Realized genetic selection differentials in Canadian Holstein dairy herds

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ABSTRACT

Estimated breeding values for a selection index, production, durability, health, and fertility traits for Canadian Holstein bulls and cows born from 1950 and 1960, respectively, were used to define and determine realized genetic selection differentials (GSD) and generation intervals along the 4-path model of genetic improvement and the variability among herds in realized GSD. The effects of some non-genetic factors on realized GSD were also determined. The mean generation intervals of the sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) pathways reduced, respectively, from 9.7, 7.5, 7.7, and 4.7 years in 1980 to 2.3, 2.5, 4.8, and 3.6 years in 2016. The realized GSD of lifetime performance index and 305-d milk, fat, and protein yields for the SB and DB paths were greater than those of the SC and DC, and realized GSD for DB were increasing for all production traits and the index after 2009. With the exception of daughter fertility (DF), we found zero to negative selection in the DC path for all the traits studied, due to the minimal opportunity for selection in that path. No clear trends were observed in realized GSD of SB, DB, or SC paths for mammary system, dairy strength, feet and legs, or herd life. The realized GSD for DF in the SB, DB, and SC remained largely negative, except after the early 2000s when positive realized GSD were observed in the SB and DB paths. The realized GSD for DF in the DC path remained positive throughout the period of the study, though mostly non-significantly different from zero, except for 2014 and 2015. Realized GSD for somatic cell score in the SB, DB, and SC paths showed increasing and favorable trends. Year of conception, housing system, agricultural region, and their interactions had significant effects on realized GSD of some traits in the SC and DC paths. We also observed considerable variations in realized

GSD among herds. The population mean realized GSD and those of the top and bottom 10% of herds could serve as benchmarks that individual herds could use to monitor their past selection and make changes if they are not moving in the intended direction.

Key words: realized genetic selection differential, generation interval, Holstein, herd

INTRODUCTION

Most livestock breeders and producers seek to maximize genetic gains in traits of economic importance. For decades, genetic selection has resulted in substantial increases in productivity in farmed livestock (Van Raden, 2004; Oltenacu and Broom, 2010; García-Ruiz et al., 2016). Genetic gain in animal productivity has a strong association with farm profitability (Thompson et al., 2015), making genetic selection important to a profitable animal farming business.

Annual genetic progress is dependent on genetic variation, accuracy of EBV, selection intensity or genetic selection differentials (**GSD**), and generation interval (**L**). Genetic selection differential is one of the tools used to measure selection applied in a national breeding program. Rather few studies have examined GSD, and those have focused mostly on production traits (Van Tassell and Van Vleck, 1991; Burnside et al., 1992; Nizamani and Berger, 1996) and fitness traits (García-Ruiz et al., 2016) in the US Holstein cattle population along the 4-path selection model (Rendel and Robertson, 1950). For milk production, Van Tassell and Van Vleck (1991) reported mean GSD of 884, 598, 235, and 28 kg in the sire-to-bull (**SB**), dam-to-bull (**DB**), sire-to-cow (**SC**), and dam-to-cow (**DC**) paths between 1967 and 1971. García-Ruiz et al. (2016) also reported mean GSD of 919, 752, 579, and 36 kg for milk yield and 42.9, 33.9, 30.3, and 1.5 kg for fat yield in the SB, DB, SC, and DC paths, respectively, between 2011 and 2015 in the US Holstein.

Some studies on selection compute GSD as the difference between the mean EBV of selected cows and the mean EBV of all cows born during the same year

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(Nizamani and Berger, 1996; Kawahara et al., 2002). Although this definition may be theoretically appropriate if selection is only within cohorts, they may not be wholly beneficial to dairy breeders, because breeders will seek to select the best bulls or cows available at any given time for breeding. In addition, the contemporary base group from which selected sires or dams' EBV are deviated in order to compute the GSD of selected sires or dams does not fully represent the contemporary group of these selected sires or dams. For instance, Nizamani and Berger (1996) and Kawahara et al. (2002) defined the GSD of sire-bulls as the mean EBV of selected sire-bulls minus the mean EBV of all cows born the same year. This has the tendency to overestimate the GSD of the sire-bulls, because they are not being compared with their true contemporaries, which are all bulls born that year. Additionally, during the pre-genomic era, when superior bulls were used for many years, the computation of a bull's GSD from its year-born mates does not entirely reflect the superiority of the selected bull in present times, as many genetically superior young bulls might be available for breeding had they been considered in the appropriate contemporary base group for comparison. When these realities are ignored, selection realized in a population using the definition of Nizamani and Berger (1996) and Kawahara et al. (2002) will be sub-optimum and may not be so relevant to dairy breeders and producers.

Genetic trends produced by organizations that work with genetic information have been the main tool producers have used to measure their past selection. Genetic trends, however, do not tell the whole story about the genetic improvement in individual dairy herds, as it is possible that few herds were intensively selecting and could be contributing to the increasing genetic trends observed in the population, while a substantial number of herds were directly selecting less for economically important traits. Also, the national genetic trends reported are for cows or bulls, and the trends are often not partitioned into the 4 pathways of selection. These have the tendency to mislead some producers into believing that they have been progressing at a certain rate when actually they are not (Jamrozik and Schaeffer, 1991). For more appropriate and accurate monitoring of genetic selection applied by dairy producers and breeders, it is important to compare the genetic merit of selected animals with all available animals of the same sex at the time of using the selected animals for breeding.

The Canadian Holstein population constitutes 93% of the national dairy cattle herd. There are about 10,000 herds of the Holstein breed, with the average herd holding 73 cows and 81% of dairy herds located in the provinces of Ontario and Quebec. About 74% of

herds are housed in tiestalls with the rest being housed in freestalls. Seventy-five percent of herds are enrolled in milk recording programs. The breeding objective of the Canadian dairy industry is balanced with selection emphases on yield, type, health, and fertility traits (Miglior et al., 2005). The majority of matings are performed via AI, with the proportion of unproven young sire usage increasing from 41.2% in 2009 to 64.7% in 2018 (CDN, 2019).

The objectives of this study were to define and determine realized GSD and generation intervals in the Canadian Holstein dairy cattle population along the 4-path selection model, and to investigate the effects of some environmental factors on realized GSD. We also sought to determine the variability among herds in terms of realized GSD.

MATERIALS AND METHODS

Data and Traits

Data used for this study consisted of genetic evaluations from April 2018; EBV for the Canadian Holstein breed were provided by the Canadian Dairy Network (CDN), and herd recording information was provided by Centre for Dairy Expertise, Valacta, Québec. Traits' EBV included 305-d milk yield (MY), 305-d fat yield (FY), 305-d protein yield (PY), SCS, herd life (HL), daughter fertility (DF), feet and legs (FL), mammary system (MS), dairy strength (DS), and lifetime performance index (LPI). The MY, FY, and PY are the expected yields of milk, fat, and protein, respectively, during 305-d lactation in herds of average management. Somatic cell score is the expected SCS of daughters during the first 3 lactations. Herd life is the number of additional lactations that daughters are expected to last due to reduced involuntary culling compared with the average bull, independent of daughter production levels. Daughter fertility is the measurement of the expected fertility of a bull's daughters, evaluated across all lactations (Van Doormaal, 2007). Feet and legs, MS, and DS are conformation traits used to classify bulls and cows within their first and subsequent lactations. Lifetime performance index is the expected lifetime profit of future progeny based on their genetic potential for production, longevity, health, and fertility. The component traits in the LPI and their weights have been changing over time since the introduction of the index in 1991. However, at every run of genetic evaluations, the most current LPI formula is used to evaluate all cows and bulls in the data file, including even animals that are long dead or culled. Therefore, the LPI trait used in this study, from 1980 to 2015,

Table 1. Groups of agricultural regions, milking systems, and housing systems in Quebec, Canada

Factor	Classes
Agricultural regions	Abitibi-Témiscamingue, Bas-Saint-Laurent, Capitale-Nationale, Centre-du-Québec, Chaudière-Appalaches, Côte-Nord, Estrie, Gaspésie-îles-de-la-Madeleine, Lanaudière, Laurentides, Laval, Mauricie, Montérégie, Montréal, Nord-du-Québec, Outaouais, Saguenay-Lac-Saint-Jean
Milking system	Milking lines, milking parlor, robot
Housing system	Tiostall, freestall

is the same as the current formula (Fall 2018) that is applied in evaluating all animals.

All traits fall within 1 of 4 trait classes: national selection index, production, durability, and health and fertility. These traits were chosen because of their contribution to any of the following: higher revenue, increased profit, or reduced cost of production (Miglior et al., 2005). In addition to trait EBV, the genetic evaluation files contained animal identification, date of birth, sire, and dam identifications. The herd information comprised herd identification, agricultural regions in Québec, and the milking system (from which housing systems were deduced). The agricultural regions, milking systems, and housing systems (**HS**) are presented in Table 1.

Records of up to 5,546,227 Holstein cows and 72,891 bulls born since 1980 were used for the analysis. The number of records varied from trait to trait because some traits have only recently been evaluated; hence, older animals do not all have EBV for all traits. The Holstein cows and bulls were the progeny of Holstein sires and dams that were born from 1950 and 1960 onward, respectively. The number of bull and cow records varied for each of the 10 traits and the path of selection, as presented in Table 2. The 72,062 SB records mean that 72,062 bulls were sired by 2,423 uniquely identifiable sires (Supplemental Table S1; <https://doi.org/10.3168/jds.2019-16890>), that these sires had EBV for MY, and that 5,546,227 cows were sired by 71,179 uniquely identifiable bulls (Supplemental Table

S1; <https://doi.org/10.3168/jds.2019-16890>) all of which had EBV for MY as well. Likewise, the 42,924 DB and 5,185,123 DC records mean that 42,924 bulls and 5,185,123 cows were born from 2,092 and 69,526 uniquely identifiable dams, respectively, all of which had EBV for MY. The relatively small number of DB compared with SB (Supplemental Table S1; <https://doi.org/10.3168/jds.2019-16890>) indicates that a strong selection leads to a small number of cows selected to produce AI bulls in addition to the limited number of males each bull-dam can produce in her lifetime in the absence of reproductive technologies. However, sire-bulls can produce many male offspring through many contract matings, from which the eventual bulls were selected for use by AI organizations. Sire identification errors may also contribute to the high numbers of SB relative to DB, as sire identification errors of up to 23% have been reported (Geldermann et al., 1986).

Realized Genetic Selection Differentials and Generation Interval

The availability period of a sire or dam used for breeding was computed as the interval between the dates of conception of their first and last progeny. For each sire or dam, the 1st and 99th percentile dates of conception of first and last progeny were used as that sire or dam's first and last usage dates, respectively. These percentiles were used to remove extreme values. For example, a sire might have been used extensively

Table 2. Number of records in each selection path¹ for each trait

Trait	SB	SC	DB	DC
LPI ²	71,520	5,505,116	41,396	4,674,470
305-d Milk yield	72,062	5,546,227	42,924	5,185,123
305-d Fat yield	72,062	5,546,227	42,924	5,185,123
305-d Protein yield	72,062	5,546,227	42,924	5,185,123
Mammary system	71,649	5,509,633	42,632	4,732,883
Dairy strength	71,649	5,509,633	42,632	4,732,883
Feet and legs	71,649	5,509,633	42,632	4,732,883
Herd life	53,113	4,655,199	42,632	4,732,883
Daughter fertility	72,891	5,510,319	41,738	4,131,071
SCS	72,062	5,546,227	42,924	5,185,123

¹SB = sire-to-bull; SC = sire-to-cow; DB = dam-to-bull; DC = dam-to-cow.

²LPI = lifetime performance index.

for breeding for 10 years and then been dormant for another 30 or 40 years before being used to produce a few cows. This could suggest that the semen of the sire had been frozen for 30 or more years before being used again—for instance, in an experimental study. The sire's availability during the period when the sire produced few offspring is deemed an outlier and, hence, would be eliminated using the 1st and 99th percentiles. In the case of dams, the 1st- and 99th-percentile dates of conception were used to remove records of outlier dams that may have frozen eggs that have been stored for a long time before being used to produce offspring. Between 29 and 64% of cases had the 1st and 99th percentile dates of conception being the same as those of the first and last progeny dates of conception. For example, we found instances of intervals of 28 years between the 99th percentile and the last date of conceptions. Bulls and cows that never produced any offspring were assumed to have been potentially available from 18 to 24 mo of age and 12 to 24 mo of age, respectively. We then computed the mean EBV of all available bulls or cows each day between 1980 and 2017. These daily mean EBV for all available bulls or cows were the contemporary groups with which the EBV of a sire or dam was compared to compute the GSD of the sire or dam. The realized GSD was therefore computed as the deviation of a parent's EBV from the mean EBV of all available bulls or cows at the time of conception of a progeny. The computation of the GSD of a parent has been illustrated in Figure 1. At the date of conception of cow 1, sires A, B, and D were available, and were all potential mates of the dam of cow 1. Therefore, the realized GSD of cow 1's sire (sire A) was computed as

the EBV of sire A minus the mean of sires A, B, and D's EBV.

We calculated the mean realized GSD for the population by year of conception for each path of selection: SB, DB, SC, and DC. The GSD was computed per year of conception because genetic materials are transmitted from parent to offspring at conception rather than the time of birth. The conception date of each animal was therefore computed as the date of birth of a progeny minus 280 d, where 280 d is the average gestation length for Holstein cows. The mean realized GSD of the top and bottom 10% of herds in Québec for each year of conception were computed for both the SC and DC paths.

Generation interval was defined as the average age of a sire or dam of a bull or cow when the offspring was born (Van Tassell and Van Vleck, 1991). Mean generation intervals were computed for each selection path by year of birth of offspring and were expressed in years (Figure 2).

Statistical Analyses

Statistical analyses were carried out on the realized GSD to determine whether environmental factors significantly influenced the GSD realized in each of the 4 paths of selection. We also sought to determine the amount of variabilities among herds in terms of the amount of selection applied for economically important traits. The realized GSD for each selection path was analyzed using the high-performance mixed (HPMIXED) procedure of SAS 9.4 (SAS Institute Inc., Cary, NC). The HPMIXED procedure was used because of the

Figure 1. Illustration of the computation of realized genetic selection differential (GSD) of a given sire (sire A) from available sires (sires A, B and D).

Figure 2. Generation intervals for the 4 paths of selection [sire-to-bull (SB), sire-to-cow (SC), dam-to-bull (DB), and dam-to-cow (DC)] by offspring birth year of the Holstein breed.

large number of observations involved and challenges regarding computing space. For the SC and DC paths, realized GSD was analyzed using model 1:

$$\begin{aligned} \text{GSD}_{ijkmn} = & \mu + \text{YOC}_i + \text{HS}_j + \text{Region}_k + \text{Herd}_{jkm} \\ & + \text{Herd} \times \text{YOC}_{ijkm} + \text{HS} \times \text{YOC}_{ij} + \text{Region} \times \text{YOC}_{ik} \\ & + \text{HS} \times \text{Region}_{jk} + e_{ijkmn}, \quad [\text{Model 1}] \end{aligned}$$

where GSD_{ijkmn} is the realized GSD for a trait (MY, FY, PY, MS, DS, FL, HL, DF, SCS, or LPI); μ is the overall mean; YOC_i is the fixed effect of the i th year of conception ($i = 1980$ to 2016); HS_j is the fixed effect of the j th housing system ($j = \text{tiestall}$ or freestall); Region_k is the fixed effect of the k th agricultural region (Table 1); Herd_{jkm} is the random effect of m th herd nested within the j th HS and the k th agricultural region $\sim N(0, \sigma_{\text{herd}}^2)$, where σ_{herd}^2 is the variance of the herd; $\text{Herd} \times \text{YOC}_{ijkm}$ is the random effect of the interaction of the m th herd nested within the j th HS and the k th agricultural region by the i th YOC $\sim N(0, \sigma_{\text{herd} \times \text{YOC}}^2)$, where $\sigma_{\text{herd} \times \text{YOC}}^2$ is the variance of herd by YOC; $\text{HS} \times \text{YOC}_{ij}$ is the fixed effect of the interaction between the j th HS and the i th YOC; $\text{Region} \times \text{YOC}_{ik}$ is the fixed effect of the interaction between the k th agricultural region and the i th YOC; $\text{HS} \times \text{Region}_{jk}$ is the fixed effect of the interaction between the j th HS and the k th agricultural region; and e_{ijkmn} is the random residual $\sim N(0, \sigma_e^2)$, where σ_e^2 is the residual variance.

Model 2 was used to analyze realized GSD of the SB and DB paths:

$$\begin{aligned} \text{GSD}_{ijk} = & \mu + \text{YOC}_i + \text{Stud}_j + \text{Stud} \\ & \times \text{YOC}_{ij} + e_{ijk}, \quad [\text{Model 2}] \end{aligned}$$

where GSD_{ijk} is the realized GSD for a trait; μ is the overall mean; YOC_i is the fixed effect of the i th year of conception ($i = 1980$ to 2016); Stud_j is the fixed effect of the j th AI center; $\text{Stud} \times \text{YOC}_{ij}$ is the fixed effect of the interaction between the j th AI center and the i th YOC; and e_{ijk} is the random residual $\sim N(0, \sigma_e^2)$, where σ_e^2 is the residual variance.

For realized GSD in the SC and DC paths, we wrote an additional model, model 3, where 1 random factor (herd or herd $\times$ YOC) was dropped at a time, and the difference in Bayesian information criteria (BIC) values between models 1 and 3 was calculated, to determine whether the random effect that was dropped was significant. This strategy was used to test the random factors in the analysis of each trait. A random factor was considered significant when the difference in BIC value between the model with and without the random effect was greater than 8. The differences in BIC values were between 558 and 69,581.

RESULTS AND DISCUSSION

Generation Intervals

Generation intervals of the SB, SC, DB, and DC paths are presented in Figure 2. All 4 paths declined in L over the 36-year period. The L of the SB dropped steadily between 1980 and 2000 from 9.7 to 6.3 years

(Figure 2). It moved up slightly afterward until after 2009, when there was a steep decline to 2.3 years in 2016. This pattern of L in SB was similar to what was reported in US Holsteins (García-Ruiz et al., 2016). The steady decline of L in the SB before the introduction of genomic selection could be attributed to more efficient progeny-testing programs in the mid-1990s (Nizamani and Berger, 1996) through the early 2000s. Also, the consolidation of AI studs in Canada between the 1980s and 1990s might have also led to higher competition among AI companies, hence the motivation to produce bulls at a faster pace. The substantial reduction in L from 2009 marked the introduction of genomic selection in the Canadian Holstein population, as proposed by Schaeffer (2006). The small decrease in L for the SC between 1980 and 2009 only culminated in about a 1-year reduction. This suggests that before the introduction of genomic EBV, dairy producers preferred to use older proven bulls for breeding because of the higher accuracy associated with the EBV of such bulls. García-Ruiz et al. (2016) also reported a lesser reduction of just 6 mo in the SC pathway, and Kawahara et al. (2002) obtained a 0.4-year increase in L in Japanese Hokkaido Holsteins between 1980 and 1998. The appreciable drop of 1.6 years in L between 2009 and 2016 for SC demonstrates the use of young genomic-tested bulls by the industry. The mean L of 5.1 years in the SC between 2011 and 2016 was similar to the 5.2 years reported in the United States between 2011 and 2015 (García-Ruiz et al., 2016). The L of the DB saw a reduction of about 40% between 1980 and 1993, after which it stayed stable until 2010. The use of reproductive technologies such as sexed semen and juvenile multiple ovulation embryo transfer (MOET; Kawahara et al., 2002) prior to the genomic era could have partly accounted for the steady reduction in DB. Also, the expansion of milk recording, better nutrition, and improved reproduction have partly helped reduce the age at first calving and shorten calving intervals, leading to reduction in L. Thereafter, we saw a steep decline, ending in a mean L of 2.5 years in 2016. The current L in the DB path confirms the predictions of Schaeffer (2006) that L will reduce to 2 years in the DB path in the era of genomic selection in dairy cattle. The modest reduction of approximately 1 year in the DC path over a 36-year period was due to the realistic need to maintain herd size and increase herd life in any profitable dairy farming business. Dairy cows become profitable only in their third lactation (Pellerin et al., 2014); thus, most producers will keep replacement cows for a longer time before replacing them. They will only cull cows when they have reproductive failures or diseases. This has contributed to the slow speed at which L has reduced in the DC. The CDN reported that the

average age of sires and dams of genotyped AI bulls in North America reduced by 55% and 25%, respectively, between 2000 and 2013 (CDN, 2018).

As of 2016, the total L of all 4 paths was 13.1 years, similar to the 13.5 years reported by García-Ruiz et al. (2016). Our total L, however, fell short of the 9.8 years predicted by Schaeffer (2006). This shortfall was due to the continuous use of relatively older sires for breeding by dairy producers: 4.6 years as opposed to the 1.5 years proposed by Schaeffer. It is expected that average L in the SC path will decline further in the future, as more producers are now using younger genomic bulls. In 2017, 67.4% of all matings by Holstein producers in Canada were done with young, unproven genomic bulls (CDN, 2018).

Realized Genetic Selection Differentials

Selection Index and Production Traits. The results of realized GSD in trait units (Supplemental Table S2; <https://doi.org/10.3168/jds.2019-16890>) and in standard deviation units (**SD units**) for the national selection index and production traits (MY, FY, PY) are presented in Figure 3. The realized GSD are presented in genetic SD units, to make it easier to compare realized selection among the selection paths and among traits. The realized GSD of LPI for the SB and DB paths were consistently higher than those of SC or DC (Figure 3a), suggesting that selection intensity for LPI among AI organizations was greater than among producers, who controlled the SC and DC pathways. Lifetime performance index, being one of the main selection indexes in Canada, serves as a tool for marketing semen by AI companies; therefore, they would naturally be inclined to place greater emphasis on this index. The realized GSD for DB increased by 0.10 SD unit between 1980 and 2006; then from 2006 to 2014, we find an increase of about 71%, translating to a 1.10-SD unit rise. This large increase was caused by selecting heifers as bull-dams based on genomic breeding values. From 1980 to 1991, the realized GSD in the SB pathway was higher than that in the DB, corroborating the findings of Burnside et al. (1992), who observed that the mean GSD of the Italian aggregate quality milk index in the 1980s were 2,328 and 1,307 for the SB and DB, respectively. The relatively smaller realized GSD of the SB compared with the DB after 1991, contrary to other reports, could perhaps be due to a fewer number of bulls sampled for progeny testing from which subsequent selection of sire-bulls was done in Canada. This could lead to several bulls with superior genetics being missed. Also, consolidation of several AI studs during the 1990s might have partly contributed to the greater realized GSD in DB compared with SB.

Artificial insemination companies have intensified their selection of bull-dams for the production of AI bulls. The use of reproductive technologies such as embryo transfer could also partly account for the high selection intensity in the DB (CDN, 2013). The trend in realized GSD of the SC was similar to that of the SB path (Figure 3a). This suggests that the breeding objective of producers might be coherent with that of AI centers; however, the selection emphasis is different. The low GSD of the SC from 1980 to 1989 was similar to the GSD of the SC for the production traits (Figure 3b–d). This indicates favorable correlation between LPI and production traits. Production traits constitute 40% of the weight of the LPI. So, although the LPI was not in existence before 1991, it was indirectly being selected through selection for other traits, such as production traits; hence the similarity in the pattern of realized GSD. The use of the current run of genetic evaluations for this study made it possible to have EBV for LPI even for older animals that were long dead before the LPI came into existence, as the current weights for LPI were applied on the data of these old animals to compute their LPI. However, this could slightly underestimate the realized GSD of older animals, as the selection criteria for these older animals could have been on some other traits not represented in the current LPI. The GSD of DC was largely stable and consistently around zero over the entire period. The mean realized GSD of 0.01 SD unit for DC was lower than the 77 reported by Burnside et al. (1992). The low selection in DC could be attributed largely to the lack of opportunity for selection in that path. Due to the low number of progeny produced per cow and the need to maintain herd size for a profitable dairy farming business, little selection was carried out in the DC pathway. We saw clear declines in realized GSD in recent years, in all selection paths. This relaxation in selection differentials has contributed to the slowing rate of genetic gain for LPI from 2014 to 2015 (CDN, 2018).

The realized GSD for production traits (MY, FY, and PY) showed similar trends for each of the selection paths (Figure 3b–d). These similarities in trends among traits are partly attributable to the strong positive genetic correlations among the production traits (Welper and Freeman, 1992; Veerkamp et al., 2001). García-Ruiz et al. (2016) also observed similarities in GSD trends for each selection path across MY, FY, and PY. Among the production traits, the GSD of the SB and DB were between 0.5 and 2.5 SD units, whereas those of the SC and DC were within 0 and 0.5 SD units, similar to the findings of Van Tassell and Van Vleck (1991). This presupposes that, although the breeding objectives of AI centers and producers might be similar, AI centers place more intense selection pressure on production

traits than do producers. Other studies, however, have reported higher selection differentials for SB and SC than for DB and DC (Burnside et al., 1992; García-Ruiz et al., 2016). The relatively low selection differentials of production traits in the SC path compared with the DB path in the Canadian Holstein population could be partly attributed to the milk quota system in Canada. The price producers are paid for milk is based on kilograms of fat and protein. Because each producer has a specific quota and is penalized for producing beyond that quota, there may be less incentive to intensify selection for production traits, even though the breeding objectives of AI centers and producers might be similar. On average, AI centers have realized slightly more selection on PY and MY than on FY. The mean realized GSD (in SD units) of these traits were 1.07 and 1.34 for FY, 1.34 and 1.36 for MY, and 1.50 and 1.63 for PY in the SB and DB paths, respectively.

The gap between the SC, on one hand, and SB and DB, on the other, was smaller for FY than those observed for MY and PY. This suggests either that dairy farmers were putting greater emphasis on FY and probably rank it high among their breeding objectives, or that AI centers were putting less emphasis on FY. The similarity of the gaps observed in MY and PY is due in part to the strong positive genetic correlation (0.81) between these 2 traits (Veerkamp et al., 2001). The SB and DB selection paths together contributed an average of 83 to 91% of the total selection applied for LPI, MY, FY, and PY in the Canadian Holstein population over the 36-year period. This demonstrates the importance of AI centers in genetic improvement in the Canadian dairy industry. In the United States, the SB and SC selection paths (73 to 90%) were the main drivers of genetic improvement in the industry (García-Ruiz et al., 2016).

Durability Traits. The dairy industry in Canada has long been interested in type traits, as animals with good conformation traits are able to sustain high milk production. Genetic evaluations for type traits started in the 1970s, and new type traits were developed over time. For instance, genetic evaluation for HL in Canada started in the early 2000s, after methods for evaluation of HL were developed by Jairath et al. (1998). We found no clear trend in realized GSD for durability traits in the 3 most influential selection paths, except for the apparent increase in the DB path for MS, FL, and HL after the year 2000 (Figure 4). For MS, the realized GSD of SC and DB were always positive, suggesting the importance that both producers and AI centers place on the selection of their males and females, respectively, for breeding. The selection intensity of the SB was also largely similar to that of the SC, except for occasional negative selection in 1987, 1988, 1995, and 1999 (Fig-

Figure 3. Mean realized genetic selection differential in standard deviation units (SD unit) per year of conception for lifetime performance index, 305-d milk yield, 305-d fat yield, and 305-d protein yield for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for the Holstein breed.

ure 4a). Mean realized GSD for MS in the SB, DB, SC, and DC were 0.44, 0.70, 0.50, and -0.11 SD units. A good mammary system, as with most type traits, affects farm profitability through reduced involuntary culling (Pérez-Cabal and Alenda, 2002). The fact that negative selection for MS occurred in DC demonstrates that dairy farmers in Canada improve their herds for MS through the selection of superior AI sires because of the minimal opportunity for selection of MS among their replacement cows. Also, the negative GSD in DC was not an indication of poor MS among replacement cows in Canadian Holstein population; rather it is only an indication of little selection emphasis in DC. The genetic improvement for MS in dairy herds occurs mainly through the other 3 selection paths.

For DS, selection in the SC was the largest, with realized GSD increasing steadily from 1989 to 2002, after which it began to decline until 2008 (Figure 4b). Between 2008 and 2015, we found an irregular pattern of rise and fall in realized GSD of the SC; however, selection differentials in this pathway were still higher than in the SB, DB, or DC. The high realized GSD of the SC suggests that selection of AI bulls was the key driver of genetic improvement for DS in the Holstein population. No clear trend of selection appears in either the SB or the DB; however, from 2002, realized GSD of the DB has remained positive, whereas that of the SB has largely been negative. The realized GSD of DC were negative throughout the study period. The similarity in trends for GSD of MS and DS, especially in the SC and DC paths, could partly be attributed to the positive genetic correlations among the groups of traits that constitute MS and DS (DeGroot et al., 2002). The GSD for MS fall within -0.20 and 1.40 SD units, whereas the GSD for DS range from -0.40 to 0.80 SD units. This indicates that the selection emphases for MS and DS, especially in the SB, DB, and SC paths, were lower than those of the production traits (0 to 2.5 SD units).

From 1980 to 1995, no trend is apparent for realized GSD of the SB, SC, and DB paths for FL (Figure 4c). During this period, the realized GSD in the paths controlled by AI centers (SB and DB) were mostly negative, suggesting that these centers did not rank FL high among their breeding objectives. After 2000, the realized GSD in SB and DB were mostly positive, possibly indicating a change in breeding objective among AI organizations. Foot- and leg-related problems have been one of the major reasons for involuntary culling among dairy cattle in Canada (CDIC, 2018). The prevalence of FL problems may be due to tiestall designs (Zurbrigg et al., 2005); hence, the observed positive realized GSD for FL in the SC across the years could be an attempt by producers to correct leg problems in their herds by

genetic means coupled with management practices they may already be undertaking. The GSD in DC was close to zero across the period of the study, due to the limitations to selection in that path. The selection emphasis placed on FL was similar to those of MS and DS. The mean GSD for FL ranged from -0.60 to 1.00 SD units.

We found no clear trend in realized GSD for HL in the SB, DB, and SC paths from 1980 to 2005 (Figure 4d). The irregular pattern during this period is similar to the findings of García-Ruiz et al. (2016). From 1981 to 2002, the realized GSD was consistently negative for the DB and mostly negative for the SB, suggesting that minimal emphasis was realized for HL by AI centers during that period. This was probably due to the fact that genetic evaluation was not available for HL at that time. Genetic evaluations for HL only became available after 2000. The GSD increased steeply in the SB and DB from 2003 and 2004, respectively. However, a sharp decline occurs in the SB from 2009, which, interestingly, marked the introduction of genomic selection in Canada. Could this be attributed, in part, to the sire sampling procedure? The realized GSD of DC remained positive at all times, similar to the results reported by García-Ruiz et al. (2016), demonstrating the importance of longevity to herd profitability among dairy farmers. Farmers will generally keep lactating cows in their herd for longer periods, provided they are trouble-free and show no diseases or injuries, until they develop problems or are no longer productive, because of the favorable effect of longer HL on overall profitability (Allaire and Gibson, 1992). The mean realized GSD for HL ranged from -0.50 to 1.50 SD units, quite similar to those of the other type traits but lower than those of production traits.

Health and Fertility Traits. The realized GSD for DF were largely negative for the SB, SC, and DB paths from 1980 to 2005 (Figure 5a). In the case of SC, the realized GSD were still negative after 2005. The mean selection differentials for the DB were low to moderately positive from 2008. The mean GSD of DC were consistently positive from 1982 to 2015. The negative realized GSD of the 3 most influential paths were partly due to the negative genetic correlation between DF and the production traits (Hoekstra et al., 1994; Kadarmideen et al., 2000). The fact that realized GSD for DF were positive after 2008 in the SB and DB could be attributed both to the deliberate effort of the industry, led by AI centers, to reverse the deterioration of fertility in Holstein cows from previous overemphasis on milk production (Miglior et al., 2005) and to the introduction of genomic selection that favors the genetic improvement of traits with low heritability (Meuwissen et al., 2001; García-Ruiz et al., 2016). The positive but small realized GSD of the DC could be mainly due to

Figure 4. Mean realized genetic selection differential in standard deviation units (SD unit) per year of conception for mammary system, dairy strength, feet and legs, and herd life for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for the Holstein breed.

culling because of reproductive failures rather than to active selection by producers for fertility in their herds. The mean realized GSD for DF ranged from -1.00 to 0.80 SD units. The selection emphasis for DF was slightly lower than that of the type traits and much lower than that of the production traits.

The realized GSD for SCS were multiplied by -1 to make interpretation easier, because until December 2018 genetic evaluations for SCS in Canada were such that lower EBV were better than higher. Our analysis revealed no clear trend in realized GSD for SCS of the 4 selection paths before 2002 (Figure 5b), although they were largely negative for the SB, DB, and SC paths. The negative realized GSD for SCS before 2002 indicated that the industry was not intensively selecting for SCS during that time. After the early 2000s, realized GSD for the SB, SC, and DB were positive, except for SB in 2015. From 1980 to 1985, the realized GSD of DC were slightly positive, but between 1986 and 2015, the GSD were essentially zero. The pattern of GSD in our study was similar to the findings of García-Ruiz et al. (2016). A favorable relationship exists between SCS and HL (Haile-Mariam et al., 2004), and thus the favorable HL observed after the early 2000s is evidence of the favorable selection differentials producers were putting on SCS. The noticeable steep increase in realized GSD in the SB and SC from 2009 could be attributable to the introduction of genomic selection that greatly favors traits with low heritability. In 2015, the realized GSD for all 4 paths edged down from previous years' values. Because SCS is an important trait for herd management, it is important for the industry to monitor selection for SCS and make a necessary revision

to its selection pressure if it is being relaxed in recent times.

Effects of Fixed Factors on Realized GSD in the SC and DC Paths

Scant information is available on the effects of YOC, HS, region, and the interactions among these factors on realized GSD among dairy farmers' herds. Tables 3 and 4 show the P -values for the effects of HS, agricultural region, $HS \times YOC$, $region \times YOC$ and $HS \times region$ on realized GSD of SC and DC paths, respectively, for 10 traits. Year of conception (not shown in the tables), $HS \times YOC$ and $Region \times YOC$ had significant effects ($P < 0.05$) on realized GSD of all traits in the SC path. Year of conception also had a significant effect ($P < 0.05$) on realized GSD of all traits in DC (not shown in tables). The significant effect of YOC on realized GSD in both the SC and DC paths might not be surprising, as breeding objectives in a country do change over time with changes in market demand (Miglior et al., 2005); hence, dairy farmers also tend to change their breeding objectives over time, translating into changes in selection emphasis as well.

Housing system had a significant effect ($P < 0.05$) only on realized GSD for DS in the SC path and LPI, FY, DS, and FL in the DC path. For DS, realized GSD in both the SC and DC were higher, on average, among tiestall operators than among freestall operators. Dairy strength, being a combination of dairy character and body capacity, was ranked very important among tiestall operators, who constitute about 84% of dairy farmers in Québec. Also, in the DC pathway, the realized

Figure 5. Mean realized genetic selection differential in standard deviation units (SD unit) per year of conception for daughter fertility and SCS for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for Holstein breed.

Table 3. Effects of housing system (HS), agricultural region (region) and HS $\times$ region on realized genetic selection differential in the sire-to-cow selection path (P -values reported for the fixed effects) and variance components of herd (HS $\times$ region), herd $\times$ YOC,¹ and residuals

Trait	Fixed effect ²			Variance component		
	HS	Region	HS $\times$ region	Herd (HS $\times$ region)	Herd $\times$ YOC	Residual
LPI ³	0.2126	0.1446	0.1141	1,450.34	3,022.32	60,635
Milk yield	0.9298	0.0057	0.1683	12,573	23,088	410,580
Fat yield	0.4828	0.1898	0.2190	11.0229	30.1971	615.34
Protein yield	0.5899	0.0198	0.3255	11.9784	21.0465	331.81
Mammary system	0.3372	0.3508	0.0626	0.6467	0.6148	13.6103
Dairy strength	0.0011	0.2206	0.0129	1.3079	1.2121	21.1901
Feet and legs	0.2783	0.3495	0.0335	0.5150	1.0646	22.7680
Herd life	0.4002	0.1191	0.1207	0.06436	0.5418	16.0305
Daughter fertility	0.1429	0.7640	0.0369	0.2076	0.8321	18.8207
SCS	0.4682	0.8892	0.6757	0.000127	0.001898	0.04742

¹YOC = year of conception ($P < 0.0001$ for all traits in the table).

²Differences are statistically significant if $P < 0.05$.

³LPI = lifetime performance index.

GSD for LPI, FY, and FL were higher in tiestall housing compared with freestalls. It was surprising to note that selection for FL was lower among freestall operators compared with tiestall operators; given that cows make relatively more movement in freestalls than in tiestalls, we would have expected freestall dairy farmers to place greater selection emphasis on FL. Also, higher incidence of leg problems has been observed in freestall HS than in tiestall systems (Cook, 2003; Sogstad et al., 2005). It is not readily clear why our observations were so.

Agricultural regions in Québec had significant effects ($P < 0.05$) on only selection differentials of MY and PY in the SC path and LPI, MY, FY, and PY in the DC path but not on those of durability, health, and fertility traits. On average, herds in Laval and Cote-Nord

place greater selection emphasis on production traits. It should be noted, however, that these regions together hosted only 5 herds.

Analysis revealed significant interactions ($P < 0.05$) between HS and YOC on realized GSD of all traits in the SC and DC except for LPI, MS, and SCS in DC. We also found significant interactions ($P < 0.05$) of the region and YOC on realized GSD of all traits in both SC and DC, except SCS in the DC path. This also suggests that differences in realized GSD among agricultural regions change over time. Producers in some of these regions could be changing their breeding objectives over time, leading to changes in their selection emphases.

We discovered significant differences ($P < 0.05$) among the interactions of HS and agricultural region

Table 4. Effects of year of conception (YOC),¹ housing system (HS), agricultural region (region), HS $\times$ YOC, Region $\times$ YOC, and HS $\times$ region on realized genetic selection differential in the dam-to-cow selection path (P -values reported for fixed effects) and variance components of herd (HS $\times$ region), herd $\times$ YOC, and residuals

Trait ²	Fixed effect ³					Variance component		
	HS	Region	HS $\times$ YOC	Region $\times$ YOC	HS $\times$ Region	Herd (HS $\times$ region)	Herd $\times$ YOC	Residual
LPI	0.0318	<0.0001	0.6220	<0.0001	0.0105	5,278.75	1,951.96	53,963
MY	0.3637	<0.0001	<0.0001	<0.0001	0.0834	24,953	8,292.76	391,313
FY	0.0011	<0.0001	0.0417	<0.0001	<0.0001	0.04356	0.01569	634.67
PY	0.6882	<0.0001	<0.0001	<0.0001	0.0870	22.2958	8.1278	307.69
MS	0.1037	0.0728	0.7090	<0.0001	0.0088	1.2849	0.3375	10.5238
DS	0.0153	0.2819	<0.0001	<0.0001	0.0071	2.0266	0.4564	14.3868
FL	0.0484	0.7824	<0.0001	<0.0001	0.0657	0.5902	0.3056	11.6493
HL	0.8447	0.1009	0.0018	<0.0001	0.3973	0.2735	0.1411	8.8568
DF	0.8369	0.3229	<0.001	<0.0001	0.4949	0.8696	0.1726	11.9890
SCS	0.0912	0.1711	0.1800	0.1099	0.0090	0.000534	0.000229	0.03230

¹ $P < 0.0001$ for all traits in the table.

²LPI = lifetime performance index; MY = 305-d milk yield; FY = 305-d fat yield; PY = 305-d protein yield; MS = mammary system; DS = dairy strength; FL = feet and legs; HL = herd life; DF = daughter fertility.

³Differences are statistically significant if $P < 0.05$.

on realized GSD of DS, FL, and DF in the SC and LPI, FY, MS, DS, and SCS in the DC.

Variations Among Herds and Herd $\times$ YOC on Realized GSD in the SC and DC Paths

All dairy farmers in Canada are likely to say they are actively selecting for economically important traits and also contributing equally to the observed genetic progress in these traits as reported by the CDN. This study is the first attempt to study variation in GSD among herds in Québec. Variability was apparent among herds in terms of realized GSD of all traits in the SC (Table 3). The variations due to herds constituted between 0.3 to 5.5% of the total variations in realized GSD of the traits studied. All the variations due to herd were significant, as measured by the large difference in BIC values between models with and without the random effect of the herd. Similarly, considerable variation occurred due to the interaction of herd by YOC on realized GSD of all traits in the SC. These comprised between 3.3 and 5.8% of the total variation in GSD. In the DC path, we also found significant variations due to herd, representing between 1.6 and 12.0% of the total variation in realized GSD, while the herd $\times$ YOC component constituted between 0.7 and 3.2% of the total variation (Table 4). The significant variations among herds in realized GSD in both SC and DC paths suggested that not all dairy farmers were directly and intensively selecting for the economically important traits, perhaps due partly to differences in semen prices and variations in herds' breeding goals. Also, limited knowledge in basic genetics among some producers may lead these producers to use any semen that sales representatives from AI companies send to their farms. This could have implications on the profitability of these dairy farms. Figure 6 illustrates the top and bottom 10% herds in the selection of AI sires for breeding cows for LPI, FY, DF, and SCS. Apart from being possible benchmarks for comparison by dairy farmers, they also served as further evidence of variations in realized GSD among herds. For LPI, the mean realized GSD of the top 10% of herds per year ranged from 1.50 to 2.50 SD units (Figure 6a). For the bottom 10% of herds, the mean realized GSD ranged from -1.00 to 0 SD units (Figure 6a). For FY, the mean realized GSD per year of conception ranged from 1.30 to 2.00 SD units in the top 10% of herds and -1.35 to -0.50 SD units in the bottom 10% of herds (Figure 6b). Figures 6c and 6d show the mean realized GSD for the top 10% and bottom 10% herds for DF and SCS, respectively. The trend in the mean realized GSD for the top 10% herds, bottom 10% herds, and entire population were all largely similar for each of the traits presented. The

mean realized GSD of the bottom 10% of herds for each trait were negative at all times, an indication that a considerable number of herds in the population were selecting less for economically important traits (Figure 6). The genetic improvement in these herds will thus lag behind that of the population.

Dairy farmers will, therefore, need to pay attention to the selection they apply in their individual herds and not use only population trends as a measure of their herds' performance but rather a benchmark for comparison. Hagan and Cue (2018) produced some suitable benchmarks with which Canadian dairy farmers could compare their herds' past selection.

Genetic selection differentials of the same selected individual herds (A, B, C, and D) for LPI, FY, DF, and FL are presented in Supplemental Figure S1 (<https://doi.org/10.3168/jds.2019-16890>). This seeks to show further evidence of the variations in selection emphases among dairy producers in Québec. The graphs indicate both variations in selection emphases from year to year for the same producer and variations in selection emphases among producers for the same periods. For instance, for LPI, the GSD of herd A were modest and between 0 and 100 LPI points between 1984 and 1999. After 1999, selection emphases consistently increased, peaking in 2013. However, herd D has seen a wobbling realized selection between 1981 and 2003, after which the trend in GSD for LPI reduced (Supplemental Figure S1a; <https://doi.org/10.3168/jds.2019-16890>).

Effects of Fixed Factors on Realized GSD in the SB and DB Paths

As with the SC and DC paths, YOC had a significant effect ($P < 0.05$) on realized GSD of all traits in both the SB and DB. This implies that different AI organizations applied varied GSD over the years. The changes in realized GSD could partly be attributed to changes in breeding objectives of the industry and AI organizations over time.

Also, AI stud and stud $\times$ YOC have significant effect ($P < 0.05$) on the realized GSD of all traits in the SB and DB paths. The significant effect ($P < 0.05$) of AI centers on realized GSD is important and suggested that not all AI centers were intensively selecting for all the economically important traits. This could in part be attributed to the different breeding objectives of AI centers. Also, it is not far-fetched for AI organizations to keep top bulls for different traits to enable them to serve a range of customers with different needs. In the current study, selection applied in both the SB and DB constituted on average 87% of the total selection realized. This indicated that AI organizations were the main drivers of genetic improvement in the population,

Figure 6. Mean realized genetic selection differential in standard deviation units (SD unit) for lifetime performance index, 305-d fat yield, daughter fertility, and SCS in the sire-to-cow path for the population, top 10%, and bottom 10% of herds.

corroborating other reports (McAllister, 1980; Cassell, 1988). For the population to optimize genetic gains, all AI organizations would need to constantly monitor and optimize their selection emphases.

CONCLUSIONS

Realized GSD and L in the Canadian Holstein dairy cattle have been investigated using the 4-path selection model. Substantial reduction in total L has occurred from 1980 (29.6 years) to 2016 (13.1 years), driven mostly by significant reductions of L in the SB, DB, and SC paths. The population mean realized GSD of the SB and DB paths were appreciably higher than those of SC and DC for the national index and production traits. However, no clear trend in realized GSD were observed for the durability, health, or fertility traits, although the GSD of DC were mostly stable and close to zero except for DF, where selection differentials in the DC were consistently above zero. Among Québec herds, YOC had a significant effect on realized GSD of all 10 traits in the SB, DB, SC, and DC paths. Also, HS, agricultural region, HS $\times$ YOC, region $\times$ YOC, and HS $\times$ region had significant effects on realized GSD of some traits in the SC and DC paths. This study has demonstrated that realized selection differentials varied considerably among herds and herd $\times$ YOC in Québec, Canada. These variations offer an opportunity to optimize genetic gains in economically important traits in the dairy industry in Canada.

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