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Comparison of breeding values among cows with exceptional longevity and their contemporary herdmates in German Holsteins

K. Abfalter[1], **W. Brade**[2], **and O. Distl**[1]

[1]Institute for Animal Breeding and Genetics, University of Veterinary Medicine Hanover, Bünteweg 17p, 30559 Hanover, Germany
[2]Chamber of Agriculture Lower Saxony, Mars-la-Tour-Straße 1–13, 26121 Oldenburg, Germany

Correspondence to: O. Distl (ottmar.distl@tiho-hannover.de)

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Abstract. The present analysis compares the estimated breeding values (EBVs), relative breeding values (RBVs), and daughter yield deviations (YDs) of cows with exceptional longevity with their contemporary herdmates. In addition, the relative breeding values of their sires were compared among these two daughter groups; the RBVs of the sires were also compared with the proportion of their daughters with exceptional longevity. Data included 5037 sires born between 1963 and 1996 with a total of 61 988 daughter; of these sires, 486 had sired daughters that completed more than nine lactations (exceptional cows) and 4957 sires had sired the contemporary herdmates. Exceptional cows had on average significantly lower EBVs for milk yield, fat and protein yield, and significantly lower YDs for milk and protein yield in the first three lactations, significantly lower RBVs for milk production and type but significantly higher RBVs for somatic cell score and functional longevity. The sires of exceptional cows had significantly higher RBVs for somatic cell count (RZS), functional longevity (RZN), and fitness (RZFit) in comparison to the sires of contemporary herdmates. Correlations among the proportion of exceptional cows per sire and RZN, RZS as well as RZFit were positive, whereas milk production (RZM) showed a negative correlation. An increase in the number of cows with exceptional longevity may be possible through a relative total breeding value with high positive weights for RZN, RZS, and RZFit but negative weights for RZM and type (RZE).

1 Introduction

Selection decisions for future sires are based on estimated breeding values (EBVs). To increase the productive life of cows, EBVs for functional longevity have been introduced for many dairy cattle breeds (Miglior et al., 2005). EBVs for functional longevity (RZN) have been available for German Holsteins since 1996. The importance of this trait stems from the decreasing trend for longevity in all milk-producing cattle breeds over more than the last 40 years. Genetic improvement of longevity has the issue that the true longevity is not available till a cow is culled. This is a major hindrance for selection of sires (Boettcher et al., 1999). Hence, waiting for the sires' daughters to complete their productive life is not reasonable. Therefore, the EBVs for functional longevity are based on a model accounting for the right censored data and the culling level for milk production within herds. To increase the reliability of RZN, type traits are included in the prediction equation because these traits are available in the first lactation and have high heritability and moderate genetic correlations with longevity (Jairath et al., 1998; Weigel et al., 1998). The type traits body depth, leg conformation, and udder depth are taken into consideration for the prediction of RZN in German Holsteins (DHV, Deutscher Holstein Verband, www.holstein-dhv.de). Forabosco et al. (2009) identified feet and leg scores, body depth, udder depth, and maternal stillbirth as indicator traits for longevity. In addition to the difficulty of predicting longevity for young sires, heritabilities for functional longevity are low with estimates be-

Table 1. Means ($\bar{x}$), standard deviations (SDs), and range of relative breeding values of the sires of exceptional cows (EX) ($n = 486$ sires) and contemporary herdmates (HGF) ($n = 4957$ sires).

	EX		HGF	
Relative breeding values of the sires	$\bar{x} \pm$ SD	Range	$\bar{x} \pm$ SD	Range
Total merit (RZG)	82.7 ± 10.7	58–113	82.3 ± 9.9	43–116
Milk production (RZM)	73.3 ± 11.9	47–114	77.1 ± 11.6	37–116
Type (RZE)	82.4 ± 9.9	57–106	85.6 ± 11.3	40–120
Somatic cell count (RZS)	105.8 ± 11.4	80–141	101.8 ± 10.7	52–139
Longevity (RZN)	108.2 ± 9.2	91–128	102.1 ± 9.3	72–135
Fitness (RZFit)	103.7 ± 9.3	82–120	96.5 ± 9.0	50–131

tween 0.04 (Vollema and Groen, 1996) and 0.11 (Eaglen et al., 2013; Sasaki, 2013).

The breeding objective for functional longevity should increase the observable longevity as well as the numbers of daughters with exceptional longevity. Therefore, the present study aims to compare breeding traits among cows with an exceptional lifespan and their contemporary herdmates using EBVs, yield deviations (YDs), and relative breeding values (RBVs) for milk production (RZM), type (RZE), somatic cell count (RZS), and functional longevity as well as the relative breeding values of their sires. In addition, the proportion of exceptional daughters was correlated with the RBVs of their sires.

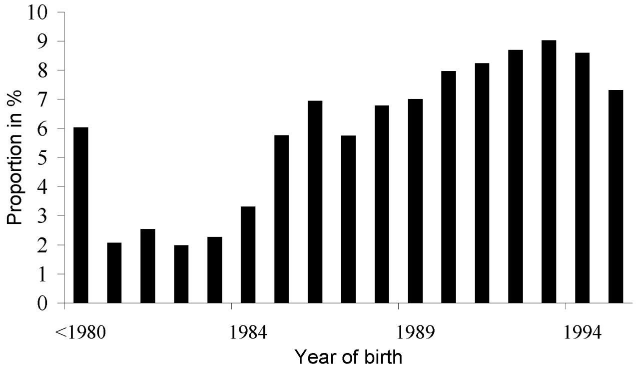

Figure 1. Distribution of the sires by their birth years.

2 Material and methods

Data for the analysis were obtained from the unified animal ownership database Vereinigte Informationssysteme Tierhaltung e.V., Verden/Aller (VIT). Two different data sets were used. The first data set included data of German Holstein dairy cows from farms where at least one cow completed eight or more lactations and/or achieved 90 000 kg milk or more in her lifetime by the years 2007 or 2008. These data comprised 61 988 cows from 446 farms, born between 1986 and 1997. Exceptional cows were defined as those cows with at least nine lactations completed. Contemporary herdmates were all other cows from the same 446 farms with less than nine lactations. Altogether, we identified 1543 exceptional cows (EX) and 60 445 contemporary herdmates (HGF) in this data set. The second data set contained the RBVs of the sires of the cows including the total merit (RZG), RZM, RZE, RZS, RZN, and fitness (RZFit). The RZFit combines RBVs for daughter fertility and maternal calving traits with the highest weights, RBVs for functional longevity, foot and leg scores with moderate weights and RBVs for somatic cell score, udder scores, and milk production with low weights (VIT, 2014). The mean RBVs of the sires including RZG, RZM, RZE, RZS, RZN, and RZFit are given for both groups in Table 1. Sires of the exceptional cows had higher means for RZS, RZN, and RZFit but lower means for RZM and RZE than the sires of the contemporary herdmates. The cows descended from a total of 5037 sires, born between 1963 and 1996 (Fig. 1). For the 5037 sires, the number of daughters per sire ranged from 1 to 4852, with an average of 12. Of these 5037 sires, 4597 had contemporary herdmate daughters and 486 sires had daughters classified as exceptional cows.

The breeding traits of the cows and the sires were compared among the exceptional cows and the contemporary herdmates using linear models.

The analysis of the EBVs, YDs, and RBVs of the cows (Y_{ij}) was performed using a general linear model (model 1):

$$Y_{ij} = \mu + \mathrm{CAT}_i + e_{ij}, \tag{1}$$

where μ is the model constant, CAT_i is the fixed effect of the ith category for contemporary herdmates and exceptional cows ($i = 1$–2), and e_{ij} is the random residual error.

This model 1 was extended by the fixed effect of birth year of the cow and the interaction between birth year of the cow and CAT. An additional model 1a was run in order to analyze the traits of the contemporary herdmates by their completed lactations. This analysis should reveal if the contemporary herdmates show differences in the EBVs, YDs, and RZMs by lactation numbers.

Table 2. Least-square means and standard deviations of the traits analyzed including daughter yield deviations (YDs), estimated breeding values, and relative breeding values (RBVs) of exceptional cows (EX) and contemporary herdmates (HGF) for milk performance (RZM), somatic cell count (RZS), type (RZE), and functional longevity (RZN) as well as P values for trait differences among EX and HGF.

Trait	EX ($n = 1543$)	HGF ($n = 60\,445$)	Total ($n = 61\,988$)	P value
EBV				
– Milk yield	-556.6 ± 527.3	-483.5 ± 578.6	-485.4 ± 577.5	< 0.0001
– Fat percentage	0.091 ± 0.25	0.068 ± 0.23	0.069 ± 0.23	0.0002
– Fat yield	-16.5 ± 19.7	-15.2 ± 21.6	-15.2 ± 21.6	0.0187
– Protein percentage	-0.004 ± 0.11	-0.008 ± 0.11	-0.008 ± 0.11	0.1109
– Protein yield	-19.6 ± 15.1	-17.4 ± 17.1	-17.5 ± 17.0	< 0.0001
– Fat or protein percentage	1.44 ± 8.31	1.38 ± 6.72	1.38 ± 6.77	0.7193
YD milk yield				
– Lactation 1	149.0 ± 410.1	214.9 ± 455.7	213.3 ± 454.8	< 0.0001
– Lactation 2	179.4 ± 407.0	238.1 ± 459.0	236.6 ± 457.9	< 0.0001
– Lactation 3	201.0 ± 432.3	264.9 ± 475.0	263.2 ± 474.1	0.0002
YD fat yield				
– Lactation 1	6.87 ± 16.6	7.73 ± 17.8	7.71 ± 17.8	0.1013
– Lactation 2	8.10 ± 18.5	8.27 ± 19.5	8.27 ± 19.5	0.7832
– Lactation 3	9.07 ± 20.2	9.43 ± 21.1	9.42 ± 21.1	0.6360
YD protein yield				
– Lactation 1	4.45 ± 11.9	6.50 ± 13.2	6.46 ± 13.1	< 0.0001
– Lactation 2	4.88 ± 12.8	6.55 ± 14.3	6.51 ± 14.2	< 0.0001
– Lactation 3	4.74 ± 13.6	6.59 ± 14.9	6.54 ± 14.8	< 0.0001
YD SCS				
– Lactation 1	0.041 ± 0.45	0.062 ± 0.43	0.061 ± 0.43	0.0933
– Lactation 2	0.047 ± 0.42	0.068 ± 0.49	0.067 ± 0.49	0.1880
– Lactation 3	0.063 ± 0.53	0.069 ± 0.50	0.069 ± 0.50	0.7517
RBV				
– RZM	70.4 ± 10.6	71.8 ± 12.1	71.7 ± 12.0	< 0.0001
– RZE	91.2 ± 7.5	91.8 ± 7.7	91.8 ± 7.7	0.0009
– RZS	110.8 ± 7.2	105.9 ± 7.6	106.1 ± 7.6	< 0.0001
– RZN	105.9 ± 4.7	102.6 ± 4.7	102.7 ± 4.7	< 0.0001

For the RBVs of the sires (Y_{ijklmn}) a mixed linear model was used (model 2):

$$Y_{ijklmn} = \mu + \mathrm{CAT}_i + \mathrm{YOB}_j + \mathrm{HLEV}_k + b_1 \mathrm{AFC}_l + \mathrm{farm}_m + e_{ijklmn}, \qquad (2)$$

where YOB_j is the fixed effect of the birth year of the cow ($j = 1$–12), HLEV_k is the fixed effect of the kth herd level for each birth year cohort calculated as average milk yield per farm using all lactation records of cows of the same birth year ($k = 1$–3 with < 6000, 6000–8000 and > 8000 kg milk, AFC_l is the age at the first calving of the cow, b_1 is the linear regression coefficient, and farm_m is the random effect of the mth farm ($m = 1$–446).

For each herd, and within the herd for each birth year of the cows, the average milk yield performance using all lactations was calculated. Thus, the herd level could vary for each herd depending on the milk performance of the cows from the respective birth year. In addition, we calculated the frequency of daughters being classified as exceptional cows for all sires in the data set. The proportion of exceptional daughters per sire was correlated with the RBVs of the sires. In this paper, we selected sires with at least one exceptional daughter and > 5 exceptional daughters to see if the correlation may be influenced by sires with a small number of exceptional daughters. Statistical analyses were performed using SAS, version 9.4 (Statistical Analysis System Institute, Cary, NC, USA, 2015) and the MEANS, GLM, MIXED, and CORR procedures.

Table 3. Least-square means and standard deviations of the traits analyzed including daughter yield deviations (YDs), estimated breeding values and relative breeding values (RBVs) of contemporary herdmates (HGF) by completed lactations for milk performance (RZM), somatic cell count (RZS), type (RZE), and functional longevity (RZN) as well as P values for trait differences among EX and HGF.

Lactation number	1–2	3–4	5–6	7–9	P value
Trait	($n = 20\,012$)	($n = 19\,196$)	($n = 13\,377$)	($n = 7860$)	
EBV					
– Milk yield	−567.9 ± 4.1	−444.4 ± 4.1	−422.7 ± 5.0	−467.7 ± 6.5	< 0.0001
– Fat percentage	0.072 ± 0.001	0.058 ± 0.001	0.070 ± 0.002	0.079 ± 0.003	< 0.0001
– Fat yield	−18.3 ± 0.15	−14.4 ± 0.15	−12.6 ± 0.19	−13.7 ± 0.24	< 0.0001
– Protein percentage	−0.003 ± 0.01	−0.012 ± 0.01	−0.011 ± 0.01	−0.011 ± 0.01	< 0.0001
– Protein yield	−19.8 ± 0.12	−16.5 ± 0.12	−15.6 ± 0.15	−16.7 ± 0.19	< 0.0001
– Fat or protein percentage	1.34 ± 0.05	1.34 ± 0.05	1.44 ± 0.06	1.44 ± 0.07	< 0.0001
YD milk yield					
– Lactation 1	211.4 ± 3.6	222.3 ± 3.7	213.9 ± 4.4	207.1 ± 5.8	< 0.0001
– Lactation 2	236.4 ± 4.1	242.8 ± 4.1	238.7 ± 4.9	229.3 ± 6.4	< 0.0001
– Lactation 3	259.0 ± 5.0	266.0 ± 4.9	268.0 ± 5.8	270.4 ± 7.6	< 0.0001
YD fat yield					
– Lactation 1	7.50 ± 0.14	8.01 ± 0.14	7.81 ± 0.17	7.50 ± 0.22	< 0.0001
– Lactation 2	8.18 ± 0.18	8.34 ± 0.17	8.46 ± 0.21	8.02 ± 0.28	< 0.0001
– Lactation 3	9.27 ± 0.22	9.46 ± 0.22	9.66 ± 0.26	9.36 ± 0.33	< 0.0001
YD protein yield					
– Lactation 1	6.37 ± 0.10	6.74 ± 0.11	6.49 ± 0.13	6.30 ± 0.17	< 0.0001
– Lactation 2	6.45 ± 0.13	6.67 ± 0.13	6.60 ± 0.15	6.40 ± 0.20	< 0.0001
– Lactation 3	6.28 ± 0.16	6.56 ± 0.15	6.78 ± 0.18	7.03 ± 0.24	< 0.0001
YD SCS					
– Lactation 1	0.065 ± 0.01	0.060 ± 0.01	0.060 ± 0.01	0.058 ± 0.01	< 0.0001
– Lactation 2	0.066 ± 0.01	0.066 ± 0.01	0.068 ± 0.01	0.075 ± 0.01	< 0.0001
– Lactation 3	0.073 ± 0.01	0.070 ± 0.01	0.061 ± 0.01	0.068 ± 0.01	< 0.0001
RBV					
– RZM	70.0 ± 0.08	72.4 ± 0.09	73.1 ± 0.10	73.1 ± 0.10	< 0.0001
– RZE	91.2 ± 0.05	91.8 ± 0.06	91.5 ± 0.07	91.7 ± 0.09	< 0.0001
– RZS	104.9 ± 0.05	105.3 ± 0.05	107.0 ± 0.06	108.5 ± 0.08	< 0.0001
– RZN	101.9 ± 0.03	102.3 ± 0.03	103.3 ± 0.04	104.2 ± 0.05	< 0.0001

Table 4. Least-square means (LSMs) with their standard errors for relative breeding values of sires of the exceptional cows (EX) and contemporary herdmates (HGF) as well as P values for differences among LSMs using model 2.

Relative breeding values of the sires	EX	HGF	P Value
Total (RZG)	80.7 ± 1.6	79.1 ± 0.9	0.2348
Milk (RZM)	71.4 ± 1.6	73.8 ± 0.8	0.0830
Somatic cell count (RZS)	105.5 ± 1.6	102.4 ± 0.8	0.0247
Type (RZE)	79.9 ± 1.7	79.3 ± 1.0	0.7057
Longevity (RZN)	109.5 ± 1.4	104.2 ± 0.7	< 0.0001
Fitness (RZFit)	103.9 ± 1.7	97.3 ± 0.6	< 0.0001

Table 5. Pearson correlations among relative breeding values of sires with the proportion of daughters classified as exceptional cows (EX) for all sires and with sires with at least one daughter and with more than five daughters classified as exceptional cow.

Relative breeding values of the sires	All sires	Sires with one or more exceptional daughters ($n = 486$)	Sires with more than five exceptional daughters ($n = 48$)
Longevity (RZN)	0.123^{c}	0.096^{a}	0.712^{c}
Total merit (RZG)	0.011	-0.010	0.144
Milk (RZM)	-0.061^{c}	-0.105^{a}	-0.338^{a}
Somatic cell count (RZS)	0.052^{b}	0.044	0.408^{b}
Type (RZE)	-0.022	-0.054	-0.068
Fitness (RZFit)	0.116^{c}	0.178^{b}	0.503^{b}

^{a} $P < 0.05$, ^{b} $P < 0.01$, ^{c} $P < 0.001$.

3 Results

For both groups, EX and HGF, least-square means (LSMs) and standard deviations for EBVs and YDs for milk performance traits and somatic cell scores (SCSs) were estimated using model 1 (Table 2). In addition, the RBVs of cows for RZM, RZE, RZS, and RZN were compared. The LSM of EBVs for milk, fat and protein yield as well as protein percentage were negative for both groups due to the genetic trend. The LSM of EBVs for all yield traits, fat percentage and YDs for milk and protein yield in the first three lactations were significantly lower in exceptional cows compared to their contemporary herdmates. The LSM of RBVs for RZM and RZE were significantly lower but significantly higher for RZS and RZN in exceptional cows than in the contemporary herdmates. The LSM for RZS and RZN of exceptional cows exceeded the corresponding LSM of RBVs of contemporary herdmates by three to five points. Using the extended model 1 including birth year and the interaction among birth year and category did not change the results for the RBVs but clearly lowered the differences among EBVs among EX and HGF. Only a significant difference remained for the EBV of fat percentage. The significance for the differences of YDs among EX and HGF were not affected by the extended model 1 with the exception of YD SCS in first-lactation cows. Here, a significant difference ($p = 0.02$) was obvious in favor of the exceptional cows.

Contemporary herdmates leaving the herd after one or two lactations had similar low EBVs for yield traits as the exceptional cows, whereas cows completing five to six lactations had the highest EBVs for these traits (Table 3). Yield deviations classified by the number of completed lactations for the contemporary herdmates were higher in each group when compared with the exceptional cows. For SCS, all different survival groups of contemporary herdmates had higher least-square means than exceptional cows. Similarly, RZS and RZN were lower in the different survival classes of contemporary herdmates.

Significant differences were found for the LSM of RBVs among the sires of exceptional cows and their contemporary herdmates using model 2 for RZS, RZN, and RZFit (Table 4). Differences among the two groups were largest for RZFit. Correlations among the proportion of daughters classified as exceptional cows with the RBVs of all their sires and sires with at least one daughter being an exceptional cow are close to zero (Table 5). Correlations deviate more from zero when only sires with more than five daughters classified as exceptional cows were employed in the correlation analysis. Significant positive correlations were seen for RZN, RZS, and RZFit. A significant negative correlation was obvious for RZM. Plots of the proportions of daughters classified as exceptional cows with the RZN of their sires are shown for sires with at least one exceptionally long-lived daughter (Fig. 2) and more than five exceptionally long-lived daughters (Fig. 3).

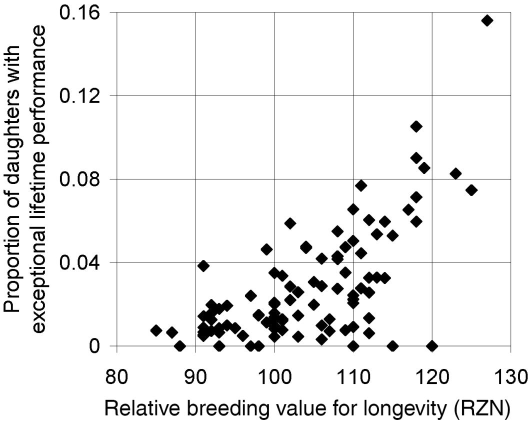

Figure 2. Proportion of exceptional cows compared with the relative breeding values for functional longevity for sires ($n = 486$).

4 Discussion

In comparison to their herdmates, exceptional cows have on average lower EBVs for milk, fat, and protein yield as well as on average lower YDs for milk and protein yield in the first three lactations. Particularly, higher means of RBVs for RZS

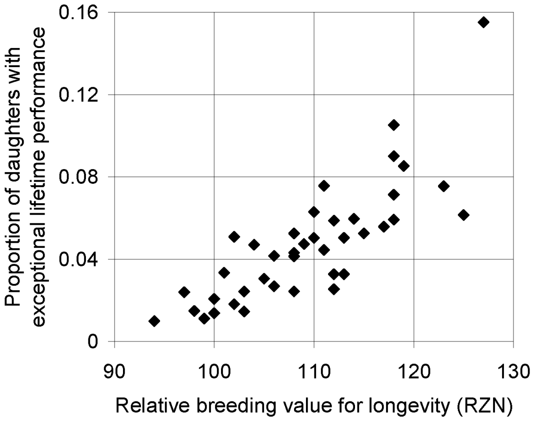

Figure 3. Proportion of exceptional cows compared with the relative breeding values for functional longevity (RZN) for sires ($n = 48$) with more than five daughters with exceptional lifetime performance.

and RZN were obvious for the exceptional cows. The main determinants for an exceptionally productive life seem to be a lower yield production at least in the first three lactations and a lower somatic cell score. In contrast to the first three lactation yields, the mean performance per lactation over the whole productive life was significantly higher in exceptional cows in comparison to their contemporary herdmates (Abfalter et al., 2012). Pritchard et al. (2013) found negative genetic correlations between functional longevity and 305-day milk and fat yield in first-lactation cows, which suggests that lower milk and fat yield in the first lactation was associated with an increased lifespan of dairy cows at the same production level. Probably energy imbalance and resulting health issues may have been the reasons for involuntary culling in first-lactation high-yielding cows. Similarly, Bicalho et al. (2014) reported that cows from sires with lower EBVs for fat yield had a higher culling risk. Also, González-Recio and Alenda (2007) suggested that high-performance cows do have more health issues and therefore a higher culling risk. A negative genetic correlation with the protein yield of first-lactation cows was not reported (Pritchard et al., 2013). In the present analysis, the lower protein yield appeared more pronounced than the lower fat yield production in the first three lactations. Cows with significantly lower protein yields but only slightly lower fat yields in the first three lactations had a higher chance of an exceptionally productive life.

The partly high genetic correlations reported for yield traits and longevity (range for r_{g} at -0.17 to 0.85; reviewed by Sasaki, 2013) could not be confirmed for exceptional cows. The reason for this result may be that despite health and fertility issues, the farmers decided to keep these cows even if they did not perform particularly well. The genetic correlation in population-wide studies mainly stems from the cows with one to six lactations and for these animals YDs for yield traits were highest in the present study. The cows with more than eight lactations seem to be very exceptional in their health, fertility, and performance.

In the present analysis, exceptional cows had higher RBVs and lower YDs for somatic cell scores, indicating a higher survival probability. Cows with somatic cell scores above the breed average had a higher culling risk than cows with lower somatic cell scores (Pritchard et al., 2013; Sewalem et al., 2006). Depending on herd average, high-cell cows did have an increased culling risk in a herd with low somatic cell scores (Caraviello et al., 2005). However, in herds with medium to high somatic cell scores, cows with very low somatic cell scores were prone to a higher culling risk, probably due to a higher mastitis risk.

Poor fertility records may have reduced the RZFit and lowered exceptional longevity in cows in this data set. This finding is in accordance with an increased culling risk for cows with fertility problems (Forabosco et al., 2009; Ferris et al., 2014). Calving traits did not have a significant genetic correlation with functional longevity (Eaglen et al., 2013) though other studies suggested higher culling risks concerning aggravated calving difficulties (Berry et al., 2004; López de Maturana et al., 2007; Sewalem et al., 2008).

The positive correlation with RZFit in the present analysis may also partly be due to the scores for foot angle and leg scores. Feet and leg scores showed positive correlation with functional longevity though their influence was not as prominent (Zavadilová et al., 2011). However, sires with high EBVs for feet and legs had a higher probability of siring offspring that survived rearing (Pritchard et al., 2013).

The improvement of exceptional longevity would require creating a combined index with negative weights for RZM and RZE but high positive weights for RZN, RZS, and RBVs of maternal fertility and calving traits. In conclusion, longevity could be improved to a population average above five lactations if the dairy farmers could select bulls with a combined index with a strong focus on maternal fertility and calving traits, somatic cell score, and functional longevity. In order to facilitate this breeding objective a total merit index RZLongevity could be calculated and provided to farmers and breeders through VIT/Verden.

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References

Abfalter, K., Brade, W., and Distl, O.: Vergleich von Lebensleistung und Leistungseffizienz zwischen extrem langlebigen Deutschen Holstein Kühen und deren zeitgleichen Herdengefährtinnen, Züchtungskunde, 84, 140–157, 2012.

Berry, D. P., Buckley, F., Dillon, P., Evans, R. D., and Veerkamp, R. F.: Genetic relationships among linear type traits, milk yield, body weight, fertility and somatic cell count in primiparous cows, Ir. J. Agric. Food Res., 43, 161–176, 2004.

Bicalho, R. C., Foditsch, C., Gilbert, R., and Oikonomou, G.: The effect of sire predicted transmitting ability for production traits on fertility, survivability, and health of Holstein dairy cows, Theriogenology, 81, 257–265, 2014.

Boettcher, P. J., Jairath, L. K., and Dekkers, J. C. M.: Genetic evaluation of herd life in Canada: Current status and future outlook, Proceedings International Workshop on Genetic Improvement of Functional Traits in cattle (GIFT): Longevity, Interbull Bulletin No. 21, 23–30, 1999.

Caraviello, D. Z., Weigel, K. A., Shook, G. E., and Ruegg, P. L.: Assessment of the impact of somatic cell count on functional longevity in Holstein and Jersey cattle using survival analysis methodology, J. Dairy Sci., 88, 804–811, 2005.

Eaglen, S. A., Coffey, M. P., Woolliams, J. A., and Wall, E.: Direct and maternal genetic relationships between calving ease, gestation length, milk production, fertility, type, and lifespan of Holstein-Friesian primiparous cows, J. Dairy Sci., 96, 4015–4025, 2013.

Forabosco, F., Jakobsen, J. H., and Fikse, W. F.: International genetic evaluation for direct longevity in dairy bulls, J. Dairy Sci., 92, 2338–2347, 2009.

Ferris, C. P., Patterson, D. C., Gordon, F. J., Watson, S., and Kilpatrick, D. J.: Calving traits, milk production, body condition, fertility, and survival of Holstein-Friesian and Norwegian Red dairy cattle on commercial dairy farms over 5 lactations, J. Dairy Sci., 97, 5206–5218, 2014.

González-Recio, O. and Alenda, R.: Genetic relationship of discrete-time survival with fertility and production in dairy cattle using bivariate models, Genet. Sel. Evol., 39, 391–404, 2007.

Jairath, L., Dekkers, J. C. M., Schaeffer, L. R., Liu, Z., Burnside, E. B., and Kolstad, B.: Genetic evaluation for herd life in Canada, J. Dairy Sci., 81, 550–562, 1998.

López de Maturana, E., Legarra, A., Varona, L., and Ugarte, E.: Analysis of fertility and dystocia in Holsteins using recursive models to handle censored and categorical data, J. Dairy Sci., 90, 2012–2024, 2007.

Miglior, F., Muir, B. L., and van Doormaal, B. J.: Selection indices in Holstein cattle of various countries, J. Dairy Sci., 88, 1255–1263, 2005.

Pritchard, T., Coffey, M., Mrode, R., and Wall, E.: Genetic parameters for production, health, fertility and longevity traits in dairy cows, Animal, 7, 34–46, 2013.

Sasaki, O.: Estimation of genetic parameters for longevity traits in dairy cattle: A review with focus on the characteristics of analytical models, Anim. Sci. J., 84, 449–460, 2013.

Sewalem, A., Miglior, F., Kistemaker, G. J., and Van Doormall, B. J.: Analysis of the relationship between somatic cell score and functional longevity in Canadian dairy cattle, J. Dairy Sci., 89, 3609–3614, 2006.

Sewalem, A., Miglior, F., Kistemaker, G. J., Sullivan, P., and Van Doormall, B. J.: Relationship between reproduction traits and functional longevity in Canadian dairy cattle, J. Dairy Sci., 91, 1660–1668, 2008.

Sasaki, O.: Estimation of genetic parameters for longevity traits in dairy cattle: A review with focus on the characteristics of analytical models, Anim. Sci. J., 84, 449–460, 2013.

VIT: Beschreibung der Zuchtwertschätzung für Milchleistungsmerkmale, Zellzahl, Exterieurmerkmale, Nutzungsdauer und Zuchtleistungsmerkmale, Verden/Aller, Germany, 2014.

Vollema, A. R. and Groen, A. F.: Genetic parameters of longevity traits of an upgrading population of dairy cattle, J. Dairy Sci., 79, 2261–2267, 1996.

Weigel, K., Lawlor Jr., T., VanRaden, P., and Wiggans, G.: Use of linear type and production data to supplement early predicted transmitting abilities for productive life, J. Dairy Sci., 81, 2040–2044, 1998.

Zavadilová, L., Němcová, E., and Stípková, M.: Effect of type traits on functional longevity of Czech Holstein cows estimated from a Cox proportional hazards model, J. Dairy Sci., 94, 4090–4099, 2011.