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Genomic evaluation of age at first calving

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ABSTRACT

From their time of birth until their first lactation, dairy heifers incur management, health, and feed expenses while not producing milk. Much effort has been made to estimate optimal ages of first calving (AFC) for cows to reduce these costs, which can be as high as \$2.50 per day, and ensure that animals are productive earlier in life. To identify AFC for 3 dairy cattle breeds (Holstein, Jersey, and Brown Swiss) that maximizes production, we retrieved phenotypic records for more than 14 million cows calving between 1997 and 2015 from the US national dairy database. The mean AFC for Holstein and Jersev has decreased by 2.4 and 2.7 mo, respectively, since 2006. When comparing the association of AFC with production and fertility traits, we found that decreased AFC was correlated with greater fertility and higher milk yield for all but the earliest group (18 to 20 mo). We also identified an unfavorable correlation of lower AFC with increasing stillbirth rates in Holstein (0.047 least squares means compared with a baseline of 24 mo) and Brown Swiss (0.062 least squares means). Finally, we identified favorable genetic correlations of lower AFC with lifetime net merit, heifer conception rate, cow conception rate, and daughter pregnancy rate in Holstein and Jersey cattle, and favorable correlations for net merit and heifer conception rate in Brown Swiss. To maximize lifetime production and reduce the effects of AFC on stillbirth, the AFC that maximizes production for Holstein and Brown Swiss is 21 to 22 mo, and for Jersey it is 20 to 21 mo. However, the effect of AFC on stillbirth reduces the benefits of calving at very young ages. Calculated genomic predicted transmitting ability for AFC showed an improvement in reliability of 20 percentage points in genomic young bulls compared with parent averages in Holstein, suggesting that genomic testing can improve selection for this trait.

Key words: genomic selection, age at first calving, trait

INTRODUCTION

Heifer rearing is a major expense for the US dairy industry, accounting for 15 to 20% of the total cost of producing milk. Total rearing costs are difficult to predict, as they appear to be influenced heavily by growth (Bach and Ahedo, 2008), estrus (Gabler et al., 2000), and mortality (Tozer and Heinrichs, 2001) in heifers. Of these, growth is perhaps the most important trait as it is frequently shown to be correlated with both BW and age at first calving (AFC; Le Cozler et al., 2008). Assuming a cost of \$2.50 per day for raising heifers (http://www.dairyherd.com/dairy-resources/ calf-heifer/manager-to-manager/Whats-it-cost-toraise-a-dairy-heifer-239463381.html; https://fvi.uwex. edu/heifermgmt/files/2015/02/Putting-a-price-tag. pdf), direct benefits for reducing AFC could be as high as \$75 per animal per month. Given that an earlier AFC allows an animal to generate income earlier, much work has been done to calculate the effects of AFC on production traits in dairy cattle (Do et al., 2013; Mohd

A prior study showed an estimated decrease in rearing costs of 18% when calving age was reduced from 25 to 21 mo (Tozer and Heinrichs, 2001). Ettema and Santos (2004) found that a reduction in AFC in first-parity Holsteins was correlated with increases in stillbirth and a lower first-lactation milk production (**FLP**), which needs to be factored into overall profitability estimates. Curran et al. (2013) found that cows calving before 24 mo have lower FLP, and reported that optimal AFC in terms of FLP and lifetime production vary with herd management characteristics, suggesting that optimal AFC may vary from herd to herd. It appears that selecting for AFC must be balanced against the reduction in FLP (Mohd Nor et al., 2013) and increased stillbirth rate to maximize the return on individual dairy cattle of any breed. Polish Holsteins calving before 23 mo of age had better fertility and lower culling risk than cows calving later (Zavadilová and Štípková, 2013). To iden-

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tify an AFC that reduces stillbirth risk and maximizes milk production in 3 major US dairy breeds [Holstein (HO), Jersey (JE), and Brown Swiss (BS)], we estimated the effect of AFC on 14 traits using data derived from the Council on Dairy Cattle Breeding's (Bowie, MD) national dairy database (https://www.uscdcb. com/cgi-bin/general/Qpublic/query-selection.cgi).

MATERIALS AND METHODS

Data consisted of records stored in the national dairy database at the Council on Dairy Cattle Breeding and included 13,947,041 Holstein, 1,205,096 Jersey, and 90,465 Brown Swiss cows with first calvings from January 1, 1997, to December 31, 2015. Sires were required to be 2 to 20 yr old and AFC was limited to 18 to 35 mo. These filters removed less than 1% of the total records for Holstein and Jersey calvings, and approximately 1.4% of the records of Brown Swiss calvings for the studied years. Statistical analyses of all traits considered in this study were performed using the general linear models procedure of SAS version 9.4 (SAS Institute Inc., Cary, NC). Traits were analyzed using the linear model

$$y = HY + YSM + AFC_i$$

where y was the trait being analyzed, HY was the herd-year of calving, YSM was the year-state-month of calving, and AFC_i was the age at first calving category $(i = 18 \text{ to } 20, 21, 22, \dots, 31, \text{ and } 32 \text{ to } 35 \text{ mo}).$ Use of state-month instead of year-state-month (YSM) to eliminate the double-counting for years in the model did not significantly change the estimates of the model (Pearson correlation of the estimates from the 2 models = 1). Age at first calving was fit as a categorical variable because previous work by our group found that fitting some quantitative trait data as covariates resulted in slightly lower correlation with actual phenotypes (Kuhn and Hutchison, 2008). Additionally, quite large differences in AFC estimates were found among our classified AFC groups, suggesting that a polynomial curve would not fit the data well.

The phenotypes analyzed included actual milk, fat, and protein yield, milk persistency, cow and heifer conception rate, daughter pregnancy rate, calving ease, and stillbirth. Lifetime traits including lifetime milk, fat, and protein yield, DIM, and days open were also examined. To calculate average milk yield per day of life, we had to estimate the days of life for each cow in the data set. Days of life were calculated by subtracting the birth date of the animal from the left-the-herd date. In cases where the animal did not have a left-theherd date, the last calving date plus DIM for the last lactation was used as an approximation. Least squares means (SAS Institute Inc.) and significance levels were computed for each AFC group. *P*-values were computed with a 2-tailed *t*-test for the null hypothesis that performance in other groups differed from the mean for 24 mo. The best AFC age groups for Holstein and Jersey were determined by identifying the AFC age group that maximized lifetime milk, fat, and protein production. Due to the variance caused by lower sample counts for Brown Swiss AFC groups, we were unable to determine an AFC that maximizes lifetime production and instead identified the AFC group that maximized heifer conception rate (**HCR**) and minimized stillbirth.

We also compared the use of our linear model against an animal model that used pedigree kinship to estimate AFC effects on actual milk production. The model we used for comparison was

$$y = HY + YSM + AFC_i + a_i,$$

where the terms HY, YSM, and AFC_i are the same for the equation above, y is the trait (in this case, actual milk yield), and a_i is the breeding value for the *i*th animal. Values were estimated using multitrait animal model software (VanRaden et al., 2014). We found that, for actual milk yield in Holsteins (Supplemental Table S1; https://doi.org/10.3168/jds.2016-12060), the predicted values were nearly identical (Pearson's r = 0.9997; P < 0.001) to the values generated by our linear model. Therefore, we chose to use the linear model for the remainder of our analysis of the effects of AFC on other production traits.

Traditional PTA

Predicted transmitting abilities for AFC were calculated using the following within-breed animal model:

$$AFC = HYS + A + e,$$

where AFC is age at first calving, HYS is the fixed effect of herd-year-season of birth, A is the random additive genetic effect, and e is the random residual error. Animal and residual error effects were distributed as $N\left(0, \mathbf{A}\sigma_a^2\right)$ and $N\left(0, \mathbf{I}\sigma_e^2\right)$, respectively, where \mathbf{A} is the numerator relationship matrix, \mathbf{I} is an identity matrix, σ_a^2 is the additive genetic variance, and σ_e^2 is the error variance. The (co)variance components were estimated using AIREMLF90 ver. 1.45 (Misztal, 1999), and multistep genomic PTA were computed using software of VanRaden et al. (2014) for the traditional evaluation and VanRaden (2008) to include genomic information.

Genomic PTA

Allele substitution effects for the 45,188 SNP used in the December 2012 US genetic evaluations were estimated from deregressed traditional PTA using an infinitesimal alleles model with a heavy-tailed prior, in which smaller effects are regressed further toward 0 and markers with larger effects are regressed less to account for a non-normal distribution of marker effects (VanRaden, 2008). Final genomic predictions combined 3 terms by selection index: (1) direct genomic prediction, (2) parent average computed from the subset of genotyped ancestors using traditional relationships, and (3) published parent average (VanRaden et al., 2009). Gains in reliability from the addition of genomic information were calculated as the difference between the realized genomic reliability and the reliability of traditional parent average (VanRaden et al., 2009).

The genomic data set included 50K SNP genotypes for 204,618 animals, 53,644 of which constituted the training population used for the prediction of SNP effects. The data set included genotypes from the BovineSNP50 BeadChip (Illumina Inc., San Diego, CA) for most bulls, as well as low-density genotypes for most cows imputed to 50K using version 2 of findhap (VanRaden et al., 2011). Approximate genetic correlations were estimated using the CORR procedure in SAS ver. 9.4.

RESULTS AND DISCUSSION

Trends in AFC

Based on records for animals with first calvings from 1997 to 2015, the overall mean AFC in the US dairy herd was 24.5 ± 2.73 mo for Holstein, 22.9 ± 2.74 mo for Jersey, and 26.3 ± 3.13 mo for Brown Swiss. This

was lower than what Nilforooshan and Edriss (2004) found in their Iranian Holstein population (26.8 mo) and Hare et al. (2006) found for HO, JE, and BS (26.9, 25.6, and 28.0 mo, respectively), suggesting increased selection for, or better management resulting in, earlier breedings in recent years. Indeed, when comparing average AFC in 1997 to 2012 (Table 1), higher percentages of HO and JE cows calved at an earlier age in more recent years compared with 1997. We found a 4-fold increase in the percentage of HO heifers that calved at 22 mo in 2012 (21.93% of all calvings) compared with the same month cutoff in 1997 (5.59%). A similar increase was observed in the earliest category of JE AFC (at 21 mo, 4.95% of all calvings in 1997; 22.78% in 2012); however, JE heifers had relatively earlier calvings than HO in 1997 to begin (at 22 mo, 11.25% and 5.59% of all JE and HO calvings, respectively). The largest discrepancy was observed in the 18 to 20 mo time frame, where 23.22% of JE calvings were observed in 2012, an increase of over 20 percentage points from 1997. Brown Swiss showed little change in percentage of breedings per AFC group from 1997 to 2012 (Pearson's r = 0.5388; P > 0.10), with a slight trend toward earlier calvings by 2012.

Maximizing Lifetime Production with AFC

Given phenotypic correlation between AFC and other production traits (Do et al., 2013; Mohd Nor et al., 2013), we sought to identify an AFC for each breed that maximizes average lifetime productive trait estimates. Ettema and Santos (2004) identified an AFC from 23 to 24.5 mo as being the economically optimal value for 3 California dairy herds, so we established a baseline AFC of 24 mo for our analysis. We calculated the least squares means for each AFC age grouping for

Table 1. Distribution of age at first calving (AFC) by month and percentage of calvings¹

AFC, mo	Holstein		Jersey		Brown Swiss	
	1997	2012	1997	2012	1997	2012
18-20	0.66	2.20	2.32	23.22	0.26	0.57
21	1.69	9.38	4.95	22.78	0.59	3.48
22	5.59	21.93	11.25	19.22	1.97	8.76
23	12.57	21.39	17.33	12.78	6.11	11.89
24	17.45	16.08	17.94	8.48	10.34	14.31
25	15.17	10.03	12.67	4.91	12.25	12.51
26	12.39	6.62	9.62	3.02	13.46	11.34
27	9.23	4.18	6.58	1.86	11.37	9.23
28	7.18	2.79	4.96	1.28	10.87	6.84
29	5.29	1.82	3.57	0.82	9.34	5.70
30	3.97	1.26	2.76	0.55	7.29	4.86
31	2.87	0.82	1.83	0.37	4.38	3.42
32 - 35	5.94	1.48	4.22	0.71	11.75	7.09

¹Values indicate percentages of all calvings; values within the same year sum to 100.

the following traits: first-lactation actual milk, fat, and protein yield, as well as lifetime milk, fat, protein, DIM, and days open. We also calculated PTA for cow conception rate, heifer conception rate, calving ease, stillbirth, and daughter pregnancy rate. For first-lactation milk and component yields, we identified the same trends as Ettema and Santos (2004), and Mohd Nor et al. (2013), where decreasing AFC reduced actual milk and component yields of the first lactation (Figure 1). Delaying AFC from 21 to 32 mo appeared to increase the first-lactation milk yield by ~1,000 kg for all 3 breeds, likely due to increased maturation of the dam; however, this represented an 11-mo delay of the onset of the first lactation. We next considered the effects of AFC on the lifetime production traits.

When looking at lifetime traits, we identified maximal production in lifetime milk, fat, protein, DIM, and days open in HO and JE cattle with an AFC of 21 mo compared with those at 24 mo (Figure 2). For HO, we noted an increase of 510 and 632 kg at 21 and 22 mo relative to 24 mo, respectively, for lifetime milk yield. WE observed a sharp decline in production in HO for the earliest AFC values that decreased under the baseline established at 24 mo, suggesting mitigating factors for animals that calved too early in the breed. Both JE and BS had consistent increases in lifetime production traits below an AFC of 22 mo, though increases identified in BS are likely an artifact due to a relatively smaller number of breedings at that AFC grouping (0.57% of all breedings in 2012). Indeed, the standard error of values for lifetime production traits in BS was far higher than in HO and JE and prevented the selection of a single age group that maximized production compared with the baseline. The only exception to the above trends was found in the lifetime days open trait, which showed precipitous declines in numbers of days open in BS cows at earlier AFC values, particularly at 22 mo. Given that the BS breed had a higher mean AFC value compared with the other breeds, we cannot rule out that much of this variance may be due to larger sample sizes in the 24 mo group (14.31%) of all calvings) compared with the 22 mo group (8.76%). Historically, BS cattle have been identified as a breed that tends to mature more slowly than other breeds (Heinrichs and Hargrove, 1994). Another interesting discrepancy was identified in JE cattle, which had increased milk, fat, and protein yields at an AFC below 21 mo compared with the other 2 breeds, which had relatively large declines in production at the same AFC value. This may be an indirect effect resulting from lower relative stillbirth and calving ease scores for JE cattle in earlier months (Table 2) versus HO (Table 3) and BS cattle (Table 4). Average milk production per day of life (Supplemental Table S2; https://doi. org/10.3168/jds.2016-12060) was consistently higher in all 3 breeds at earlier AFC categories. All 3 breeds had

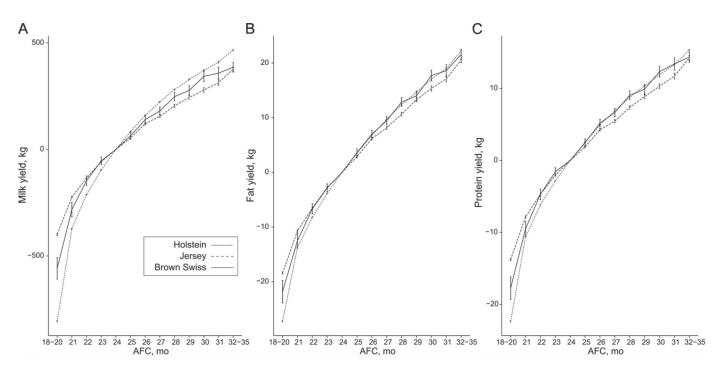


Figure 1. Least squares means of each age at first calving (AFC) group compared with a baseline of 24 mo for actual first-lactation (A) milk yield, (B) fat yield, and (C) protein yield in Holstein, Jersey, and Brown Swiss cattle. Standard errors are represented as bars above each data point.

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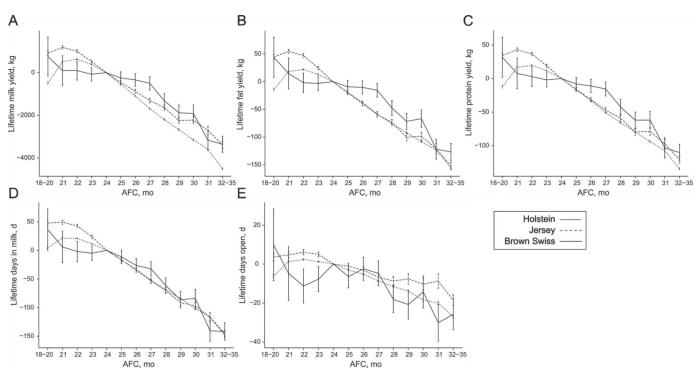


Figure 2. Least squares means of each age at first calving (AFC) group compared with a baseline of 24 mo for lifetime (A) milk yield, (B) fat yield, (C) protein yield, (D) DIM, and (E) lifetime days open in Holstein, Jersey, and Brown Swiss cattle. Standard errors are represented as bars extending from each data point.

a higher milk per day of life value at the earliest AFC categories, suggesting that animals able to breed earlier likely stay in the herd longer. Whereas this may be due to improved fertility and health of the animals in this AFC category, our results still suggest that AFC may serve as a reliable indirect indicator of general animal survivability and productivity.

Earlier AFC groups had improved effects for CCR, HCR, DPR, and calving ease (Tables 2, 3, and 4); however, they also had negative effects on stillbirth rates for all 3 breeds, suggesting that early-AFC heifers were able to get pregnant faster due to high fertility and were able to deliver calves easier, but were less likely to deliver a live calf. The increasing trend of stillbirth incidence was similar to the trend observed by Ettema and Santos (2004); however, they found higher proportions of stillbirths in AFC groups of 23 to 25 mo. Intuitively, higher HCR relative to 24 mo of AFC for HO (0.221),

Table 2. Least squares means for age at first calving (AFC) groups of Jersey cows relative to 24 mo for PTA of cow conception rate (CCR), heifer conception rate (HCR), and daughter pregnancy rate (DPR) and the phenotypes calving ease (CE) and stillbirth (SB)

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AFC, mo	CCR	HCR	CE	SB	DPR
18-20	0.188†	0.315†	-0.020**	0.015†	0.116†
21	0.158^{+}	0.221^{+}	-0.008	0.003	0.111†
22	0.095^{+}	0.128^{+}	-0.012*	-0.002	0.067^{+}
23	0.040^{+}	0.056^{+}	0.003	0.001	0.025^{*}
24	0	0	0	0	0
25	-0.040^{+}	-0.041^{+}	-0.002	0.005	-0.032^{**}
26	-0.052^{+}	-0.082^{+}	0.008	0.003	-0.033^{*}
27	-0.065^{+}	-0.107^{+}	0.023	0.016^{*}	-0.046^{**}
28	-0.086^{+}	-0.146^{+}	0.039^{*}	0.009	-0.056^{**}
29	-0.092^{+}	-0.172^{+}	0.065^{**}	0.034	-0.044*
30	-0.118^{+}	-0.181^{+}	0.097^{+}	0.029	-0.089^{+}
31	-0.089^{+}	-0.194^{+}	-0.026	0.015	-0.042
32 - 35	-0.065^{+}	-0.146^{+}	0.108^{+}	0.034^{*}	-0.004

P < 0.05, P < 0.01, P < 0.001.

Table 3. Least squares means for age at first calving (AFC) groups of Holstein cows relative to 24 mo for PTA of cow conception rate (CCR), heifer conception rate (HCR), and daughter pregnancy rate (DPR) and the phenotypes of calving ease (CE), and stillbirth (SB)

AFC, mo	CCR	HCR	CE	SB	DPR
18-20	0.100†	0.221†	-0.035^{\dagger}	0.047^{+}	0.101†
21	0.163^{+}	0.279^{+}	-0.028^{+}	0.015^{+}	0.147^{+}
22	0.137^{+}	0.206^{+}	-0.018^{+}	0.006^{+}	0.126^{+}
23	0.073^{+}	0.097^{+}	-0.008^{+}	0.002^{+}	0.068^{+}
24	0	0	0	0	0
25	-0.053^{\dagger}	-0.083^{\dagger}	0.007^{+}	-0.001	-0.054^{\dagger}
26	-0.086^{+}	-0.148^{+}	0.013^{+}	-0.001*	-0.084^{+}
27	-0.112^{+}	-0.194^{+}	0.023^{+}	-0.001	-0.111^{+}
28	-0.132^{+}	-0.235^{+}	0.030^{+}	0.002	-0.132^{+}
29	-0.142^{+}	-0.268^{+}	0.032^{+}	-0.001	-0.140^{+}
30	-0.161^{+}	-0.297^{+}	0.042^{+}	0.003	-0.156^{+}
31	-0.167^{+}	-0.318^{+}	0.051^{+}	0.004^{*}	-0.162^{+}
32 - 35	-0.164^{+}	-0.347^{++}	0.087^{+}	0.007^{+}	-0.161^{+}

 $*P < 0.05, \dagger P < 0.001.$

JE (0.315), and BS (0.380) for the 18 to 20 mo AFC groups suggest that these animals may enter puberty faster than other AFC groups or are more likely to become pregnant on the first service attempt. Increased stillbirth effects for HO (0.047) and BS (0.062) at 18 to 20 mo counteract this increase in fertility, suggesting that animals are able to conceive but have far riskier pregnancies due to immature reproductive systems, smaller BW, or other confounding factors. The confluence of these trends suggest that an optimum AFC value can be identified that minimizes stillbirth effects while maximizing increased lifetime production. We were able to identify an optimum AFC of 21 to 22 mo for BS cattle by maximizing HCR (0.335) and reducing stillbirth (0.016) observations.

When field data are used to identify optimal management practices (e.g., Kuhn et al., 2005), a risk of bias exists because farmers may avoid practices that they believe to be undesirable or less profitable and only survivors contribute data for analysis. Considerable heterogeneity also exists among management practices adopted on farms. This is typically accounted for by including management effects in the model so that performance on different farms is comparable. When herd-year effects were removed from the models used in the current study and effects were recomputed, the preferable AFC remained unchanged (results not shown). This suggests that the reported values of 21 to 22 mo for BS and HO and 20 to 21 mo for JE do represent the most desirable ages at which to calve heifers of those breeds.

Sire Evaluations

Summary statistics for sire evaluations by breed are shown in Table 5. Genetic trends, estimated by regression of PTA on sire birth year (data not shown), were negative across time for HO and JE, suggesting that

Table 4. Least squares means for age at first calving (AFC) groups of Brown Swiss cows relative to 24 mo for PTA of cow conception rate (CCR), heifer conception rate (HCR), and daughter pregnancy rate (DPR) and the phenotypes of calving ease (CE), and stillbirth (SB)

AFC, mo	CCR	HCR	CE	SB	DPR		
18-20	0.415†	0.380†	-0.132	0.062*	0.163		
21	0.204^{*}	0.335^{+}	-0.004	0.016	0.085		
22	0.179^{*}	0.195^{+}	-0.013	0.003	0.087		
23	0.094^{*}	0.071*	0.014	0.019^{**}	0.075^{*}		
24	0	0	0	0	0		
25	0.012	-0.078*	0.031	0.011^{+}	0.042		
26	-0.032	-0.097^{**}	0.013	0.011	0.035		
27	-0.081	-0.181^{+}	0.000	0.005	0.003		
28	-0.084	-0.171^{+}	0.022	0.004	0.024		
29	-0.079	-0.175^{+}	0.033	0.022	0.014		
30	-0.077	-0.226^{+}	-0.018	-0.015	0.041		
31	-0.104	-0.233^{+}	0.015	-0.003	0.032		
32 - 35	-0.109*	-0.233^{+}	0.074	0.028	0.065		

 $*P < 0.05, **P < 0.01, \dagger P < 0.001.$

Breed^1	Sire status ²	N	$\mathrm{Mean}\pm\mathrm{SD}$	Minimum	Maximum	${\rm Mean}\ {\rm REL}^3$	$\operatorname{PA}\operatorname{REL}^4$
BS	A	30	-0.3 ± 0.5	-1.2	0.6	65	32
	G	57	-0.4 ± 0.5	-1.7	0.6	32	21
	Р	89	-0.2 ± 0.4	-1.4	1.0	37	25
HO	А	518	-3.7 ± 2.5	-9.4	7.9	82	38
	G	2,173	-5.0 ± 1.9	-11.4	4.1	66	24
	Р	3,976	-4.3 ± 2.2	-10.9	5.2	69	30
JE	А	118	-0.2 ± 0.2	-0.6	0.3	77	37
	G	401	-0.2 ± 0.2	-0.7	0.3	51	26
	Р	515	-0.2 ± 0.1	-0.6	0.5	56	31

Table 5. Summary statistics of sire evaluations for age at first calving (days), sire genomic PTA reliabilities, and parent average reliabilities

 $^{1}BS = Brown Swiss, HO = Holstein, and JE = Jersey.$

 ^{2}A = active bull; G = genotyped bull >12 mo old with <10 daughters being actively marketed; P = young bull not actively marketed.

³REL = average reliability of sire genomic PTA.

 ${}^{4}\text{PA}$ REL = average reliability of parent average PTA.

AFC is decreasing over time. This confirms observations made on the percentage of all calvings at AFC groups between 1997 and 2012 (Table 1), where a trend toward an earlier AFC was identified in HO and JE. For BS cows, the genetic trend remained constant over time, which is also consistent with comparisons of calvings from 1997 to 2012. It also appears that selection for shorter AFC may be happening indirectly, as HO genotyped and not actively marketed bulls have PTA that average less than 0 (Table 5). Bull sire status in Table 5 refers to the following categories: A bulls are in active AI; G bulls are genotyped, older than 1 yr with less than 10 daughters being marketed; and P bulls are young bulls that are not being actively marketed. Either through indirect selection for AFC by breeding high-HCR heifers or through direct selection of heifers that mature earlier, it appears that cattle breeders are already targeting early AFC animals in HO. The trend was less substantial in JE and BS for different reasons. It appears that the JE herd has almost reached an AFC for the breed (46% of all calvings at ≤ 21 mo; Table 1) that maximizes production, whereas BS trends show almost no selection for the trait. Additional factors may have precluded the selection of earlier AFC in BS; however, we cannot rule out the possibility of the influence of management decisions on the trait. Calculated genomic PTA for AFC suggest that this trait can be reliably predicted in genomically tested sires, as we discovered a 42-, 25-, and 11-percentage point increase in reliability compared with parent averages in HO, JE, and BS sires (Table 5). Reliabilities of prediction in BS may have been hampered by the low number of sires in the reference population used for the estimate, as reliabilities for BS genotyped and young sires were only 32 and 37%, respectively. Genomic PTA reliabilities for AFC for G and P sires of the HO and JE breeds are comparable to genomic reliabilities for productive traits (Wiggans et al., 2016).

Approximate genetic correlations of AFC with other traits (Table 6) show that increasing AFC results in lower yield, poorer longevity, reduced fertility, and lower lifetime profit. These correlations may explain the observed genetic trend because the lifetime net merit index (NM\$; VanRaden and Cole, 2014) places considerable emphasis on milk components yield, fertility, and longevity. When looking at correlations of AFC with individual traits, some notable differences were observed within the BS breed. It appears that milk yield (-0.03) is not significantly affected by increasing AFC, whereas fat percentage (0.05) increases with AFC. This suggests that breeding goals for BS that maximize components may be indirectly selecting sires with higher PTA for AFC. The incorporation of AFC into BS mating programs or indexes may provide more benefit to the breed than in HO and JE because of the large difference in current and our selected AFC ideal for the breed and the improvement of NM\$, as shown by the correlation of the index with AFC (-0.44).

We noted that earlier AFC is likely an indirect effect that is exhibited by animals that have better growth, health, or fertility traits in the population. For exam-

Table 6. Genetic correlations among sire evaluations for age at first calving (with reliabilities ≥ 0.90) and PTA of other traits for Brown Swiss (BS), Holstein (HO), and Jersey (JE) bulls

Trait^1	$\begin{array}{c} BS\\ (n=37) \end{array}$	$\begin{array}{c} \mathrm{HO} \\ \mathrm{(n=1,886)} \end{array}$	${\rm JE} \atop (n=261)$
Milk	-0.03	-0.43^{\dagger}	-0.49^{+}
Fat	0.05	-0.41^{+}	-0.64^{\dagger}
Protein	-0.38*	-0.53^{\dagger}	-0.61^{+}
Daughter pregnancy rate	-0.41*	-0.30^{\dagger}	0.07
HCR	-0.49^{**}	-0.45^{\dagger}	-0.25^{\dagger}
CCR	-0.50^{**}	-0.27^{\dagger}	0.04
Productive life	-0.37^{*}	-0.34^{\dagger}	-0.46^{\dagger}
Net merit	-0.44^{**}	-0.54^{+}	-0.72^{+}

¹HCR = heifer conception rate; CCR = cow conception rate. *P < 0.05, **P < 0.01, and †P < 0.001. ple, bovine respiratory disease incidence has a strong inverse correlation with animal survival (Bach, 2011; Stanton et al., 2012), which may be a contributor to an increase in AFC in affected animals. Given the paucity of incidence data in the national database, it is difficult to assess the effects of bovine respiratory disease and other calfhood illnesses on AFC, so we cannot rule out the effects of animal health on this trait. The main benefit of selecting for AFC over other covariates is in the completeness of the calving records and the lower cost of collecting this data over a more expensive phenotype, such as ADG. Individual management strategies that are designed to increase milk yield may benefit from genetic selection for earlier AFC due to its desirable phenotypic correlations with other traits. To identify an optimal AFC for this and other such management goals, controlled experiments that quantify the effects of breeding early AFC heifers later than predicted by the genomic model are needed.

Economic Impact and Potential for Inclusion in NM\$

The direct benefits of a reduction of AFC from 24 to 22 mo in Holstein would include a reduction of \$150 in heifer rearing costs (estimated at \sim \$75 per month per heifer). Indirect benefits derived from the same 2-mo reduction in AFC in Holstein would be an increase in lifetime milk yield of 632 kg, but an increase of 1% in stillbirths. If the value per calf is \$200 per animal and milk price is \$0.37 per kilogram, the estimated indirect benefits and costs of these traits are -\$2 and \$236 for stillbirths and increased lifetime milk, respectively. This suggests that the cumulative indirect benefits (\$234) of reducing AFC outweigh the direct benefits (\$150); however, we would like to emphasize that the relationships estimated here are nonlinear and would not apply to further reduction of AFC to 18 to 20 mo in the Holstein breed. Further reduction in AFC away from the optimal values identified in our study would increase stillbirth and potentially lower lifetime milk production, putatively offsetting any benefits. Adverse effects on stillbirth can be managed through careful mate selection (Cole et al., 2007), but farmers and consumers may prefer management strategies that avoid increased calf deaths. It is difficult account for those preferences when computing economic values.

Given the correlation of AFC with other production traits, AFC would only receive the \$2.50 per day direct value in the NM\$ index (https://aipl.arsusda.gov/reference/nmcalc-2014.htm). Given its standard deviation of 2.5 d of true transmitting ability in active AI Holstein bulls (Table 5), AFC would account for no more than 3% of emphasis in NM\$ [2.5 SD \times \$2.50 direct value/(2.5 SD × \$2.50 direct value + \$193 SD of true transmitting ability from 2017 NM\$) = $\sim 3\%$]. If AFC is included in the NM\$ index, HCR would be given less emphasis than its current value (2.3 NM\$) given the high correlation it has with AFC (-0.49 genetic correlation in Holstein). Inclusion of this trait in the index will result in economic benefit to dairy producers with the added caveat that there is an intermediate optimum for AFC that reduces costs (i.e., stillbirth) and maximizes lifetime production.

CONCLUSIONS

Our results show that an ideal AFC that maximizes production is actually 2 to 5 mo lower than the current breed average for HO, and BS, suggesting that selection for an earlier AFC may improve profitability in HO and BS cattle. Earlier AFC is favorably correlated with NM\$, production, and fertility traits, suggesting that selection for the trait may improve herd performance over time. However, we confirmed a concerning trend where the earliest AFC groups had higher incidence of stillbirth in HO and BS cattle. This suggests that there should be a selection index for the breeds which includes AFC, maximizes lifetime production and fertility and minimizes stillbirth incidence. Our data suggest that AFC genomic PTA can be predicted with reliabilities averaging 66% for young and 82% for daughter-proven HO sires and 51% for young and 77% for daughterproven JE sires with some moderate successes in BS sires (reliabilities = 32 to 65%). Selection for the AFC in these 3 breeds of cattle that maximizes lifetime production is likely to coincide with improved HCR, productive life, and overall profitability. Bulls should be selected using an index that includes AFC, and phenotypic stillbirth trends should be monitored closely to identify any undesirable changes resulting from management practices which seek to minimize AFC.

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