm} = random residual effect

Data were analyzed using the DMU software package (Madsen and Jensen, 2010). The average of the variances, the heritability or the correlation estimates (μ^*) was calculated by means of the following formula because the data subsets differed in size:

$$\mu^* = \frac{1}{SW} \sum_{i=1}^4 \frac{\mu_i}{SE_i^2}$$

where μ_i was the parameter estimate from subset i or the average of the estimates if the parameter was

computed more than once within each subset. The latter concerned the heritability estimated. The sum of weights (SW) was calculated using the following formula:

$$SW = \sum_{i=1}^4 \frac{1}{SE_i^2}$$

where SE_i is the standard error of the estimate from subset i or the average standard error if the parameter was computed more than once within each subset.

Descriptive statistics

Table 1 shows the basic descriptive statistics of four datasets that were used for estimation of genetic parameters. There were no substantial differences between data subsets. The subsets contained 103 499, 75 541, 92 211, and 91 261 first lactation observations and 59 937, 53 024, 53 466, and 41 291 observations in the second lactation. Corresponding pedigree files included 267 363, 238 820, 230 343, and 267 363 animals, respectively. The number of HYS was 9591, 7808, 8643, 7736, the number of herds was 365, 332, 348, 308, the number of sires was 1341, 1136, 1372, 1163 in datasets 1 to 4, respectively. 593 sires were common to all four datasets.

RESULTS AND DISCUSSION

Heritability

Average variance component estimates and corresponding heritabilities for the 7 first lactation traits are shown in Table 2. Also the resulting estimates of

variances and (co)variances for particular analyzed subsets were similar. The values are not presented here and they are available from the authors. Additive variance was slightly larger than the herd-year variance for LPL. Management practices tended to have a greater influence on production than on fertility and longevity traits, leading to a larger difference between total heritability and within-herd heritability, especially for production traits (see Table 2), as was similarly found by Tiezzi et al. (2011).

Estimated heritability for LPL within herds was small (0.09) but higher than the value of 0.03 reported by Zavadilová and Štípková (2012) for Czech Holsteins or 0.04 by Páchová et al. (2005). The within-herd heritability reported in our study was similar to results of Vollema and Groen (1998), who reported an estimate of 0.07 in Danish Holsteins using linear model analysis of functional longevity.

Within-herd heritability estimates for MY1, FY1, and PY1 were 0.34, 0.29, and 0.29, respectively (Table 2). These are higher than previous estimates from Czech data by Dědková and Wolf (2001), who found heritabilities of 0.28, 0.24, and 0.25, and higher than those of Zink et al. (2012), who reported 0.21, 0.21, and 0.23 for MY1, FY1, and PY1, respectively.

Within-herd heritabilities of fertility traits were low, 0.05 for CFI1, 0.06 for DO1, and 0.03 for FLI1. These estimates are slightly higher than those of Zink et al. (2012), who reported 0.04, 0.04, and 0.03 for CFI1, DO1, and FLI1, respectively, for Czech Holsteins. Current results are, however, concurrent with other recent research. In Canadian Holsteins, Jamrozik et al. (2005) reported 0.10 and 0.07, and Sun et al. (2009) reported values of 0.08 and 0.03 for CFI1 and FLI1, respectively, in Danish Holsteins. Corresponding estimates for

Table 2. Variance components and total heritability (h_T^2) and within herd heritability (h_W^2) estimates \pm SE of longevity (LPL), milk (MY1), fat (FY1), protein yield (PY1), days from calving to first insemination (CFI1), days open (DO1), and days between first and last insemination (FLI1) in first parity Holstein cows (weighted average of four datasets)

	LPL (days)	MY1 (kg)	FY1 (kg)	PY1 (kg)	CFI1 (days)	DO1 (days)	FLI1 (days)
Additive variance (α_a^2)	28 056 \pm 2 256	435 888 \pm 13 508	545.0 \pm 20.2	356.0 \pm 12.5	49.6 \pm 5.0	223.6 \pm 19.7	103.4 \pm 12.7
Herd-year variance (α_{hy}^2)	21 404 \pm 1 225	706 893 \pm 21 164	1 168.5 \pm 35.5	901.5 \pm 29.9	138.9 \pm 4.7	265.7 \pm 10.9	175.2 \pm 8.4
Residual variance (α_e^2)	324 578 \pm 2 224	829 282 \pm 9 735	1 353.7 \pm 15.2	857.7 \pm 9.5	964.1 \pm 6.1	4 133.6 \pm 24.3	3 530.8 \pm 18.8
Total variance (α_t^2)	374 039	1 972 063	3 067.1	2 115.1	1 152.6	4 622.9	3 809.4
$h_T^2 = \alpha_a^2 / \alpha_t^2$	0.07 \pm 0.008	0.22 \pm 0.009	0.18 \pm 0.010	0.17 \pm 0.012	0.04 \pm 0.006	0.05 \pm 0.006	0.03 \pm 0.004
$h_W^2 = \alpha_a^2 / (\alpha_a^2 + \alpha_e^2)$	0.09 \pm 0.006	0.34 \pm 0.009	0.29 \pm 0.010	0.29 \pm 0.009	0.05 \pm 0.005	0.06 \pm 0.004	0.03 \pm 0.003

Table 3. Variance components and total heritability (h_T^2) and within herd heritability (h_W^2) estimates \pm SE of days from calving to first insemination (CFI2), days open (DO2), and days between first and last insemination (FLI2) in second parity Holstein cows (weighted average of four datasets)

	CFI2 (days)	DO2 (days)	FLI2 (days)
Additive variance (α_a^2)	22.0 \pm 3.01	6.3 \pm 0.76	19.4 \pm 2.98
Herd-year variance (α_{hy}^2)	97.0 \pm 4.05	3.3 \pm 0.27	95.4 \pm 4.12
Residual variance (α_e^2)	717.9 \pm 5.68	151.0 \pm 1.01	819.2 \pm 5.68
Total variance (α_T^2)	836.9	160.7	934.0
$h_T^2 = \alpha_a^2/\alpha_T^2$	0.03 \pm 0.006	0.04 \pm 0.004	0.02 \pm 0.009
$h_W^2 = \alpha_a^2/(\alpha_a^2 + \alpha_e^2)$	0.03 \pm 0.005	0.04 \pm 0.005	0.02 \pm 0.009

within-herd heritability of FLI1 by Roxström et al. (2001) and Andersen-Ranberg et al. (2005) were 0.03 each. Other published heritability estimates for FLI1 ranged from 0.03 to 0.04 (Dechow et al., 2001; Wall et al., 2003).

Our estimates of within-herd heritability for fertility traits in the second lactation (Table 3) were lower (CFI2 0.03, DO2 0.04, FLI2 0.02) than those in the first lactation. Probably due to the culling in the first lactation, genetic and herd-year variances were considerably reduced for second parity cows leading to lower estimates of heritability. This reduces the scope for selection for female fertility in the second parity cows. In contrast, Raheja et al. (1989) and Tiezzi et al. (2012) detected a smaller reduction in heritabilities of fertility traits for second parity cows than reported in the present paper.

Genetic correlations between longevity and the first lactation traits

Estimated genetic correlations between longevity, fertility, and production traits are shown in Table 4.

Those between longevity and fertility were favourable, ranging from -0.37 to -0.44 . These estimates were lower than those between survival to next lactation and days open (-0.78) as reported by González-Recio and Alenda (2007), suggesting that reduced genetic potential for functional longevity was associated with reduced genetic value for fertility. However, the correlation between functional longevity and CFI1 (0.25) was unfavourable in the study of Roxström and Stranberg (2002).

Modest unfavourable genetic correlations were found between longevity and FY1 (0.18) and PY1 (0.15). This indicates that genetically reduced functional longevity is associated with increased genetic potential for fat and protein production. Dematawewa and Berger (1998) reported genetic correlations of longevity with MY1, FY1, and PY1 in the first lactation of 0.16, 0.20, -0.13 , respectively. In contrast, Roxström and Stranberg (2002) reported a positive correlation between functional longevity and PY1 of 0.07, smaller than found in our study.

Estimated genetic correlations between fertility traits and milk production traits were moderate to high (0.48 to 0.65) and unfavourable, suggesting

Table 4. Estimates \pm SE of genetic correlations between longevity (LPL), milk (MY1), fat (FY1), protein yield (PY1), days from calving to first insemination (CFI1), days open (DO1), and days between first and last insemination (FLI1) for first parity Holstein cows (weighted average of four datasets)

	LPL (days)	CFI1 (days)	DO1 (days)	FLI1 (days)	MY1 (kg)	FY1 (kg)
CFI1 (days)	-0.39 ± 0.057					
DO1 (days)	-0.44 ± 0.055	0.83 ± 0.033				
FLI1 (days)	-0.37 ± 0.068	0.53 ± 0.071	0.92 ± 0.015			
MY1 (kg)	0.00 ± 0.040	0.52 ± 0.040	0.65 ± 0.034	0.60 ± 0.045		
FY1 (kg)	-0.18 ± 0.041	0.48 ± 0.042	0.59 ± 0.037	0.54 ± 0.049	0.69 ± 0.012	
PY1 (kg)	-0.15 ± 0.041	0.49 ± 0.042	0.63 ± 0.035	0.60 ± 0.046	0.91 ± 0.004	0.77 ± 0.010

all correlations are significant at $P < 0.01$ except the correlation between MY and LPL

that cows genetically predisposed to yield high amount of milk are also more likely to be less fertile. This is in agreement with other studies reporting genetic correlations of 0.30 to 0.50 between the interval from calving to first insemination and protein yield (Kadarmideen et al., 2000; Roxström et al., 2001; Andersen-Ranberg et al., 2005). For Czech Holsteins, Zink et al. (2012) reported positive but slightly lower genetic correlations between milk production and fertility traits than those found in our study. As suggested by Andersen-Ranberg et al. (2005), the correlation between fertility and milk production traits may be influenced by individual farmer decisions if, for example, high-yielding cows are inseminated later than cows with low or moderate yields. However, this is not a common practice in the Czech Republic. The genetic correlations between test-day milk yield closest to 90 DIM and CFI1 or to FLI1 (0.07 and 0.05, respectively) published by Sewalem et al. (2010) for Canadian Holsteins were substantially smaller than our estimates. Similarly, Raheja et al. (1989) reported genetic correlations close to zero between fertility and production in the first three lactations for Canadian Holsteins. Sewalem et al. (2010) explained the absence of any appreciable correlation between milk production and female fertility by Canada's longstanding balanced breeding approach that includes selection for high production combined with superior conformation traits to support production levels. However, Czech farmers are reluctant to cull high-yielding cows despite repeated unsuccessful inseminations. As concluded by Royal et al. (2002), although genetic correlations between milk production and fertility

traits are unfavourable, they are not unity; it is not inevitable that fertility will decline as genetic merit for milk yield increases. Good management can foster high fertility and high yield in cows, but it will become increasingly difficult in the long term to maintain the current standards if fertility is not included in the breeding objective, as supported by findings of Dematawewa and Berger (1998).

Herd-year and residual correlations in the first lactation

The estimated herd-year and residual correlations between longevity, fertility, and production traits are shown in Tables 5 and 6, respectively. The highest herd-year correlations were those among the production traits MY1, FY1, and PY1. High herd-year correlations were also found between DO1 and CFI1 (0.56) and between DO1 and FLI1 (0.70), suggesting that contemporarily, herd environments influencing one variable, tended also to change the other. The herd-year correlation between CFI1 and FLI1 was negative but slight (−0.09). Andersen-Ranberg et al. (2005) reported positive herd-year correlations between non-return rate for first parity cows and interval from calving to first insemination (0.51). Similarly to our results (−0.13), Andersen-Ranberg et al. (2005) found small negative herd-year correlations between CFI1 and PY1 (−0.20). In our study, LPL was negatively correlated with milk production traits on a herd-year basis, indicating an antagonistic environmental relationship between longevity and milk production during first lactation.

Table 5. Estimates ± SE of herd-year correlations between longevity (LPL), milk (MY1), fat (FY1), protein yield (PY1), days from calving to first insemination (CFI1), days open (DO1), and days between first and last insemination (FLI1) for first parity Holstein cows (weighted average of four datasets)

	LPL (days)	CFI1 (days)	DO1 (days)	FLI1 (days)	MY1 (kg)	FY1 (kg)
CFI1 (days)	0.05 ± 0.030					
DO 1 (days)	0.02 ± 0.033	0.56 ± 0.020				
FLI1 (days)	0.05 ± 0.035	−0.2 ± 0.030	0.70 ± 0.016			
MY1 (kg)	−0.28 ± 0.029	−0.14 ± 0.024	−0.14 ± 0.027	−0.06 ± 0.028		
FY1 (kg)	−0.32 ± 0.026	−0.11 ± 0.024	−0.10 ± 0.028	−0.03 ± 0.028	0.86 ± 0.005	
PY1 (kg)	−0.37 ± 0.027	−0.13 ± 0.024	−0.13 ± 0.027	−0.06 ± 0.028	0.98 ± 0.001	0.77 ± 0.005

correlations ≥ 0.06 in absolute value are significant at $P < 0.05$

correlations ≥ 0.10 in absolute value are significant at $P < 0.01$

Table 6. Estimates \pm SE of residual correlations between longevity (LPL), milk (MY1), fat (FY1), protein yield (PY1), days from calving to first insemination (CFI1), days open (DO1), and days between first and last insemination (FLI1) for first parity Holstein cows (weighted average of four datasets)

	LPL (days)	CFI1 (days)	DO1 (days)	FLI1 (days)	MY1 (kg)	FY1 (kg)
CFI1 (days)	0.00 \pm 0.005					
DO1 (days)	0.02 \pm 0.005	0.39 \pm 0.004				
FLI1 (days)	0.03 \pm 0.004	-0.09 \pm 0.004	0.87 \pm 0.002			
MY1 (kg)	0.15 \pm 0.006	0.05 \pm 0.005	0.20 \pm 0.006	0.18 \pm 0.006		
FY1 (kg)	0.06 \pm 0.006	0.07 \pm 0.006	0.20 \pm 0.006	0.17 \pm 0.005	0.95 \pm 0.003	
PY1 (kg)	0.07 \pm 0.007	0.06 \pm 0.005	0.22 \pm 0.006	0.19 \pm 0.006	0.97 \pm 0.002	0.86 \pm 0.002

all correlations are significant at $P < 0.01$ except the correlation between LPL and MY1

Residual correlations among variables were small except among production traits (> 0.85) and between DO1 and CFI1 (0.39) and DO1 and FLI1 (0.87), showing that on an individual cow basis, length of DO1 is more closely related to FLI1 than to CFI1, i.e. to the number of inseminations. Andersen-Ranberg et al. (2005) reported a 0.22 residual correlation between CFI1 and PY1, higher than that observed in our study (0.06).

Correlations between traits in the first and second lactation

Estimated genetic correlations among longevity and fertility traits in the first vs. second lactation are shown in Table 7. Genetic correlations between LPL and fertility traits were favourable, ranging from -0.25 to -0.43 , with the exception of LPL with FLI2 (0.28). This positive relationship is undesirable because low fertility (FLI2) is genetically associated with acceptable functional longevity (LPL).

In contrast to the first lactation, cows that did not conceive at the first insemination (long FLI2) exhibited longer functional longevity. A probable explanation is that farmers were reluctant to cull cows during the second lactation despite a repeated inability to conceive which would cause prolonged calving interval and therefore LPL extension. This would be at the expense of lower fertility. In addition, farmers may unintentionally promote formation of the genetic relationship between reduced fertility and functional longevity, thus they give the less fertile cows the opportunity to become pregnant.

Pinedo and De Vries (2010) reported higher risk of death for cows with longer DO in the previous lactation compared with cows with shorter DO. As a possible contributing factor they mentioned over-conditioning of cows toward the end of lactation when milk production is lower and feed intake has not been correspondingly reduced as an explanation for higher risk of death or culling of cows. These cows may have metabolic

Table 7. Estimates \pm SE of genetic correlations of longevity (LPL) and days from calving to first insemination (CFI1), days open (DO1), and days between first and last insemination (FLI1) in first parity with days from calving to first insemination (CFI2), days open (DO2), and days between first and last insemination (FLI2) in second lactation of Holstein cows (weighted average of the four datasets)

		2 nd Lactation			
		LPL (days)	CFI2 (days)	DO2 (days)	FLI 2 (days)
1 st Lactation	CFI1 (days)	-0.39 \pm 0.056	0.93 \pm 0.046	0.33 \pm 0.080	-0.80 \pm 0.064
	DO1 (days)	-0.43 \pm 0.055	0.60 \pm 0.077	0.40 \pm 0.076	-0.44 \pm 0.092
	FLI1 (days)	-0.37 \pm 0.067	0.13 \pm 0.106	0.35 \pm 0.087	0.09 \pm 0.114
	LPL (days)		-0.39 \pm 0.078	-0.25 \pm 0.089	0.28 \pm 0.089

correlations ≥ 0.30 in absolute value are significant at $P < 0.01$

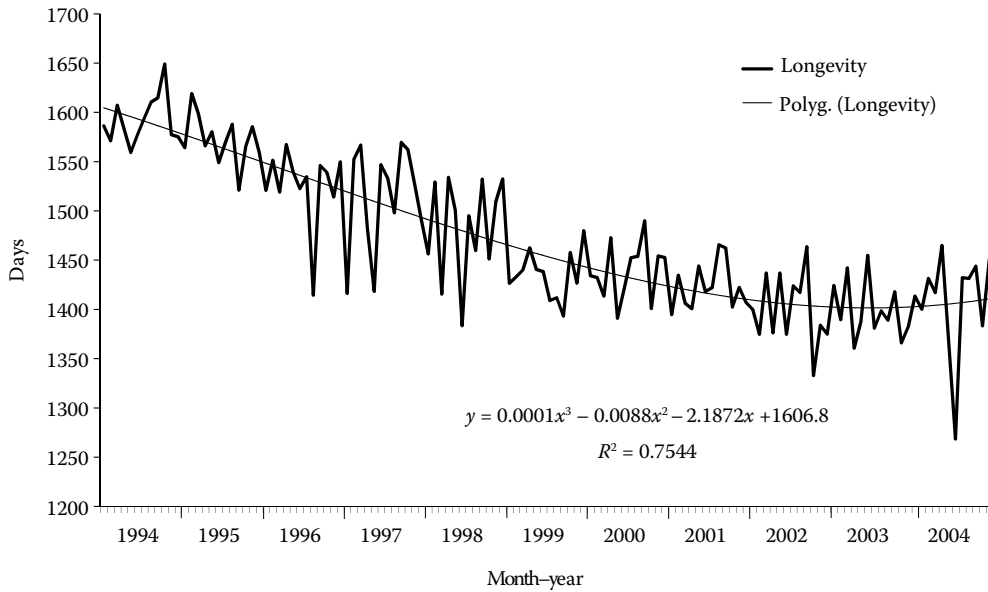


Figure 1. BLUE of month-year at first calving effects for longevity from January 1994 to December 2004

problems as a consequence of increased DO around subsequent calving (Heuer et al., 1999). Moreover, Pinedo and De Vries (2010) suggest that healthier cows that have a better transition after calving may be more likely to conceive promptly and may also be more likely to survive in the future.

The genetic correlation between CFI1 and CFI2 was high (0.93), whereas the genetic correlation between DO1 and DO2 was moderate (0.40) and that between

FLI1 and FLI2 (0.09) was low and not significant. These results indicate that none of the evaluated fertility traits can be considered to be biologically the same trait in the first vs. second lactation. Tiezzi et al. (2012) reported very high genetic correlations (> 0.92) between all the interval fertility traits in the subsequent lactation, whereas Raheja et al. (1989) found very low genetic relationship between fertility in the first and second lactations.

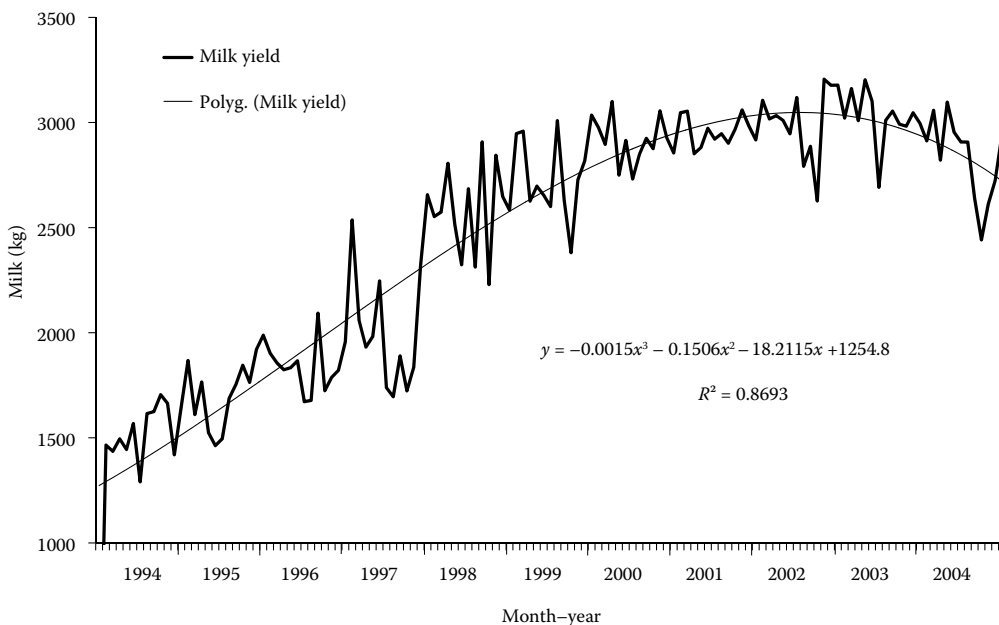


Figure 2. BLUE of month-year at first calving effects for milk production in first lactation from January 1994 to December 2004

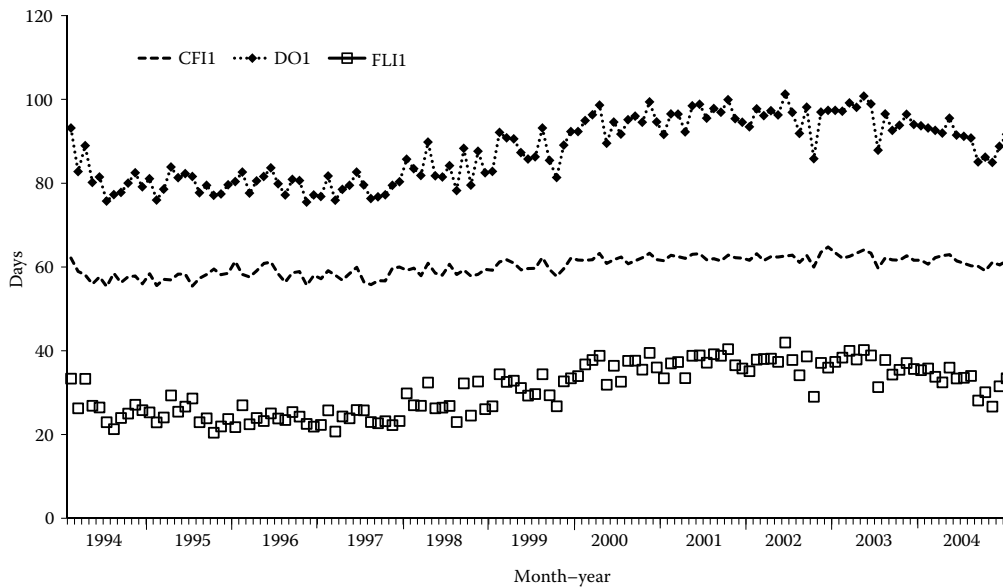


Figure 3. BLUE of month-year at first calving effects for days from calving to first insemination (CFI1), days open (DO1), and days between first and last insemination (FLI1) in first lactation from January 1994 to December 2004

All of the herd-year and residual effects correlations of longevity with fertility traits in the first and second lactation were low (< 0.08 ; data not shown).

Environmental effects

The best linear unbiased estimate (BLUE) for month-year of first calving effects for functional longevity (Figure 1) declined between years 1994–2002. Over these years, deleterious influences of the environment on longevity apparently accumulated. Probably, this was caused by a constant decline in the number of cows in the Czech Republic due to

the unfavourable economic situation. Culled cows could not therefore express their genetic value for longevity. In contrast, the BLUE for month-year of first calving effects for milk production in the first lactation (Figure 2) increased between the years 1994–2004. A possible explanation is that in reducing the number of cows in a herd, farmers culled first of all the low yielding animals. The BLUE for month-year of first calving effects for DO1 and FLI1 (Figure 3) increased slightly between the years 1994–2004, whereas CFI1 remained essentially constant during this period. This could indicate efforts of the breeders to improve environmental conditions to prevent reduced fertility.

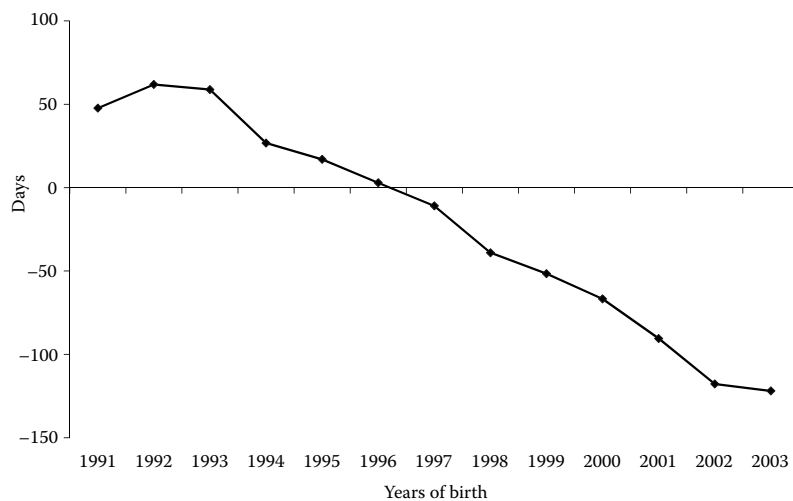


Figure 4. Genetic trend for length of productive life of cows (mean breeding values of cows by year of birth)

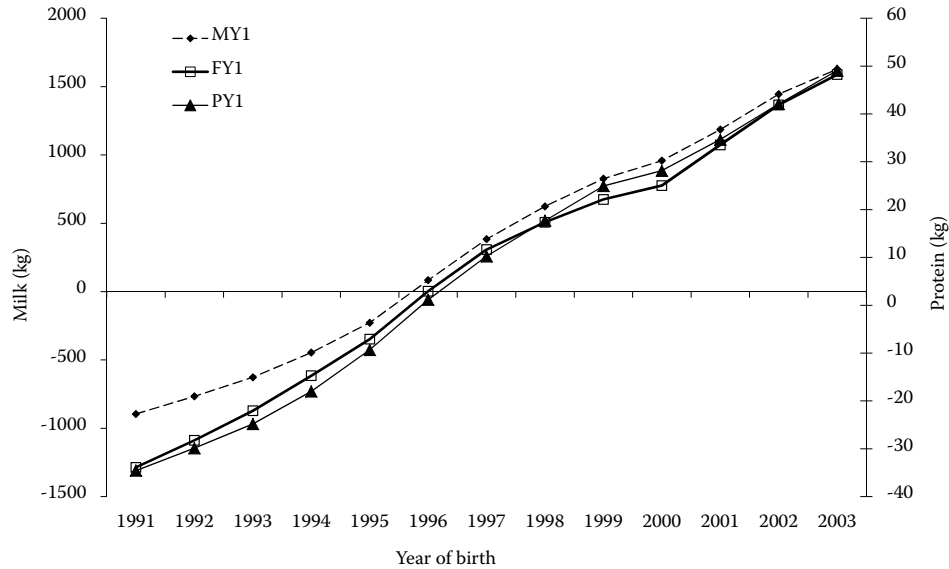


Figure 5. Genetic trend for production traits in first lactation: milk yield (MY1), fat yield (FY1), and protein yield (PY1) (mean breeding values of cows by year of birth)

Genetic trends

Genetic trends for fertility and production traits in the first lactation and for LPL were expressed as mean breeding values of cows (BV) by year of birth. Breeding values were estimated using the whole dataset. Average cow BV for LPL decreased across the entire period (Figure 4), while average cow BV for MY1, FY1, and PY1 increased (Figure 5). Thus, the estimated genetic change for longevity was unfavourable. Similarly, the genetic changes in FLI1 were unfavourable in the period from 1991 to 2003 (Figure 6).

CONCLUSION

Knowledge of genetic relationships among longevity, female fertility, and milk production traits is necessary for economically rational dairy cattle genetic improvement programs. This report is the first step for development of a selection index focused on functional traits in Czech Holsteins. Unfavourable genetic correlations of milk production and fertility with longevity were identified. The relationship between fertility and functional longevity was negative, suggesting that reduced genetic potential for functional longevity could

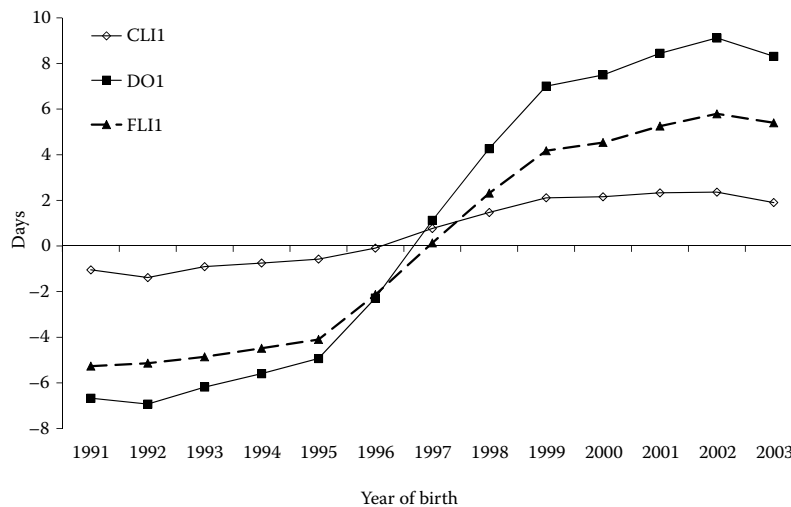


Figure 6. Genetic trend for fertility traits: for days from calving to first insemination (CFI1), days open (DO1), and days between first and last insemination (FLI1) (mean breeding values of cows by year of birth)

foster genetically impaired fertility and vice versa. During the second lactation, there was an unfavourable (positive) genetic correlation between functional longevity and interval between the first and last insemination, suggesting an arising genetic antagonism between fertility and functional longevity. Our study confirmed that increasing genetic potential for milk yield corresponded to a reduced breeding value for functional longevity and a slight decline in fertility traits (especially an increased interval between first and final insemination). For these reasons, it is important to develop a selection index including longevity, female fertility, and production traits. The substantial, unfavourable genetic correlations found in this study suggest that incorporating female reproductive measures in selection indices could be effective in reducing deterioration of reproductive performance of cows selected for production traits.

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REFERENCES

- Andersen-Ranberg I.M., Klemetsdal G., Heringstad B., Steine T. (2005): Heritabilities, genetic correlations, and genetic change for female fertility protein yield in Norwegian dairy cattle. *Journal of Dairy Science*, 88, 348–355.
- Dechow C.D., Rogers G.W., Clay J.S. (2001): Heritabilities and correlations among body condition scores, production traits, and reproductive performance. *Journal of Dairy Science*, 84, 266–275.
- Dědková L., Wolf J. (2001): Estimation of genetic parameters for milk production traits in Czech dairy cattle populations. *Czech Journal of Animal Science*, 46, 292–301.
- Dematawewa C.M.B., Berger P.J. (1998): Genetic and phenotypic parameters for 305-day yield fertility and survival in Holsteins. *Journal of Dairy Science*, 81, 2700–2709.
- Ducrocq V.P., Quaas R.L., Pollak E.J., Casella G. (1988): Length of productive life of dairy cows. 2. Variance component estimation and sire evaluation. *Journal of Dairy Science*, 71, 3071–3079.
- González-Recio O., Alenda R. (2007): Genetic relationship of discrete-time survival with fertility and production in dairy cattle using bivariate models. *Genetics Selection Evolution*, 39, 391–404.
- González-Recio O., Pérez-Cabal M.A., Alenda R. (2004): Economic value of female fertility and its relationship with profit in Spanish dairy cattle. *Journal of Dairy Science*, 87, 3053–3061.
- Heuer C., Schukken Y.H., Dobbelaar P. (1999): Postpartum body condition score and results from the first test day milk as predictors of disease, fertility, yield, and culling in commercial dairy herds. *Journal of Dairy Science*, 82, 295–304.
- Jamrozik J., Fatehi J., Kistemaker G.J., Schaeffer L.R. (2005): Estimates of genetic parameters for Canadian Holstein female reproduction traits. *Journal of Dairy Science*, 88, 2199–2208.
- Kadarmideen H., Thompson N.R., Simm G. (2000): Linear and threshold model genetic parameters for disease, fertility and milk production in dairy cattle. *Animal Science*, 71, 411–419.
- Madsen P., Jensen J. (2010): DMU – a package for analysing multivariate mixed models. Version 6, release 5.0. Aarhus University, Foulum, Denmark. Available from www.dmu.agrsci.dk (accessed June 1, 2011).
- Miglior F., Muir B.L., Van Doormaal B.J. (2005): Selection indices in Holstein cattle of various countries. *Journal of Dairy Science*, 88, 1255–1263.
- Páchová E., Zavadilová L., Sölkner J. (2005): Genetic evaluation of the length of productive life in Holstein cattle in the Czech Republic. *Czech Journal of Animal Science*, 50, 493–498.
- Pinedo P.J., De Vries A. (2010): Effect of days to conception in the previous lactation on the risk of death and live culling around calving. *Journal of Dairy Science*, 93, 968–977.
- Pryce J.E., Royal M.D., Garnsworthy P.C., Mao I.L. (2004): Fertility in the high-producing cows. *Livestock Production Science*, 86, 125–135.
- Raheja K.L., Burnside E.B., Schaeffer L.R. (1989): Relationships between fertility and production in Holstein dairy cattle in different lactations. *Journal of Dairy Science*, 72, 2670–2678.

- Royal M.D., Flint A.P.F., Woolliams J.A. (2002): Genetic and phenotypic relationships among endocrine and traditional fertility traits and production traits in Holstein-Friesian dairy cows. *Journal of Dairy Science*, 85, 958–967.
- Roxström A., Strandberg E. (2002): Genetic analysis of functional, fertility-, mastitis-, and production-determined length of productive life in Swedish dairy cattle. *Livestock Production Science*, 74, 125–135.
- Roxström A., Strandberg E., Berglund B., Emanuelson U., Philipsson J. (2001): Genetic and environmental correlations among female fertility traits and milk production in different parities of Swedish Red and White dairy cattle. *Acta Agriculturae Scandinavica, Section A – Animal Science*, 51, 7–14.
- Sewalem A., Miglior F., Kistemaker G.J., Van Doormaal B.J. (2008): Relationship between fertility traits and longevity in Canadian dairy cattle. *Journal of Dairy Science*, 91, 1660–1668.
- Sewalem A., Kistemaker G.J., Miglior F. (2010): Relationship between female fertility and production traits in Canadian Holsteins. *Journal of Dairy Science*, 93, 4427–4434.
- Sun C., Madsen P., Nielsen U.S., Zhang Y., Lund M.S., Su G. (2009): Comparison between a sire model and an animal model for genetic evaluation of fertility traits in Danish Holstein population. *Journal of Dairy Science*, 92, 4063–4071.
- Tiezzi F., Maltecca C., Penasa M., Cecchinato A., Chang Y.M., Bittante G. (2011): Genetic analysis of fertility in the Italian Brown Swiss population using different models and trait definitions. *Journal of Dairy Science*, 94, 6162–6172.
- Tiezzi F., Maltecca C., Cecchinato A., Penasa M., Bittante G. (2012): Genetic parameters for fertility of dairy heifers and cows at different parities and relationship with production traits in first lactation. *Journal of Dairy Science*, 95, 7355–7362.
- Vollema A.R., Groen A.F. (1998): A comparison of breeding value predictors for longevity using a linear model and survival analysis. *Journal of Dairy Science*, 81, 3315–3320.
- Wall E., Brotherstone S., Woolliams J.A., Banos G., Coffey M.P. (2003): Genetic evaluation of fertility using direct and correlated traits. *Journal of Dairy Science*, 86, 4093–4102.
- Zavadilová L., Štípková M. (2012): Genetic correlations between longevity and conformation traits in the Czech Holstein population. *Journal of Dairy Science*, 95, 125–136.
- Zink V., Lassen J., Štípková M. (2012): Genetic parameters for female fertility and milk production traits in first-parity Czech Holstein cows. *Czech Journal of Animal Science*, 57, 108–114.

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