GENETIC SELECTION IN CANADIAN DAIRY CATTLE

by

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ABSTRACT

Genetic evaluations for April 2018, which were computed by Canadian Dairy Network, dairy herd information, and lactation records of Holstein cows from Lactanet, were used to (i) compute realized genetic selection differentials (GSD) for economically important traits in Holstein, Ayrshire, Jersey, and Brown Swiss herds in Canada, (ii) investigate generation intervals in four dairy cattle populations, (iii) estimate genetic parameters for milk production, lactation body weight, SCS, and profit indicator traits in Holstein cows in Québec, and (iv) develop a prototype tool and visualization model to monitor selection realized in individual dairy herds. A new approach that would be more relevant to dairy producers has been used to compute realized GSD of traits of economic importance in four dairy cattle breeds in Canada. Significant GSDs were being realized for production, durability, health, fertility traits, and lifetime performance index (LPI). Greater selections were realized in the dam-to-bull (DB) and sire-to-bull (SB) pathways of selection compared with selection realized in the sire-to-cow (SC) and dam-to-cow (DC) pathways; little to no selection was realized for production, durability, and health traits in the DC path in the four dairy cattle breeds. Apart from year of conception, other non-genetic factors were mostly unimportant on the realized GSD for economically important traits while significant variations existed among herds in their realized GSD.

Generation intervals (L) in all four paths of selection have been decreasing from 1980 to 2016. There have been 55%, 41%, 46%, and 38% reductions in total L in the Holstein, Ayrshire, Jersey, and Brown Swiss populations between 1980 and 2016, respectively. A significant proportion of the reductions in L occurred in the last 8 years (2009 to 2016). Herd and herd*year of birth explained significant proportion of the variations in L. This study has demonstrated that herds that used younger Artificial Insemination bulls for breeding increased their annual genetic progress at a faster rate.

First to fourth lactation records of Holstein cows in Québec were used to estimate genetic and phenotypic parameters of milk production, somatic cell score (SCS), lactation body weight (BWT), cumulative milk value (MV), cumulative feed cost (FC), and margin over feed cost (MOFC). Heritability estimates for milk production traits, BWT, MV, and MOFC were moderate whereas heritability estimates for SCS and FC were low. Genetic correlations among the traits studied ranged from low to high. Strong genetic correlations existed between the same traits in different lactations with the greatest correlations found between adjacent lactations. An attempt has been made to illustrate that it is possible to slow or halt the positive genetic trends in cow body weight by incorporating BWT and milk production traits into a simple selection index.

Finally, a prototype software tool and visualization model were developed to help dairy producers and advisors monitor GSD in their herds, and compare the selection they are making with a number of benchmarks. The concept of this prototype software tool is applicable to all livestock species for which genetic evaluations are routinely computed and published. It is expected that producers would use this software tool to monitor what selection they are making in their herds and make changes if they are moving in an unintended direction.

RÉSUMÉ

Les évaluations génétiques pour le mois d'avril 2018, calculées par le Réseau laitier canadien, et l'information sur les troupeaux laitiers et les relevés de lactation des vaches Holstein provenant de Lactanet, ont été utilisés pour (i) calculer les écarts de sélection génétique (ÉSG) réalisés pour les traits économiquement importants pour les troupeaux Holstein, Ayrshire, Jersey et Suisse Brune au Canada, (ii) étudier les intervalles de générations dans quatre populations de vaches laitières, (iii) estimer les paramètres génétiques de la production laitière, du poids des vaches en lactation, de la cote de cellules somatiques (CCS) et des traits indicateurs de profit chez les vaches Holstein au Québec, et (iv) développer un prototype d'outil et un modèle de visualisation pour surveiller la sélection réalisée dans les troupeaux laitiers individuels. Une nouvelle approche qui serait plus pertinente pour les producteurs laitiers a été utilisée pour calculer les ÉSG des traits d'importance économique. D'importants ÉSG ont été obtenus pour la production, la durabilité, la santé, les traits de fertilité et l'indice de performance à vie (IPV). De plus grandes sélections ont été réalisées dans les méthodes de sélection femelle à mâle (DB) et mâle à mâle (SB) comparativement à d'autres méthodes; peu ou pas de sélection a été réalisée pour la production, la durabilité et les traits de santé dans la méthode femelle à femelle (DC) dans les quatre races de bovins laitiers. Mis à part l'année de conception (YOC), les autres facteurs non génétiques n'avaient majoritairement pas d'importance sur l'ÉSG réalisé pour les traits économiquement importants alors qu'il existait des variations significatives entre les troupeaux dans leur ÉSG réalisé.

Les intervalles de génération (L) dans les quatre méthodes de sélection ont diminué de 1980 à 2016. Il y a eu des réductions de 55 %, 41 %, 46 % et 38 % du L total dans les populations de Holstein, Ayrshire, Jersey et Suisse Brune entre 1980 et 2016, respectivement. Une proportion importante des réductions de L s'est produite au cours des huit dernières années (2009 à 2016). Le troupeau et l'interaction entre l’année de naissance et le troupeau expliquent une proportion significative des variations de L. Cette étude a démontré que les troupeaux qui utilisent de jeunes taureaux d’insémination artificielle pour la reproduction augmentent leur progrès génétique annuel à un rythme plus rapide.

Les données de la première à la quatrième lactation des vaches Holstein au Québec ont été utilisées pour estimer les paramètres génétiques et phénotypiques de la production laitière, de la CCS, du poids des vaches en lactation (BWT), de la valeur cumulative du lait (MV), du coût cumulatif des aliments (FC) et de la marge sur le coût des aliments (MOFC). Les estimations de l'héritabilité pour les traits de production laitière, BWT, MV et MOFC étaient modérées tandis que l'héritabilité pour le CCS et FC était faible. Il existe diverses corrélations génétiques entre les traits étudiés. Il existe de fortes corrélations génétiques entre les mêmes traits dans différentes lactations avec la plus grande corrélation observée entre les lactations adjacentes. On a tenté d'illustrer qu'il est possible de ralentir ou d'arrêter les tendances génétiques croissantes du poids des vaches en incorporant les traits de la production laitière en utilisant un indice de sélection simple.

Finalement, un prototype d'outil et de modèle de visualisation ont été mis au point pour aider les producteurs laitiers et les conseillers à surveiller l’ÉSG dans leurs troupeaux et à comparer leur sélection à certains repères. Le concept de ce prototype d'outil est applicable à toutes les espèces animales pour lesquelles des évaluations génétiques sont régulièrement calculées et publiées. Nous nous attendons à ce que les producteurs utilisent cet outil logiciel pour surveiller la sélection qu'ils font dans leurs troupeaux et apporter des changements s'ils vont dans une direction non voulue.

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CONTRIBUTIONS TO KNOWLEDGE

CHAPTER III

This chapter looks at the realized genetic selection for key production, durability, health, and fertility traits, and LPI in Canadian Holstein herds. The original contribution of this chapter is that it is the first comprehensive report of genetic selection differentials (GSD) in Canadian Holstein cattle population using EBV that are computed by Lactanet. The chapter is the maiden report of determining the variations in realized GSD in Holstein dairy herds in Québec or any other Holstein population. The effects of non-genetic factors on realized GSD in pathways controlled by dairy producers and Artificial Insemination (AI) centers were also assessed. This chapter also introduces the concept of available bulls and cows at each time a bull or cow is used for breeding, and the EBV of bull/cow used for breeding is compared with the average EBV of all available bulls/cows at the time of breeding. The chapter has been accepted for publication in the Journal of Dairy Science.

CHAPTER IV

In this chapter, realized GSD for production, durability, health, and fertility traits in herds of three Canadian minor dairy cattle breeds (Ayrshire, Jersey, and Brown Swiss) were determined. Variations in realized GSD among minor dairy herds were computed, and the effects of non-genetic factors on realized GSD in dairy herds were also determined. This is the first study of realized GSD for economically important traits in minor dairy cattle breeds in Canada and the second study for any minor dairy breeds in North America besides that of the Jersey population in the USA. The chapter has been submitted to the Journal of Dairy Science and is currently under revision.

CHAPTER V

This chapter assesses the importance of ancillary traits in the breeding objectives of Canadian dairy producers and the amount of selection emphases producers apply on these traits. Estimated breeding values of ancillary traits were used to calculate GSD that producers of Holstein, Ayrshire, Jersey, and Brown Swiss breeds realized in their herds. The mean realized GSD for LPI – sub-indices of durability (LPI-DUR), and health and fertility (LPI-HF) for the four dairy cattle populations were also determined. This study also determined whether the top 10% available bulls for LPI-DUR, and LPI-HF in each year were being used for breeding by dairy producers of the four dairy cattle populations.

CHAPTER VI

Chapter VI describes the generation intervals in Holstein, Ayrshire, Jersey, and Brown Swiss populations in Canada between 1980 and 2016. The chapter also reported the effects of some environmental factors on generation intervals in herds of the four dairy cattle populations. Variations in generation intervals realized among herds of Canadian dairy producers and AI studs were assessed. This study is the first comprehensive report of generation intervals along the four pathways of selection in Canadian dairy herds. The chapter has been accepted for publication in the Canadian Journal of Animal Science.

CHAPTER VII

Genetic parameters for cow lactation body weight, milk production, SCS, and profit indicator traits have been computed for Holstein cows in Québec born from 2008. This chapter updates the literature of genetic parameters for milk production traits, SCS, cumulative milk value, cumulative feed cost, and margin over feed cost in Holstein cows in Québec. Genetic parameters for lactation body weight have also been computed. The inclusion of lactation body weight in a selection index comprising milk production traits have been proposed to slow or halt the positive genetic trends in cow body weight. The chapter has been submitted to Livestock Science and is currently under revision.

CHAPTER VIII

A prototype software tool has been developed to allow dairy producers and/or agricultural advisors to monitor the genetic selection differentials that dairy farms are making. The prototype has been developed using four dairy cattle breeds but it can be equally applied to other livestock species for which genetic evaluations are routinely computed. Appropriate benchmarks have been identified and created by which dairy producers could compared their selection emphases for economically important traits with.

CONTRIBUTIONS OF AUTHORS

Six co-authored manuscripts have been presented in this thesis. Authors of manuscript 1, 2, and 3 (Chapters III, IV, and V) are Bernard Ato Hagan, José Moro-Mendez, and Roger I. Cue. **Bernard A. Hagan** analyzed the data for the studies, produced graphs, and wrote the manuscripts. **Roger I. Cue** and **José Moro-Mendez** conceptualized the experimental ideas and reviewed the manuscripts.

Authors of manuscripts 4, 5, and 6 (Chapter VI, VII, and VIII) are Bernard A. Hagan and Roger I. Cue. **Bernard A. Hagan** conceptualized the experimental ideas for chapters vi and vii, analyzed the data for manuscripts 4, 5, and 6 and wrote the manuscripts. **Roger I. Cue** conceptualized the experimental ideas for chapters vi, vii, and viii and reviewed all the manuscripts.

Chapters 3 and 6 have been published in the Journal of Dairy Science and Canadian Journal of Animal Science, respectively. Chapter 8 has been published in conference proceedings of 14th International Conference on Precision Agriculture in Montreal, Québec, Canada with the full paper being prepared for submission to the Journal of Computers and Electronics in Agriculture.
Chapters 4 and 7 have been submitted to the Journal of Dairy Science and Livestock Science, respectively, and are currently under review. Chapter 5 is being reviewed by co-authors before submission to a selected journal.

Table of Contents

List of Tables

List of Figures

LIST OF ABBREVIATIONS

AI	Artificial Insemination
ANG	Angularity
b	Regression Coefficient
BCS	Body Condition Score
BIC	Bayesian Information Criteria
BWT	Lactation Body Weight
CDN	Canadian Dairy Network
CONF	Conformation
CSD	Cumulative Selection Differential
DB	Dam-to-Bull
DC	Dam-to-Cow
DCA	Daughter Calving Ability
DF	Daughter Fertility
DHI	Dairy Herd Information
DIM	Days-in-milk
DIM_BWT	Days-in-Milk when body weight was recorded
DOB	Date of Birth
DOC	Date of Conception
DS	Dairy Strength
DSS	Decision support system
EBV	Estimated Breeding Value
FC	Cumulative Feed Cost
FEC	Faecal Egg Count
FEC1	Faecal Egg Count measured in mid to late January
FEC2	Faecal Egg Count recorded in late February to early March
F%	Fat percentage
FL	Feet and legs
FY	305-day Fat Yield
G_C	Genetic values
HPMIXED	High Performance Mixed

ΔGy	Annual genetic gain
GSD	Genetic Selection Differential
h^2	Heritability
HH	Hoof Health
HL	Herd Life
HS	Housing System
HY	Herd-Year
L	Generation interval
LL	Lactation length
LP	Lactation Persistency
LPI	Lifetime Performance Index
LPI-DUR	Lifetime Performance Index sub-index for Durability
LPI-HF	Lifetime Performance Index sub-index for Health and Fertility
LPI-PROD	Lifetime Performance Index sub-index for Production
i	Selection intensity
MOET	Multiple Ovulation Embryo Transfer
MOFC	Margin over Feed Cost
MR	Milking Rate
MS	Mammary System
MSP	Milking Speed
MT	Milking Temperament
MV	Cumulative Milk Value
MY	305-day Milk Yield
PBV	Predicted Breeding Value
P%	Protein Percentage
Pro$	Pro Dollar Index
PY	305-day Protein Yield
R	Response to selection
$rEBV$	Accuracy of EBV
RUMP	Rump
SB	Sire-to-Bull

SC	Sire-to-Cow
SCC	Somatic Cell Count
SCS	Somatic Cell Score
sd	standard deviation
SD	Selection Differential
STA	Stature
T or YOB	Year of birth
UDD	Udder Depth
UDT	Udder Texture
UK	United Kingdom
USA	United States of America
WIM	Week in Milk
YOC	Year of Conception

1 CHAPTER I

1.1 Introduction

Most livestock producers and breeders seek to maximize genetic gains for economically important traits and at the same time increase the rate at which genetic gains are achieved. Annual rate of genetic gain (ΔGy) is a function of selection intensity (i), accuracy of estimated breeding values (r_{EBV}), genetic standard deviation (σg), and generation intervals (L).

$$\Delta G_y = i.r_{EBV}.\sigma_g/L$$

This suggests that accurate and intensified genetic selection of breeding objective traits and minimizing generation intervals are appropriate strategies that can be used to maximize the annual genetic progress in any livestock population.

Genetic selection has brought substantial increases in productivity of farmed livestock (Pryce *et al.*, 2001; VanRaden, 2004; Oltenacu and Broom, 2010) and efficiency of production (Thornton, 2010) both of which have partly contributed, in real terms, to the reduction in global food prices (Piesse and Thirtle, 2009). In livestock production, genetic gain has a strong association with farm profitability (Thompson *et al.*, 2015), thus making genetic selection an essential factor to a profitable animal farming business.

The Canadian dairy industry plays key roles in the global dairy business through the export of some dairy products and superior genetics to other parts of the world. The annual milk production for all dairy cattle breeds in Canada has been increasing since the last century. Milk yield of Holstein cows has increased from an average of 9,118 kg/yr in 1991 to 12,492 kg/yr in 2017 (www.cdn.ca, August 15, 2019), an increase of approximately 1.6% per year. The increasing milk production levels can be attributed to both management and genetics. It is estimated that 56% of improvement in milk, fat, and protein yields in Holstein cattle is due to genetics (www.uscdcb.com, August 20, 2019). Apart from production traits, there have also been improvements in durability, health, and reproduction traits. Production, durability, and health and fertility traits are the major groups of traits that constitute most national selection indices for dairy cattle (Miglior *et al.*, 2005) and influence profitability of cows. Genetic selection has played a key role in improvements in the dairy industry. Annual genetic gain of over 3% of the trait mean is realizable if genetic selection in continuously and logically made (Simm *et al.*, 2005).

The amount of genetic selection applied in livestock population is measured by the genetic selection differential (GSD). The total selection applied in any livestock population is a composite of selection in the four pathways of genetic improvement as proposed by Rendel and Robertson (1950). These pathways are sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths. Whilst there is evidence of overall genetic improvement in all Canadian dairy cattle populations, it is not clear what the contribution of dairy producers, who control the SC and DC paths, is to this genetic improvement. It is therefore not surprising for producers to think and say, “we are directly selecting for economically important traits since the population genetic trends for economic traits are increasing”. The issue, however, is that the positive trends could be due to intense selection emphases of few producers or AI centers within the population. Not enough tools are available for producers to monitor the past selections producers have made within their herds. It would thus be important for producers and the industry at large to have adequate tools to routinely monitor the success of selective breeding programs, measure the efficiency of selection practices historically applied, and measure current selection practices in their herds and population.

There are rather few studies on GSD in dairy cattle, which studies focused mainly on production traits in nucleus or entire populations of Holstein breed in the USA, Japan, and Italy (Van Tassell and Van Vleck, 1991; Burnside *et al.*, 1992; Kawahara *et al.*, 2004; García-Ruiz *et* *al.*, 2016) and Jersey population in the USA (Nizamani and Berger, 1996). There are no reports of GSD in Canadian dairy cattle populations, and also variations in GSD of most economically important traits among herds in Canada and other parts of the world.

1.1.1 Objectives

The general objective of this thesis was to investigate realized genetic selection differentials among Canadian dairy cattle herds.

Specific objectives were

- i. compute realized GSD for major production, durability, health, and fertility traits along the four-path selection model across many years of conception in the Holstein dairy cattle breed
- ii. compute realized GSD for major production, durability, health, and fertility traits along the four-path selection model across many years of conception in three minor dairy cattle breeds (Ayrshire, Jersey, and Brown Swiss)
- iii. estimate realized GSD for auxiliary traits in four Canadian dairy cattle breeds identified above
- iv. investigate generation intervals in four Canadian dairy cattle breeds identified above
- v. estimate genetic parameters for lactation body weight, milk production, health, and profit indicator traits in Holstein cows in Québec
- vi. develop a prototype software tool and visualization model that dairy producers and agricultural advisors can use to monitor applied GSD in their herds on an on-going basis.

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2 CHAPTER II: Literature Review

2.1 Importance of selection experiments

Selection experiments in livestock species started as far back as the beginning of the 20th century with laying performance in poultry (Lerner, 1958). Hill (2011) outlined some important reasons for long term selection experiments over the years and why such experiments may still be relevant. Selection experiments were essentially undertaken to obtain information on the genetic architecture of quantitative traits, estimate additive genetic variances and covariances among traits under selection, determine theoretical predictions of genetic progress, heritability of traits in the base populations, and test for genotype by environment interaction (Hill, 1980, 2011; Eisen, 1994). Results of selection experiments are needed to enable animal producers to make informed decisions in managing herds and improve economically important traits (Koch *et al.*, 1994). Several authors have also used selection experiments to estimate direct and correlated responses, genotype x environment interactions, and realized heritability in various species of animals (Bishop, 1993; Koch *et al.*, 1994; Swallow *et al.*, 1998; Burrow and Corbet, 2000). Other benefits of long-term selection applications have been outlined by Burnside (1996).

Mice and drosophila have often been the model or pilot organisms for many long-term selection experiments in the past and they have been used to demonstrate selection theories, estimate some genetic parameters, and demonstrate evidence of selection limits (Falconer, 1953; Byrne *et al.*, 1973; Falconer, 1973; Sharp *et al.*, 1984; Bunger *et al.*, 1994; Zwaan *et al.*, 1995; Nielsen *et al.*, 1997) due to the shorter generation intervals of mice and drosophila, and the relatively low cost of experiments involving these organisms. A contrary view that the real cost of experiments involving pilot animals was higher than larger animals has been expressed by Blair, personal communication as cited in Burnside (1996). However, for several decades, selection has also been used to bring about significant changes in economically important traits in various livestock populations such as poultry (Dunnington and Siegel, 1996; Nestor *et al.*, 2000), swine (Nguyen and Mcphee, 2005; Schwab *et al.*, 2006), sheep (Morris *et al.*, 1997), and beef cattle (Buchanan *et al.*, 1982; Koch *et al.*, 2004).

2.2 Selection

Natural selection is one of the evolutionary forces that brings about changes in allele and genotype frequencies in large random mating population (Falconer and Mackay, 1996). Artificial genetic selection is the process of choosing individuals that are superior for specific traits to become parents of the next generation of animals using the individuals estimated breeding values (EBV). Genetic selection is an effective tool that has brought genetic changes in livestock populations during the first half of the 20th century (Dunn, 1951) and beyond. Genetic gain is the increase in performance achieved through artificial selection (Xu *et al.*, 2017).

2.2.1 Methods for estimating genetic gain

In animal breeding, annual genetic gain which depicts the genetic difference between a selected population and its offspring population, is a function of genetic selection differential and generation interval. Two methods have often been used to estimate the rate of genetic gains or genetic progress in a population. The first is the regression of genetic values of animals (EBV) on animals' year of birth (Van Tassell and Van Vleck, 1991; Nizamani and Berger, 1996; Chegini *et al.*, 2013) as illustrated below:

$$\Delta G \text{ per year} = b_{GC}T \qquad \textbf{[Equation 2.1]}$$

where ΔG per year = expected annual genetic gain

b_{Gc} = estimated regression of average predicted genetic values of cows (Gc) on year of birth (T)

The second approach is the formula of García-Ruiz *et al.* (2016), based on the method of Rendel and Robertson (1950), using the genetic selection differentials in the four paths of genetic improvement and the generation intervals in each of the four paths of selection as shown below:

$$\Delta Gy = \frac{\Delta G_{SB} + \Delta G_{DB} + \Delta G_{SC} + \Delta G_{DC}}{L_{SB} + L_{DB} + L_{SC} + L_{DC}} \quad \textbf{[Equation 2.2]}$$

where ΔGy = annual genetic change

ΔG = estimated genetic superiority of the selected animals over their contemporaries born in the same year

L = Generation interval

In dairy cattle, few workers have used the second approach to estimate annual genetic gains in production, reproduction, and health traits (Nizamani and Berger, 1996; García-Ruiz *et al.*, 2016). The next two sections will briefly review genetic selection differential and generation interval as they apply to annual genetic change.

2.3 Genetic selection differential

Selection differential is used to compare the amount of selection pressure applied in breeding programs (Falconer and Mackay, 1996). It is defined as the average phenotypic superiority of selected parents over the mean of their contemporary groups. Realized and expected selection differentials have been computed and expressed in either trait units or standard deviation units in a number of selection experiments, some of which will be reviewed in later sections. Genetic selection differential, on the other hand, is the computation of selection differentials using animals' EBV rather than their phenotypic values. There have been variations in the computations of selection differentials among authors, but all are essentially based on the principles of quantitative genetics stipulated by Falconer and Mackay (1996).

In a study on adaptive traits in northern pike, a recreational fish, Arlinghaus *et al.* (2009) computed selection differential as the difference in trait means before and after selection. Brown and Cue (1992) calculated genetic selection differential as the difference between bull proofs and the average proof of all bulls available for service within a given period. In a study on observed and theoretical genetic trends in Italian Friesian cattle, Burnside *et al.* (1992) estimated realized GSD as the difference between the average EBV of all parents of each progeny birth year and the average EBV of all Italian cows born a generation interval earlier. Van Tassell and Van Vleck (1991) and García-Ruiz *et al.* (2016) have computed GSD as the deviation of each parent's predicted breeding value (PBV) from the average PBV of an appropriate base group of the same birth year.

Genetic selection differential is a function of selection intensity (i), accuracy of EBV (r_{EBV}), and genetic standard deviation (σg) of the trait. The equation for GSD is presented below:

$$GSD = i.r_{EBV}.\sigma_g \qquad \textbf{[Equation 2.3]}$$

Realized GSD are either weighted by the number of progeny or unweighted. Weighted GSD partly account for the effects of natural selection (Falconer and Mackay, 1996). The ratio of weighted to unweighted GSD has been used as a measure of the extent of usage of selected sires or dams for breeding in a population, and a measure of the effects of natural selection on fertility of sires or dams (Koch *et al.*, 1994). Thus, ratios greater than one indicate that selected sires or dams are extensively being used for breeding. The concept of cumulative selection differential (CSD) has often been used in beef cattle breeding, and it is the sum of an individual's selection differential and the average selection differential of their parents. Cumulative selection differential measures the total past selection applied in a population (Koch *et al.*, 1994). Two different approaches of computing CSD were proposed by Pattie (1965) and Newman *et al.* (1973).

2.4 Generation interval

Generation interval (L) is often the average age of parents when their progeny were born. Falconer and Mackay (1996) defined L as the interval between the matings made in successive generations. Mathematically, L is calculated as the interval between the dates of birth of parents and progeny expressed in days or years (Burnside *et al.*, 1992; Kawahara *et al.*, 2004).

The next few sections attempts to briefly review selection differentials and generation intervals in selection experiments in mice, sheep, beef cattle, and dairy cattle.

2.5 Selection experiments in mice

2.5.1 Selection differentials

Selection experiments with mice were very popular in the past to understand the genetic variations in quantitative traits and compute realized heritabilities for quantitative traits. Such experiments are, however, not common in recent times due to funding difficulties and the availability of new methods for deeper studies of biology of animal species (Hill, 2011). About six decades ago, Falconer (1953) reported results of divergent selection experiments in mice where he selected for large and small body weight at 6 weeks of age. After 11 generations of selection in each line, he reported mean weighted and unweighted selection differential of 1.50 and 1.51 grams, respectively, in the large line. For the small line, the realized mean weighted and unweighted selection differentials were 1.32 and 1.33 grams, respectively. The lack of difference between the weighted and unweighted selection differentials in both lines was attributed to the absence of differential fertility for parents of both lines. Falconer's experiment did not partition the total selection differentials into the four component paths of selection.

Sharp *et al.* (1984) reported mean CSD of 37.3, -36.9, and 1.0 grams, respectively, for high, low, and control lines of mice between the ages of 4 and 6 weeks selected for feed intake. For gonad fat pad per body weight, they reported mean CSD of 16.9, -10.7, and 0.8 mg/g, respectively, for high, low, and control lines. In selecting for increased (high) and decreased (low) heat loss in male mice, Nielsen *et al.* (1997) reported mean realized CSD of 145.1 and -105.0 $\mathrm{kcal.kg^{-0.75}.d^{-1}}$ for high and low lines, respectively, after 15 generations. There are several other studies of selection in mice (Bradford, 1968, 1971; Swallow *et al.*, 1998; Bunger *et al.*, 1994). Selection experiments with mice involved divergent lines and the estimation of realized heritabilities for various traits ranging from production to heat dissipation. There are differences in the mean selection differentials in the divergent lines, however, no statistical test was carried out to determine if these differences were significant. Also, most of the selection experiments in mice were phenotypic selections.

In mouse selection experiments, responses to selection were measured by keeping either selected and unselected control lines or divergent lines for many generations. The differences in mean values of traits between selected and unselected lines served as the measure of response to selection. From the selection response, realized heritability for a trait can be computed from the formula presented below:

$$\textit{Realized } h^2 = R/SD \qquad \textbf{[Equation 2.4]}$$

where R = Response to selection

SD = Selection differential

2.5.2 Generation intervals in mice

Generation intervals are not usually important in mice selection experiments because mating times in mice experiments are determined by experimenters, and thus there are only few reports of L in the literature. Generation intervals in mice are in weeks and often not relevant if they are not studied over time or compared between populations. Nielsen *et al.* (1997) achieved an L of 15 weeks in parity one mice while Falconer (1953) achieved L of 9, 12.5, and 16 weeks in parities 1, 2, and 3 mice, respectively.

2.6 Selection experiments in sheep

2.6.1 Selection differentials

The literature is lacking in information on selection differentials in sheep, probably due to relatively high cost involved with such experiments. In New Zealand Romney sheep born between 1979 and 1992, Morris *et al.* (1997) observed mean CSD of -1.03 and 1.07 $\log_e$ units for faecal nematode egg count recorded in mid to late January (FEC1) for resistant and susceptible lines, respectively. For FEC recorded in late February to early March (FEC2), the mean CSD were -1.39 and 0.91 $\log_e$ units for resistant and susceptible lines, respectively. These selection differentials translated into 0.36 and 0.30 σ_p per generation for resistant and susceptible lines, respectively. About 54% of the selection differentials for FEC were accumulated in the last 4 years (1989 to 1992) of the study period. This suggested that selection differentials for FEC were increasing over time. Johnson *et al.* (1995), however, reported higher selection differential of 0.75 σ_p per generation for yearling weight or body weight in Romney sheep born between 1967 and 1990. Morris *et al.* (1997) attributed the low realized selection differentials in their study to selection based largely on phenotypic performance in the early years, and dilution of selection for FEC by simultaneous selection for post-weaning weight gain in the later years. Both Morris *et al.* (1997) and Johnson *et al.* (1995) did not partition the results of the selection differentials into the four pathways of selection.

In a selection experiment with Suffolk sheep in the UK, Simm *et al.* (2002) reported unweighted average selection intensities of 1.48 and 0.33 for an index of live weight, ultrasonic muscle, and fat depth at an adjusted constant age of 150 days in male and female selected lines, respectively, over a 9-year period. Selection intensities of -0.07 and 0.05 were observed in male and female control lines, respectively. Bhuiyan and Curran (1995) reported a mean selection differential of 7 LLB/EJ for prolificacy (expressed per 100 ewes) in Romney ewes born between 1983 and 1988. The mean selection differential for the last 3 years was 8.27 LLB/EJ suggesting that realized selection differentials increased with time. Similar selection differentials have been reported for cannon bone length (Atkins and Thompson, 1986), and greasy fleece weight (Blair, 1986). The breeding objectives of the sheep experiments ranged from improvement in production to health and fertility traits. The selection differentials have not been partitioned into the 4-path selection model.

Responses to selection in sheep experiments have also been computed as the differences in performance of selected and control unselected lines after several generations of selection (Anderson and Curran, 1990; Bhuiyan and Curran, 1995; Johnson *et al.*, 1995; Simm *et al.*, 2002). Differences between selected and control lines have been used to evaluation sheep breeding programs for many years (Hill, 1972; Mann *et al.*, 1978). Annual responses of between 1 and 2% of trait means were observed for production and reproduction traits in Romney (Bhuiyan and Curran, 1995; Johnson *et al.*, 1995) and Suffolk (Simm *et al.*, 2002) sheep. The sheep experiments reviewed involved small nucleus flocks with a few hundreds or thousands of sheep, and relatively few number of years of selection in nucleus or experimental flocks.

2.6.2 Generation intervals in sheep

Morris *et al.* (1997) reported mean generation intervals of between 3.14 and 3.40 years for the male path, and between 3.56 and 3.61 years for the female path. However, Johnson *et al.* (1995) reported lower L (2.7 years) in the same breed of sheep in a slightly different production system. Joakimsen (1969) reviewed L in all four paths of selection in five Norwegian sheep breeds. The mean L in the four paths ranged from 3.7 to 4.1 years. Cameron and Bracken (1992) reported the lowest mean L of 1.87 and 1.92 years for low and high lines, respectively, of Texel-Oxford sheep selected for carcass leanness. The lowest L in the study was because both rams and ewes were mated at 7 months of age and ewes were culled at 4 years of age. The reduction of L in especially the male pathways has positive influence on profit as it increases the rate at which superior breeding males are produced and used for breeding in a flock, thereby increasing the flock's performance for breeding objective traits at a faster rate. The L in the female pathways cannot be reduced beyond a certain age as females only become sexually mature for breeding at a certain age in the absence of reproductive technologies. In addition, producers will want to keep breeding ewes for longer period of time to enable them undergo many parturitions to increase the profitability of such breeding ewes.

2.7 Selection experiments in beef cattle

2.7.1 Selection differentials

There have been quite a number of long-term selection experiments in beef cattle in different countries. Newman *et al.* (1973) were one of the first researchers to estimate selection differentials in Canadian beef cattle. For yearling weight, they reported mean realized selection differentials of 69.1, 24.8, 67.8, and 25.8 kg in the SB, DB, SC, and DC paths, respectively, in beef Shorthorn cattle in a nucleus herd in Brandon, and 65.8, 24.1, 66.7, and 24.4 kg for SB, DB, SC, and DC paths, respectively, at the Lacombe herd. Unintended selection differentials of -2.7 and 7.6 kg attributed to natural selection were observed in unselected control lines (Newman *et al.*, 1973). In New Zealand, Baker *et al.* 1991 observed lower mean selection differentials for yearling weight in Angus (7.6 kg) and Hereford (6.0 kg) beef cattle with an unintended mean selection differential of 0.36 kg per year in an Angus control line.

In a selection experiment in three lines of Hereford cattle in Nebraska between 1960 and 1977, Buchanan *et al.* (1982) reported mid-parent selection differentials per generation of between 0.87 σ and 1.06 σ for weaning weight, yearling weight, muscle score, and index of yearling weight and muscle score. Similar mid-parent selection differentials have been reported for similar primary traits at Agricultural Experiment station in Nevada (Chevraux and Bailey, 1977). The study of Buchanan *et al.* (1982) showed that even with selection pressure for primary objective traits, there was appreciable unintended selection in other traits (birth weight, weaning weight, pre-weaning daily gain, and post-weaning daily gain) due to the genetic correlations among traits. Similar findings have been reported elsewhere (Koch *et al.*, 1994; Pereira *et al.*, 2008). Lower mean mid-parent selection differentials per generation for weaning and yearling weights in Hereford (Frahm *et al.*, 1985) and Angus (Aaron *et al.*, 1986) beef cattle have been reported.

Higher mean weighted selection differentials of between 1.10 σ and 1.72 σ for sires, and between 0.24 σ and 0.61 σ for dams were realized for yearling weight in Caracu and Nelore beef cattle breeds in Brazil (Razook *et al.*, 1998; Knackfuss *et al.*, 2006; Pereira *et al.*, 2008). Similar selection differentials of 1.75 σ and 0.25 σ were realized in Hereford sires and dams, respectively

(Koch *et al.*, 1994). Selection differentials in the sire paths were higher than the dam paths as the sire path was reported to contribute between 86% and 95% of the total realized selection differentials in two beef herds in Iowa State University (Hassen and Willham, 1998).

All the studies of selection reviewed in beef cattle involved selection in experimental or nucleus herds. They involved herds with relatively smaller numbers, and traits studied were primarily production traits, which is not surprising as body weights and feed efficiency were the key breeding objectives of beef breeders and major drivers of profit in the beef industry. Little information has been reported on selection for reproduction and health traits in beef cattle. The selection differentials realized were below the maximum selection differentials attainable due to reasons such as set selection criteria or constraints, and loss of focus on selection objectives (Pereira *et al.*, 2008).

Genetic trends for yearling weight by regressing cumulative selection differentials on year of birth have been reported in several populations of beef cattle in Brazil (Mercadante *et al.*, 2003; Knackfuss *et al.*, 2006; Pereira *et al.*, 2008), Canada (Sharma *et al.*, 1985), New Zealand (Baker *et al.*, 1991), and the USA (Koch *et al.*, 1994). The genetic trends ranged from 0.27 kg/year to 11.31 kg/year.

2.7.2 Generation intervals in beef cattle

The average generation intervals for beef cattle experiments were within the range of 3 to 6 years (Baker *et al.*, 1991; Parnell *et al.*, 1997; Mercadante *et al.*, 2003; Knackfuss *et al.*, 2006). Most of the studies reviewed reported L of the male and female paths whilst Hassen and Willham (1998) reported the mean L in all four paths of selection, SB (2.7 to 3.4 years), DB (2.5 to 3.2 years), SC (3.3 to 5.2 years), and DC (3.1 to 4.1 years) in three synthetic lines of beef cattle across two herds.

2.8 Selection in dairy cattle

2.8.1 Selection differentials

Only a few long-term selection experiments have been reported in dairy cattle. This could be due to the longer generation intervals of dairy cows and the high cost of selection experiments involving dairy cattle. In a review, McAllister and Lee (1994) reported important heterotic effects of annualized discounted net returns in a Holstein-Red and White synthetic line cross. There were studies of selection differentials in mostly Holstein populations in the USA, Italy, and Japan. Selection differentials reported for dairy cattle were for all four pathways of selection as proposed by Rendel and Robertson (1950).

In Holstein cattle in the north eastern USA, Van Tassell and Van Vleck (1991) reported average weighted GSD of 405, 395, 239, and 42 kg for milk yield in the SB, DB, SC, and DC paths, respectively. Lower unweighted GSD of 97 and -12 kg were observed for the SB and SC paths which suggested that genetically superior bulls for milk yield were being heavily used for breeding. The mean GSD for the last 5 years of Van Tassell and Van Vleck's study (1974 to 1978) were higher for the SB (884 kg) and DB (598 kg), but remained unchanged for the SC (235 kg) and lower for the DC (28 kg) path. This was an indication that whilst AI companies were intensively selecting for milk during the later period of the study, selection pressures of producers were either unchanged or declining. The producers' selection actions in recent times were partly attributed to selection for traits other than milk production and partly to higher levels of involuntary culling of sick and unproductive replacement cows. It is also possible that producers' selection could have been due to better producer management.

Burnside *et al.* (1992) estimated the rates of genetic progress theoretically possible in a modern AI and progeny testing scheme in relation to what was actually achieved in Italian Friesian population between 1972 and 1988. The actual mean weighted GSD for milk yield, in the study of Burnside and coworkers, were 2237, 1237, 1208, and 90 kg for the SB, DB, SC, and DC paths, respectively. These GSDs were higher than those reported by Van Tassell and Van Vleck (1991) although the GSD ranked identical for all four pathways. The mean GSD for fat and protein yields in four pathways ranged from 3 to 80 kg and ranked similar as that of milk yield (Burnside *et al.*, 1992). Nizamani and Berger (1996) and García-Ruiz *et al.* (2016) have both reported different rankings for weighted GSD of milk yield in registered Jersey and Holstein populations, respectively, in the USA. In both studies, GSD of the SC path was higher than that of the DB.

For milk yield, Nizamani and Berger (1996) reported mean weighted GSD of 493, 307, 351, and 34 kg in the SB, DB, SC, and DC paths, respectively, for Jersey cows born between 1960 and 1987. The ranking of unweighted GSD for the four selection pathways reported by Nizamani and Berger (1996) were, however, similar to those of Van Tassell and Van Vleck (1991) and Burnside *et al.* (1992). The unweighted mean GSD for milk yield were 240, 269, 109, and 18 kg for SB, DB, SC, and DC paths, respectively (Nizamani and Berger, 1996).

García-Ruiz *et al.* (2016) reported mean weighted GSD for milk yield of 823, 286, 522, and 41 kg for SB, DB, SC, and DC, respectively, in USA Holstein cows born between 1981 and 1985. The GSD for the same trait in Italian Friesian population born around the same period were considerably higher than those in the USA and these were attributed to the heavy importation of semen from North America into the Italian population.

In Japanese Hokkaido Holstein born between 1980 and 1990, Kawahara *et al.* (2004) reported positive trends in GSD for milk, fat, and protein yields in the SB, DB, SC, but not the DC path. An interesting observation in this study was the change in ranking of GSD for milk and fat yields. The mean realized GSD for milk yield were 2.19, 1.69, 1.57, and <0.10 genetic standard deviation units while those for fat yield were 2.28, 1.85, 2.40, and <0.10 in the SB, DB, SC, and DC paths, respectively. These results suggest that the breeding objectives of producers might be different from those of AI companies, hence the differences in selection emphases.

In all the studies reviewed, the GSD of the DC path were low (Van Tassell and Van Vleck, 1991; Burnside *et al.*, 1992; Nizamani and Berger, 1996; Kawahara *et al.*, 2004; García-Ruiz *et al.*, 2016) and this was explained by the lack of opportunity for selection in the DC path, and the limitation of the need for replacement cows within a herd. The SB path was the greatest contributor to the total GSD in the studies reviewed. In addition, the mean GSD of the later years of the studies were mostly higher than the overall mean GSD for the entire study periods, indications of increasing GSD over time.

Annual genetic trends in dairy cattle have often been estimated by regression of mean EBV on year of birth or the ratio of average GSD to average L. Van Tassell and Van Vleck (1991) reported mean realized annual genetic gain of 34.9 kg/year for milk but this was lower than the theoretically possible value of 96 kg/year in that population. This was an indication that there was still further opportunity to intensify selection for milk production. Burnside *et al.* (1992), on the other hand, reported realized annual genetic gain of 247 kg/year in Italian Friesian population which was similar to the maximum theoretically possible value. Annual genetic gain of 43.6 kg/year in USA Jersey (Nizamani and Berger, 1996) and 70 kg/year in USA Holstein (García-Ruiz *et al.*, 2016) born between 1981 and 1990 have been reported. The Canadian dairy industry through the Canadian Dairy Network (CDN) calculates and reports on the genetic trends of key traits in the Holstein cows (Table 2.1) but there are no reports of the selection emphases in the various paths of selection that brought about this genetic change.

Table 2.1 Comparison of total 5-year genetic gains realized by traits before and after the introduction of genomics in Canada

	Total Gain Realized	
Trait	**Before genomics (2004 – 2009)**	**Last 5 years (2011 – 2016)**
Milk yield (kg)	355	603
Fat yield (kg)	14.0	29.8
Protein yield (kg)	11.8	24.0
Fat deviation (%)	0.01	0.07
Protein deviation (%)	0.00	0.04
Conformation	3.20	5.06
Mammary system	3.19	4.94
Feet and legs	1.86	3.99
Dairy strength	1.78	2.63
Rump	1.34	1.05
Herd life	1.12	3.36
Somatic cell score	0.04	0.12
Mastitis resistance	0.92	2.46
Metabolic disease	0.10	1.42
Persistency	-0.22	1.41
Daughter fertility	-0.72	1.06
Milking speed	0.06	0.51
Milking temperament	-0.09	1.89
Daughter calving ability	0.23	2.29

Sourced from the Canadian Dairy Network website (www.cdn.ca, August 23, 2019).

All the studies of GSD in dairy cattle have focused on selection emphases in entire populations of either Holstein or Jersey, but not one of them has examined the variations in realized selection differentials among selection pathways controlled by producers and AI centres. The population average GSDs are important indicators of trends in selection emphases in the population, but they could be influenced greatly by intense selection by a few herds or AI centres. The existence of intense selection by a few herds could give wrong indications to some producers and breeders that they are improving at a certain rate when in fact they are not. It therefore behooves on the industry to determine variabilities in the realized GSD among dairy producers in the major dairy cattle populations. This could be used to develop specific tools to enable groups of producers in a given agricultural region, or using particular housing systems, to monitor their selection emphases for economically important traits that influence profitability of producers' herd operations.

Despite Canada's prominent status in the global dairy industry, there has not been any comprehensive study of GSD in Canadian dairy cattle populations. The works of Rapitta *et al.* (1988) estimated L and selection intensities of young sires in AI studs while Brown and Cue (1992) determined differences that AI organizations and dairy producers placed on type and production traits by assessing selection emphases for bulls by official and owner sampler herds relative to bulls selected by AI centres. The two studies in Canada involved relatively few records of Ayrshire and Holstein breeds, but did not entirely explore the selection practices of producers who are major stakeholders in the dairy industry. It is important to investigate the selection emphases applied to breeding objectives traits by both AI centres and dairy producers (herds) in Canada by completely estimating the GSD and L in all four pathways of selection for major and minor dairy cattle breeds (Holstein, Ayrshire, Jersey, and Brown Swiss) across an exhaustive list of traits of economic importance since 1980. The results will be used to design a monitoring tool which dairy producers could use to monitor the selection producers are making in their herds on an on-going basis and compare their herds' performance with appropriate benchmarks.

2.8.2 Generation intervals in dairy cattle

Most studies on selection differentials in dairy cattle also reported L. The mean L for the four paths of genetic improvement have been summarised in Table 2.2 below.

Table 2.2 Mean generation intervals (in years) for the four paths of selection as reported in dairy cattle breeds by various authors across different countries

Breed	SB[1]	DB	SC	DC	Country	Period	References
Holstein	7.6	5.6	7.0	4.7	USA	1960 – 79	Lee et al. (1985)
Holstein	9.5 – 11	7.4 – 7.6	-	-	Canada	1980 – 86	Rapitta et al. (1988)
Holstein	10.2	6.4	9.3	5.1	USA	1955 – 78	Van Tassell and Van Vleck (1991)
Friesian	10.5	5.6	9.0	4.5	Italy	1980 – 90	Burnside et al. (1992)
Jersey	9.3	5.8	7.6	4.5	USA	1965 – 90	Nizamani and Berger (1996)
Holstein	7.8	5.0	8.0	4.5	Japan	1980 – 98	Kawahara et al. (2004)
Holstein	2.6	2.8	5.2	3.5	USA	2011 – 15	García-Ruiz et al. (2016)

[1] SB – Sire-to-bull; DB – Dam-to-bull; SC – Sire-to-cow; DC – Dam-to-cow

2.9 Economically important traits

In the dairy cattle industry, traits of economic importance are characteristics in cows or bulls that add economic value to cows or bulls and thereby contribute to the profitability of the animals. Most breeding objectives in animal breeding programs seek to improve economically important traits. Selection emphases are, thus, put on these traits to improve the traits. Generally, economically important traits in dairy cattle are recognized as traits that serve at least one of the following functions: contribute to higher revenue, contribute to increased profit due to longer herd life of cows, or reduce the cost of production. The traits are broadly classified as production, durability, and health and fertility. A number of individual traits are combined to form selection index. Different indices are created and selected for in different countries and these indices reflect most countries' breeding objectives (Miglior *et al.*, 2005).

2.9.1 Production traits

Milk production traits have been the main traits for selection in the past due to the relative ease and objective means of recording production traits and their strong relationship with cow profitability. The key production traits of dairy cattle are 305-day milk (MY), fat (FY), protein (PY) yields, fat (F%), and protein (P%) percentages. Production or yield traits have positive economic values (Mulder and Jansen, 2001) and currently constitute between 40 and 55% of the weight of the lifetime performance index (LPI) for Holstein, Ayrshire, Brown Swiss, and Jersey dairy breeds in Canada (www.cdn.ca, August 27, 2019). The moderate heritabilities for production traits (Miglior *et al.*, 2007) have enabled appreciable genetic progress to be made for production traits in the dairy industry. The importance of production traits in breeding programs many years ago are diminishing as breeding goals are becoming broader with time (Miglior *et al.*, 2017). Moderate to strong and positive genetic correlations exist among yield traits (Miglior *et al.*, 2007), while there are moderate genetic correlations between yield and some type and conformation traits (De Haas *et al.*, 2007). Milk production traits have unfavorable genetic correlations with fertility (Veerkamp *et al.*, 2001) and health related traits (Pritchard *et al.*, 2013).

2.9.2 Durability traits

Durability traits comprised of conformation or type and longevity traits; and conformation traits were long suggested for consideration in selection programs together with production traits (Copeland, 1938). Some key durability traits included in the Canadian LPI are mammary system

(MS), feet and legs (FL), dairy strength (DS), rump (RUMP), hoof health (HH), and herd life (HL). Durability traits constitute between 27 and 40% of the weight of the LPI of the Ayrshire, Brown Swiss, Holstein, and Jersey cattle breeds (www.cdn.ca, August 27, 2019). Heritability estimates for conformation traits are mostly moderate (Koenen and Groen, 1998; De Haas *et al.*, 2007) and heritability estimate of longevity is low (Short and Lawlor, 1992; Sewalem *et al.*, 2005). The genetic correlations among conformation traits are mostly moderate (De Haas *et al.*, 2007), and similar to the correlations between conformation and milk production traits (De Haas *et al.*, 2007). Cow longevity has low to moderate genetic correlations with conformation traits ranging from -0.28 to 0.47 (Mrode *et al.*, 2000). Conformation traits generally have favorable genetic correlations with fertility traits and somatic cell score (SCS) (Van Dorp *et al.*, 1998; Kadarmideen, 2004). Among the durability traits, herd life had a high economic value (Mulder and Jansen, 2001) and was second to the economic values of milk production traits (Allaire and Gibson, 1992). The economic values of the conformation traits were mostly low and negative (Mulder and Jansen, 2001). The low, but heritable, values of longevity traits in addition to the moderate correlations between longevity and conformation traits make longevity traits eligible for inclusion in a selection index, in an attempt to improve overall cow profitability. Many dairy producing countries have routine genetic evaluations for longevity (Miglior *et al.*, 2005).

2.9.3 Health and fertility traits

Health and reproductive traits are important traits in Canadian dairy industry. They contribute between 15 and 22% of the weight of the LPI for the Canadian dairy cattle breeds (www.cdn.ca, August 28, 2019). The main traits that constitute the health and fertility sub-group are daughter fertility (DF), mastitis resistance, SCS, udder depth (UDD), milking speed (MSP), and lactation persistency (LP). The heritability estimates for fertility traits are low (Pryce *et al.*, 1998; Veerkamp *et al.*, 2001; Pritchard *et al.*, 2013) similar to health-related traits (Pryce *et al.*, 1998; Van Dorp *et al.*, 1998). Fertility traits have antagonistic relationship with milk production traits (Pryce and Veerkamp, 2001; Kadarmideen, 2004; VanRaden *et al.*, 2004) but favorable genetic correlations with health traits (Morris *et al.*, 2011; Pritchard *et al.*, 2013). The higher economic values of fertility (Pryce and Veerkamp, 2001) and health (Sadeghi-Sefidmazgi *et al.*, 2011) traits have contributed to the inclusion of fertility and health traits in most national breeding goals and selection indices (Miglior *et al.*, 2005). Considerable genetic gains have been realized for fertility and health traits in the era of genomic selection (García-Ruiz *et al.*, 2016).

2.9.4 Selection indices

Most national breeding goals are many and tend to be balanced (Miglior *et al.*, 2005), comprising a combination of production, durability, and health and fertility traits. In the study of national selection indices of 15 countries, Miglior *et al.* (2005) observed average relative emphases of 59.5, 28, and 12.5% for production, durability, and health and fertility traits, respectively. This suggested that production was still important in the breeding goals of most countries. The relative emphasis on production has, however, been reducing and is expected to reduce further if welfare traits are included in national selection indices (Oltenacu and Broom, 2010) for dairy cattle. The LPI is one of the main selection indices used in Canada. The relative weights of production, durability, and health and fertility in the LPI are different for the different breeds of dairy cattle. The LPI for Holstein cattle, for instance, has relative emphasis of 40%, 40%, and 20% for production, durability, and health and fertility, respectively (www.cdn.ca, August 30, 2019). Beside the LPI, the Canadian dairy industry also has sub-indices for the three groups of traits. These are the LPI sub-indices for production (LPI-PROD), durability (LPI-DUR), and health and fertility (LPI-HF). The pro dollar index (Pro$) is a selection index that has recently been introduced for the Canadian dairy industry. Genetic trends are produced and reported for the LPI, but not the sub-indices. Being one of the marketing tools of AI centres, it will be interesting to determine the selection emphases both producers and AI organizations put on the LPI for the various breeds of cattle in Canada. The only report of realized GSD of a selection index in the literature was the Italian aggregate quality milk index (Burnside *et al.*, 1992).

2.10 Impact of genetic selection on rates of inbreeding

Current advances in genetic selection programs have led to increase rates of genetic gains in most national breeding programs and also increased the rates of inbreeding in these programs (Weigel, 2001). Inbreeding is a function of selection intensity (Weigel, 2001). The intensification of selection intensities could result in increased incidences of genetically related animals with high EBV for economically important traits being selected and used for breeding. In the dairy cattle industry where traditional progeny testing schemes were very common in the past in the absence of genomic information, bull calves were selected for progeny testing using their parental average breeding values. Full-sibs with high EBV will, thus, be selected together and this can increase the rate of inbreeding (Hayes *et al.*, 2009). Under genomic selection, rate of inbreeding per generation has been projected to decrease due to Mendelian sampling (Hayes *et al.*, 2009), but the rate of inbreeding per year may increase due to the reduction in generation intervals (VanRaden *et al.*, 2011) as reductions in generation intervals, in especially the male-to-female path, have characterized genomic selection (García-Ruiz *et al.*, 2016). A balance between genetic gains and rates of inbreeding is sought in many breeding programs (Quinton *et al.*, 1992) hence optimum genetic gains should be desired in national breeding program to sustain such programs. A number of methods have been proposed for controlling inbreeding in livestock populations (Weigel, 2001). Several mate selection programs have been proposed to be useful tools to minimize rates of inbreeding whilst optimizing genetic gains in livestock populations (Toro and Perez-Enciso, 1990; Klieve *et al.*, 1994; Fernández and Toro, 1999; Weigel and Lin, 2000).

2.11 Tools for monitoring genetic selection

There are very few tools available to dairy producers to use to monitor their selection emphases for breeding objective traits within their herds. AlphaMate program, developed in the UK for animal and cross- and self- pollinating plant populations, has been designed to optimize selection, maintain genetic diversity, and mate allocation in both animal and plant breeding programs (Gorjanc and Hickey, 2018). Similarly, ZPLAN is a tool designed to optimize selection strategies in livestock breeding (Willam *et al.*, 2008). In Australia, beef breeders have tools for measuring genetic trends in individual beef herds (Johnston, 2007). Many authors have indicated reasons why many national breeding programs do not realize the expected genetic gains on breeding objective traits after selection (Van Tassell and Van Vleck, 1991; Burnside *et al.*, 1992; García-Ruiz *et al.*, 2016). One of the key reasons was the selection emphases on traits other than breeding objective traits. Currently in Canada, the only available tool dairy producers use to monitor their selection are the genetic trends for 16 traits calculated by Canadian Dairy Network. These trends serve as the only benchmark for producers to monitor their selection with. Production and management characteristics of dairy herds are different; therefore, producers may need localized or customized benchmarks to monitor the selection in their herds and make necessary changes if they are not moving in the right or expected direction.

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CONNECTING STATEMENT

The next chapters of this thesis are based on manuscripts prepared and submitted or ready for submission to selected journals. Chapter 3 has been accepted for publication in the Journal of Dairy Science (JDS) and is currently in-press. Chapter 4 has been submitted to the JDS and is currently under revision. Chapter 5 is under review by the authors and will be submitted for publication in the JDS. Chapter 6 has been accepted for publication in the Canadian Journal of Animal Science and is currently in-press. Chapters 7 has been submitted to Livestock Science and is currently under revision. Chapter 8 is being reveiwed by authors for submission to Journal of Computers and Electronics in Agriculture, respectively. Lastly, chapter 9 puts everything into perspective in a general discussion and conclusion.

3 CHAPTER III: Realized genetic selection differentials in Canadian Holstein dairy herds

There is a tendency for dairy producers to say they are selecting and improving their herds' performance because the population genetic trends are increasing. This study sought to determine what selection Holstein producers and AI centers are making and the variabilities in the selections realized among herds. Analysis of EBV data indicated that there were variations in selection realized by both producers and AI centers. These variations offer further opportunity to increase genetic gains in the Canadian dairy industry. Besides the year of conception, other environmental factors studied generally did not have important effect on selection achieved for economically important traits.

RUNNING TITLE: FULL-LENGTH RESEARCH PAPER

Realized genetic selection differentials in Canadian Holstein dairy herds

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3.1 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.

Keywords: realized genetic selection differential, generation interval, Holstein, herd

3.2 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 (VanRaden, 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, SC, DB, 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 (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 from to compute the GSDs 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 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 was 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 were 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 Québec. About 74% of herds are housed in tie stalls with the rest being housed in free stalls. 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 (Canadian Dairy Network, 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.

3.3 MATERIALS AND METHODS

3.3.1 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-day milk yield **(MY)**, 305-day fat yield **(FY)**, 305-day protein yield **(PY)**, somatic cell score

(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-day 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, 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 which are long dead or culled. Therefore, the LPI trait used in this study, from 1980 to 2015, 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, increase 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 3.1.

Table 3.1 Groups of agricultural regions, milking systems, and housing systems in Québec, 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	Tie stall, free stall

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 onwards, respectively. The number of bull and cow records varied for each of the 10 traits and the path of selection, as presented in Table 3.2. The 72,062 SB records mean that 72,062 bulls were sired by 2,423 uniquely identifiable sires (Supplemental Table S3.5), that these sires had EBV for MY, and that 5,546,227 cows were sired by 71,179 uniquely identifiable bulls (Supplemental Table S3.5) 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 S3.5) 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 the DB, as sire identification errors of up to 23% have been reported (Geldermann et al., 1986).

Table 3.2 Number of records in each selection path[1] for each trait

Trait	SB	SC	DB	DC
LPI[2]	71,520	5,505,116	41,396	4,674,470
305-day Milk yield	72,062	5,546,227	42,924	5,185,123
305-day Fat yield	72,062	5,546,227	42,924	5,185,123
305-day 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
Somatic cell score	72,062	5,546,227	42,924	5,185,123

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

[2] LPI – lifetime performance index.

3.3.2 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 that had been used extensively 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 months of age and 12 to 24 months of age, respectively. We then computed the mean EBV of all available bulls or cows each day between 1980 and 2017. These mean EBVs per day 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 3.1. 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 by subtracting 280 days, being the average gestation length for Holstein cows, from the date of birth of a progeny. 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 **(L)** 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 expressed in years (Figure 3.2).

3.3.3 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 of the 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 large number of observations involved and challenges regarding computing space. For the SC and DC paths, realized GSD was analyzed using [model 3.1]:

$$GSD_{ijkmn} = \mu + YOC_i + HS_j + Region_k + Herd_{jkm} + Herd*YOC_{ijkm} + HS*YOC_{ij} + Region*YOC_{ik} + HS*Region_{jk} + e_{ijkmn}, \qquad \textbf{[Model 3.1]}$$

where GSD_{ijkmn} is the realized genetic selection differential 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 ith year of conception (i = 1980 to 2016);

HS_j is the fixed effect of the jth housing system (j = Tie stall or Free stall);

$Region_k$ is the fixed effect of the kth agricultural region (Table 3.1);

$Herd_{jkm}$ is the random effect of mth herd nested within the jth HS and the kth agricultural region ~ $N(0, \sigma^2_{herd})$ where σ^2_{herd} is the variance of herd;

$Herd*YOC_{ijkm}$ is the random effect of the interaction of the mth herd nested within the jth HS and the kth agricultural region by the ith YOC ~ $N(0, \sigma^2_{herd*YOC})$ where $\sigma^2_{herd*YOC}$ is the variance of herd by YOC;

$HS*YOC_{ij}$ is the fixed effect of the interaction between the jth HS and the ith YOC;

$Region*YOC_{ik}$ is the fixed effect of the interaction between the kth agricultural region and the ith YOC;

$HS*Region_{jk}$ is the fixed effect of the interaction between the jth HS and the kth agricultural region;

and e_{ijkmn} is the random residual ~ $N(0, \sigma^2_e)$ where σ^2_e is the residual variance.

[Model 3.2] was used to analyze realized GSD of the SB and DB paths:

$$GSD_{ijk} = \mu + YOC_i + Stud_j + Stud*YOC_{ij} + e_{ijk}, \qquad \textbf{[Model 3.2]}$$

where GSD_{ijk} is the realized genetic selection differential for a trait;

μ is the overall mean;

YOC_i is the fixed effect of the ith year of conception (i = 1980 to 2016);

$Stud_j$ is the fixed effect of the jth AI center (j = 1, …, 191);

$Stud*YOC_{ij}$ is the fixed effect of the interaction between the jth AI center and the ith YOC;

e_{ijk} is the random residual ~ $N(0, \sigma^2_e)$.

σ^2_e is the residual variance.

For realized GSDs in the SC and DC paths, we wrote an additional model, Model 3.3, where 1 random factor (herd or herd*YOC) was dropped at a time, and the difference in Bayesian Information Criteria **(BIC)** values between models 3.1 and 3.3 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 a random effect was greater than 8. The differences in BIC values were between 558 and 69,581.

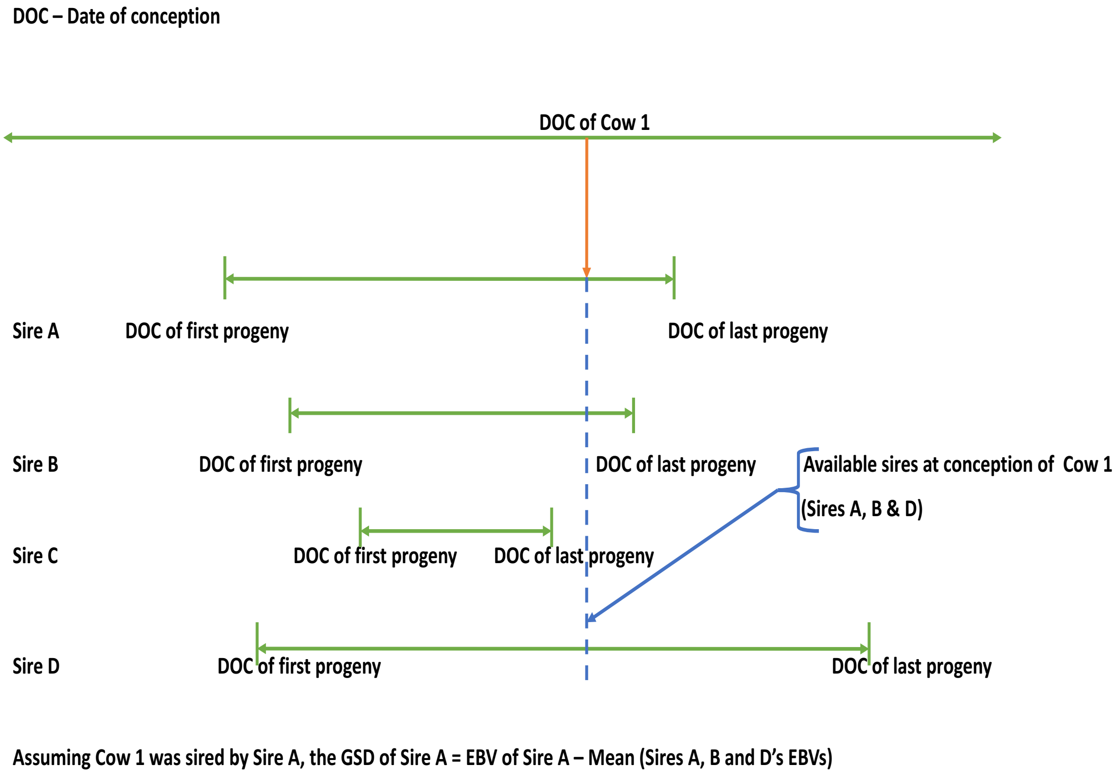

Figure 3.1 Illustration of the computation of realized genetic selection differential of a given sire (sire A) from available sires (sires A, B, and D).

3.4 RESULTS AND DISCUSSION

3.4.1 Generation Intervals

Generation intervals of the SB, SC, DB, and DC paths are presented in Figure 3.2. All 4 paths declined in L over 36-year period. The L of the SB dropped steadily between 1980 and 2000 from 9.7 to 6.3 years (Figure 3.2). 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.

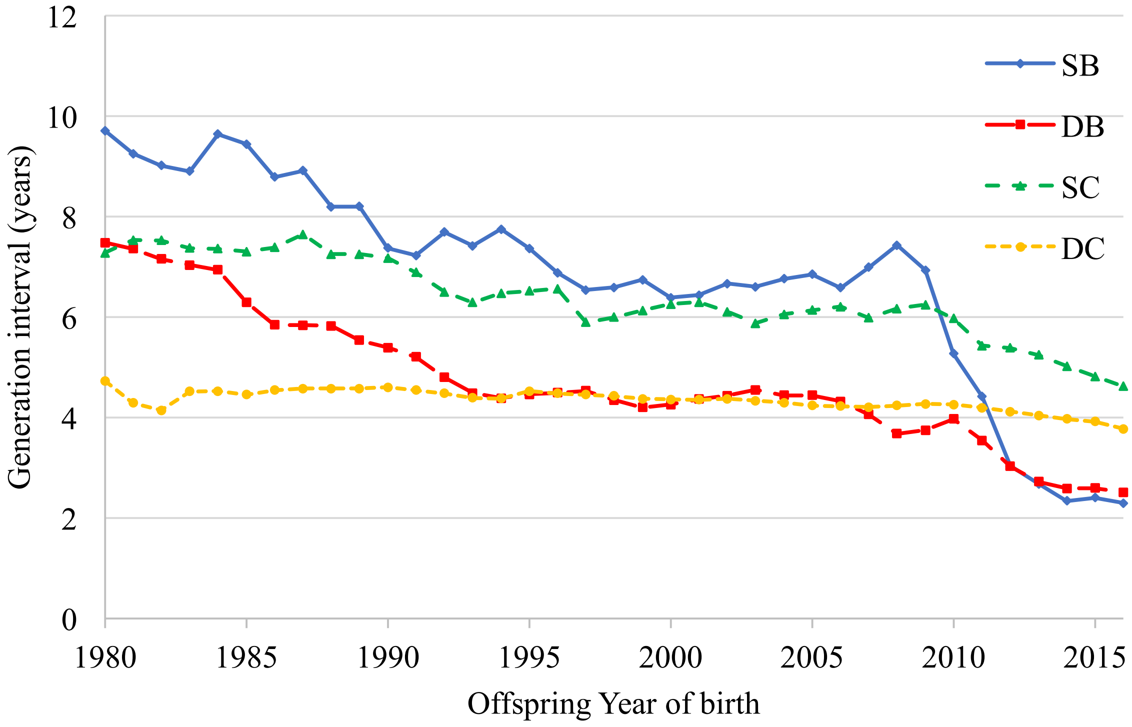

Figure 3.2 Generation intervals for the 4 paths of selection [sire-to-bull (SB), sire-to-cow (SC), dam-to-bull (DB), and dam-to-cow (DC)] by offspring birth year of the Holstein breed.

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 was 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 months in the SC pathway, and Kawahara et al. (2002) obtained a 0.4-year increase in L in Japanese Hokkaido Holstein 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 US 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, there was 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 profitability 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 (Canadian Dairy Network, 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 reduce further in the future, as more producers are now using genomic bulls. In 2017, 67.4% of all matings by Holstein producers in Canada was done with young, unproven genomic bulls (Canadian Dairy Network, 2018).

3.4.2 Realized Genetic Selection Differentials

3.4.2.1 Selection index and Production Traits

The results of realized GSD in trait units (Supplemental Table S3.6) and in standard deviation units **(sd unit)** for the national selection index and production traits (MY, FY, PY) are presented in Figure 3.3. The realized GSDs are presented in genetic standard deviation 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 the SC and DC (Figure 3.3a), 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 into a 1.10-sd unit rise. This large increase was in all likelihood 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 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 the DB compared with SB. Artificial Insemination companies have intensified their selection of bull-dams for the production of AI bulls. The use of reproductive technology such as embryo transfer could also partly account for the high selection intensity in the DB (Canadian Dairy Network, 2013). The trend in realized GSD of the SC was similar to that of the SB path (Figure 3.3a). 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 those for the production traits (Figure 3.3b-d). This signifies favorable correlation between the LPI and production traits. Production traits constitute 40% of the weight of the LPI. So, though LPI was not in existence before to 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 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 old animals, as the selection criteria for these old 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 to the need to maintain herd size for 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 (Canadian Dairy Network, 2018).

The realized GSD for the production traits (MY, FY, and PY) showed similar trends for each of the selection paths (Figure 3.3b-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 finding 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 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 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 hand, was smaller for FY than those observed for MY and PY. This suggests that either 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 – 90%) were the main drivers of genetic improvement in the industry (García-Ruiz et al., 2016).

3.4.2.2 Durability Traits

The dairy industry in Canada have 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, the 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 each of the 3 most influential selection paths, except for the apparent increase in the DB path for

MS, FL, and HL after the year 2000 (Fig. 3.4). 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 the SC, except for occasional negative selection in 1987, 1988, 1995, and 1999 (Figure 3.4a). 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 minimum 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 3.4b). 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 bull 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 and 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 – 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 3.4c). 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. Feet- and legs-related problems have been one of the major reasons for involuntary culling among dairy cattle in Canada (Canadian Dairy Information Centre, 2018). The prevalence of FL problems may be due to tie-stall designs (Zurbrigg et al., 2005); hence, the observed positive realized GSDs 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 3.4d). 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

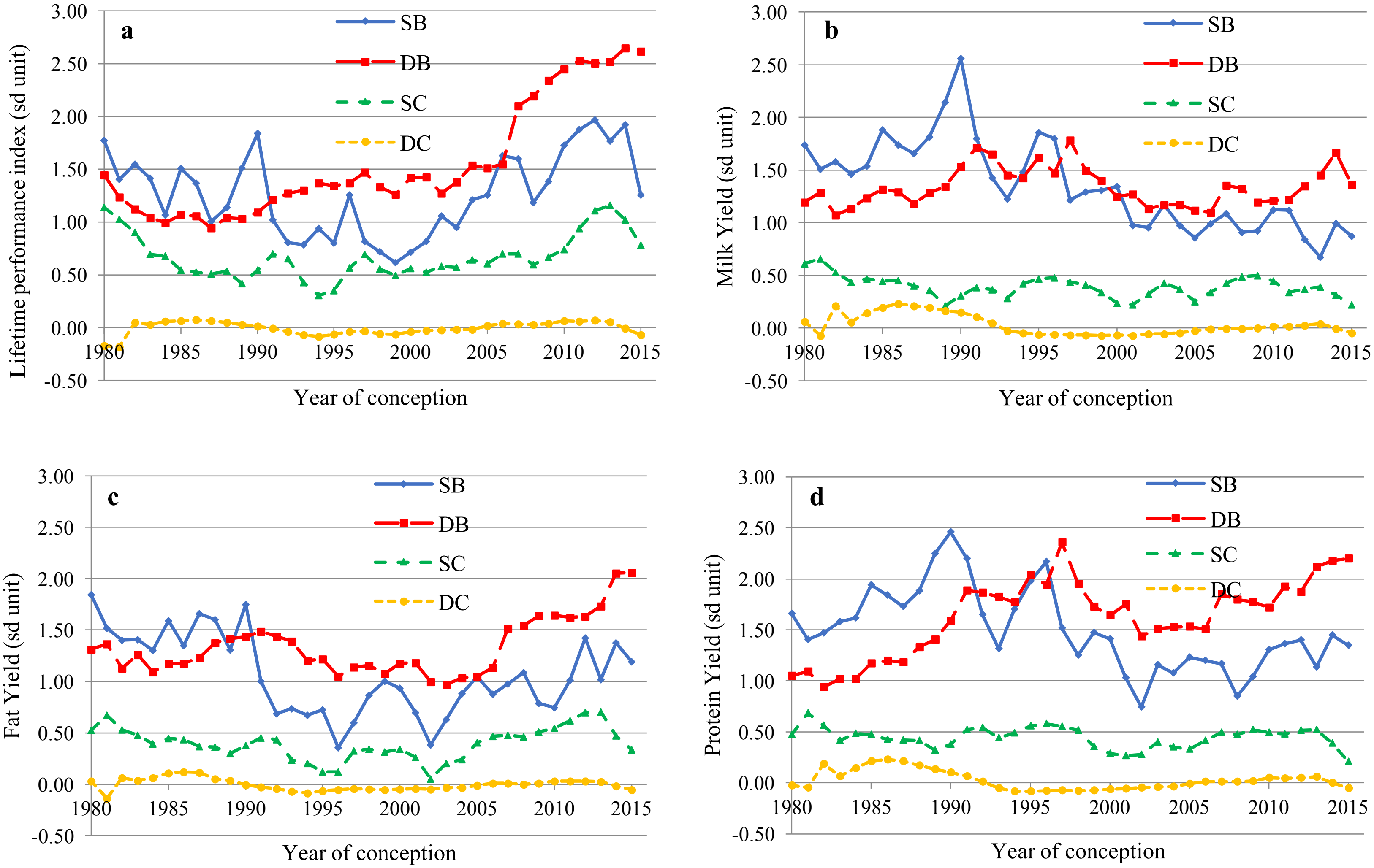

Figure 3.3a-d Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for Lifetime performance index, 305-day milk yield, 305-day fat yield and 305-day protein yield for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for Holstein breed.

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.

3.4.2.3 Health and Fertility Traits

The realized GSD for DF were largely negative for the SB, SC, and DB paths from 1980 to 2005 (Figure 3.5a). 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 to both 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 culling because of reproductive failures rather than 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

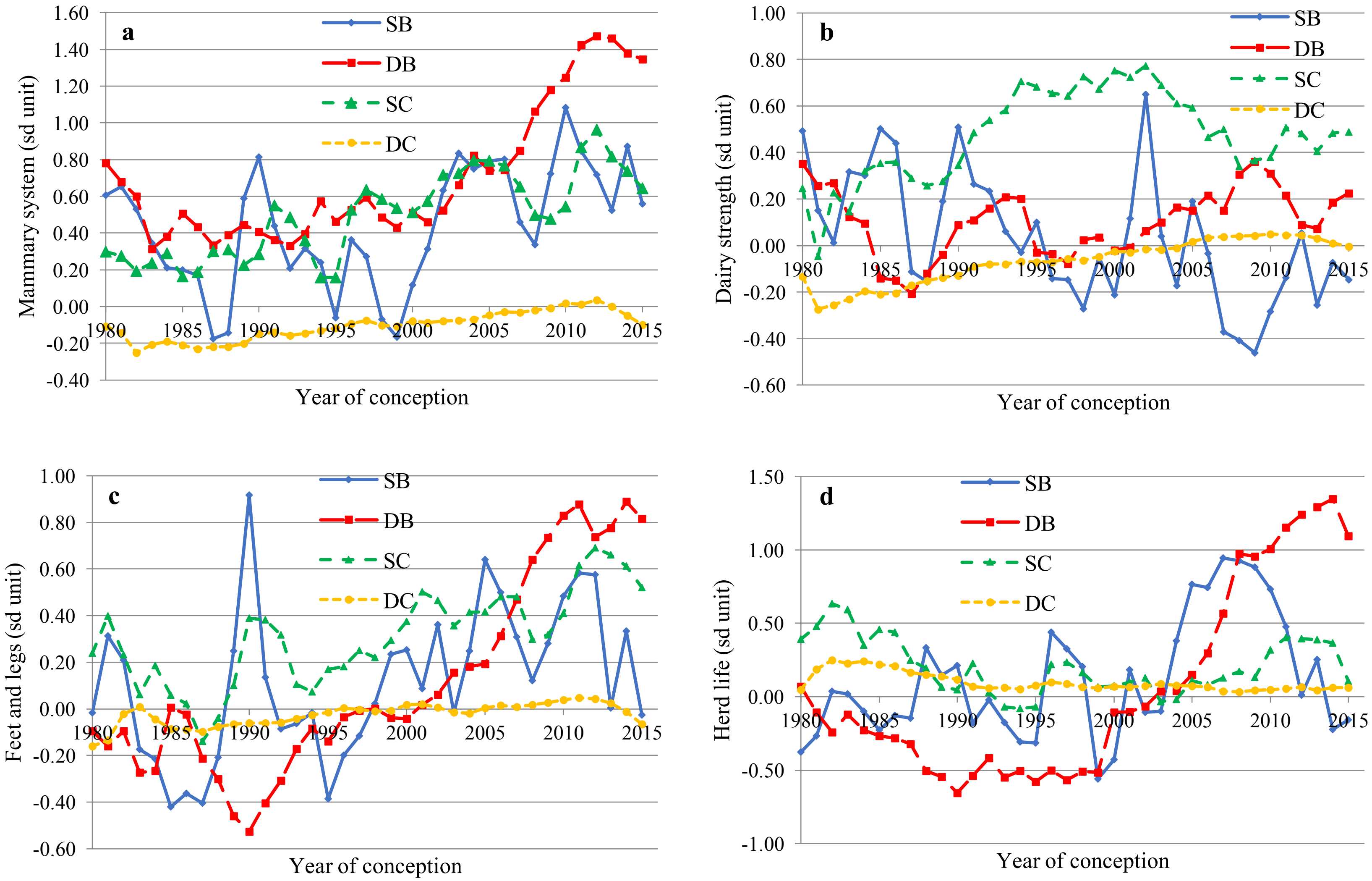

Figure 3.4a-d Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for mammary system, dairy strength, feet and legs, and herd life for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for Holstein breed.

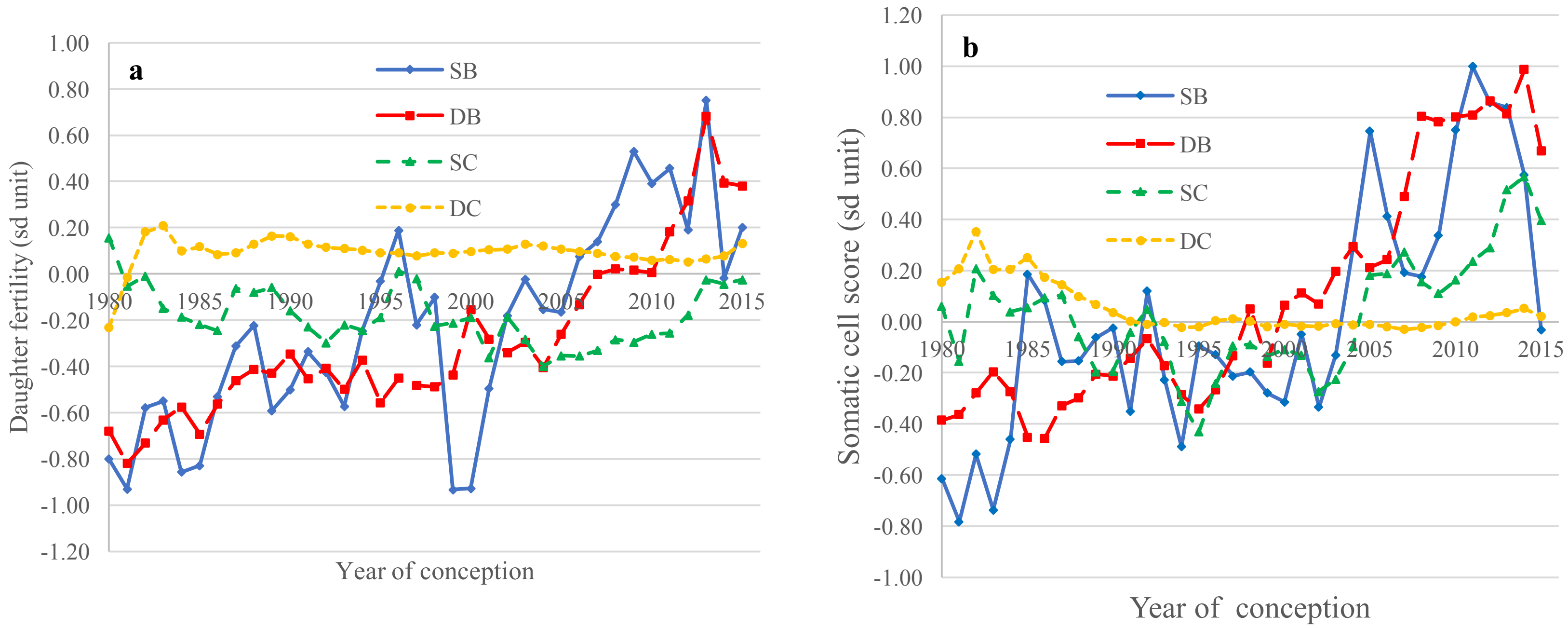

Figure 3.5a-b Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for daughter fertility and somatic cell score for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) for Holstein breed.

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 the 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 3.5b), 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 attributed 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.

3.4.3 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 3.3 and 3.4 show the *P*-values for the effects of HS, agricultural region, HS*YOC, region*YOC and HS*region on realized GSD of SC and DC paths, respectively, for 10 traits. Year of conception (not shown in table), HS*YOC and Region*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 table). 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 in changes in selection emphasis as well.

Table 3.3 Effects of Housing system (HS), agricultural region (Region), and HS*Region on realized Genetic Selection Differential in Sire-to-Cow selection path (P-values reported for the fixed effects) and variance components of herd(HS*Region), herd*YOC[3], and residuals

	Fixed effects[2]			Variance components		
Trait	HS	Region	HS*Region	Herd(HS*Region)	Herd*YOC	Residual
LPI[1]	0.2126	0.1446	0.1141	1450.34	3022.32	60635
Milk yield	0.9298	0.0057	0.1683	12573	23088	410580
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	0.00107	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
Somatic Cell Score	0.4682	0.8892	0.6757	0.000127	0.001898	0.04742

[1] LPI – lifetime performance index.

[2] Differences are statistically significant if *P*<0.05.

[3] YOC – Year of conception (*P*<0.0001 for all traits in the table).

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 tie stall operators than among free stall operators. Dairy strength, being a combination of dairy character and body capacity, was ranked very important among tie stall operators, who constitute about 84% of dairy farmers in Québec. Also, in the DC pathway, the realized GSD for LPI, FY, and FL were higher in tie stalls compared with free stalls. It was surprising to note that selection for FL was lower among free stall operators compared with tie stall operators; given that cows make relatively more movement in free stalls than in tie stalls, we would have expected free stall dairy farmers to place greater selection emphasis on FL. Also, higher incidence of leg problems has been observed in free stalls HS than in tie stalls 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 the 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 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.

Table 3.4 Effects of Year of conception (YOC3), Housing system (HS), agricultural region (Region), HS*YOC, Region*YOC and HS*Region on realized Genetic Selection Differential in the Dam-to-Cow selection path (P-values reported for the fixed effects) and variance components of herd(HS*Region), herd*YOC, and residuals

[1]Trait	[2]Fixed effects					Variance components		
	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
LPI	0.0318	<0.0001	0.6220	<0.0001	0.0105	5278.75	1951.96	53963
MY	0.3637	<0.0001	<0.0001	<0.0001	0.0834	24953	8292.76	391313
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] LPI – lifetime performance index; MY – 305-day milk yield; 305-day FY – fat yield; 305-day PY- protein yield; MS – mammary system; DS –dairy strength; FL – feet and legs; HL – herd life; DF – daughter fertility; SCS – somatic cell score.

[2] Differences are statistically significant if *P*<0.05.

[3] YOC - Year of conception (*P*<0.0001 for all traits in the table).

We discovered significant differences (P<0.05) among the interactions of HS and agricultural region on realized GSD of DS, FL, and DF in the SC and LPI, FY, MS, DS, and SCS in the DC.

3.4.4 Variations among herds and herd*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 3.3). 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 found significant variations due to herd, representing between 1.6 and 12.0% of the total variation in realized GSD, while the herd*YOC component constituted between 0.7 and 3.2% of the total variation (Table 3.4). 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 3.6 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 3.6a). For the bottom 10% of herds, the mean realized GSD ranged from -1.00 to 0 sd units (Figure 3.6a). For FY, the mean realized GSD per year of conception ranged from 1.30 to 2.00 sd units in the top 10% herds and -1.35 to -0.50 sd units in the bottom 10% herds (Figure 3.6b). Figures 3.6c and 3.6d show the mean realized GSD for the top 10% and bottom 10% of herds for DF and SCS. 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 3.6). 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 four randomly selected individual herds (A, B, C, and D) for LPI, FY, DF, and FL are presented in Supplemental Figure S3.7. 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 S3.7a).

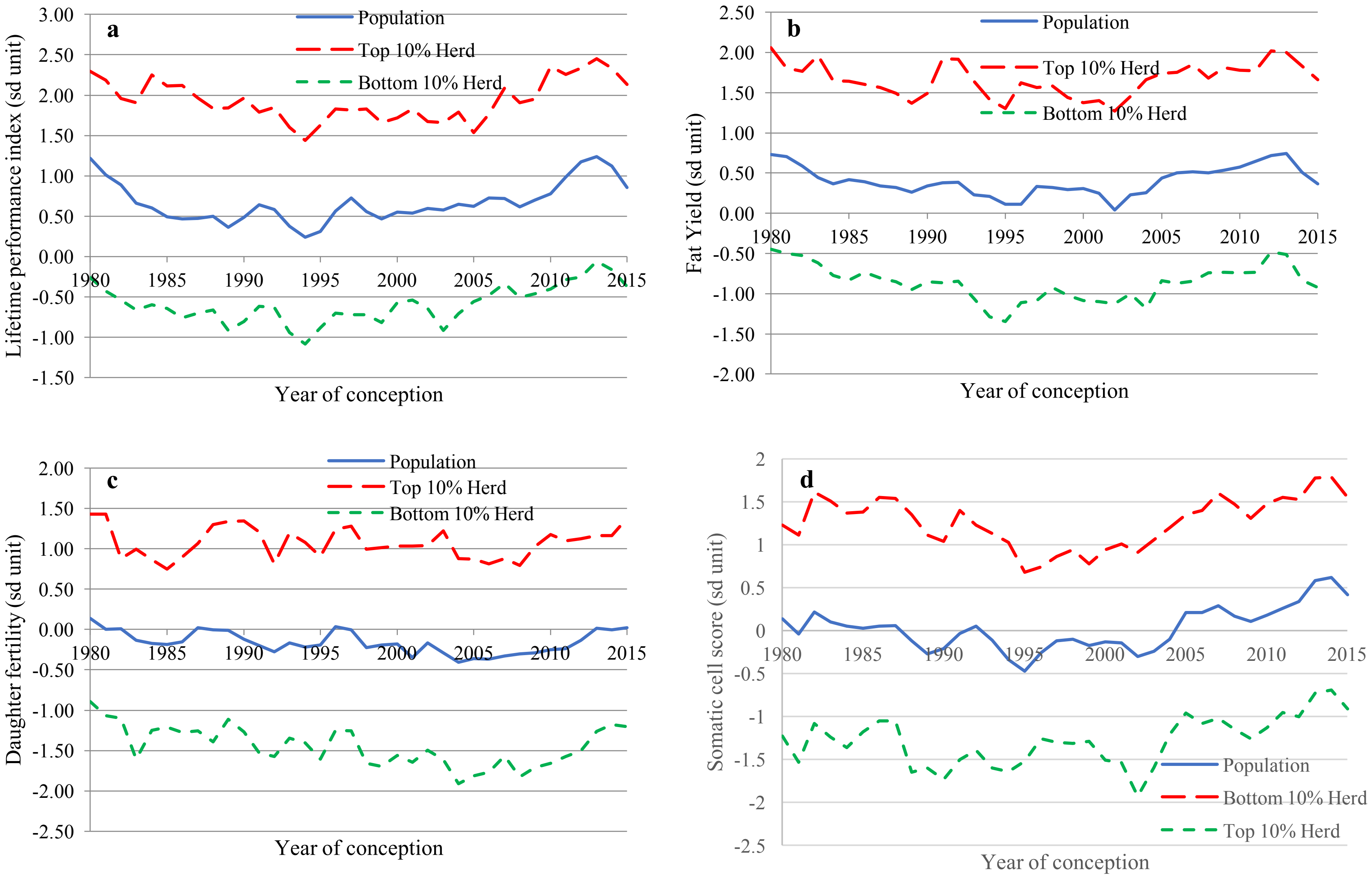

Figure 3.6a-d Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) for life performance index, 305-day fat yield, daughter fertility and somatic cell score in the sire-to-cow for the population, Top 10%, and Bottom 10% herds.

3.4.5 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*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-fetch 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 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.

3.5 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 means 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 trends 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*YOC, region*YOC, and HS*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*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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Table S3.5 Number of unique sires and dams of bulls and cows in each selection path for each trait

Trait	Sires of Bulls	Sires of Cows	Dams of Bulls	Dams of Cows
LPI[1]	2,347	62,012	2,036	63,523
305-day milk yield	2,423	71,179	2,092	69,526
305-day fat yield	2,423	71,179	2,092	69,526
305-day protein yield	2,423	71,179	2,092	69,526
Mammary system	2,393	64,065	2,070	65,303
Dairy strength	2,393	64,065	2,070	65,303
Feet and legs	2,393	64,065	2,070	65,303
Herd life	1,110	10,724	2,070	65,303
Daughter fertility	2,909	63,345	2,031	54,920
Somatic cell score	2,423	71,179	2,092	69,526

[1] LPI – lifetime performance index

Table S3.6 Average realized Genetic Selection Differential (GSD) for the four paths of selection (SB, DB, SC, and DC) for 10 traits for the study period (1980 to 2015) and the last 10 years (2006 to 2015) of the study

		Year of conception	
Trait	Selection path	1980 – 2015	2006 – 2015
Lifetime Performance Index	SB[1]	292.61	407.54
	DB	341.66	572.84
	SC	167.58	240.17
	DC	-0.74	8.12
Milk yield, kg	SB	847.37	704.09
	DB	815.04	873.72
	SC	252.10	278.01
	DC	15.05	2.64
Fat yield, kg	SB	25.48	28.41
	DB	31.02	43.05
	SC	9.83	14.64
	DC	-0.15	0.20
Protein yield, kg	SB	27.41	26.28
	DB	28.34	35.66
	SC	8.20	9.71
	DC	0.29	0.40
Mammary system	SB	1.64	2.60
	DB	2.39	4.56
	SC	1.88	2.78
	DC	-0.30	-0.07
Dairy strength	SB	0.14	-1.01
	DB	0.45	1.04
	SC	2.29	2.24
	DC	-0.21	0.14
Feet and legs	SB	0.50	1.35
	DB	0.42	2.79
	SC	1.51	2.34
	DC	-0.07	0.05
Herd life	SB	0.50	1.77
	DB	0.20	3.00
	SC	0.82	1.04
	DC	0.27	0.16
SCS	SB	-0.002	-0.088
	DB	-0.016	-0.114
	SC	-0.002	-0.059
	DC	-0.006	-0.001
DF	SB	-0.76	1.35
	DB	-0.91	0.64
	SC	-0.77	-0.96
	DC	0.29	0.30

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

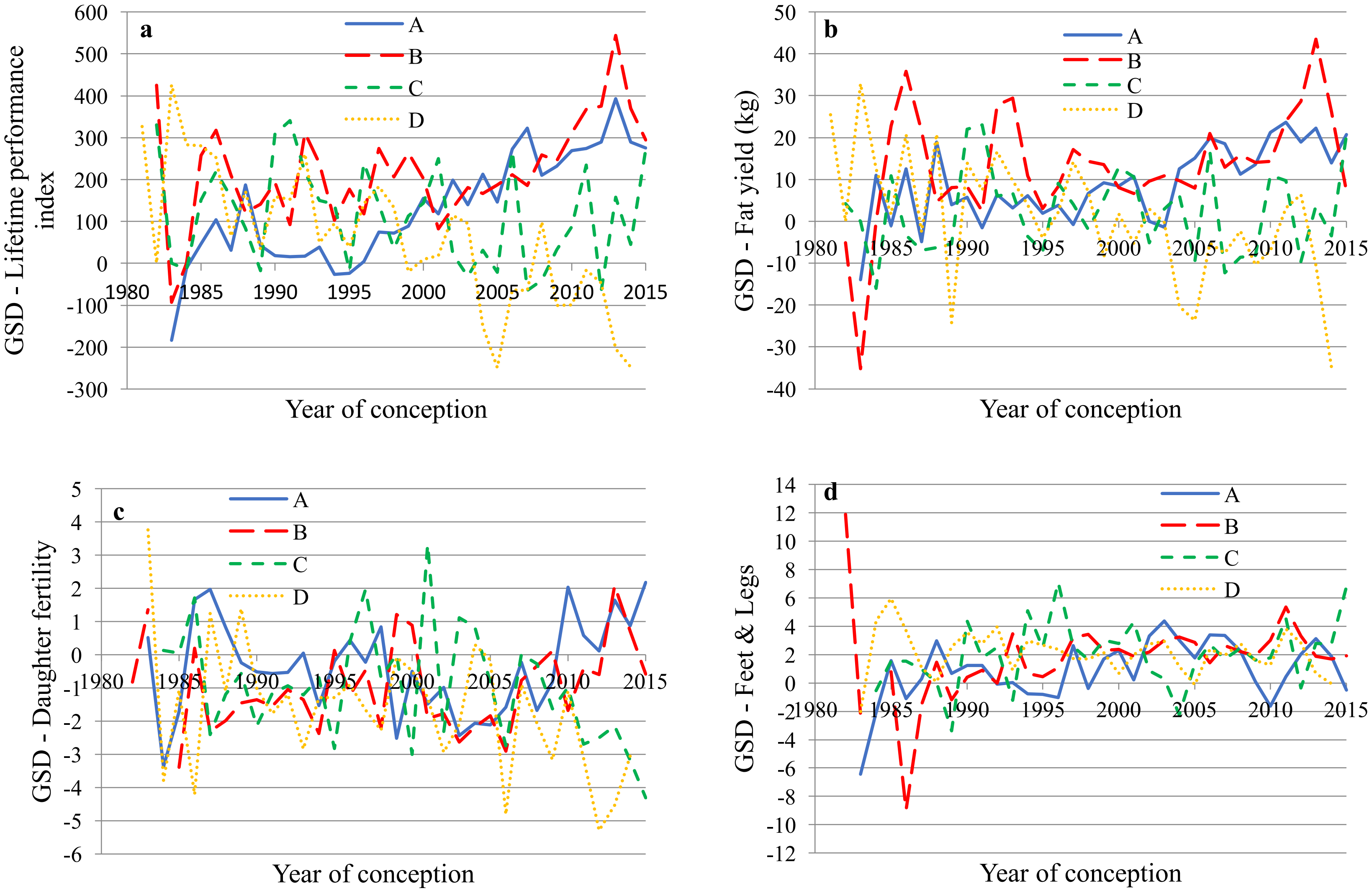

Figure S3.7a-d Mean realized genetic selection differential (GSD) of lifetime performance index, 305-day fat yield, daughter fertility, and feet and legs for sires of cows in four randomly selected herds A, B, C, and D.

CONNECTING STATEMENT

Chapter III of this thesis presents realized genetic selection differentials of 10 economically important traits and an index in the Holstein dairy cattle breeds in Canada along the four pathways of genetic improvement. The Holstein breed is the most popular dairy breed in the country. The chapter also examined variations in GSD among dairy herds in Québec. Chapter IV looks at the realized GSD for economically important traits in three minor dairy cattle breeds of Canada (Ayrshire, Jersey, and Brown Swiss). Although the minor dairy cattle breeds in Canada constitute only approximately 7% of the total dairy cattle herd, they offer several advantages and are important in the overall dairy industry of the country. It is therefore imperative to also study the GSD in the four pathways of genetic improvement in the minor dairy cattle breeds.

4 CHAPTER IV: Realized genetic selection differentials in Canadian Ayrshire, Jersey, and Brown Swiss dairy cattle populations

Minor dairy cattle breeds are important to Canada's dairy industry as they have several unique characteristics that need to be preserved and improved. The hundreds of producers keeping Ayrshire, Jersey, and Brown Swiss breeds are also selecting since there are increasing genetic trends in some key traits in these minor breeds. Estimated breeding values were used to determine the selection emphases producers of minor dairy breeds were making for economically important traits and the amount of variations in realized selection among producers' herds. Considerable variations in realized selection existed among herds and this offers opportunity to further increase genetic gains.

RUNNING TITLE: FULL-LENGTH RESEARCH PAPER

Realized genetic selection differentials in Canadian Ayrshire, Jersey, and Brown Swiss dairy cattle populations

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4.1 ABSTRACT

Estimated breeding values for a national selection index, production, durability, and health and fertility traits from Canadian Ayrshire, Jersey, and Brown Swiss bulls and cows born from 1950 and 1960, respectively, were used to determine realized genetic selection differentials (GSD) along the sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) pathways of genetic improvement. We also determined the variations in realized GSD due to herds and herd*year of conception in addition to the effects of some environmental factors on realized GSD of the SC and DC paths. The mean realized GSD of the DB were higher than those of other paths and were increasing for lifetime performance index (LPI), 305-day milk yield (MY), 305-day fat yield (FY), and 305-day protein yield (PY) in all three-dairy cattle populations. We observed no clear trends in realized GSD for type traits in all three dairy cattle breeds, except for the apparent increasing trends in realized GSD of mammary system (MS), dairy strength (DS), and feet and legs (FL) in the DB and SC paths of the Ayrshire breed. There were no clear patterns observed in the realized GSD of daughter fertility (DF) in the SB, DB, and SC paths of all dairy cattle breeds. Realized GSD for somatic cell score (SCS) showed increasing and favorable trends in the 3 most influential selection paths (SB, DB, and SC). Year of conception (YOC) influenced realized GSD of Artificial Insemination (AI) bulls in Ayrshire, Jersey, and Brown Swiss dairy populations. Housing system, agricultural region, and their interaction had mostly little influence on the selection achieved in the SC and DC paths. We observed considerable variations among herds in their realized selection in the SC and DC paths in all three dairy cattle breeds. There were appreciable and significant variations in realized GSD due to herd*YOC in the SC but not the DC path. This study demonstrates that variations exist among herds of minor dairy cattle breeds in their selection for economically important traits. These variations offer opportunities for further improvements in the minor dairy cattle populations.

Keywords: Ayrshire, Brown Swiss, Jersey, realized genetic selection differential, herd

4.2 INTRODUCTION

The dairy industry, today, has an efficient and reliable genetic evaluation system using well-run progeny testing and genomic evaluation systems which have made it easier to identify the genetically superior animals in the population. Issues, however, are whether most producers are directly selecting and using these superior animals for breeding to improve their herds' performance and that of the entire population. Secondly, are the genetic values being used for management and genetic decision-making to improve herd efficiency and profitability in a consistent and methodological fashion. It is only through continuous selection of superior parents that genetic gains would be achieved within individual herds.

Dairy producers play important roles in national genetic improvement programs because dairy producers are many in numbers compared with Artificial Insemination **(AI)** centers, control the sire-to-cow **(SC)** and dam-to-cow **(DC)** paths of selection, and producers' selection activities contribute between 10 and 32% of the total genetic gains observed in a population (McAllister, 1980; Cassell, 1988). Favorable genetic selection causes genetic gains which are associated with farm profitability (Falconer and Mackay, 1996; Thompson et al., 2015).

The Canadian Dairy Network **(CDN)** reports genetic trends for 16 key traits for all dairy cattle breeds in the country (Canadian Dairy Network, 2019). Although these genetic trends serve as means of monitoring the genetic progress in the population, national genetic trends do not capture the diversity in selection emphasis present in a population. Genetic trends, therefore, do not necessarily present a clear picture of what selection an individual producer is making within his or her herd. Producers may incorrectly assume that they are making progress in their herds and at the same rate of progress in the population since the population genetic trends are reported to be increasing. The increasing population genetic trend could possibly be due to a few herds within the population who were selecting more intensively. Also, the rising trends may be due mostly to high selection intensities mostly achieved by AI centers. Both selection differentials and generation intervals are important factors to producers and breeders because producers have control and can manipulate these factors in their herds to improve their herds' performance. To maximize annual genetic progress in their herds, dairy producers can either increase the genetic selection differential **(GSD)** for breeding objective traits and/or reduce the generation intervals of the sires and/or dams that producers use for breeding in their herd.

There are rather few studies that have examined GSD, that these studies have focused on production traits in the Holstein dairy breed (Van Tassell and Van Vleck, 1991; Kawahara et al., 2004; García-Ruiz et al., 2016; Hagan et al., 2020). The Holstein breed is the major commercial dairy breed in the World. In Canada, this breed constitutes 93% of the dairy population (Canadian Dairy Information Centre, 2017). Despite their relatively low numbers in the dairy population, minor dairy cattle breeds such as Ayrshire, Jersey, Brown Swiss, and Guernsey are important for several reasons. Some of these breeds have strong genetic potentials for higher fat and protein yields compared with the Holstein. Also, the reproductive performance of some of these minor dairy cattle breeds is superior to the Holsteins (Norman et al., 2009; Washburn et al., 2002). It will, therefore, be important to also study the selection realized for some key traits in the lesser dairy cattle breeds in Canada as they play vital roles in the dairy industry of the country. Also, latest contribution of producers' selection efforts to the total genetic gains in the population are needed as the present literature on the contribution of the SC and DC paths to the total genetic gains in Canadian dairy cattle is about 3 decades old.

The only report of GSD in dairy cattle breed other than Holstein is the US Jersey (Nizamani and Berger, 1996). This study focused on only production traits (milk, fat, and protein yields) in the larger Jersey population without estimation of variations in realized GSD among herds. For milk yield, Nizamani and Berger (1996) reported mean weighted GSD of 730.5, 494.7, 321.1, and 29.3 kg for the sire-to-bull **(SB)**, dam-to-bull **(DB)**, SC, and DC paths, respectively, between 1982 and 1986.

The objectives of this study were to determine realized GSD in the Canadian Ayrshire, Jersey, and Brown Swiss dairy cattle populations along the 4-path selection model, and to investigate the effects of some environmental factors on realized GSD for AI bulls and replacement cows. Lastly, we determined the variability among herds in terms of realized GSD.

4.3 MATERIALS AND METHODS

4.3.1 Data and traits

Data used for this study consisted of genetic evaluations from April 2018; EBV for the Canadian Ayrshire, Jersey, and Brown Swiss breeds provided by Lactanet [formerly "CDN" (genetic evaluations) and Valacta (herd recording information)]. The genetic evaluation files contained information on animal identification, date of birth, sire and dam identifications, and trait EBV. Traits studied were 305-day milk yield **(MY)**, 305-day fat yield **(FY)**, 305-day protein yield **(PY)**, somatic cell score **(SCS)**, herd life **(HL)**, daughter fertility **(DF)**, feet and legs **(FL)**, mammary system **(MS)**, dairy strength **(DS)**, and lifetime performance index **(LPI)**. The trait definitions have been provided by CDN (Van Doormaal, 2007) and subsequently described in

Hagan et al. (2020). The traits contribute to any one of the following: increase revenue, increase profit, or reduced cost of production (Miglior et al., 2005). The herd information file comprises herd identification, agricultural regions in Quebec **(region)**, and the milking system which was used to deduce the housing systems **(HS)**. The regions, milking systems, and HS are presented in Table 4.1.

Table 4.1 Groups of agricultural regions, milking systems, and housing systems in Québec, Canada

Factor	Classes
Agricultural region	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	Tie-stall, free stall

Before editing the data sets, the Ayrshire, Jersey, and Brown Swiss EBV files contained records on 10,187, 20,478, and 6,292 bulls and 251,793, 210,941, and 44,135 cows born from 1900 and 1925, respectively. After editing of the data sets by removing records of all cows and bulls born before 1980 or sires and dams born before 1950 and 1960, respectively, the maximum number of records for bulls and cows born from 1980 are presented in Table 4.2. These number of records varied from trait to trait because some traits have only recently been evaluated; therefore, older animals do not all have EBV for all traits. The cows and bulls of the 3 dairy cattle populations were the progeny of sires and dams born from 1950 and 1960 onwards, respectively. The 1,332

SB records mean that 1,332 bulls were sired by 268 uniquely identifiable sires (Appendix Table S4.9), that these sires had EBV for the 10 traits. Also, the 192,458 SC records mean that 192,458 cows were sired by 4,075 uniquely identifiable sires (Appendix Table S4.9), that these sires had EBVs for the 10 traits. There were relatively smaller number of records in the DB path compared with the SB path which suggests that there was strong selection for bull dams compared with bull sires together with the limited number of males each bull-dam can produce during her lifetime in the absence of reproductive technologies.

Table 4.2 Number of computed GSD records for each path[1] of selection (SB, SC, DB, and DC) for the Ayrshire, Jersey, and Brown Swiss dairy cattle breeds

Breed	SB	SC	DB	DC
Ayrshire	1,332	192,458	1,230	170,983
Jersey	6,295	148,686	3,314	132,168
Brown Swiss	1,557	29,179	1,102	23,456

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

4.3.2 Realized Genetic Selection Differentials

Realized GSD of a sire or dam was defined and computed as the difference between the EBV of a sire or dam and the mean EBV of all available bulls or cows at the time of conception of a progeny. The determination of availability of a cow or bull and detailed definition of realized GSD has been described in Hagan et al. (2020). Mean realized GSD for the population was calculated by year of conception of progeny **(YOC)** for each of the 4 pathways: SB, DB, SC, and DC. Year of conception was computed from the date of conception of a progeny, which was determined as the date of birth of a progeny minus 280 days (being the average gestation length of a cow).

4.3.3 Statistical analyses

Realized GSD of the SC and DC selection paths were analyzed using the high-performance mixed **(HPMIXED)** procedure of SAS 9.4 (SAS Institute Inc., Cary, NC). The HPMIXED procedure of SAS was used to overcome the challenges we encountered with regard to limited computing space. The statistical analyses were carried out to essentially determine the influence of some environmental factors on realized GSD in the producers' controlled pathways. We also sought to determine the amount of variations in realized GSD among herds. The model used for the analyses is presented below:

$$\mathrm{GSD}_{ijkmn} = \mu + \mathrm{YOC}_i + \mathrm{HS}_j + \mathrm{Region}_k + \mathrm{Herd}_{jkm} + \mathrm{Herd{*}YOC}_{ijkm} + \mathrm{HS{*}YOC}_{ij} + \mathrm{Region{*}YOC}_{ik} + \mathrm{HS{*}Region}_{jk} + e_{ijkmn}$$

where GSD_{ijkmn} is the realized genetic selection differential of sire of cow or dam of cow for a trait (LPI, MY, FY, PY, MS, DS, FL, HL, DF, or SCS);

μ is the overall mean;

YOC_i is the fixed effect of the ith year of conception (i = 1980 to 2015);

HS_j is the fixed effect of the jth housing system (j = Tie stall, Free stall);

Region_k is the fixed effect of the kth agricultural region (Table 4.1);

Herd_{jkm} is the random effect of mth herd nested within jth HS and kth region $\sim N(0, \sigma^2_{herd})$, where σ^2_{herd} is the variance of herd;

$\mathrm{Herd{*}YOC}_{ijkm}$ is the random effect of the interaction of the mth herd nested within the jth HS and kth region by the ith YOC $\sim N(0, \sigma^2_{herd*YOC})$ where $\sigma^2_{\mathrm{herd*YOC}}$ is the variance of herd by YOC;

$\mathrm{HS{*}YOC}_{ij}$ is the fixed effect of the interaction between the jth HS and ith YOC;

$\mathrm{Region{*}\ YOC}_{ik}$ is the fixed effect of the interaction between the kth region and ith YOC;

$\mathrm{HS{*}Region}_{jk}$ is the fixed effect of the interaction between the jth HS and kth region;

and e_{ijkmn} is the random residual ~ $N(0, \sigma^2_e)$, where σ^2_e is the residual variance.

For each of the pathways, we wrote an additional model where one random factor (herd or herd*YOC) was dropped at a time, and the difference in Bayesian Information Criterion **(BIC)** values between the first (full model) and second (one random factor dropped) models were calculated to determine whether the random effect that was dropped was significant. 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 22 and 6584, 0 and 2400, and -4 and 863 for Ayrshire, Jersey, and Brown Swiss breeds, respectively.

4.4 RESULTS AND DISCUSSION

4.4.1 Realized Genetic Selection Differentials

4.4.1.1 Selection index and production traits

Mean realized GSD of LPI and production traits (MY, FY, and PY) for Ayrshire, Jersey, and Brown Swiss breeds are presented in Figures 4.1, 4.4, and 4.7, respectively. The realized GSD have been presented in trait units as shown in appendix supplemental tables (Tables S4.10, S4.11, and S4.12) and standard deviation units **(sd unit)** as presented in Figures 4.1, 4.4, and 4.7. The presentation of the realized GSD in genetic sd units will enable the comparison of realized GSD among selections paths and among traits. The realized GSD for LPI showed similar trends for each selection path in the three breeds (Figures 4.1a, 4.4a, and 4.7a). In all three breeds, realized GSD of the DB was the highest when compared with other paths of selection. For the Brown Swiss, the mean annual realized GSD of the DB increased gradually from 1980 to 1994 after which it began to decline. The mean realized GSD for LPI in the DB between 1980 and 2015 were 1.24, 1.41, and

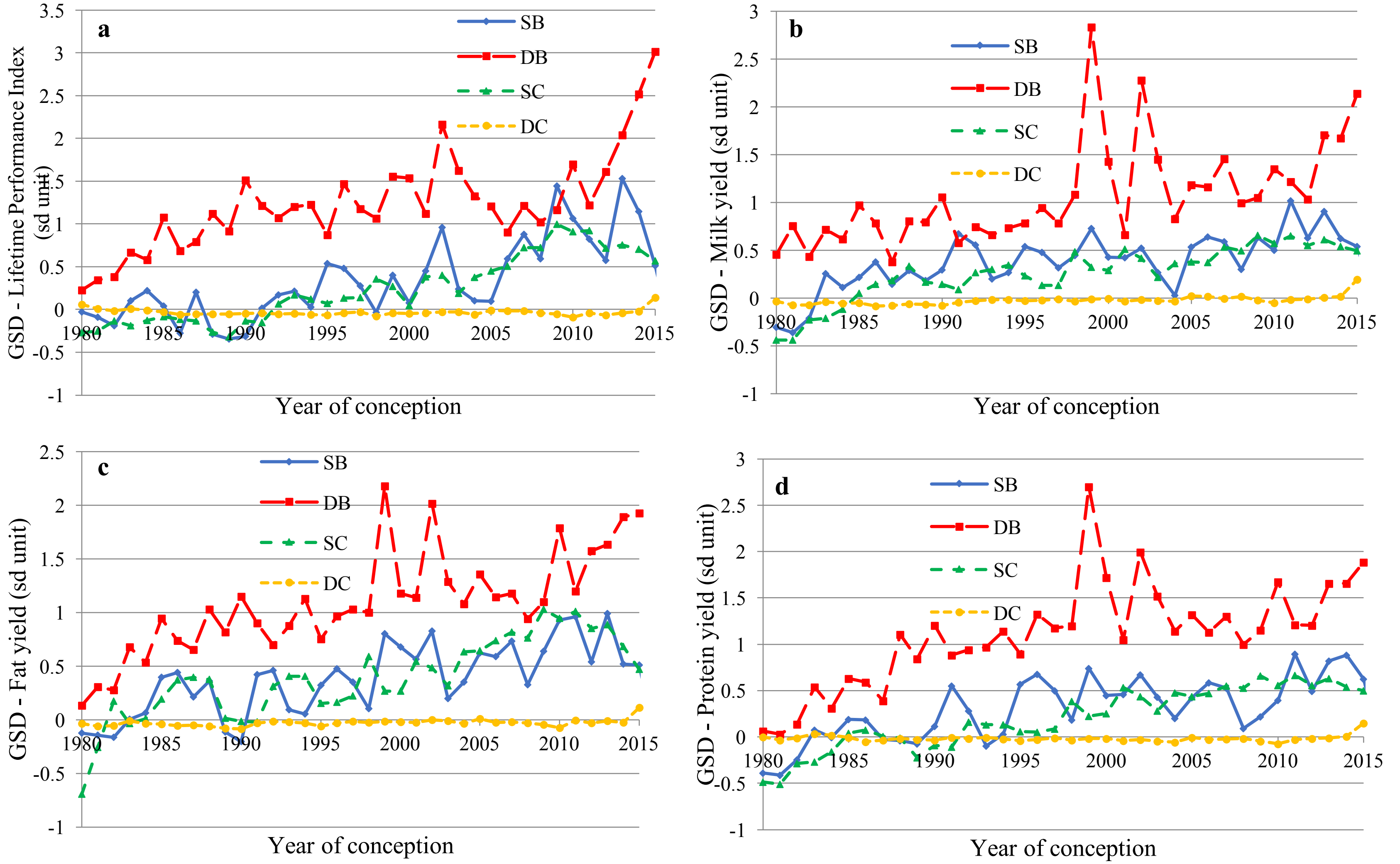

Figure 4.1a-d Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for Lifetime performance index, 305-day milk yield, 305-day fat yield and 305-day protein yield for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for Ayrshire breed.

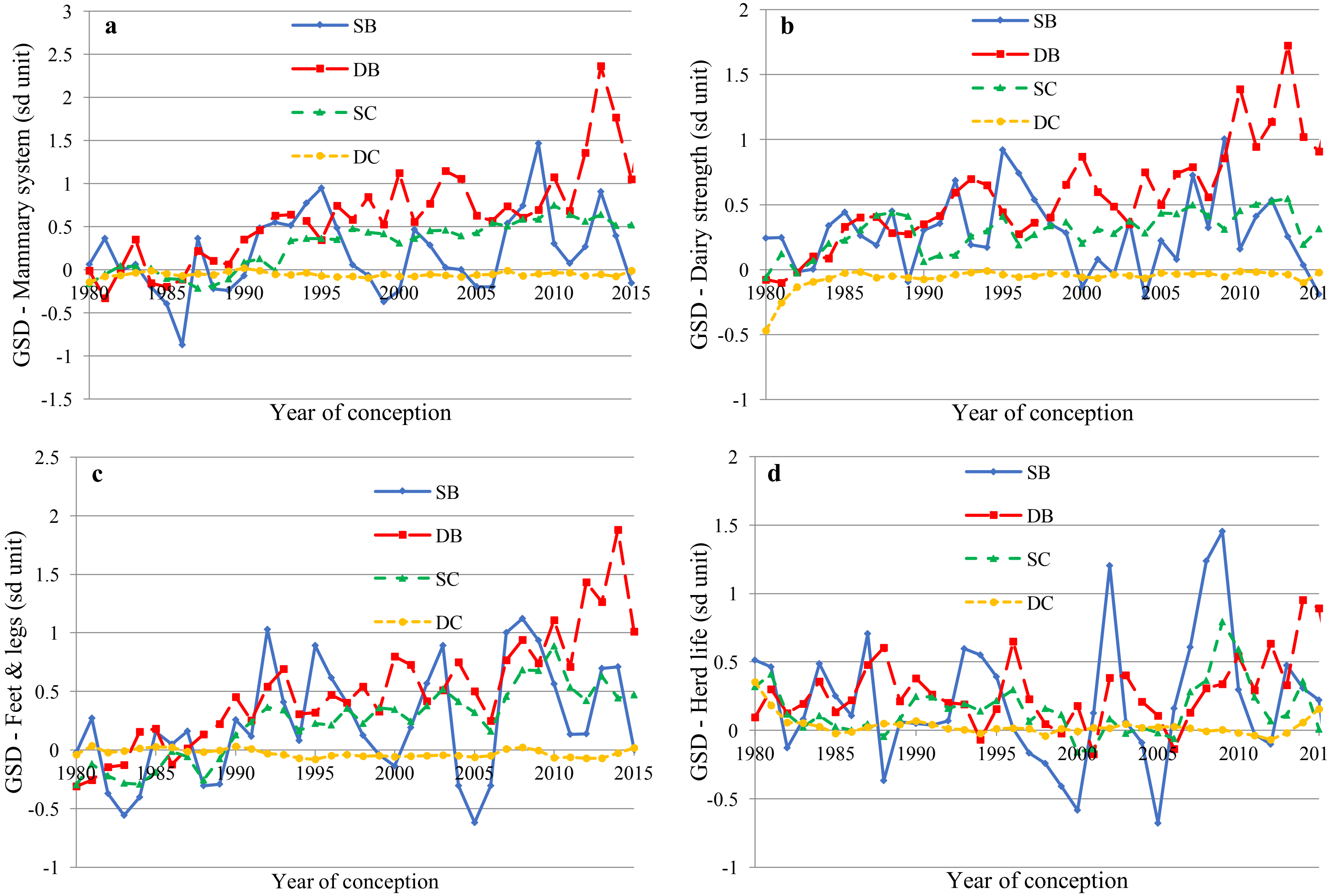

Figure 4.2a-d Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for mammary system, dairy strength, feet and legs, and herd life for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for Ayrshire breed.

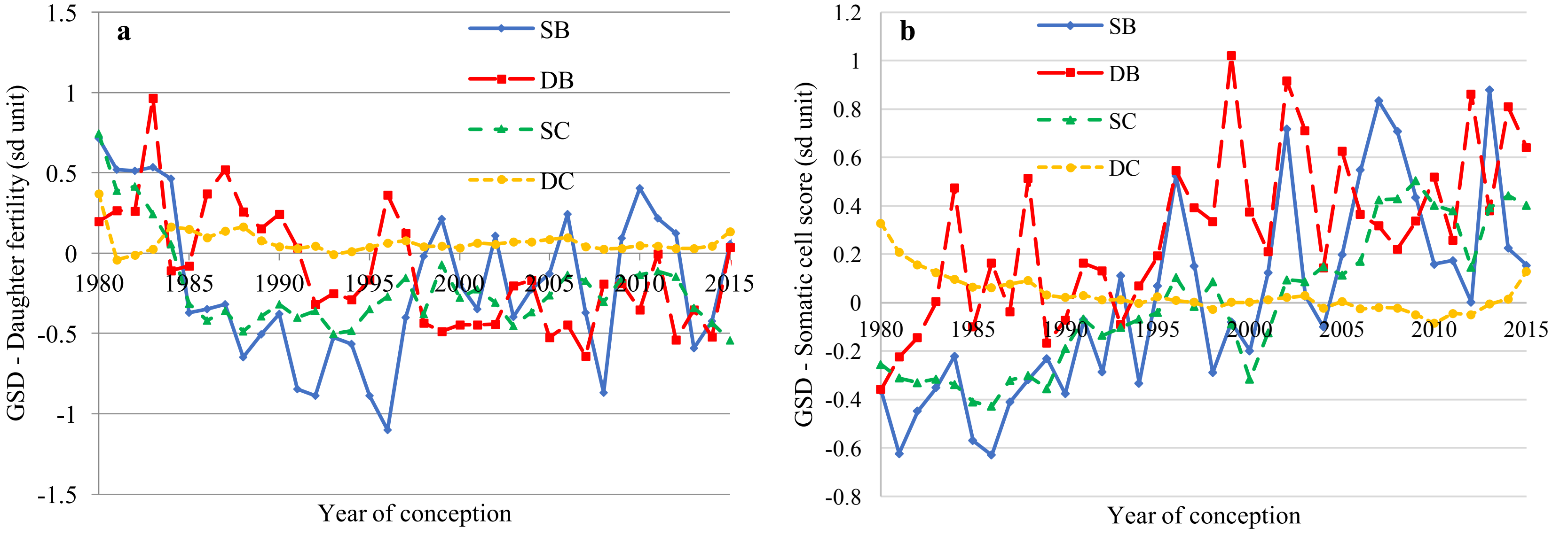

Figure 4.3a-b Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for daughter fertility and somatic cell score for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) for Ayrshire breed.

1.02 sd unit for the Ayrshire, Jersey, and Brown Swiss populations, respectively. The trends in realized GSD in the SB and SC paths were largely similar, and these were the case for all three dairy breeds. This similarity in trends of realized GSD is an indication that both AI centers and dairy producers of the three minor dairy cattle breeds were putting similar selection emphases in terms of sire selection for breeding. There was negative realized GSD in DC for each of the breeds although not statistically different from zero. The mean realized GSD in DC between 1980 and 2015 for the Ayrshire, Jersey, and Brown Swiss breeds were -0.04, -0.09, and -0.05 sd unit, respectively. The negative and close to zero mean realized GSD in the DC of the three breeds were similar to the 0.01 sd unit observed in the DC path of the Canadian Holstein population (Hagan et al., 2020) and these can be attributed to lack of opportunity for selection in the DC path. Cows produce small numbers of offspring in their lifetime, hence, there are few female calves to select from to replace a milking cow especially in the absence of sexed semen. Also, Canadian producers need to maintain herd size to partly meet their milk production quota; hence, selection in the DC is due more to involuntary culling rather than actual selection. However, Burnside et al. (1992) reported a low, but positive selection differential of 77 points in the DC for Italian aggregate index in the Friesian-Holstein population in Italy.

For any one particular selection path, the 3 dairy cattle breeds showed similar trends in realized GSD for the same trait (MY, FY, or PY) (Figures 4.1b-d, 4.4b-d, and 4.7b-d). The similarity in trends among the production traits was due partly to the strong positive genetic correlations among the production traits (Veerkamp et al. 2001). In the Ayrshire population, selection realized in the SB and SC were similar and both fell behind the DB. Canaza-Cayo et al. (2016) and Silva et al. (2001) have also reported higher selection differentials for 305-day milk yield in DB than other paths of selection. Other studies have, however, reported greater selection differentials in SB relative to DB (Nizamani and Berger, 1996; García-Ruiz et al., 2016). The lesser realized GSD we observed in the SB compared with the DB could partly be attributed to probably the less strict sire sampling procedure for progeny testing in Canada compared with the USA. The numbers of bulls sampled for progeny testing may not be large enough therefore good and superior bulls may be ignored or missed. In addition, the inherent defects of bull selection using parent average which is less reliable compared to the use of genomic EBV partly contributed to lesser realized GSD. The lower realized GSD in the SB and SC compared with the DB could be partly attributed to the milk quota system in Canada. Within the Canadian milk quota system, dairy producers are penalized when they produce more butter fat and protein than their acquired milk quota. Producers may not have an incentive to intensify selection for production traits.

In the Jersey population, the realized GSD of the SB and DB were considerably higher than those of the SC and DC for production traits. The realized GSDs of the SB and DB paths were similar in the Jersey population, unlike the Ayrshire population where the realized GSD of the SB and SC were similar for production traits. The high and similar realized GSD of the SB and DB paths in the Jersey suggest that genetic improvement in Canadian Jersey breed were mainly driven by AI centers. The realized GSD in the SB and DB increased gradually before 1990, after which they remained stable. Before 2007, there were little genetic selections achieved for MY, FY, and PY among dairy producers in their use of AI sires for breeding. Selection realized in the SC path, however, began to increase steadily after 2007. The mean realized GSD of SC were -0.07, 0.02, and 0.02 sd unit for MY, FY, and PY, respectively. These were lower than the mean realized GSD for MY (0.27), FY (0.39), and PY (0.20) in the SC of the Ayrshire breed. This suggests that overall little selections were realized for production traits in the Jersey population. The mean realized GSD for MY, FY, and PY in this study were considerably lower than the mean GSD for milk, fat, and protein yields in the registered US Jersey population born between 1960 and 1990 (Nizamani and Berger, 1996). There was largely zero selection realized for production traits in the DC due to the lack of selection opportunity in that path similar to the findings of the DC in the Ayrshire population.

For the Brown Swiss population, the annual mean realized GSD in the DB was gradually increasing from 1980 to the mid-1990s for all production traits after which it began to decline gradually until 2006. There was an apparent increase from 2006. No clear trends were observed in realized GSD in SB and SC except for the observation of predominantly negative realized GSD for MY, FY, and PY in the 1980s. The realized selections in the DC were essentially zero for all production traits.

4.4.1.2 Durability traits

The mean realized GSD per YOC for MS, DS, FL, and HL for all 4 selection paths in Ayrshire, Jersey, and Brown Swiss breeds are presented in Figures 4.2, 4.5, and 4.8, respectively. There were increasing trends in realized GSD for MS, DS, and FL in the DB and SC, but not the SB of the Ayrshire breed. The realized GSD of the SB wobbled around from year to year. The increasing realized GSD of dams of bulls and sires of cows suggest that both AI centers and dairy producers of Ayrshire population considered type traits important in their breeding objectives. The trends in realized GSD for MS and DS were more similar for each of the selection paths than the trends for FL and HL due possibly to the strong positive genetic correlation between MS and DS (DeGroot et al., 2002). For HL, there were no clear trends in realized GSD of the SB, DB, and SC paths. This could be attributed to the fact that genetic evaluations for herd life only began recently (early 2000s), hence, producers were not actively selecting on this trait. There was little selection realized in the DC for any of the type traits studied except for the positive realized GSD for HL from 2012.

In the Ayrshire breed, the mean total realized GSD of all paths between 1980 and 2015 were 1.03, 1.08, 0.93, and 0.68 sd unit for MS, DS, FL, and HL, respectively. The mean total GSDs in the Ayrshire population are confirmations of the annual genetic trends of 0.6, 0.4, 0.6, and 0.4 for MS, DS, FL, and HL, respectively, reported by CDN over a 10-year period between 2006 and 2016 (Canadian Dairy Network, 2019).

For the Jersey population, we observed no clear trends in realized GSD in the SB, DB, and SC paths for all the type traits. The realized GSD for the type traits in the SC were largely positive and mostly higher than those of other paths (SB, DB, and DC). In the SC, the mean realized GSD for MS, DS, FL, and HL were 0.34, 0.37, 0.23, and 0.04 sd unit, respectively. These were slightly higher than mean GSD of 0.29 and 0.29 sd unit for MS and DS, respectively, in the SC of the Ayrshire breed. The generally higher realized GSD for type traits in the SC compared with other paths give an indication of the importance of type traits in the breeding objectives of Jersey dairy producers. There were largely negative realized GSD for type traits in the SB and DB suggesting type traits were probably not so important to AI organizations keeping Jersey cows; hence, the less selection emphases on type traits. The realized GSD in the DC was largely stable and below zero, however, there was a marginally increasing trend in realized GSD for HL in the DC from 2012.

The mean total realized GSD for the period of 1980 and 2015 for MS, DS, FL, and HL were -0.02, -0.30, -0.41, and -0.59 sd units, respectively. This translated in the relatively smaller genetic gains for the type traits obtained in the Jersey population compared with the Ayrshire and Brown Swiss populations (Canadian Dairy Network, 2019). The annual genetic trends for MS, DS, FL, and HL were 0.4, 0.1, 0.1, and 0.1, respectively, for the period between 2006 and 2016 in the Jersey population.

In the Brown Swiss breed, there were no apparent trends in realized GSD for the type traits in the 3 most influential pathways (SB, DB, and SC). However, the mean total realized GSD of all paths between 1980 and 2015 were 0.63, 0.52, 0.54, and -0.22 sd unit for MS, DS, FL, and HL, respectively. This suggests that there were total selections realized for some type traits (MS, DS, and FL) in the Brown Swiss population. This is confirmed by the annual genetic trends of 0.5, 0.3, and 0.2 per year

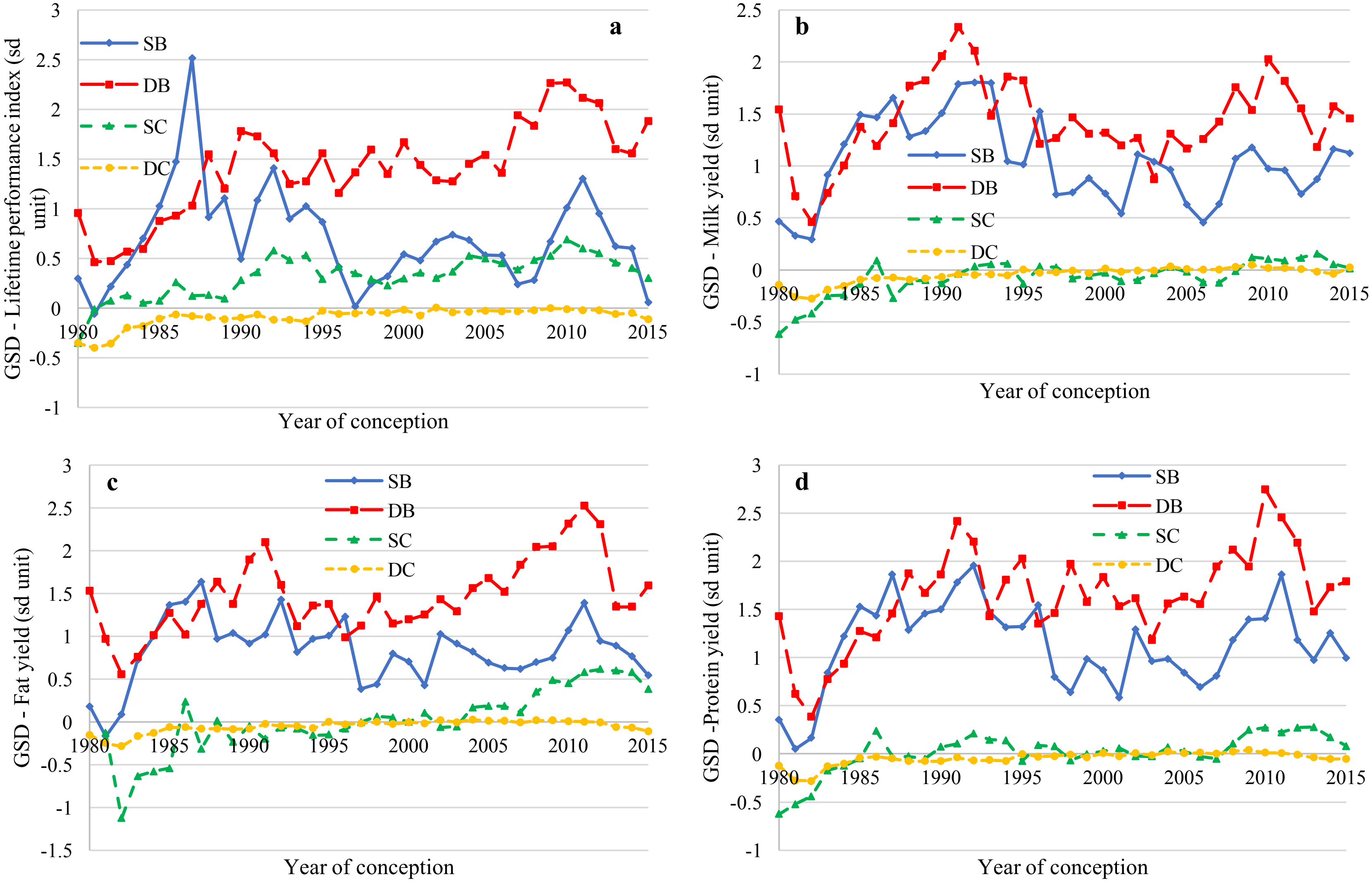

Figure 4.4a-d Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for Lifetime performance index, 305-day milk yield, 305-day fat yield and 305-day protein yield for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for Jersey breed.

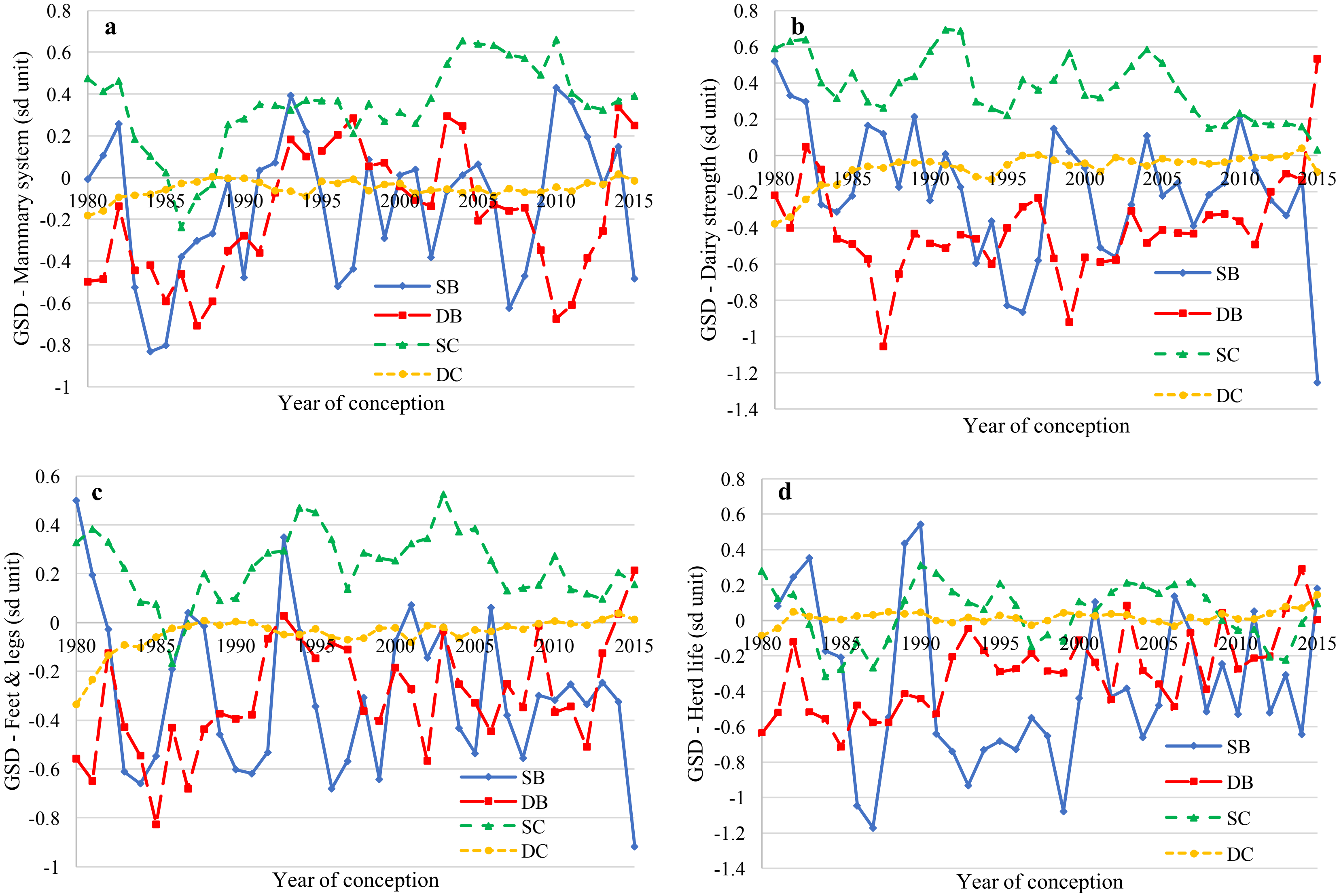

Figure 4.5a-d Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for mammary system, dairy strength, feet and legs, and herd life for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for Jersey breed.

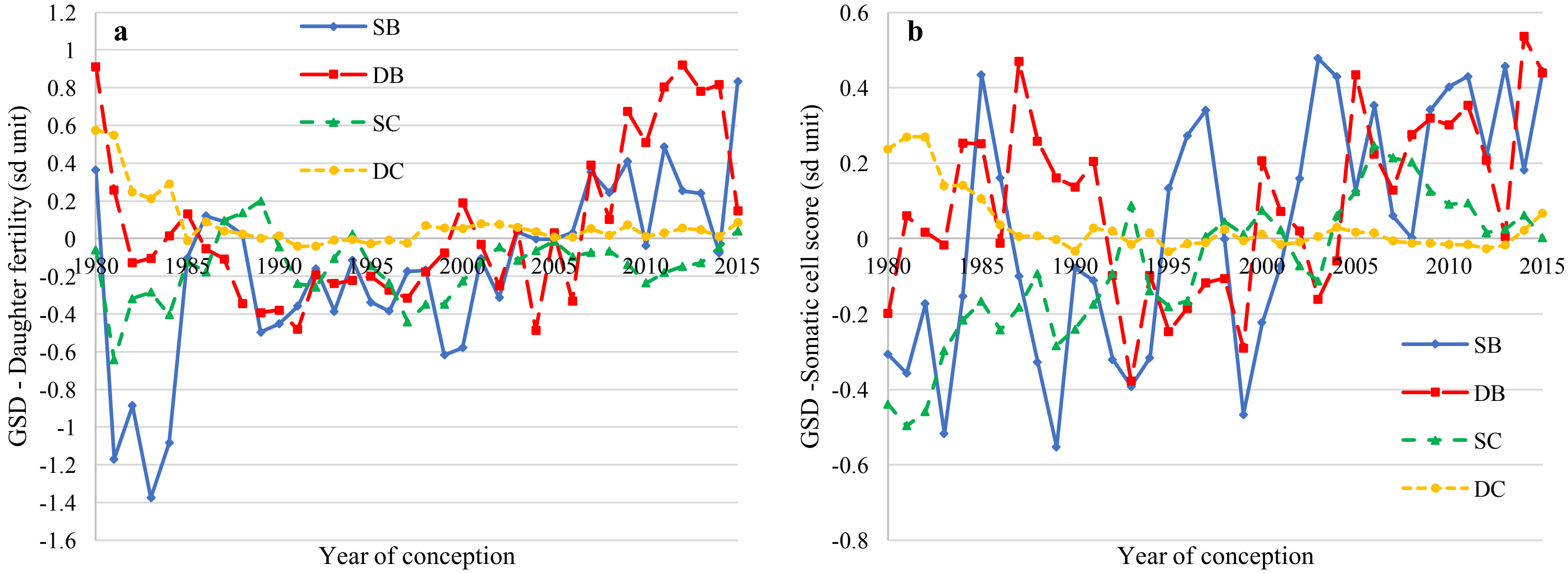

Figure 4.6a-b Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for daughter fertility and somatic cell score for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) for Jersey breed.

for MS, DS, and FL, respectively, for a 10-year period reported by CDN (Canadian Dairy Network, 2019). Unlike MS, DS, and FL, mean realized GSD of HL in the DC was slightly above zero (0.02 SD unit), though not statistically different from zero, demonstrating the practice where producers will generally keep healthy replacement cows in their herds for a longer period of time provided they are trouble-free to improve overall farm profitability (Allaire and Gibson, 1992). This explanation is applicable for the Ayrshire, Jersey, and Brown Swiss populations. The mean annual realized GSD for HL in the three breeds ranged from -1.44 to 1.16 sd unit.

The selection realized for type traits were lower than the production traits. This could partly be attributed to the higher economic weights of production traits in breeding goals of producers.

4.4.1.3 Health and fertility traits

The mean realized GSD for DF in SB, DB, and SC paths showed no clear trend and were largely negative for the Ayrshire, Jersey, and Brown Swiss breeds (Figures 4.3a, 4.6a, and 4.9a). The largely negative realized GSD in the 3 pathways could partly be attributed to the negative genetic correlations between fertility and yield traits (Kadarmideen et al., 2000) and also the low heritability for fertility traits (Jamrozik et al., 2005). However, mean realized GSD for DF in the DC were positive; 0.07 sd unit in both the Ayrshire and Jersey breeds, but not the Brown Swiss breed (-0.01 sd unit). The positive selection realized for DF in the DC of Ayrshire and Jersey populations was similar to the findings in the Canadian Holstein population (Hagan et al., 2020), and these are probably due to the practice of culling infertile cows in dairy herds in order to achieve pregnancy and sustain lactations to meet milk quota; lactation can only begin after the birth of a calf. The selection emphases for DF were lower than those of production and type traits and this was not surprising as intensified selection for production in the past had led to a correlated reduction in fertility because of the negative genetic correlations that exist between production and fertility traits.

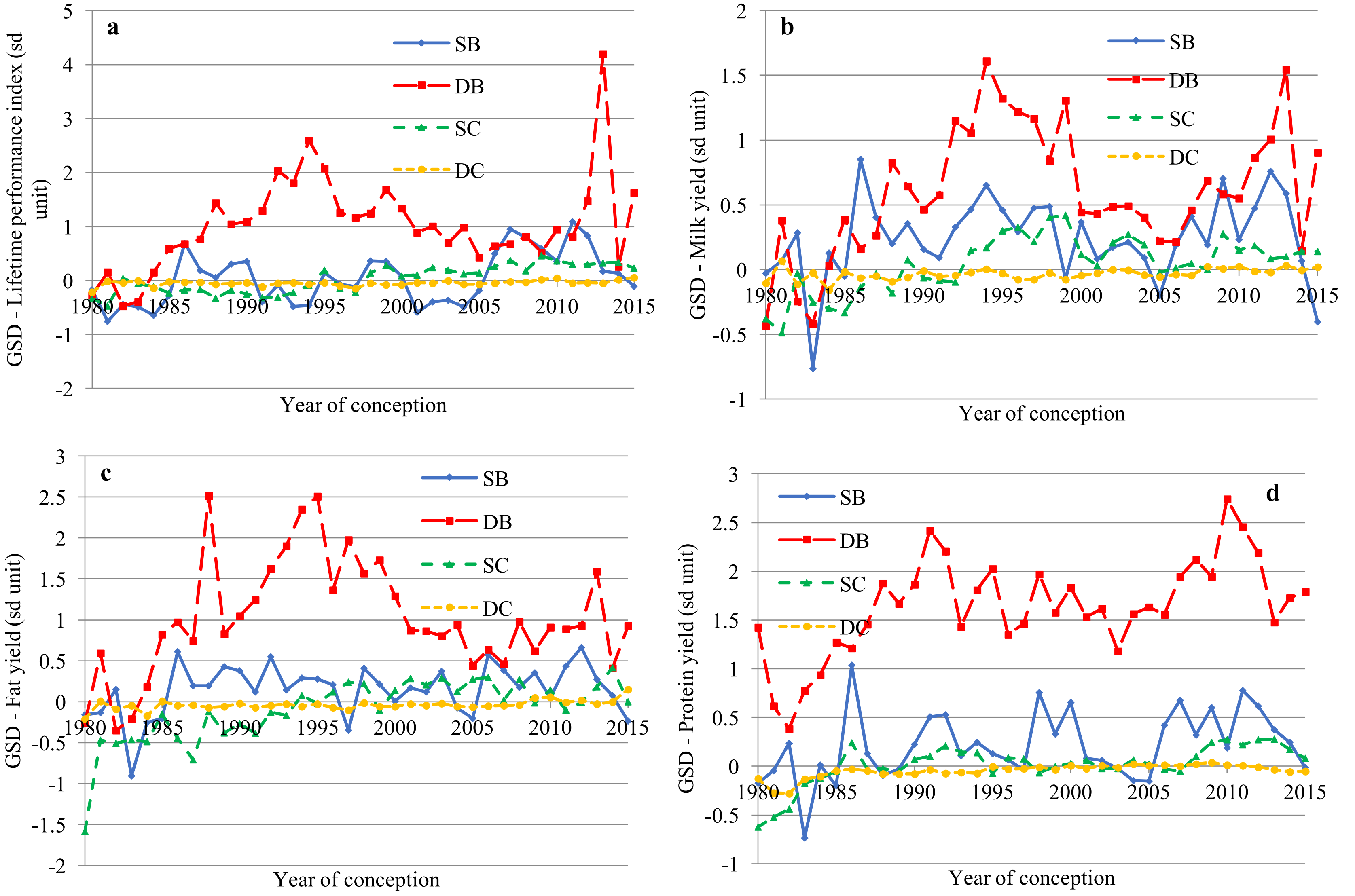

Figure 4.7a-d Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for Lifetime performance index, 305-day milk yield, 305-day fat yield and 305-day protein yield for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) for Brown Swiss breed.

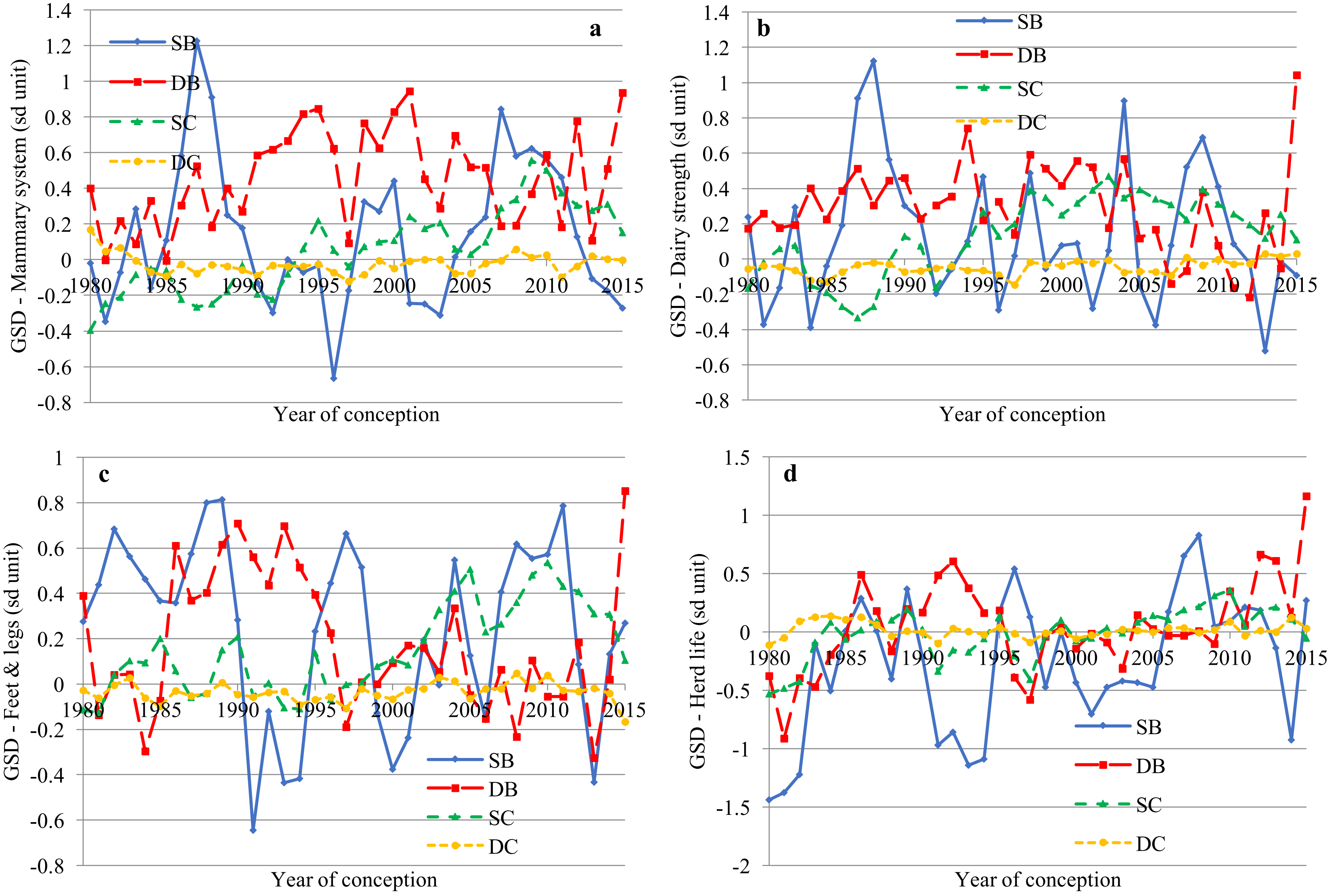

Figure 4.8a-d Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for mammary system, dairy strength, feet and legs, and herd life for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) paths for Brown Swiss breed.

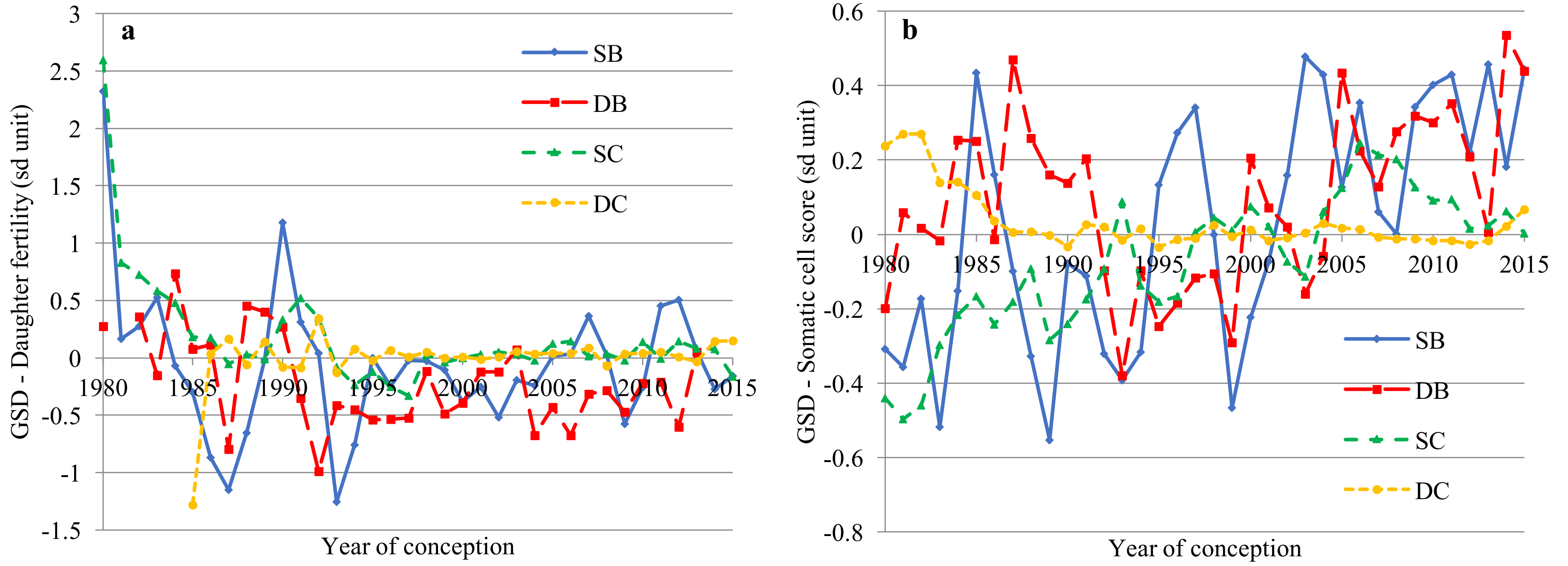

Figure 4.9a-b Mean realized genetic selection differential (GSD) in standard deviation unit (sd unit) per year of conception for daughter fertility and somatic cell score for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) for Brown Swiss breed.

Before December 2018, the genetic evaluations for SCS in Canada were such that lower values were better than higher values. To make the interpretation easier, the SCS were multiplied by -1. There were seemingly increasing trends in realized GSD for SCS in the SB, DB, and SC paths in all 3 cattle breeds (Figures 4.3b, 4.6b, and 4.9b). The realized GSD for SCS were mainly positive and favorable in the SB, DB, and SC from 2005. In the Ayrshire population, the realized GSD for HL largely increased and were above zero from 2005; the same period realized GSD for SCS were above zero. This could be attributed to the favorable genetic correlation between HL and SCS (Haile-Mariam et al., 2004). The mean total realized GSD between 1980 and 2015 were 0.32, 0.08, and 0.08 sd unit for Ayrshire, Jersey, and Brown Swiss populations, respectively. These were higher than the mean total realized GSD for DF in Ayrshire (-0.45), Jersey (-0.19), and Brown Swiss (-0.08) populations.

4.4.2 Effects of environment on realized GSD in the SC and DC paths of the Ayrshire, Jersey, and Brown Swiss dairy breeds

The *P*-values for the effects of YOC, HS, region, HS*YOC, region*YOC, and HS*region on realized GSD for 10 traits in the SC and DC paths are presented in Tables 4.3 and 4.4 for Ayrshire, Tables 4.5 and 4.6 for Jersey, and Tables 4.7 and 4.8 for Brown Swiss, respectively. Year of conception had significant effect ($P<0.05$) on realized GSD of all traits in the SC (not shown in table) of all breeds except the effect of YOC on realized GSD of FL in the Brown Swiss breed. The significant effect ($P<0.05$) of YOC on realized GSD in the SC could be an indication of changing breeding objectives of the industry and Ayrshire, Jersey, and Brown Swiss producers over time due perhaps to changes in market demands (Miglior et al., 2005) over time resulting in changes in selection emphases by producers.

Table 4.3 Effects of Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the sire-to-cow selection path (*P*-values for fixed effects) and the percentage of total variance in GSD explained by Herd(HS*Region), Herd*YOC[3], and residuals for the Ayrshire breed

	Fixed effect[2]					Percentage of total variance		
Trait[1]	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
LPI	0.8029	0.6337	0.9396	0.0016	0.6376	1.90	4.75	93.35
MY	0.9324	0.2232	0.4425	0.1591	0.3299	4.05	4.52	91.43
FY	0.8286	0.2998	0.4047	0.0079	0.4178	4.58	9.57	85.85
PY	0.6198	0.2400	0.5787	0.0011	0.6452	3.85	5.03	91.12
MS	0.9037	0.7388	0.7749	0.2340	0.7842	2.97	4.53	92.50
DS	0.2273	0.8474	0.6324	0.6490	0.3742	2.81	4.11	93.08
FL	0.7057	0.7102	0.8838	0.0050	0.8803	1.82	4.81	93.37
HL	0.7994	0.4787	0.2638	0.1871	0.8064	0.60	3.98	95.42
DF	0.5260	0.2536	0.0428	0.7047	0.6788	0.64	3.98	95.38
SCS	0.4638	0.9557	0.8142	0.6065	0.4944	0.60	30.17	69.23

[1] LPI – lifetime performance index; MY – 305-day milk yield; FY – 305-day fat yield; PY – 305-day protein yield; MS – mammary system; DS – dairy strength; FL – feet and legs; HL – herd life; DF – daughter fertility; SCS – somatic cell score.

[2] Fixed effects are statistically significant if $P<0.05$.

[3] YOC – Year of conception ($P<0.0001$ for all traits in the table).

Table 4.4 Effects of Year of conception (YOC), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the dam-to-cow selection path (*P*-values for fixed effects) and the percentage of total variance in GSD explained by Herd(HS*Region), Herd*YOC, and residuals for the Ayrshire breed

	Fixed effect[2]						Percentage of total variance		
Trait[1]	YOC	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residuals
LPI	0.0003	0.2450	0.0576	0.2863	<0.0001	0.5139	7.21	2.30	90.49
MY	0.0016	0.3385	0.0600	0.9032	0.0045	0.7948	8.37	1.64	89.99
FY	0.0715	0.2086	0.0502	0.8083	0.0035	0.6121	8.09	2.22	89.69
PY	0.0059	0.1822	0.0256	0.9319	0.0371	0.6597	8.33	2.37	89.30
MS	0.3000	0.9203	0.7891	0.9979	0.2575	0.8354	7.91	2.17	89.92
DS	0.7088	0.3285	0.7621	0.7440	0.5340	0.5813	9.54	1.67	88.79
FL	0.0203	0.6541	0.7594	0.9831	0.3553	0.8132	6.74	2.11	91.15
HL	0.0517	0.9039	0.7255	0.0319	0.1704	0.6989	3.00	0.80	96.20
DF	0.7907	0.4414	0.4142	0.0006	0.9451	0.5883	7.46	0.73	91.80
SCS	0.0529	0.0497	0.3127	0.8445	0.5711	0.4753	1.95	1.27	96.78

[1] LPI – lifetime performance index; MY – 305-day milk yield; FY – 305-day fat yield; PY – 305-day protein yield; MS – mammary system; DS – dairy strength; FL – feet and legs; HL – herd life; DF – daughter fertility; SCS – somatic cell score.

[2] Fixed effects are statistically significant if $P<0.05$.

Apart from YOC, other environmental factors did not mostly have significant effects ($P>0.05$) on realized GSD in the SC except for the effects of HS*YOC on realized GSD for DF (0.0428) and region*YOC on realized GSD for LPI (0.0016), FY (0.0079), PY (0.0011), and FL (0.0050) in Ayrshire breed. The effect of region*YOC was also significant ($P<0.05$) on realized GSD of FY and FL, and HS*region on realized GSD of LPI in the SC path of the Jersey breed. In the Brown Swiss breed, the effect of HS was significant ($P<0.05$) on realized GSD of LPI in the SC. Similarly, the effect of region*YOC was significant ($P<0.05$) on realized GSD of all type traits (MS, DS, FL, and HL) in the SC; and the effect of HS*region was significant ($P<0.05$) in the realized GSD of MY and FY. The significant effects ($P<0.05$) of region*YOC on realized GSD for LPI, FY, PY, and FL in the Ayrshire, and FY and FL in the Jersey, and MS, DS, FL, and HL in the Brown Swiss breed suggest that among the agricultural regions, there were differences in selection realized for some traits over time. The results indicate that apart from YOC, the other environmental factors generally had little influence on realized selection for economically important traits in the SC path of the Ayrshire, Jersey, and Brown Swiss populations.

Table 4.5 Effects of Year of conception (YOC), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the sire-to-cow selection path (*P*-values for fixed effects) and the percentage of total variance in GSD explained by Herd(HS*Region), Herd*YOC[3], and residuals for the Jersey breed

	Fixed effect[2]					Percentage of total variance		
Trait[1]	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
LPI	0.7770	0.4218	0.6788	0.3833	0.0489	3.92	7.35	88.73
MY	0.8061	0.9379	0.9392	0.1522	0.5143	9.10	8.81	82.09
FY	0.3791	0.6755	0.7843	0.0010	0.6339	6.97	18.30	74.73
PY	0.9453	0.8549	0.8075	0.3070	0.5982	10.84	9.01	80.15
MS	0.3047	0.5954	0.7789	0.8597	0.5777	6.77	7.50	85.73
DS	0.0567	0.9250	0.5067	0.9923	0.4359	5.43	8.89	85.68
FL	0.8085	0.4964	0.8988	0.0323	0.6560	7.03	6.80	86.17
HL	0.5229	0.8275	0.9087	0.3871	0.8108	3.75	5.25	91.00
DF	0.0567	0.9250	0.5067	0.9923	0.4359	1.13	6.30	92.57
SCS	0.3572	0.9199	0.7095	0.1940	0.0674	0.71	5.71	93.58

[1] LPI – lifetime performance index; MY – 305-day milk yield; FY – 305-day fat yield; PY – 305-day protein yield; MS – mammary system; DS – dairy strength; FL – feet and legs; HL – herd life; DF – daughter fertility; SCS – somatic cell score.

[2] Fixed effects are statistically significant if $P<0.05$.

[3] YOC – Year of conception ($P<0.0001$ for all traits in the table).

Table 4.6 Effects of Year of conception (YOC), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the dam-to-cow selection path (P-values for fixed effects) and the percentage of total variance in GSD explained by Herd(HS*Region), Herd*YOC, and residuals for the Jersey breed

	Fixed effect[2]						Percentage of total variance		
Trait[1]	YOC	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
LPI	0.3953	0.4458	0.0108	0.7043	0.8566	0.0503	10.21	2.92	86.87
MY	0.2233	0.9151	0.1532	0.9873	0.6492	0.2369	11.36	2.72	85.92
FY	0.2948	0.6387	0.1016	0.5812	0.9683	0.2365	11.03	3.57	85.40
PY	0.2078	0.6107	0.1236	0.8941	0.8366	0.1288	12.40	3.79	83.81
MS	0.0756	0.9858	0.6932	0.2151	0.8714	0.3632	15.47	1.97	82.56
DS	0.0437	0.3087	0.6554	0.8829	0.0935	0.4779	11.88	2.47	85.65
FL	0.2829	0.7863	0.3766	0.4692	0.2140	0.8371	14.61	2.15	83.24
HL	0.3014	0.5934	0.6121	0.9832	0.6037	0.8722	11.66	1.27	87.07
DF	0.8196	0.4707	0.2261	0.4330	0.3165	0.1285	7.95	1.05	91.00
SCS	0.6349	0.2139	0.7559	0.6641	0.0035	0.2713	3.89	0.00	96.11

[1] LPI – lifetime performance index; MY – 305-day milk yield; FY – 305-day fat yield; PY – 305-day protein yield; MS – mammary system; DS – dairy strength; FL – feet and legs; HL – herd life; DF – daughter fertility; SCS – somatic cell score.

[2] Fixed effects are statistically significant if $P<0.05$.

In the DC, YOC had a significant effect ($P<0.05$) on the realized GSD of LPI, MY, PY, and FL in the Ayrshire population. This is interesting as there is little opportunity for selection in the DC path, but the significant changes in selection realized for FL could mostly be due to involuntary culling of lamed replacement cows over time. Housing system did not have a significant effect ($P>0.05$) on realized GSD of all traits except SCS ($P=0.0497$). Free stall herds recorded on average slightly higher and favorable realized GSD for SCS than tie stall herds. In Norwegian dairy herds, higher clinical mastitis rates were reported in tie stalls than free stall herds (Valde et al., 1997). However, for conformation traits, Paakala et al. (2018) observed a significant effect of HS on the selection preference of Finnish Ayrshire AI bulls. They found that automatic and loose housing herds valued conformation traits higher than tie-stall herds.

Whilst region did not have any significant effect (*P*>0.05) on realized GSD for all 10 traits in the DC of the Ayrshire breed except for PY, there was a significant interaction (*P*<0.05) between region and YOC on realized GSD for production traits (MY, FY, and PY) and LPI in the DC. The interaction between HS and region did not have a significant effect (*P*>0.05) on selection realized for any of the 10 traits.

In the DC path of the Jersey population, all the environmental factors and their interactions did not have significant effect (*P*>0.05) on realized GSD of all 10 traits except for the effects of YOC and region on realized GSD for DS and LPI, respectively (Table 4.6). For the Brown Swiss population, YOC and region did not have significant effects (*P*>0.05) on realized GSD of all 10 traits except for the effect of YOC on realized GSD of FL in the DC path (Table 4.8). Housing system had a significant effect on only the realized GSD of SCS while HS*YOC had a significant effect (*P*<0.05) on realized GSD of DF. There were significant interactions (*P*<0.05) of region and YOC on realized GSD of MS, DS, and FL, and HS*region also had a significant effect (*P*<0.05) on realized GSD of MY in the DC path of the Brown Swiss population.

4.4.3 Variations among herds and herd*YOC on realized GSD in the SC and DC paths of the Ayrshire, Jersey, and Brown Swiss dairy breeds

There were considerable variations among herds in the selection realized for economically important traits in both the SC and DC paths of the Ayrshire, Jersey, and Brown Swiss populations (Tables 4.3 to 4.8). In the Ayrshire population, variations due to herd constituted between 0.6 and 4.6% of the total variation in realized GSD observed in the SC path. In the Jersey and Brown Swiss breeds, variations due to herd were between 0.7 and 10.8%, and between 0.5 and 4.6% of the total variations observed, respectively, in realized GSD for traits studied in the SC path. We observed greater variabilities in selection realized for production traits (MY, FY, and PY) in the Ayrshire (3.9 – 4.6%) and Jersey (7.0 – 10.8%) compared with type, and health and fertility traits. Moderate variations were observed among herds in their selection pressures for type traits (3.8 – 7.0%) in the Jersey breed. However, in the Brown Swiss breed, the variations due to herd were relatively lower for production traits (1.3 – 2.2%) compared with type traits (1.3 – 4.6%) but not health and fertility traits (0.5 – 1.7%).

Table 4.7 Effects of Year of conception (YOC), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the sire-to-cow selection path (*P*-values for fixed effects) and the percentage of total variance in GSD explained by Herd(HS*Region), Herd*YOC, and residuals for the Brown Swiss breed

	Fixed effect[2]						Percentage of total variance		
Trait[1]	YOC	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
LPI	<0.0001	0.0391	0.4522	0.6715	0.6271	0.2742	1.44	9.70	88.86
MY	0.0056	0.1546	0.6474	0.0953	0.4555	0.0238	1.49	6.08	92.43
FY	<0.0001	0.1842	0.8096	0.6556	0.4906	0.0421	1.30	20.37	78.33
PY	<0.0001	0.0994	0.6193	0.4575	0.3890	0.1089	2.16	7.39	90.45
MS	0.0050	0.6229	0.0789	0.9813	0.0055	0.5241	3.86	7.26	88.88
DS	<0.0001	0.2448	0.0942	0.9252	0.0285	0.4669	4.55	11.73	83.72
FL	0.4792	0.0924	0.9961	0.8859	0.0039	0.9310	1.58	6.79	91.63
HL	0.0038	0.2004	0.2663	0.7488	0.0023	0.5722	1.29	7.27	91.44
DF	0.0001	0.9563	0.9620	0.4711	0.7495	0.2367	1.66	10.59	87.75
SCS	<0.0001	0.9957	0.4164	0.8842	0.5546	0.8345	0.53	8.39	91.08

[1] LPI – lifetime performance index; MY – 305-day milk yield; FY – 305-day fat yield; PY – 305-day protein yield; MS – mammary system; DS – dairy strength; FL – feet and legs; HL – herd life; DF – daughter fertility; SCS – somatic cell score.

[2] Fixed effects are statistically significant if $P<0.05$.

Table 4.8 Effects of Year of conception (YOC), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the dam-to-cow selection path (*P*-values for fixed effects) and the percentage of total variance in GSD explained by Herd(HS*Region), Herd*YOC, and residuals for the Brown Swiss breed

	Fixed effects[2]						Percentage of total variance		
Trait[1]	YOC	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residuals
LPI	0.6832	0.1914	0.0625	0.5171	0.0778	0.0539	10.25	0.00	89.75
MY	0.3562	0.3865	0.3094	0.7742	0.3592	0.0332	13.84	1.04	85.12
FY	0.7435	0.3325	0.0955	0.4270	0.1868	0.1615	11.19	0.57	88.24
PY	0.6758	0.8848	0.1317	0.5175	0.2410	0.1447	12.25	0.48	87.27
MS	0.6486	0.1679	0.8767	0.1616	0.0001	0.2834	15.00	0.00	85.00
DS	0.6749	0.5977	0.9402	0.4157	<0.0001	0.5919	16.61	0.00	83.39
FL	0.0356	0.6977	0.9128	0.1795	0.0439	0.1792	5.36	0.00	94.64
HL	0.7550	0.1102	0.9691	0.8507	0.1135	0.3743	7.22	0.81	91.97
DF	0.0931	0.9403	0.5300	0.0173	0.0545	0.5882	16.70	0.87	82.43
SCS	0.3091	0.0172	0.4131	0.2874	0.3108	0.7750	6.28	0.00	93.72

[1] LPI – lifetime performance index; MY – 305-day milk yield; FY – 305-day fat yield; PY – 305-day protein yield; MS – mammary system; DS – dairy strength; FL – feet and legs; HL – herd life; DF – daughter fertility; SCS – somatic cell score.

[2] Fixed effects are statistically significant if $P<0.05$.

There were also significant variations due to Herd*YOC on realized GSD of traits in the SC path of Ayrshire, Jersey, and Brown Swiss breeds with the variations ranging from 4.0 to 30.2%, 5.3 to 18.3%, and 6.1 to 20.4%, respectively, of the total variation in realized GSD (Tables 4.3, 4.5, and 4.7). The significant variations in GSD in the SC due to herd*YOC are indications that selection emphases for economically important traits changes with time among Ayrshire, Jersey, and Brown Swiss herds.

In the DC of the Ayrshire population, herd significantly accounted for between 2.0 and 9.54% of the total variation in realized GSD (Table 4.4). The greatest variation in realized GSD due to herd was observed for production traits (MY, FY, and PY) and DF, DS, and MS (7.5 – 9.5%). The higher variations among herds for GSD of DF in DC could be due to the active culling of unproductive cows among dairy herds (Bascom and Young, 1998). Herds which have in the past consistently culled out unproductive cows might put minimal selection emphasis on DF in recent times compared with those that have not done so before or in a long while. Also, it is possible that some herds have better management than other herds, and therefore they do not perceive the need to breed for better fertility. There were relatively smaller but significant variations in realized GSDs due to herd*YOC compared with the variations due to herd, in the DC path of the Ayrshire population, ranging from 0.7 to 2.4% of the total variations in GSD.

In the Jersey population, variations in realized GSD due to herd explained between 3.9 and 15.5% of the total variations in realized GSDs in the DC path (Table 4.6). Greater variabilities were observed among producers in realized GSD for type traits (11.7 to 15.5%) compared with production, health, and fertility traits. Since Jersey cattle are noted to yield higher fat and protein percentages compared with other dairy breeds, there might be relatively little differences in the amount of selection emphases producers put on yield traits while there may be greater variabilities in selection for type traits among producers of Jersey breed. There were also considerable variations among herds in the realized GSD for health and fertility traits (3.9 to 8.0%). There were minimal variations due to herd*YOC on realized GSD. The variations due to herd*YOC were significant for all traits studied, except FL and SCS.

In the Brown Swiss population, variations in realized GSD due to herd constituted between 5.4 and 16.7% of the total variations in realized GSD while herd*YOC component explained only little (0.0 to 1.0%) of the total variation in realized GSD (Table 4.8). The little variations in GSD of Brown Swiss herds over time suggest that selection emphases in DC path tend to be the same from year to year.

For the SC path of all breeds, all the variations in realized GSD due to herd and herd*YOC were significant. These suggest that not all dairy producers were actively selecting for economically important traits in their choice of AI sires for breeding. It could be an indication of differences in breeding objectives of dairy farms across Québec. The little to no selection realized in economically important traits among some herds would have adverse implications on the profitability of these dairy farms in the long term. It is not clear if these producers were aware of the selection emphases they are making and achieving and its implications on their farms' profitability.

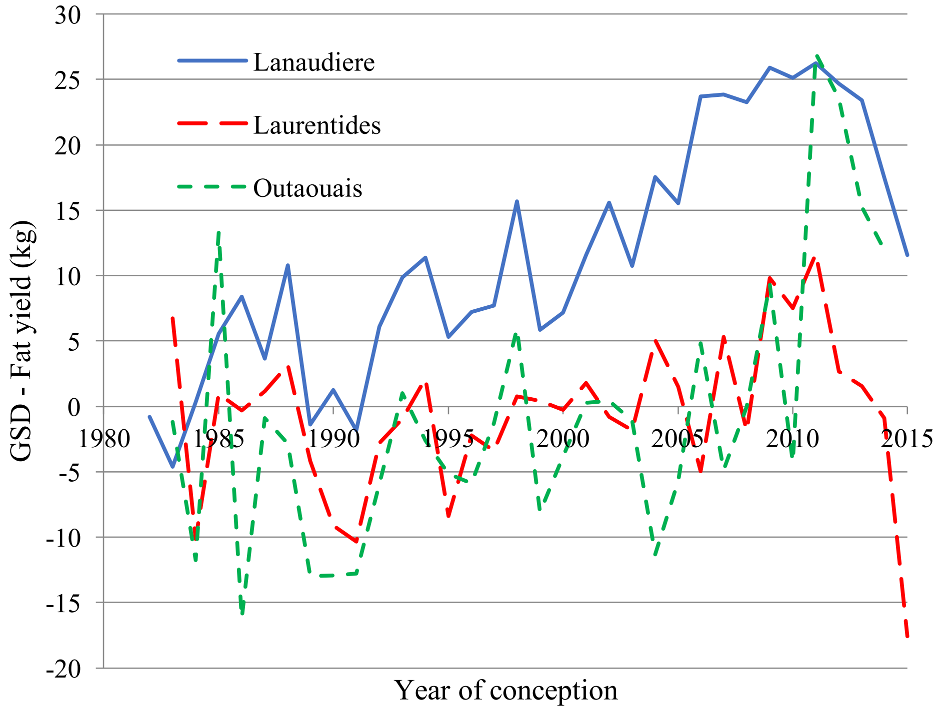

Figure 4.10 Mean genetic selection differential (GSD) for fat yield for three selected agricultural regions; Lanaudiere, Laurentides and Outaouais of the Ayrshire breed.

4.4.4 General discussion

Breeding objectives of dairy industries around the world have been evolving over the years (Miglior et al., 2005). Breeding objectives of the second half of the last century were mainly production oriented traits (Miglior et al., 2005; Miglior et al., 2017). This partly explains why the GSDs for the production traits (MY, FY, and PY) in the SB and DB paths from 1980 to 2000 were higher than the GSDs for durability, health, and fertility traits at the same period in each of the 3 dairy populations (Ayrshire, Jersey, and Brown Swiss). In the 21st century, breeding objectives have been more broadened to include reproduction and health traits in most dairy producing countries (Miglior et al., 2005). This has partly contributed to the relatively higher selection emphases for durability traits and SCS in especially the Ayrshire breed from 2001 to 2015 compared with the preceding years (1980 – 2000).

Genomic evaluation in the Canadian Ayrshire breed started in 2013, and this has improved the accuracy of EBVs of traits, therefore the higher GSDs of especially production traits in the DB path of the Ayrshire breed. Since genomic selection has a positive influence on the GSD and genetic gains of lowly heritable traits (García-Ruiz et al., 2016), the GSDs of DF in the SB and DB paths were expected to be high and positive in the period after the introduction of genomic selection in the Ayrshire, Jersey, and Brown Swiss breeds. Genomic selection started in 2009 for the Jersey and Brown Swiss breeds and 2013 for the Ayrshire breed (Wiggans et al., 2017); however, genomic selection seems to have positively influenced the GSDs of DF in the SB and DB paths of the Jersey breed but not the Ayrshire and Brown Swiss breeds.

The largely positive GSDs of LPI, production, and durability traits in the SB, DB, and SC paths are in agreement with the positive genetic trends for LPI, durability, and production traits reported by

Canadian Dairy Network between 2006 and 2016 for the Canadian Ayrshire, Jersey, and Brown Swiss populations (Canadian Dairy Network, 2019).

Information is scant on the effects of environmental factors on selection emphases applied by producers for economically important traits in dairy cattle. We would expect that some environmental factors such as HS, region, and YOC will influence the GSD realized by dairy producers. The significant effect of YOC on the GSDs for economically important traits in the SC path could practically be attributed to instances where producers could change their selection emphases for traits over time to correct for certain shortfalls within herds. For example, a producer who notices increased incidences of leg problems among his or her herd could put more selection emphasis on feet and legs over time to correct for the leg problem in addition to the use of management strategies. After correction of the problem, the producer may revert to putting more emphases on other traits such as fat yield to meet his or her monthly kg fat quota.

The significant interaction of region*YOC could be due to changes in breeding objectives over time among herds in some of the agricultural regions. To further illustrate this interaction, the mean realized GSD per YOC was plotted for three selected agricultural regions; Lanaudiere, Laurentides, and Outaouais (Figure 4.10). The difference in realized GSD between Lanaudiere and Laurentides tended to widen over time while the realized GSD of Laurentides and Outaouais overlap one another over time. Year of conception was mostly unimportant in the realized GSD of traits in the DC path. The observed significant effect (P=0.0356) of YOC on realized GSD of FL in the DC path of the Ayrshire breed might be a deliberate attempt to control leg-related problems among cows in the herds of some producers during certain periods over the 36-year period.

Genetic trends reported by most national breeding programs might give the impression that all producers or AI centers are making the same or similar selection for economically important traits. It was therefore important in this study to determine the variations in GSDs realized by dairy producers. The considerable and significant variations in realized GSD due to herd indicate that not all producers were intensively selecting for economically important traits. This could be due partly to differences in herds' breeding objectives and partly to differences in semen prices. Also, some producers who might lack clear, consistent, well established, and well defined breeding goals may be prone to use semen from sires with diverse genetic potentials throughout the year, hence the observed variations in realized GSD.

As with the Ayrshire population, greater variabilities were observed among herds keeping the Jersey breed for production traits (7.0 – 10.8%) compared to the type, health, and fertility traits in the Jersey breed. This suggests that there was greater variability in the inclusion and selection emphases producers put on production traits in their total breeding objectives compared with other traits. The considerable variations in GSDs among herds offer opportunities to optimize genetic gains in economically important traits in the minor dairy cattle breeds in Canada as producers could intensify their selection emphases for breeding objective traits. Appropriate tools could thus be developed to enable dairy producers monitor the selection emphases they apply for economically important traits within their herds and compare their selection emphases with suitable benchmarks to enable them make necessary changes if they are not moving in intended direction.

4.5 CONCLUSIONS

Realized GSD attained by Canadian dairy producers of the Ayrshire, Jersey, and Brown Swiss dairy cattle breeds have been investigated along the 4-path selection model. The population average realized GSDs of the DB path were appreciably higher than those of SB, SC, and DC paths for the national selection index and production traits in the Ayrshire and Brown Swiss populations but not the

Jersey population. There was continuously increasing selection realized for SCS in the SB, DB, and SC paths in all 3 cattle breeds.

Year of conception was the main environmental factor that significantly influenced the realized GSD of AI sires (SC path). Other environmental factors studied were mostly not important on selection realized in the SC and DC paths in the Ayrshire, Jersey, and Brown Swiss populations. There were considerable variations among herds in selection realized for AI sires (SC) and replacement cows (DC) in all 3 dairy cattle populations. This study has demonstrated that realized GSD vary considerably among Ayrshire, Jersey, and Brown Swiss herds in Québec. Appropriate tools may thus be needed for dairy producers to monitor the amount of selection they are making and how much selection emphases individual dairy producers are making for economically important traits.

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Table S4.9 Maximum number of unique sires and dams of bulls and cows in each selection path for the three breeds

Breed	Sires of Bulls	Sires of Cows	Dams of Bulls	Dams of Cows
Ayrshire	268	4,075	798	111,157
Jersey	623	4,463	1,417	86,148
Brown Swiss	259	1,717	546	16,775

Table S4.10 Average realized genetic selection differential for the 4 paths of selection[1] (SB, DB, SC, and DC) for 10 traits for all the study period (1980 to 2015) and the last 10 years (2006 to 2015) for the Ayrshire breed

		Year of conception	
Trait	Selection path	1980 – 2015	2006 – 2015
Lifetime Performance Index	SB[1]	101.73	240.24
	DB	322.88	451.40
	SC	83.02	245.57
	DC	-7.17	-6.70
Milk yield, kg	SB	188.13	292.21
	DB	507.15	689.68
	SC	142.02	284.23
	DC	-8.56	8.26
Fat yield, kg	SB	8.71	14.34
	DB	22.05	32.07
	SC	8.36	18.05
	DC	-0.45	-0.33
Protein yield, kg	SB	6.08	10.49
	DB	18.10	25.12
	SC	3.93	10.45
	DC	-0.22	-0.14
Mammary system	SB	0.87	1.78
	DB	2.28	4.09
	SC	1.31	2.63
	DC	-0.16	-0.17
Dairy strength	SB	1.22	1.47
	DB	2.11	3.47
	SC	1.27	1.89
	DC	-0.19	-0.14
Feet and legs	SB	0.88	2.13
	DB	1.74	3.58
	SC	1.13	2.58
	DC	-0.09	-0.10
Herd life	SB	0.64	1.16

	DB	0.97	1.43
	SC	0.65	1.11
	DC	0.07	0.04
Somatic Cell Score	SB	0.002	-0.076
	DB	-0.047	-0.070
	SC	0.001	-0.074
	DC	-0.003	0.003
Daughter Fertility	SB	-0.83	-0.47
	DB	-0.68	-1.44
	SC	-0.95	-1.05
	DC	0.21	0.20

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

Table S4.11 Average realized genetic selection differential for the 4 paths of selection[1] (SB, DB, SC, and DC) for 10 traits for all the study period (1980 to 2015) and the last 10 years (2006 to 2015) for the Jersey breed

		Year of conception	
Trait	Selection path	1980 – 2015	2006 – 2015
Lifetime Performance Index	SB[1]	142.10	150.86
	DB	281.60	383.34
	SC	79.69	124.87
	DC	-16.83	-8.70
Milk yield, kg	SB	560.52	500.32
	DB	763.94	816.20
	SC	-36.56	27.79
	DC	-19.90	6.89
Fat yield, kg	SB	19.45	18.61
	DB	32.95	42.97
	SC	0.88	12.11
	DC	-0.99	-0.53
Protein yield, kg	SB	17.85	17.14
	DB	26.83	31.49
	SC	0.63	3.56
	DC	-0.62	-0.11
Mammary system	SB	-0.39	-0.26
	DB	-0.46	-0.75
	SC	1.50	2.19
	DC	-0.15	-0.17
Dairy strength	SB	-0.79	-0.84
	DB	-1.04	-0.76
	SC	1.99	0.91
	DC	-0.23	-0.09
Feet and legs	SB	-1.21	-1.29
	DB	-0.97	-0.66
	SC	1.20	0.88
	DC	-0.16	-0.01
Herd life	SB	-1.15	-0.79
	DB	-0.81	-0.37
	SC	0.19	0.05
	DC	0.06	0.14
Somatic Cell Score	SB	-0.003	-0.037
	DB	-0.009	-0.028
	SC	0.014	-0.017
	DC	-0.005	0.0001
Daughter Fertility	SB	-0.82	1.08
	DB	0.20	1.77
	SC	-0.64	-0.55
	DC	0.18	0.14

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

Table S4.12 Average realized genetic selection differential for the 4 paths of selection[1] (SB, DB, SC, and DC) for 10 traits for the study period (1980 to 2015) and the last 10 years (2006 to 2015) for the Brown Swiss breed

		Year of conception	
Trait	Selection path	1980 – 2015	2006 – 2015
Lifetime Performance Index	SB[1]	18.17	142.05
	DB	226.76	237.99
	SC	8.34	105.42
	DC	-15.01	-3.32
Milk yield, kg	SB	96.54	146.27
	DB	215.04	234.17
	SC	21.32	53.98
	DC	-16.39	-1.05
Fat yield, kg	SB	2.18	4.39
	DB	16.09	15.56
	SC	-1.83	2.39
	DC	-0.74	0.18
Protein yield, kg	SB	2.51	5.74
	DB	11.38	12.04
	SC	-0.11	2.84
	DC	-0.63	-0.40
Mammary system	SB	0.59	1.18
	DB	1.84	2.16
	SC	0.28	1.42
	DC	-0.09	-0.01
Dairy strength	SB	0.53	0.60
	DB	1.23	0.95
	SC	0.66	1.18
	DC	-0.17	-0.07
Feet and legs	SB	0.94	1.41
	DB	0.64	0.20
	SC	0.73	1.61
	DC	-0.13	-0.10
Herd life	SB	-1.03	0.74
	DB	0.08	0.56
	SC	-0.02	0.81
	DC	0.03	0.10
Somatic Cell Score	SB	0.014	-0.069
	DB	-0.025	-0.077
	SC	0.012	-0.030
	DC	-0.002	0.002
Daughter Fertility	SB	-0.18	-0.04
	DB	-0.46	-1.38
	SC	1.01	0.21
	DC	0.23	0.17

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

CONNECTING STATEMENT

Chapters III and IV present the GSD of major economically important traits in the Holstein, Ayrshire, Jersey, and Brown Swiss dairy cattle breeds in Canada along the four pathways of genetic improvement. The effects of year of conception, housing system, agricultural regions, and their interactions on the realized GSDs were also determined. The profitability of dairy cows does not hinge on only the major economically important traits but on all traits for which genetic evaluations are calculated. The next chapter, V, examines the realized GSD of ancillary traits in the Holstein, Ayrshire, Jersey, and Brown Swiss dairy cattle breeds in Canada. The chapter also examines effects of some environmental factors on the realized GSD of ancillary traits in the producers controlled pathways (sire-to-cow and dam-to-cow paths).

5 CHAPTER V: What selection is realized for ancillary traits in Canadian dairy cattle breeds?

Ancillary traits in dairy cattle breeds are important as they confer unique characteristics to dairy cows and contribute considerably to the profitability of dairy cows. Holstein, Ayrshire, Jersey, and Brown Swiss producers would be interested in improving ancillary traits in their herds to partly sustain the high milk production of their cows. Estimated breeding values were used to determine the selection emphases producers of Canadian dairy breeds were making for ancillary traits and the amount of variations in realized selection among producers' herds. Significant variations in realized selection existed among herds and this offer opportunity to further increase genetic gains for ancillary traits.

RUNNING TITLE: FULL-LENGTH RESEARCH PAPER

What selection is realized for ancillary traits in Canadian dairy cattle breeds?

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5.1 ABSTRACT

Estimated breeding values for ancillary type and functional traits of Canadian Holstein, Ayrshire, Jersey, and Brown Swiss bulls and cows born from 1950 and 1960, respectively, were used to estimate the realized genetic selection differential (GSD) for selection indices of type and functional traits along the 4 paths of genetic improvement. The effects of some environmental factors on realized GSD of the sire-to-cow (SC) and dam-to-cow (DC) paths and variations in realized GSD of ancillary type and functional traits due to herd and herd by year of conception (herd*YOC) were also investigated. The mean total realized GSD for the lifetime performance sub-index for type traits, LPI-durability (LPI-DUR) between 1980 and 2015 were higher than the mean total realized GSD for the health and fertility sub-index, LPI-health and fertility (LPI-HF) in all breeds except the Jersey. The top 10% available bulls for LPI-DUR and LPI-HF for each year were being utilized for breeding by some dairy producers of the 4 dairy cattle populations. The effect of YOC was mostly significant ($P<0.05$) on the realized GSD for ancillary type and functional traits in the SC, but not the DC path. Housing system had some significant influence on the realized GSD of type, but not functional traits. Other environmental factors did not have significant influence ($P>0.05$) on the realized GSD of ancillary type and functional traits in the SC and DC paths in all dairy cattle breeds. There were considerable and significant variations in realized GSD due to herd and herd*YOC in the SC and DC paths. The appreciable variations in realized GSD due to herd suggest there is opportunity to further increase genetic improvement of ancillary type and functional traits in Canadian dairy cattle breeds.

Keywords: realized genetic selection differential, herd, ancillary type and functional traits, Holstein

5.2 INTRODUCTION

The profitability of the dairy industry is not dependent on only production traits but on all economically important traits (Funk, 1993). Dairy producers have for a long time selected for production traits because of the higher revenue associated with yield traits, the availability of EBV for yield traits to select on, and the ease in objectively measuring and recording yield traits. The over-emphasis on selecting for production traits has resulted in deterioration of fitness traits (Pryce et al., 1998; Royal et al., 2002; Kadarmideen et al., 2003; Pryce et al., 2004) in dairy cattle. Most national breeding programs have recognized the importance of ancillary traits to animal welfare (Oltenacu and Broom, 2010) and profitability and have started including such traits in their selection indices.

The average composition of type and fitness traits is still less than 50% in 14 out of the 15 national selection indices earlier studied (Miglior et al., 2005). In Canada, apart from the Holstein and Ayrshire breeds, type and fitness traits constitute less than 50% of the national index, lifetime performance index **(LPI)**, for other dairy cattle breeds (Canadian Dairy Network, 2019). The breeding objectives of individual dairy herds might differ slightly based on producers' needs. It is expected that dairy producers in countries with little or no restriction on the marketing of milk and milk products will put greater selection emphasis on production compared with type and functional traits to increase revenues from their farming operations. However, in Canada, where there is a supply management coupled with quota-based system, it is expected that producers will probably put more selection emphasis on type and fitness traits compared with production traits as producers cannot produce and sell quantities of milk beyond their purchased milk quota without being penalized.

Genetic selection differential **(GSD)**, which is the measure of the amount of selection applied, have been studied in Holstein (Van Tassell and Van Vleck, 1991; Kawahara et al., 2002; García-Ruiz et al., 2016) and Jersey (Nizamani and Berger, 1996) breeds. Canaza-Cayo et al. (2016) and Silva et al. (20001) have also studied selection differentials in Girolando and Mantiqueira cattle, respectively, in Brazil. The few studies on selection differentials focused on mostly milk production traits with little report on reproduction (García-Ruiz et al., 2016; Canaza-Cayo et al., 2016) and health-related (García-Ruiz et al., 2016) traits. Selection differentials for type traits have also been reported in Canadian Holstein cows (Hagan et al., 2020). Average GSDs of 1.15, 0.78, 0.42, and 0.06 for daughter fertility in the SB, DB, SC, and DC paths, respectively, in US Holsten cows born between 2011 and 2015 have been reported (García-Ruiz et al., 2016). However, there are no reports of GSD for ancillary type and functional traits in dairy cattle populations.

National genetic trends computed by most national breeding programs are relevant as they give an overview of the performance of the population for key traits. Although there are genetic evaluations for ancillary traits in Canada, there are no reports of population genetic trends for these traits. It will be interesting to know how important dairy producers consider ancillary type and functional traits in their breeding objectives and whether they are directly or indirectly selecting for ancillary traits.

The objectives of this study were to measure the realized GSD of ancillary type and functional traits of Canadian Holstein, Ayrshire, Jersey, and Brown Swiss dairy cattle breeds and determine the variations in realized GSD in the SC and DC selection paths. We also determined the effects of some environmental factors and their interactions on the realized GSD for ancillary traits.

5.3 MATERIALS AND METHODS

5.3.1 Data and traits

Data for this study were the April 2018 run of genetic evaluations provided by Lactanet (formerly Canadian Dairy Network, **CDN** (responsible for calculations of genetic evaluations of dairy breeds) and Valacta (in charge of herd recordings in Québec and the Atlantic provinces)). The EBV files contained information on animal identification, date of birth, sire and dam identifications, and trait EBV. The ancillary traits studied were angularity **(ANG)**, body condition score **(BCS)**, conformation **(CONF)**, daughter calving ability **(DCA)**, lactation persistency **(LP)**, milking rate **(MR)**, milking speed **(MSP)**, milking temperament **(MT)**, rump **(RUMP)**, stature **(STA)**, udder depth **(UDD)**, udder texture **(UDT)**, and lifetime performance sub-indices for type **(LPI-DUR)** and health and fertility **(LPI-HF)**. The composition and weights of the traits in the LPI-DUR and LPI-HF indices for Canadian Holstein, Ayrshire, Jersey, and Brown Swiss breeds are described by Canadian Dairy Network (2019). The LPI-DUR index consists of type traits which include herd life, mammary system, feet and legs, hoof health, dairy strength, and rump. The LPI-HF index generally comprise health and fertility related traits and these include daughter fertility, mastitis resistance, somatic cell score, udder depth, milking speed, and lactation persistency. Van Doormaal (2007) has given comprehensive definitions of traits and the scales of measurement for these traits in Canada. For instance, MSP is measured on a scale of 70% to 95% with the breed average being 85% (Van Doormaal et al., 2009). The information in the herd recording file are presented in Table 5.1.

The original EBV files contained records of up to 203,696, 10,187, 20,478, and 6,292 bulls and 6,204,898, 251,793, 210,941, and 44,135 cows of the Holstein, Ayrshire, Jersey, and Brown Swiss breeds, respectively. These animals were born between 1883 and 2017. We carried out series

Table 5.1 Groups of agricultural regions, milking systems, and housing systems in Québec, Canada

Factor	Classes
Agricultural region	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	Tie-stall, free stall

of editing on the data after which we analyzed the data of cows born from 1980. These cows should be progeny of sires and dams born from 1950 and 1960 onwards, respectively. Any bull and cow born from 1980 with parents born before 1950 (sires) and 1960 (dams) were removed. The number of records vary from trait to trait as some traits were more recently evaluated. The maximum number of trait records for each path of selection for all the dairy cattle breeds studied after editing are presented in Table 5.2.

Table 5.2 Maximum number of records for each path[1] of selection (SB, SC, DB, and DC) for the Holstein, Ayrshire, Jersey, and Brown Swiss breeds

Breed	**SB**	**SC**	**DB**	**DC**
Holstein	73,864	5,546,227	42,924	5,185,123
Ayrshire	1,334	193,083	1,248	181,218
Jersey	6,434	149,439	3,525	149,143
Brown Swiss	1,563	29,723	1,129	25,970

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

The maximum number of records of 1,563 in the SB path of the Brown Swiss breed mean that 1,563 bulls were sired by 259 uniquely identifiable sires (Table S5.11), that these sires had EBV for the traits studied. Also, the 29,723 SC records for the Brown Swiss mean that 29,723 cows were sired by 1,785 uniquely identifiable sires (Table S5.11), and that these sires had complete information on trait EBV.

5.3.2 Realized Genetic Selection Differentials

Realized GSD was calculated as the EBV of a sire or dam minus the mean EBV of all available bulls or cows at the time of conception of a progeny of this sire or dam (Hagan et al., 2020). A bull or cow's availability period was determined from the dates of conception of the first and last progeny of this bull or cow. Detailed description of computation of a bull or cow's availability period is given in Hagan et al. (2020). The conception date of a progeny was computed as the date of birth of the progeny minus 280 days, which is the mean gestation period of cows.

The mean realized GSD for LPI-DUR and LPI-HF indices for each dairy cattle population were computed for each year of conception (YOC) in each of the selection pathways: SB, DB, SC, and DC. This was to give an overview of the overall selection emphasis both artificial insemination (AI) centers and dairy producers put on ancillary type, health, and fertility traits. The mean GSD of AI sires (sires of cows), top and bottom 10% sires of cows that were used for breeding, and the top 10% bulls available for use in terms of LPI-DUR and LPI-HF were computed for each year of conception and for each breed.

5.3.3 Statistical analyses

Statistical analyses were undertaken on the realized GSD of individual traits in only herds in the province of Québec. We used herds in Québec because we had access to information on Québec herds which was provided by Lactanet. There were 1,911,679 SC and 1,826,054 DC records for the Holstein breed; 82,333 SC and 81,544 DC records for the Ayrshire breed; 29,674 SC and 29,093 DC records for the Jersey breed; and 8,516 SC and 7,960 DC records for the Brown Swiss breed.

Realized GSD of the SC and DC were analyzed using the high-performance mixed **(HPMIXED)** procedure of SAS 9.4 (SAS Institute Inc., Cary, NC). The model used for the analyses is presented below in model 5.1:

$$GSD_{ijkmn} = \mu + YOC_i + HS_j + region_k + Herd_{jkm} + Herd*YOC_{ijkm} + HS*YOC_{ij} + region*YOC_{ik} + HS*region_{jk} + e_{ijkmn} \qquad \textbf{[Model 5.1]}$$

where GSD_{ijkmn} is the realized genetic selection differential of a sire of cow or dam of cow for a trait (ANG, BCS, CONF, DCA, LP, MR, MSP, MT, RUMP, STA, UDD, or UDT);

μ is the overall mean;

YOC_i is the fixed effect of the ith year of conception (i = 1980, …, 2016);

HS_j is the fixed effect of the jth housing system (j = Tie stall or Free stall);

$Region_k$ is the fixed effect of the kth agricultural region (Table 5.1);

$Herd_{jkm}$ is the random effect of the mth herd nested within the jth HS and the kth agricultural region $\sim N(0, \sigma^2_{herd})$ where σ^2_{herd} is variance of herd;

$Herd*YOC_{ijkm}$ is the random interaction of the mth herd nested within the jth HS and kth region by the ith YOC $\sim N(0, \sigma^2_{herd*YOC})$ where $\sigma^2_{herd*YOC}$ is variance of herd by YOC;

$HS*YOC_{ij}$ is the fixed effect of the interaction between the jth HS and the ith YOC;

$Region* YOC_{ik}$ is the fixed effect of the interaction between the kth agricultural region and the ith YOC;

$HS*region_{jk}$ is the fixed effect of the interaction between the jth HS and the kth agricultural region; and e_{ijkmn} is the random residual $\sim N(0, \sigma^2_e)$ where σ^2_e is the residual variance.

Subsequent models with either the herd or herd*YOC dropped were used in analyzing the data of both the SC and DC. The difference in Bayesian Information Criteria **(BIC)** between models with all random factors present and one random factor dropped was used to determine whether the variation in a random factor was significant or not. When the difference in BIC value was greater than 8, the random factor was considered to be significant.

5.4 RESULTS AND DISCUSSION

5.4.1 Population Realized Genetic Selection Differentials

5.4.1.1 Selection indices

Mean realized GSDs per YOC for the two selection indices, LPI-DUR and LPI-HF, of the Holstein, Ayrshire, Jersey, and Brown Swiss breeds in standard deviation units **(sd unit)** are presented in Figure 5.1, 5.2, 5.3, and 5.4, respectively. Generally, some selection for the type index were realized in Holstein, Ayrshire, and Brown Swiss populations but not the Jersey (Figures 5.1a, 5.2a, 5.3a, and 5.4a). The total of the mean realized GSDs of all four pathways of selection for LPI-DUR in the Holstein, Ayrshire, Jersey, and Brown Swiss populations between 1980 and 2016 were 0.30, 0.22, -0.08, and 0.06 sd units, respectively. In both Holstein and Ayrshire populations, the DB and SC paths have been the main drivers of total realized GSD for the type index (LPI-DUR), especially after the year 2000. However, in the Jersey population, producers improved type traits through the SC as there were mostly negative realized GSD for LPI-DUR in the AI centers controlled pathways (SB and DB) and the DC path. There were irregular patterns of realized GSD for the type index in the Brown Swiss population. In all four dairy cattle populations, the realized GSD in the DC path were negative and not significantly different from zero. The mean realized GSD for the type index (LPI-DUR) in the DC path were -0.061, -0.004, -0.052, and -0.020 sd units for Holstein, Ayrshire, Jersey, and Brown Swiss breeds, respectively. However, the mean realized GSD for the type index in the SC were 0.51, 0.14, 0.32, and 0.32 sd units for the Holstein, Ayrshire, Jersey, and Brown Swiss breeds, respectively. This indicates that dairy producers directly improve their herds for the type index mainly through selection of AI bulls and not replacement cows. This could probably be due to the little opportunity for selection in the DC path because of the relatively small number of offspring produced by cows during their lifetime. Apart from the small number of offspring per cow, the high rate of involuntary culling among replacement cows due to health-related issues and reproductive failures leave a further reduced number of female offspring for producers to select from to replace their milking cows.

The realized GSDs for LPI-DUR before the year 2000 were generally lower than those from 2000 onwards. Many of the ancillary type traits were not available to the industry as EBVs or selection indices before the mid-1990s, therefore the lower realized GSDs for the type index prior to the year 2000 would be at best measuring selection differentials based on genetic correlations to production and conformation traits that were available for selection at the period or at worst due to random mating. In addition, the lower realized GSD for LPI-DUR was partly due to the greater focus on selection for production traits before the end of the last century (Miglior et al., 2017) which production traits have unfavorable genetic correlations with some type traits (e.g. BCS, muscularity, and rump width) in Holstein, Brown Swiss, and Red and White breeds (De Haas et al., 2007). The increasing trends in LPI-DUR in recent times in the Holstein and Ayrshire populations are partly due to the changes in selection focus from mostly yield traits to a more balanced breeding goal (Miglior et al., 2005; Miglior et al., 2017) which put considerable emphasis on type traits.

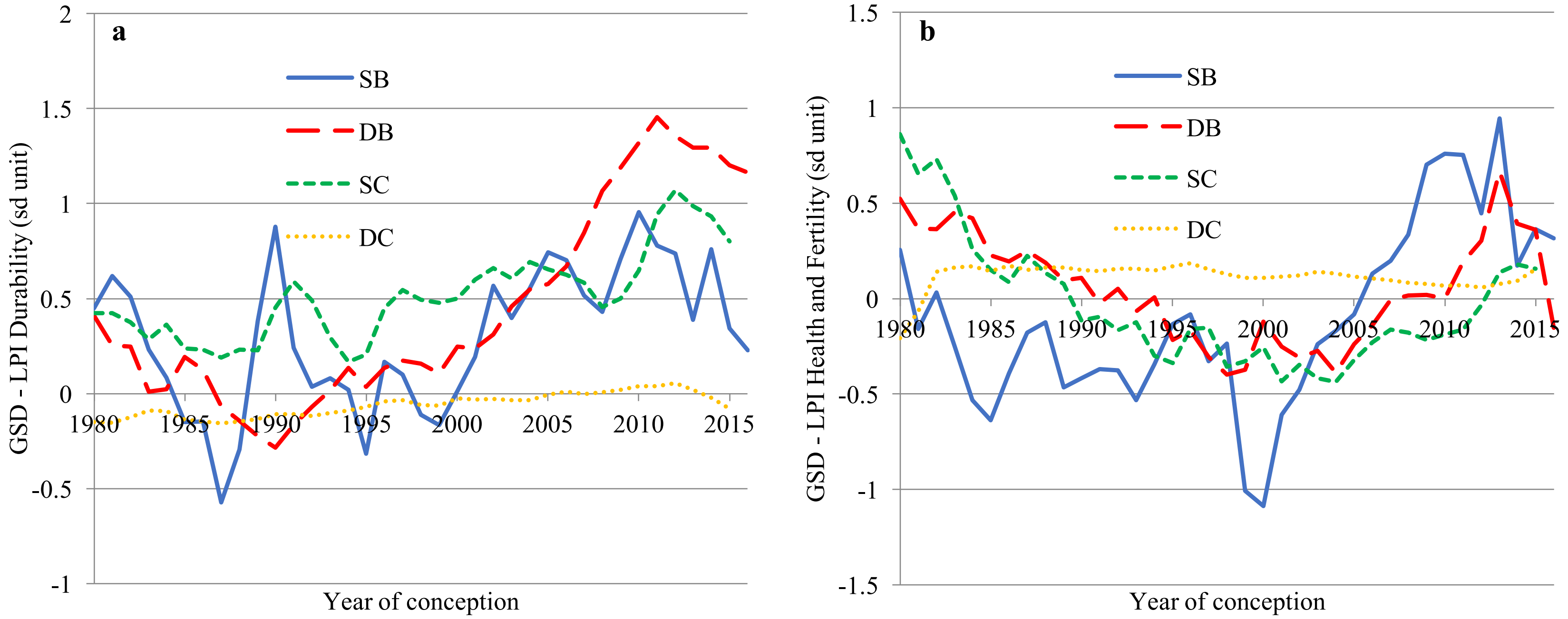

Figure 5.1a-b Mean realized genetic selection differential (GSD) in standard deviation units (sd units) per year of conception for a) LPI-durability and b) LPI-health and fertility for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) for Holstein breed.

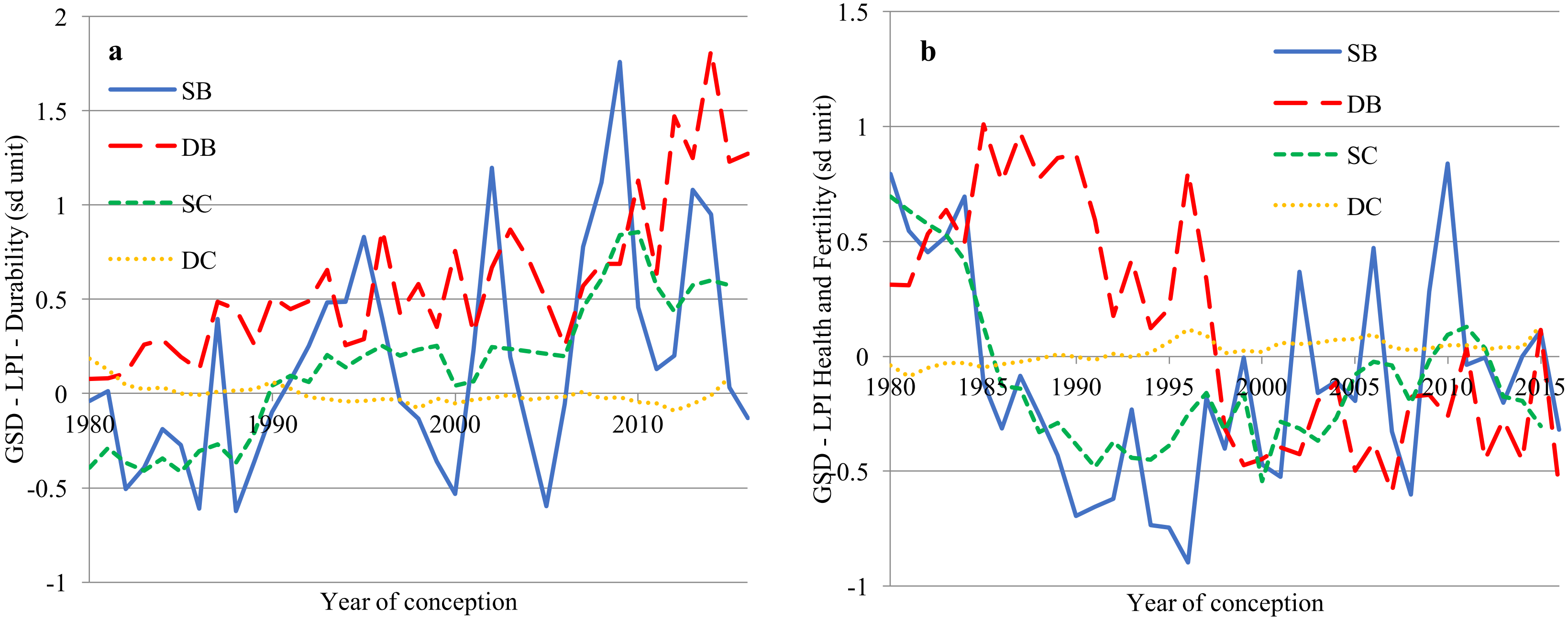

Figure 5.2a-b Mean realized genetic selection differential (GSD) in standard deviation units (sd units) per year of conception for a) LPI-durability and b) LPI-health and fertility for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) for Ayrshire breed.

The mean GSD of LPI-DUR by YOC for the top 10% and bottom 10% sires used in each population, and the top 10% available bulls in each population have been computed and presented in Figures S5.5a, S5.6a, S5.7a, and S5.8a. In the Holstein, Ayrshire, and Jersey populations, the mean GSD of LPI-DUR by YOC for the top 10% available bulls were below the mean GSD of the top 10% sires that were actually used. This is an indication that a considerable number of producers of Holstein, Ayrshire, and Jersey breeds were using the top 10% or even higher available bulls for LPI-DUR for breeding yearly. However, for the Brown Swiss population, the mean GSD per YOC for the top 10% available bulls were similar to the top 10% sires that were used for breeding. This suggests that a considerable number of herds of the Brown Swiss population were indeed using the top 10% available bulls for breeding. The mean GSD of LPI-DUR by YOC for the bottom 10% sires used for breeding in all the 4 dairy cattle populations were below zero. This is interesting as we would have expected the mean GSD of the bottom 10% sires used for breeding to be around zero. The negative mean GSD for the bottom 10% sires used for breeding is an indication that a considerable number of producers were not directly selecting for type traits through the type index. This does not give an indication that such producers were not improving their herds for type traits, but rather they were not directly improving their herds for type through the LPI-DUR. Such producers could indirectly be improving their herds for type traits through the selection realized by AI centers. There will, thus, be a genetic lag between the performance of the population or AI centers and that of herds that were not directly selecting for the type index.

Realized GSD for LPI-HF has been mostly negative in the SB, DB, and SC paths (Figures 5.1b, 5.2b, 5.3b, and 5.4b). The mean total realized GSD for Holstein, Ayrshire, Jersey, and Brown Swiss populations between 1980 and 2016 were 0.01, -0.02, -0.04, and -0.004 sd units, respectively. There were, however, marginal selections realized for LPI-HF in the DC path of the

Holstein (0.11) and Brown Swiss (0.03), but not the Ayrshire (0.02) and Jersey (0.01) breeds. The marginal selections realized in the DC path could be due mainly to active culling of unproductive replacement cows in producers' herds. However, the zero to negative total selection realized for the health and fertility index could partly be due to the negative genetic correlations between production and fertility traits (Berry et al., 2003; Kadarmideen, 2004).

The mean GSDs of LPI-HF by YOC for the top 10% and bottom 10% sires used for breeding and the top 10% available bulls in each population have been computed and presented in Figures S5.5b, S5.6b, S5.7b, and S5.8b. In all dairy populations studied, the mean GSDs of LPI-HF by YOC for top 10% available bulls were similar to the mean GSDs of the top 10% sires used for breeding. The similarity in the means suggests that a considerable proportion of producers were using the top 10% available bulls for LPI-HF traits for breeding. The mean GSDs of LPI-HF per YOC for the bottom 10% sires used for breeding in each of the dairy populations were negative, an indication that a proportion of dairy producers of the four dairy breeds were not directly selecting for the health and fertility index. The appreciable gap between the GSDs of the top 10% and bottom 10% sires used for breeding in the Holstein, Ayrshire, Jersey, and Brown Swiss populations suggests that there are considerable variations in the selection realized for LPI-HF index among producers. The overall average GSDs of the sires used for breeding in each of the 4 dairy populations were stable and close to zero.

The mean realized GSD for the ancillary type and functional traits for the entire study period (1980 to 2015) and the last 10 years of the study period (2006 to 2015) in the Holstein, Ayrshire, Jersey, and Brown Swiss populations are presented in supplemental Tables S5.12, S5.13, S5.14, and S5.15, respectively. The mean realized GSD for the last 10 years were generally higher than the overall mean realized GSD. This observation is partly due to intensification of selection

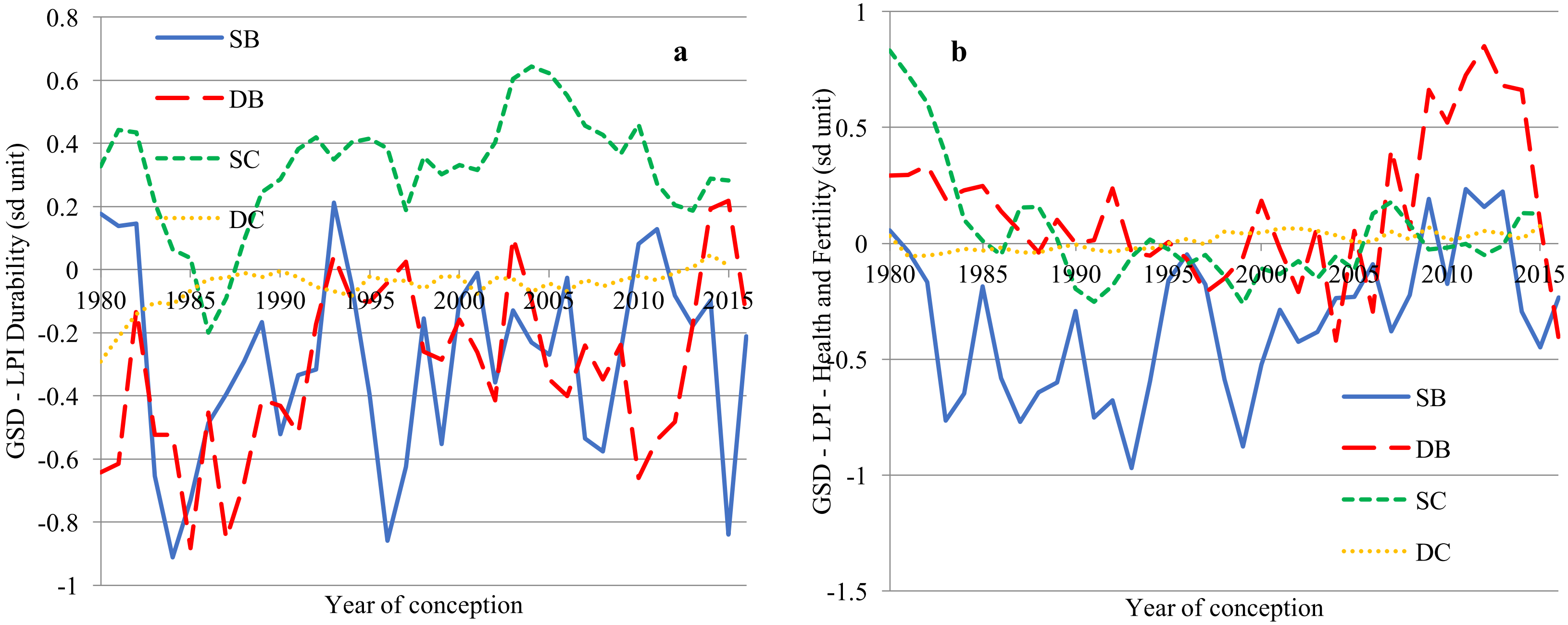

Figure 5.3a-b Mean realized genetic selection differential (GSD) in standard deviation units (sd units) per year of conception for a) LPI-durability and b) LPI-health and fertility for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) for Jersey breed.

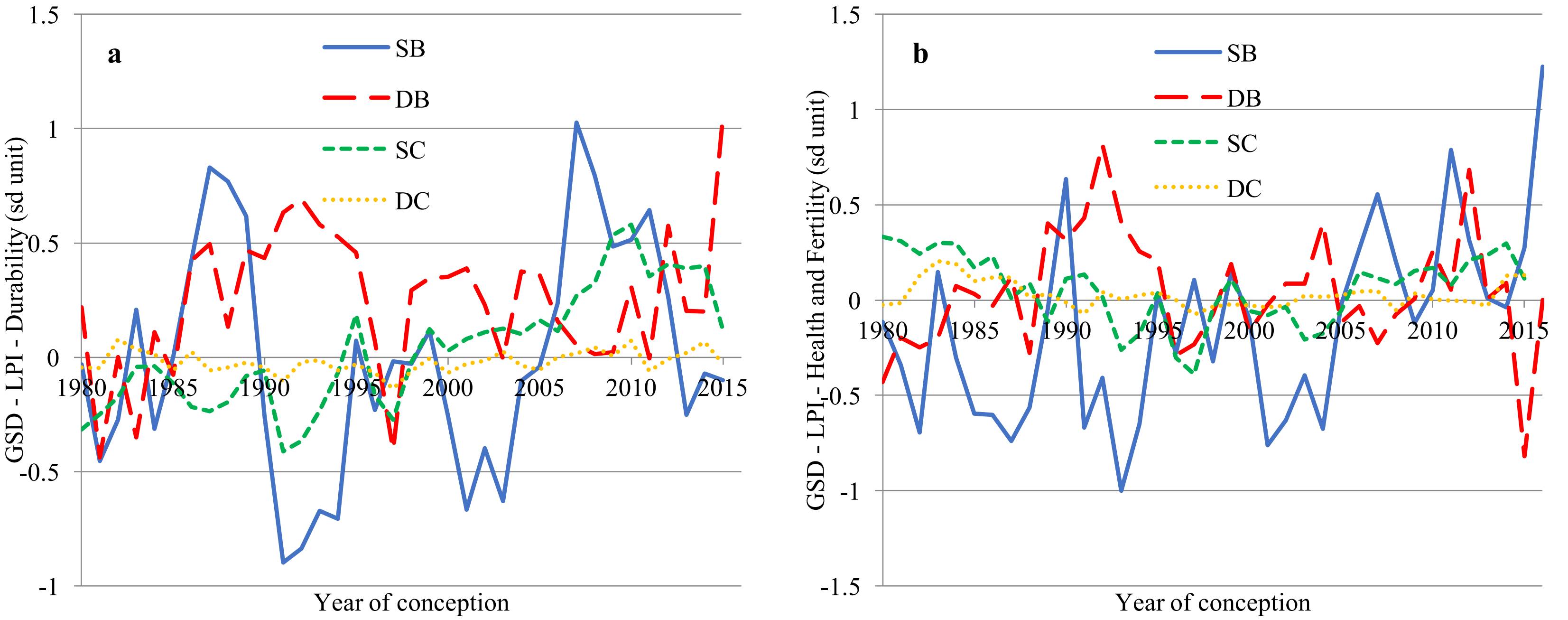

Figure 5.4a-b Mean realized genetic selection differential (GSD) in standard deviation units (sd units) per year of conception for a) LPI-durability and b) LPI-health and fertility for sire-to-bull (SB), dam-to-bull (DB), sire-to-cow (SC), and dam-to-cow (DC) for Brown Swiss breed.

for ancillary type, health, and fertility traits in recent times due to the inclusion of these traits in the Canadian national breeding objectives. The introduction of genomic evaluations has also made it possible to realize more intense selection for lowly heritable traits (García-Ruiz et al., 2016) such as some ancillary type, health and fertility traits.

5.4.2 Environmental influence on realized GSD of ancillary type and functional traits in the SC and DC paths and variations in realized GSD

5.4.2.1 Holstein breed

The effects of YOC, HS, agricultural region, and the interactions among these factors on realized GSD of ancillary traits in the SC and DC paths of the Holstein population are presented in Tables 5.3 and 5.4, respectively. The *P*-values from the statistical tests for each trait analyzed are presented in the tables. Year of conception (not shown in table) had significant effect ($P<0.05$) on the realized GSD of all ancillary type and functional traits in the SC and DC paths except MR (0.7539) and MSP (0.0672) in the DC path. This suggests that the selection emphases that Holstein producers put on ancillary type and functional traits change over time possibly to correct for time bound functional defects among producers' herds. In addition, the significant effect ($P<0.05$) of YOC on realized GSD could be attributed to changes in breeding objectives of the industry, due possibly to changes in market demands (Miglior et al., 2005) over time.

Housing system did not have a significant effect ($P>0.05$) on realized GSD of most of the traits studied except ANG and STA in the SC (Table 5.3), and ANG and CONF in the DC path (Table 5.4). This observation agrees favorably with Paakala et al. (2018) who reported a significant effect of HS on selection preference for conformation traits in Finnish Holstein and Ayrshire breeds. They observed that conformation traits were valued higher in free stall housing systems than traditional tie-stall barns. The fixed and limited sizes of tie-stalls may have influenced

Table 5.3 Effects of Year of conception (YOC[3]), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the sire-to-cow selection path (P-values for fixed effects) and the variance components of Herd(HS*Region), Herd*YOC, and residuals for the Holstein breed

	Fixed effect[2]					Variance components		
Trait[1]	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
ANG	0.0093	0.3927	<0.0001	<0.0001	0.0131	1.2006	0.8194	21.2662
BCS	0.1664	0.8121	<0.0001	<0.0001	0.0825	0.6888	0.1521	17.2403
CONF	0.1223	0.1607	<0.0001	<0.0001	0.0235	0.8612	1.2469	14.4351
RUMP	0.0677	0.3002	<0.0001	<0.0001	0.0080	0.9038	0.4315	21.4754
STA	0.0067	0.5437	<0.0001	<0.0001	0.0081	0.9736	0.4781	19.7679
DCA	0.6728	0.6833	<0.0001	<0.0001	0.0158	0.8464	0.09795	20.1040
LP	0.0773	0.0957	<0.0001	<0.0001	0.1715	0.9495	0.1842	23.6369
MR	0.4038	0.8746	<0.0001	<0.0001	0.7975	0.6802	0.06493	18.61
MSP	0.3372	0.3508	<0.0001	<0.0001	0.0626	0.6148	0.6467	13.6103
MT	0.9342	0.2261	0.0001	<0.0001	0.2831	0.9500	0.07288	24.1991
UDD	0.1825	0.0477	<0.0001	<0.0001	0.3681	0.4353	0.04373	8.8791
UDT	0.2047	0.3738	<0.0001	<0.0001	0.2061	1.0874	0.7734	21.3002

[1] ANG – angularity; BCS – body condition score; CONF – conformation; RUMP – rump; STA – stature; DCA – daughter calving ability; LP – lactation persistency; MR – milking rate; MSP – milking speed; MT – milking temperament; UDD – udder depth; UDT – udder temperament.

[2] Fixed effects are statistically significant if $P<0.05$.

[3] YOC - Year of conception ($P<0.0001$ for all traits in the table).

producers from putting greater emphasis on selection for size to perhaps prevent cows from being uncomfortable in their stalls. Agricultural region did not have significant effect ($P>0.05$) on realized GSD of all traits in the SC and DC paths except UDD (0.0477) in the SC and LP (0.0001) in the DC. The largely non-significant effects ($P>0.05$) of HS and region on realized GSD suggest that apart from YOC, other environmental factors did not greatly influence the amount of selection pressures Holstein producers put on ancillary type and functional traits in their herds.

Table 5.4 Effects of Year of conception (YOC[3]), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the dam-to-cow selection path (P-values for fixed effects) and the variance components of Herd(HS*Region), Herd*YOC, and residuals for the Holstein breed

Trait[1]	Fixed effect[2]					Variance components		
	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
ANG	0.0269	0.0653	<0.0001	<0.0001	0.0039	1.4878	0.4034	15.0324
BCS	0.1859	0.1596	<0.0001	<0.0001	0.2203	0.4038	0.1528	9.7047
CONF	0.0460	0.2095	<0.0001	<0.0001	0.0067	1.9804	0.0500	11.0441
RUMP	0.5809	0.9256	<0.0001	<0.0001	0.0104	0.6488	0.1815	12.7292
STA	0.0183	0.0096	0.0090	0.3263	0.3393	2.7184	0.02903	17.0440
DCA	0.7309	0.8390	0.0003	<0.0001	0.1096	0.6177	0.1944	10.9061
LP	0.8583	0.0001	0.2482	<0.0001	0.2044	1.6438	0.2974	21.3622
MR	0.6762	0.7064	0.9956	0.9845	0.9168	0.2847	0.1211	10.3971
MSP	0.9510	0.2316	<0.0001	<0.0001	<0.0001	0.01264	0.007416	15.6472
MT	0.5876	0.9729	0.0013	0.7104	0.2439	0.2652	0.1190	14.4871
UDD	0.6099	0.4192	0.4655	0.3318	0.2737	0.1696	0.00922	5.9450
UDT	0.3210	0.0017	0.4448	0.1772	0.1175	2.3456	0.08428	13.6416

[1] ANG – angularity; BCS – body condition score; CONF – conformation; RUMP – rump; STA – stature; DCA – daughter calving ability; LP – lactation persistency; MR – milking rate; MSP – milking speed; MT – milking temperament; UDD – udder depth; UDT – udder temperament.

[2] Fixed effects are statistically significant if $P<0.05$.

[3] YOC - Year of conception ($P<0.0001$ for all traits in the table).

The effects of interactions between HS and YOC, and region by YOC were significant ($P<0.05$) on the realized GSD of all traits in the SC path and many traits in the DC path (Tables 5.3 and 5.4). This indicates that there were differences in realized GSD within housing systems and agricultural regions from year to year. This could be attributed to changes in selection pressures applied by producers within a given HS or region over time. The interaction between HS and region were significant (*P*<0.05) for realized GSD of mostly ancillary type traits in the SC (ANG, CONF, RUMP, STA) and DC paths (ANG, CONF, RUMP), but not the ancillary functional traits with the exception of DCA in the SC path.

There were significant variations in realized GSD due to herds for ancillary type and functional traits of both the SC and DC paths as presented in Tables 5.3 and 5.4, respectively. The variations in total realized GSD due to herd constituted between 3.5 and 5.2% of the total variations realized in the SC path and between 3.9 and 15.1% of the total variations in the DC path. The variations in realized GSD due to herd were slightly higher for ancillary type traits than for functional traits. All the variations due to herd in both the SC and DC paths were significant (differences in BIC values were greater than 8) suggesting that whilst some dairy producers of the Holstein breed were intensively selecting for ancillary type and functional traits, other producers were selecting less or not directly selecting for these traits. The variations in realized GSD due to herd*YOC ranged from 0.3 to 7.5% for the SC and between 0.4 and 2.4% for the DC path.

5.4.2.2 Ayrshire breed

The effects of YOC, HS, region, HS*YOC, region*YOC, and HS*region on realized GSD of ancillary type and functional traits in the SC and DC paths are presented in Tables 5.5 and 5.6, respectively. Year of conception had significant effect (*P*<0.05) on realized GSD for all traits in the SC (not shown in table) but not the DC path. This suggests that whilst selection emphasis for ancillary type and functional traits changes from year to year in the selection of AI bulls, it remains generally the same in the selection of replacement cows in the Ayrshire population. The non-significant effect of YOC on realized GSD in the DC path could be due partly to the little to no selection realized in the DC path.

Table 5.5 Effects of Year of conception (YOC[3]), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the sire-to-cow selection path (*P*-values for fixed effects) and the variance components of Herd(HS*Region), Herd*YOC, and residuals for the Ayrshire breed

	[2]Fixed effects					Variance components		
Trait[1]	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
ANG	0.4055	0.5958	0.6449	0.0307	0.6673	0.3695	0.8600	19.6177
BCS	0.3390	0.0155	0.8875	0.0586	0.0218	0.1152	0.9224	23.7919
CONF	0.7738	0.8546	0.7919	0.0278	0.7227	0.7606	0.8734	15.6751
RUMP	0.9280	0.9962	0.9222	0.5915	0.4827	0.9722	1.2811	25.4124
STA	0.3944	0.9051	0.5049	0.1137	0.1919	0.6229	0.6770	17.3746
DCA	0.1363	0.4188	0.2542	0.3786	0.7193	0.2083	1.0196	23.8806
LP	0.7354	0.9434	0.1943	0.0242	0.0960	0.3185	0.8502	21.6272
MR	0.0801	0.0698	0.9345	0.0067	0.1200	0.08551	0.8743	20.8951
MSP	0.2731	0.4410	0.0099	0.0082	0.4157	0.1530	1.5105	20.8951
MT	0.3011	0.8229	0.1685	0.4835	0.3328	0.05501	0.7823	21.0410
UDD	0.7039	0.8747	0.3261	0.2349	0.8143	0.03187	0.3534	9.3397
UDT	0.9572	0.6194	0.6849	0.1765	0.8696	0.4025	0.8739	18.5363

[1]ANG – angularity; BCS – body condition score; CONF – conformation; RUMP – rump; STA – stature; DCA – daughter calving ability; LP – lactation persistency; MR – milking rate; MSP – ilking speed; MT – milking temperament; UDD – udder depth; UDT – udder temperament.

[2]Fixed effects are statistically significant if $P<0.05$.

[3]YOC - Year of conception ($P<0.0001$ for all traits in the table).

The effects of HS and region were mostly not important to the realized GSD of AI bulls and replacement cows in the Ayrshire population. The non-significant effect ($P>0.05$) of HS on selection realized for ancillary type traits is contrary to the findings of Paakala et al. (2018) in Finnish Ayrshire population. The interactions between HS and YOC, region and YOC, and HS and region were mostly not significant (*P*>0.05) and unimportant on realized GSD of SC and DC paths.

Table 5.6 Effects of Year of conception (YOC), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the dam-to-cow selection path (*P*-values for fixed effects) and the variance components of Herd(HS*Region), Herd*YOC, and residuals for the Ayrshire breed

	Fixed effect[2]						Variance components		
Trait[1]	YOC	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
ANG	0.3284	0.4508	0.8461	0.7967	0.2488	0.8335	1.1119	0.1976	11.9136
BCS	0.6011	0.2351	0.0739	0.5676	0.0421	0.0234	0.3237	0.07941	10.5353
CONF	0.2010	0.4658	0.8151	0.9840	0.1553	0.9096	1.3850	0.3169	10.0398
RUMP	0.5261	0.1091	0.4562	0.1074	0.5827	0.6466	1.3564	0.2382	12.4530
STA	0.1290	0.4358	0.7987	0.2962	0.2453	0.6327	1.4135	0.1839	13.7070
DCA	0.2616	0.0165	0.6471	0.2747	0.3153	0.2005	1.8351	0.2373	17.6859
LP	0.8130	0.5767	0.9714	0.6499	0.6117	0.8940	3.0216	0.3431	19.8101
MR	0.9454	0.9400	0.2504	0.9087	0.7639	0.2094	0.4930	0.1120	11.3829
MSP	0.9327	0.6075	0.8993	0.1260	0.8867	0.7846	0.3080	0.1413	15.5462
MT	0.6362	0.7150	0.4414	0.9997	0.9883	0.6195	0.1714	0.06307	10.2264
UDD	0.0001	0.0025	0.0195	0.3962	0.0519	0.0002	130.16	17.6624	146.56
UDT	0.0620	0.6516	0.8896	0.8588	0.2262	0.8429	0.8660	0.2048	11.0851

[1] ANG – angularity; BCS – body condition score; CONF – conformation; RUMP – rump; STA – stature; DCA – daughter calving ability; LP – lactation persistency; MR – milking rate; MSP – milking speed; MT – milking temperament; UDD – udder depth; UDT – udder temperament.

[2] Fixed effects are statistically significant if $P<0.05$.

There were considerable variations in realized GSD in the SC and DC paths of the Ayrshire population. The variations due to herd ranged from 0.3 to 4.4% in the SC and 1.6 to 44.2% in the DC path. All the variations due to herd were significant. This suggests that there were considerable variations in the selection emphases Ayrshire producers put on ancillary type and functional traits.

The variations due to herd*YOC ranged between 3.6 and 6.7% in the SC, and between 0.6 and 6.0% in the DC. All the variations due to herd*YOC were significant (differences in BIC values > 8) except for MR in the DC path. The considerable variabilities in realized GSD due to herd suggest that not all Ayrshire producers were intensively selecting for ancillary type and functional traits. This could be attributed to differences in breeding objectives of various Ayrshire producers. In addition, it is possible some producers are not even aware they are falling behind in their selection emphases for ancillary type and fitness traits.

5.4.2.3 Jersey breed

As with the Holstein and Ayrshire breeds, YOC had significant effect ($P<0.05$) on realized GSD of all traits in the SC path of the Jersey population (not shown in table). However, in the DC, the effect of YOC was only significant ($P<0.05$) for mostly realized GSD of ancillary type traits (BCS, CONF, RUMP, STA), but not functional traits (Table 5.8). This is an indication that selection emphases for ancillary type traits change over time whereas selection emphases for ancillary functional traits remain largely the same in the selection of replacement cows.

Other environmental factors studied were mostly not important in the realized GSD for ancillary type and functional traits of both the SC and DC paths (Tables 5.7 and 5.8). However, the effect of HS on realized GSD of two type traits, ANG and RUMP, were significant ($P<0.05$) in the SC path, corroborating the findings of Paakala et al. (2018). Our findings suggest that HS and regions are not major considerations in the amount of selection pressure applied on functional traits by Jersey producers. The interactions between HS and YOC, region and YOC, and HS and region were mostly not important in the selection emphases for ancillary type and functional traits in the SC. However, the effects of HS*YOC and region*YOC were significant ($P<0.05$) on the realized selection for RUMP and MSP of the SC path. In the DC path, the effects of HS*YOC, region*YOC, and HS*region were also largely unimportant in the selection achieved for ancillary type and functional traits in the Jersey breed. There were, however, significant effect ($P<0.05$) of region*YOC on realized GSD for ANG, STA, and UDD, and significant effect ($P<0.05$) of HS*region on realized GSD for ANG in the DC.

Table 5.7 Effects of Year of conception (YOC[3]), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the sire-to-cow selection path (*P*-values for fixed effects) and the variance components of Herd(HS*Region), Herd*YOC, and residuals for the Jersey breed

	Fixed effect[2]					Variance components		
Trait[1]	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
ANG	0.0489	0.6837	0.2826	0.1255	0.2319	0.3440	2.0034	23.7807
BCS	0.9828	0.9856	0.7227	0.1048	0.0800	1.0548	1.4871	18.8035
CONF	0.4144	0.6276	0.5602	0.1397	0.5868	2.2804	1.8870	18.9573
RUMP	0.0234	0.8498	0.0320	0.0002	0.4968	1.4473	1.6709	24.1110
STA	0.2017	0.8556	0.4866	0.6148	0.4310	0.8101	1.5909	21.0173
DCA	0.4143	0.3665	0.9678	0.9456	0.3247	0.3859	1.2211	19.5110
LP	0.8004	0.7566	0.5747	0.0020	0.9566	0.7686	1.3828	18.6148
MR	0.5166	0.8982	0.9932	0.9157	0.6816	0.2591	1.0805	17.7304
MSP	0.5443	0.2731	0.0406	0.0003	0.1131	0.2941	1.4037	22.4654
MT	0.1538	0.0026	0.1124	0.1539	0.2411	0.2045	1.2210	19.2324
UDD	0.9510	0.1133	0.6629	0.5480	0.9529	0.06856	0.4301	6.7153
UDT	0.4144	0.7868	0.9912	0.2605	0.7380	1.0404	1.6488	20.8451

[1] ANG – angularity; BCS – body condition score; CONF – conformation; RUMP – rump; STA – stature; DCA – daughter calving ability; LP – lactation persistency; MR – milking rate; MSP – milking speed; MT – milking temperament; UDD – udder depth; UDT – udder temperament.

[2] Fixed effects are statistically significant if $P<0.05$.

[3] YOC - Year of conception ($P<0.0001$ for all traits in the table).

In the SC path, herd explained between 1.0% and 9.9% of the total variation in realized GSD whereas herd explained between 2.1 and 22.3% of the total variation in realized GSD in the DC path (Tables 5.7 and 5.8). The amount of variations in realized GSD explained by herd were all significant. Generally, herd explained larger amount of the variations in realized GSD for the ancillary type traits compared with ancillary functional traits in both the SC and DC paths. The mean variation in GSD due to herd was 5% for type traits as against 2.1% for functional traits. This suggests that Canadian Jersey producers put relatively similar selection emphasis on ancillary functional traits in their herds compared with type traits. The significant variations in realized GSD due to herd for both ancillary type and functional traits also suggest that not all producers were selecting intensively for ancillary type and functional traits. Ancillary type and functional traits are economically important traits in dairy production in that they contribute to increase profit and reduction in cost of production (Miglior et al., 2005); hence, it is expected that some producers will include such traits in their breeding objectives thereby increasing selection emphasis for such traits. The unfavorable relationship between type and production traits calls for the inclusion of ancillary type traits in the breeding objectives of producers as a way of perhaps maintaining cow appearance (Grantham et al., 1974) and also enable high producing cows to maintain or sustain their high production. Also, the moderate heritability of type traits (Rupp and Boichard, 1999) means intensifying selection for ancillary type traits is expected to yield considerable genetic response. In recent times, the use of more balanced selection indices to address health and fertility challenges in dairy herds (Miglior et al., 2017) has enabled both producers and breeders to achieve sizeable genetic improvement in most economically important traits. The variations in realized GSD of ancillary functional traits explained by herd also suggest differences in selection emphasis for these traits among producers. The moderate heritabilities for MR, MSP, and MT (Miller et al., 1976; Sewalem et al., 2011) offer opportunity for decent genetic responses to be obtained in these traits if producers intensify selection for ancillary functional traits or include them in their breeding objectives.

Table 5.8 Effects of Year of conception (YOC), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the dam-to-cow selection path (*P*-values for fixed effects) and the variance components of Herd(HS*Region), Herd*YOC, and residuals for the Jersey breed

	Fixed effect[2]						Variance components		
Trait[1]	YOC	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
ANG	0.4970	0.5233	0.0029	0.8755	0.0233	<0.0001	1.2662	0.1273	15.2051
BCS	0.0021	0.4746	0.4465	0.6655	0.8585	0.0667	1.1855	0.3404	10.4864
CONF	0.0081	0.8122	0.4426	0.3217	0.2503	0.5998	2.8450	0.3863	11.6982
RUMP	0.0028	0.2808	0.5111	0.4443	0.8726	0.4646	1.5645	0.2968	13.2533
STA	0.0301	0.7984	0.3465	0.5832	0.0132	0.7312	1.8168	0.1830	17.9373
DCA	0.6071	0.3192	0.0124	0.8759	0.8792	0.9397	3.9643	0.4209	13.5371
LP	0.8940	0.4794	0.8091	0.9837	0.1340	0.6333	1.8221	0.2024	14.8224
MR	0.8951	0.4365	0.9858	0.4193	0.9995	0.9355	0.5051	0.1397	9.8216
MSP	0.7334	0.2377	0.4030	0.7494	0.1094	0.0822	0.3546	0.004109	16.4683
MT	0.9499	0.5355	0.8311	0.8052	0.9984	0.6759	0.6109	0	15.3481
UDD	0.0003	0.7669	0.4462	0.5192	0.0131	0.3172	66.1979	23.7633	207.38
UDT	0.8295	0.7374	0.1458	0.8754	0.0519	0.3571	1.3381	0.2205	11.2741

[1] ANG – angularity; BCS – body condition score; CONF – conformation; RUMP – rump; STA – stature; DCA – daughter calving ability; LP – lactation persistency; MR – milking rate; MSP – milking speed; MT – milking temperament; UDD – udder depth; UDT – udder temperament

[2] Fixed effects are statistically significant if $P<0.05$.

The variations in realized GSD due to herd*YOC ranged from 5.7 to 8.2% in the SC and from 0 to 8% in the DC path. These indicate that herd*YOC also explains considerable part of the observed variation in GSD realized by producers. Most of the variations due to herd*YOC were significant except for ANG, MR, MSP, MT, and STA in the DC path.

5.4.2.4 Brown Swiss

In the Brown Swiss population, YOC had significant effect ($P<0.05$) on the realized GSD of all ancillary type and functional traits in the SC (not shown in table), but not the DC path. In the DC, the effects of YOC was only significant on realized GSD of MT (Table 5.10). This is an indication that the selection pressure producers put on the selection of AI bulls changes with time but there is no change in the selection pressure put on the selection of replacement cows over time. The non-significant effect ($P>0.05$) of YOC on realized GSD in the DC path could be partly attributed to the little opportunity for selection in the DC path. The need for producers to maintain herd size in order for producers to meet their milk quota does not allow producers to intensively select for ancillary type and functional traits in the DC path. Selection in the DC path is mainly through involuntary culling due to health-related issues and reproductive failures.

Housing system and region did not have significant effect ($P<0.05$) on realized GSD in both the SC (Table 5.9) and DC (Table 5.10) except for ANG in the SC. Likewise, the effect of HS*YOC was unimportant in the selection realized in the SC and DC paths. However, the effect of region*YOC was significant ($P<0.05$) on the realized GSD for ancillary type traits (CONF, RUMP, STA) in both the SC and DC paths. In addition, the effect of region*YOC was significant ($P<0.05$) on the realized GSD for UDT and MSP in the SC and DC paths, respectively. The effect of the interaction between HS and region was also unimportant in the realized GSD for ancillary type and functional traits in the SC and DC paths except for MR of the DC path. Apart from YOC, other environmental factors studied were mostly unimportant in the realized GSD for ancillary type and functional traits in the Brown Swiss population.

Table 5.9 Effects of Year of conception (YOC[3]), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the sire-to-cow selection path (*P*-values for fixed effects) and the variance components of Herd(HS*Region), Herd*YOC, and residuals for the Brown Swiss breed

	Fixed effect[2]					Variance components		
Trait[1]	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
ANG	0.1128	0.0226	0.9206	0.2754	0.4437	1.3138	3.2473	24.5605
BCS	0.6553	0.6611	0.9082	0.8966	0.6290	0.6492	2.9497	23.5013
CONF	0.2547	0.0654	0.9950	<0.0001	0.5669	1.1330	1.7261	20.0116
RUMP	0.8077	0.0611	0.9029	0.0293	0.2180	0.5475	1.3333	23.5572
STA	0.4177	0.2511	0.5168	0.0458	0.6342	0.5711	1.9121	18.2949
DCA	0.8142	0.5542	0.8372	0.5045	0.6421	0.2812	2.6317	21.5537
LP	0.9579	0.6669	0.8702	0.3175	0.8059	0.4789	0.9180	18.2440
MR	0.8626	0.6580	0.9835	0.9765	0.9458	0.0359	1.5983	12.6895
MSP	0.2542	0.7953	0.5170	0.1704	0.4358	0	2.7465	24.6183
MT	0.9732	0.6879	0.1313	0.5476	0.1237	0.0970	1.8730	19.5831
UDD	0.6312	0.4914	0.2504	0.8684	0.7592	0.0131	0.4255	6.0991
UDT	0.0864	0.0625	0.7923	0.0004	0.3924	0.6760	2.1267	22.0903

[1]ANG – angularity; BCS – body condition score; CONF – conformation; RUMP – rump; STA – stature; DCA – daughter calving ability; LP – lactation persistency; MR – milking rate; MSP – milking speed; MT – milking temperament; UDD – udder depth; UDT – udder temperament

[3]YOC - Year of conception (*P*<0.0001 for all traits in the table).

The variations in realized GSD explained by herd and herd*YOC ranged from 0 to 5% and from 4.7 to 11.2%, respectively in the SC path (Table 5.9). For the DC path, herd and herd*YOC explained between 2.8 and 22%, and between 0 and 11.2%, respectively, of the total variation in realized GSD for ancillary type and functional traits. The variations in realized GSD due to herd were all significant whereas the variations due to herd*YOC were mostly significant. In both the SC and DC paths, the variations in realized GSD explained by herd were generally larger for the ancillary type traits than those of ancillary functional traits. The greater variations in realized GSD due to herds suggest that there were considerable variabilities in the selection emphases Brown Swiss producers were applying on ancillary type and functional traits.

Table 5.10 Effects of Year of conception (YOC), Housing system (HS), Region, HS*YOC, Region*YOC, and HS*Region on realized genetic selection differential in the dam-to-cow selection path (*P*-values for fixed effects) and the variance components of Herd(HS*Region), Herd*YOC, and residuals for the Brown Swiss breed

	Fixed effect[2]						Variance components		
Trait[1]	YOC	HS	Region	HS*YOC	Region*YOC	HS*Region	Herd	Herd*YOC	Residual
ANG	0.8806	0.7617	0.9733	0.4228	<0.0001	0.6880	4.2520	0.0490	16.3935
BCS	0.9928	0.6730	0.9890	0.8068	0.9831	0.6873	1.6354	0.3433	10.6155
CONF	0.5095	0.1563	0.9405	0.2348	<0.0001	0.0978	2.7298	0	15.7979
RUMP	0.9720	0.4677	0.9750	0.9199	<0.0001	0.0889	1.2587	0.3076	14.7306
STA	0.4098	0.7114	0.7406	0.4264	0.0132	0.3701	1.0731	0	16.1248
DCA	0.8052	0.4530	0.7674	0.8998	0.9994	0.2009	3.1011	0.7615	14.8303
LP	0.0590	0.3903	0.5390	0.6304	0.4760	0.2291	1.8112	0.0447	14.7592
MR	0.0917	0.1083	0.2112	0.4611	0.9994	0.0010	0.3737	0.1168	5.8931
MSP	0.3052	0.2896	0.2707	0.8979	0.0089	0.6959	0.2943	0	10.3543
MT	0.0193	0.3577	0.5543	0.5081	0.5024	0.3903	0.4621	0	12.7507
UDD	0.4189	0.5458	0.6415	0.8988	1.0000	0.9631	76.7905	38.9917	232.96
UDT	0.6950	0.2605	0.8684	0.6507	0.0057	0.2074	2.2000	0.2064	14.6808

[1] ANG – angularity; BCS – body condition score; CONF – conformation; RUMP – rump; STA – stature; DCA – daughter calving ability; LP – lactation persistency; MR – milking rate; MSP – milking speed; MT – milking temperament; UDD – udder depth; UDT – udder temperament.

[2] Fixed effects are statistically significant if $P<0.05$.

5.5 CONCLUSIONS

Dairy producers of Holstein, Ayrshire, Jersey, and Brown Swiss breeds in Canada considered ancillary type and functional traits important in their breeding objectives as they put considerable selection emphases on these traits in especially the selection of AI bulls used for breeding. From the durability, and health and fertility sub-indices, LPI-DUR and LPI-HF, genetic improvement of type traits among producers' herds were mainly achieved through selection of AI bulls while genetic improvement for health and fertility traits were mainly achieved through selection of replacement cows. Considerable proportion of dairy producers of Holstein, Ayrshire, Jersey, and Brown Swiss breeds were using the top 10% available bulls for LPI-DUR and LPI-HF index for breeding in their herds while an appreciable number of producers were also not directly selecting for these two indices. Apart from YOC, other environmental factors studied were largely unimportant in the realized GSD in both the SC and DC paths. Herd and herd*YOC explained moderate amounts of the variation in total realized GSD in the SC and DC paths in all 4 dairy cattle breeds. The considerable variations in realized GSD for ancillary type and functional traits suggest that not all producers were directly selecting intensively for these traits, hence, there was opportunity to increase the selection emphases to optimize genetic gains for ancillary traits in Canadian Holstein, Ayrshire, Jersey, and Brown Swiss herds. Appropriate tools could also be developed to enable dairy producers monitor their selection emphasis for economically important traits in their herds and make the necessary changes if they are not moving in intended direction.

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Table S5.11 Maximum number of unique sires and dams of bulls and cows in each selection path for the Holstein, Ayrshire, Jersey, and Brown Swiss breeds

Breed	Sires of Bulls	Sires of Cows	Dams of Bulls	Dams of Cows
Holstein	2,393	64,065	14,200	2,883,078
Ayrshire	271	4,132	809	112,044
Jersey	618	4,623	1,452	87,724
Brown Swiss	259	1,785	545	16,332

Table S5.12 Average realized genetic selection differential for the four paths[1] of selection (SB, DB, SC, and DC) for 12 traits for all the study period (1980 to 2015) and the last 10 years (2006 to 2015) in the Holstein breed

		Year of conception	
Trait	Selection path	1980 – 2015	2006 – 2015
Angularity	SB	2.456	0.064
	DB	2.335	1.455
	SC	3.088	2.897
	DC	-0.273	0.067
Body Condition Score	SB	-2.056	0.590
	DB	-2.240	0.483
	SC	-1.296	-1.467
	DC	0.292	0.088
Conformation	SB	1.022	1.724
	DB	1.557	3.927
	SC	2.456	3.120
	DC	-0.234	0.046
Daughter Calving Ability	SB	0.550	2.262
	DB	-0.036	1.833
	SC	-0.016	0.462
	DC	0.197	0.116
Lactation Persistency	SB	0.237	0.546
	DB	0.659	2.005

	SC	0.006	0.384
	DC	-0.247	-0.151
Milking Rate	SB	-0.773	1.018
	DB	-0.446	0.886
	SC	-0.045	0.684
	DC	0.043	-0.009
Milking Speed	SB	0.477	1.108
	DB	2.391	4.555
	SC	-0.367	-0.296
	DC	-0.016	0.002
Milking Temperament	SB	0.399	1.892
	DB	0.083	0.941
	SC	0.322	-0.189
	DC	0.041	0.071
Rump	SB	-0.675	-1.248
	DB	18.930	7.845
	SC	1.294	1.321
	DC	0.192	0.171
Stature	SB	0.263	-0.177
	DB	1.125	1.782
	SC	1.884	2.377
	DC	-0.145	-0.102
Udder Texture	SB	1.656	1.964
	DB	2.214	3.261
	SC	2.260	3.263
	DC	-0.023	-0.015
Udder Depth	SB	0.734	0.345
	DB	0.145	0.127
	SC	0.659	0.490
	DC	-2.772	-2.465

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

Table S5.13 Average realized genetic selection differential for the four paths[1] of selection (SB, DB, SC, and DC) for 12 traits for all the study period (1980 to 2015) and the last 10 years (2006 to 2015) in the Ayrshire breed

Trait	Selection path	Year of conception	
		1980 – 2015	2006 – 2015
Angularity	SB	1.869	1.774
	DB	2.212	3.296
	SC	1.836	2.542
	DC	-0.246	-0.202
Body Condition Score	SB	-1.397	-0.705
	DB	-0.569	-0.290
	SC	-1.102	-0.996
	DC	0.110	0.070
Conformation	SB	1.119	1.941
	DB	2.424	4.470
	SC	1.559	2.783
	DC	-0.190	-0.147
Daughter Calving Ability	SB	-1.923	1.128
	DB	-0.137	0.164
	SC	-1.583	0.142
	DC	0.689	0.235
Lactation Persistency	SB	-0.568	0.662
	DB	0.153	1.708
	SC	-0.819	-0.214
	DC	0.007	-0.025
Milking Rate	SB	-0.043	0.769
	DB	0.534	0.632
	SC	-0.099	1.105
	DC	-0.030	-0.096
Milking Speed	SB	0.213	0.822
	DB	0.334	0.307
	SC	-0.337	0.380
	DC	-0.047	0.003
Milking Temperament	SB	0.498	0.144
	DB	0.181	1.175
	SC	0.157	-0.053
	DC	-0.048	0.047

Rump	SB	0.505	0.447
	DB	1.220	1.635
	SC	0.938	1.399
	DC	-0.151	-0.162
Stature	SB	0.671	0.657
	DB	1.979	2.354
	SC	0.895	1.066
	DC	-0.208	-0.074
Udder Texture	SB	1.285	2.222
	DB	2.529	4.403
	SC	1.331	2.950
	DC	-0.192	-0.236
Udder Depth	SB	0.529	0.164
	DB	0.066	0.072
	SC	0.441	0.156
	DC	-5.325	-5.253

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

Table S5.14 Average realized genetic selection differential for the four paths[1] of selection (SB, DB, SC, and DC) for 12 traits for all the study period (1980 to 2015) and the last 10 years (2006 to 2015) in the Jersey breed

		Year of conception	
Trait	Selection path	1980 – 2015	2006 – 2015
Angularity	SB	2.070	1.287
	DB	2.014	2.435
	SC	1.783	1.256
	DC	-0.271	-0.088
Body Condition Score	SB	-3.786	-1.827
	DB	-4.214	-2.674
	SC	0.309	-0.250
	DC	0.098	0.009
Conformation	SB	-0.936	-0.738
	DB	-1.241	-0.932
	SC	1.966	1.864
	DC	-0.225	-0.116
Daughter Calving Ability	SB	0.418	1.650
	DB	1.171	2.856
	SC	-1.204	-1.281
	DC	0.212	0.318
Lactation Persistency	SB	0.715	1.301
	DB	0.611	1.964
	SC	-0.633	-0.334
	DC	0.115	0.027
Milking Rate	SB	-1.563	-0.769
	DB	-1.470	-1.575
	SC	-0.091	0.571
	DC	0.041	0.006
Milking Speed	SB	1.197	0.997
	DB	0.093	0.996
	SC	0.084	-0.104
	DC	0.037	0.049
Milking Temperament	SB	-0.821	0.805
	DB	0.561	0.396
	SC	-0.185	0.452
	DC	-0.015	-0.064

Rump	SB	-1.458	-0.964
	DB	-2.346	-1.239
	SC	1.603	1.050
	DC	-0.149	-0.082
Stature	SB	-0.935	0.142
	DB	-1.184	-0.383
	SC	1.456	0.688
	DC	-0.215	-0.179
Udder Texture	SB	0.314	-0.336
	DB	0.259	-0.376
	SC	1.381	1.740
	DC	-0.222	-0.145
Udder Depth	SB	0.694	-0.113
	DB	0.663	-0.041
	SC	-0.042	-0.076
	DC	-4.576	-5.167

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

Table S5.15 Average realized genetic selection differential for the four paths[1] of selection (SB, DB, SC, and DC) for 12 traits for all the study period (1980 to 2015) and the last 10 years (2006 to 2015) in the Brown Swiss breed

		Year of conception	
Trait	Selection path	1980 – 2015	2006 – 2015
Angularity	SB	0.718	0.383
	DB	1.665	1.437
	SC	0.597	0.893
	DC	-0.178	-0.069
Body Condition Score	SB	-0.683	-0.101
	DB	-1.105	-0.810
	SC	0.137	-0.203
	DC	0.098	0.170
Conformation	SB	0.703	1.229
	DB	1.668	1.848
	SC	0.675	1.660
	DC	-0.185	0.001
Daughter Calving Ability	SB	-0.757	0.183
	DB	-0.630	-0.984
	SC	0.249	0.492
	DC	-0.214	0.234
Lactation Persistency	SB	0.449	0.457
	DB	1.468	1.085
	SC	0.125	1.109
	DC	-0.089	-0.184
Milking Rate	SB	0.047	0.672
	DB	-0.472	-0.129
	SC	-0.042	0.277
	DC	-0.018	-0.082
Milking Speed	SB	-0.181	0.523
	DB	-0.096	-0.007
	SC	-0.120	0.291
	DC	0.068	0.055
Milking Temperament	SB	-0.279	1.641
	DB	0.224	1.050
	SC	-0.158	0.356
	DC	0.008	-0.050

Rump	SB	-0.474	0.296
	DB	-0.216	-0.400
	SC	-0.153	0.320
	DC	-0.031	0.081
Stature	SB	0.296	0.657
	DB	0.720	-0.533
	SC	0.357	0.649
	DC	-0.065	0.012
Udder Texture	SB	0.861	0.866
	DB	1.745	2.300
	SC	0.411	1.364
	DC	-0.146	-0.077
Udder Depth	SB	0.591	0.112
	DB	-0.309	-0.845
	SC	0.393	0.179
	DC	-5.464	-0.735

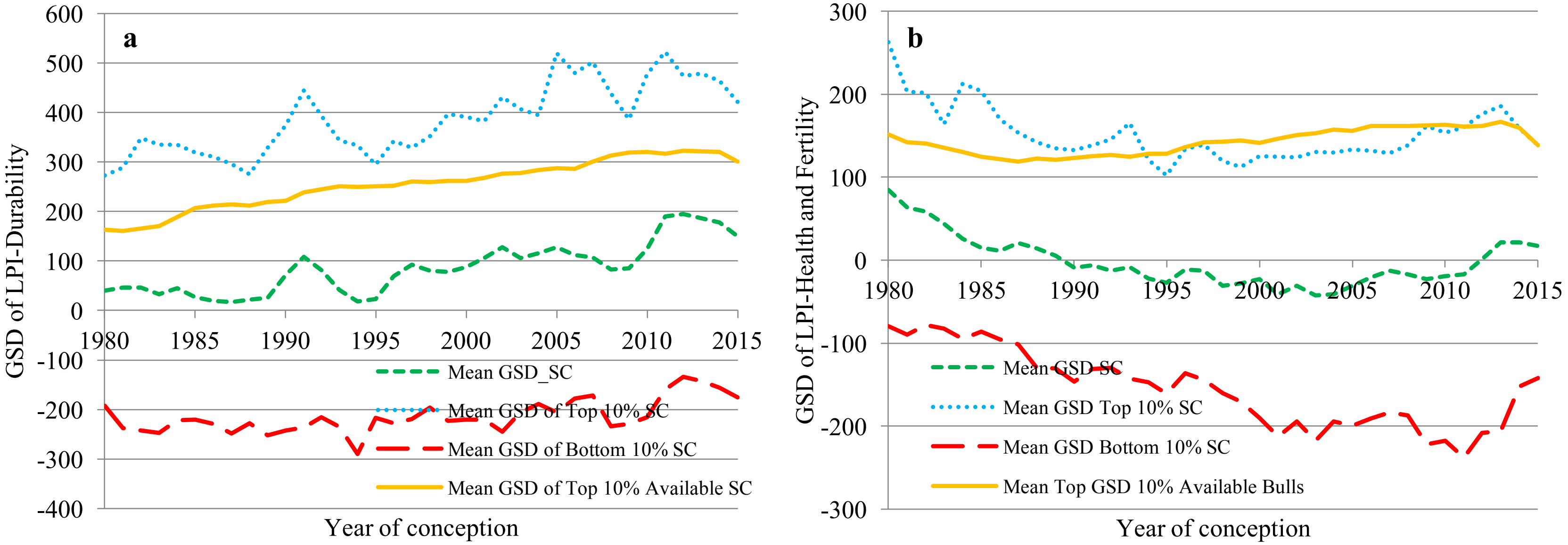

Figure S5.5a-b Mean realized genetic selection differential (GSD) in trait units per year of conception for sires of cows (GSD SC), top 10% sires used (Top 10% SC), bottom 10% sires (Bottom 10% SC), and Top 10% available bulls (Top 10% Available Bulls) for a) LPI-durability and b) LPI-health and fertility in the Holstein breed.

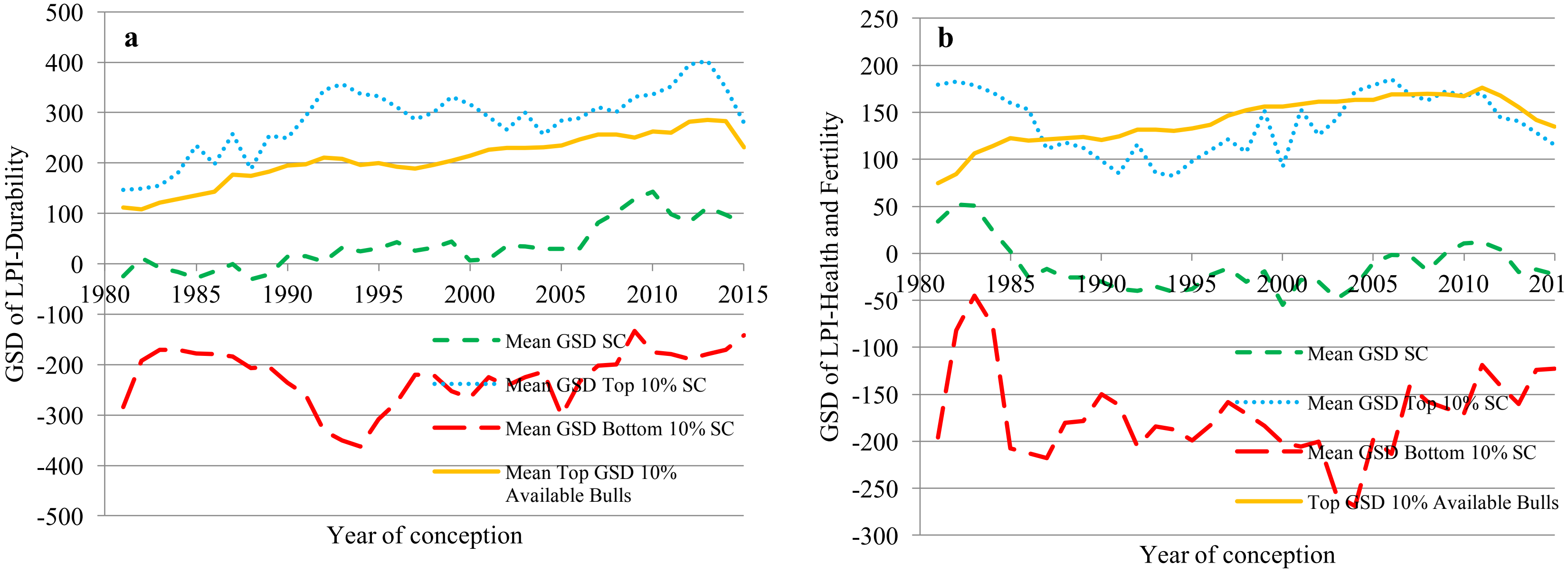

Figure S5.6a-b Mean realized genetic selection differential (GSD) in trait units per year of conception for sires of cows (GSD SC), top 10% sires used (Top 10% SC), bottom 10% sires used (Bottom 10% SC), and top 10% available bulls (Top 10% Available Bulls) for a) LPI-durability and b) LPI-health and fertility in the Ayrshire breed.

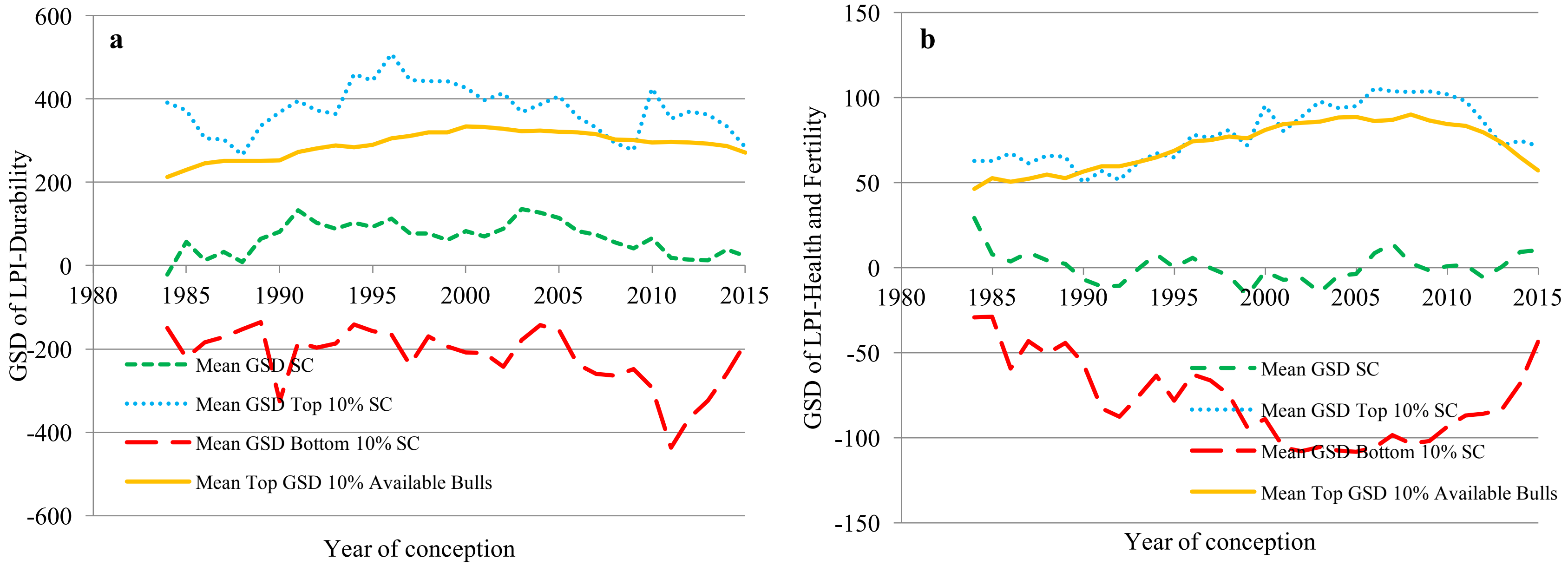

Figure S5.7a-b Mean realized genetic selection differential (GSD) in trait units per year of conception for sires of cows (GSD SC), top 10% sires used (Top 10% SC), bottom 10% sires used (Bottom 10% SC), and top 10% available bulls (Top 10% Available Bulls) for a) LPI-durability and b) LPI-health and fertility in the Jersey breed.

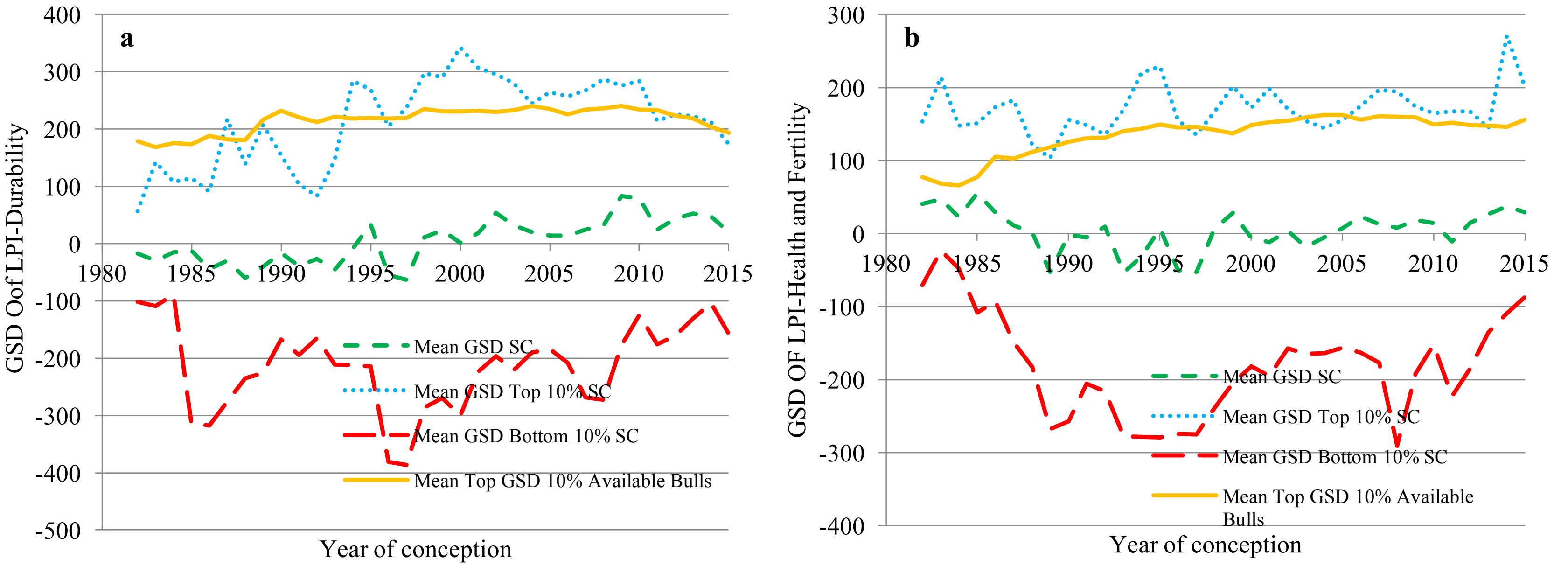

Figure S5.8a-b Mean realized genetic selection differential (GSD) in trait units per year of conception for sires of cows (GSD SC), top 10% sires used (Top 10% SC), bottom 10% sires used (Bottom 10% SC), and top 10% available bulls (Top 10% Available Bulls) for a) LPI-durability and b) LPI-health and fertility in the Brown Swiss breed.

CONNECTING STATEMENT

Chapter V examined the realized GSD for ancillary type and functional traits in Canadian Holstein, Ayrshire, Jersey, and Brown Swiss breeds. Annual rate of genetic improvement in any livestock population is a function of both genetic selection differentials and generation intervals. Chapter VI of this thesis therefore examines the generation intervals in the Canadian Holstein, Ayrshire, Jersey, and Brown Swiss dairy cattle populations along the four-path selection model. The effects of environmental factors on generation intervals and variations in generation intervals due to herd and AI centers were also determined.

6 CHAPTER VI: Generation intervals in Canadian dairy cattle herds

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6.1 ABSTRACT

Genetic evaluation records for the Canadian Holstein, Ayrshire, Jersey, and Brown Swiss bulls and cows born from 1950 and 1960, respectively, were used to study the generation intervals (L) along the four-path selection model. The objectives of the study were to determine the L in the four dairy cattle breeds and the effects of some environmental factors and variations among herds or artificial insemination (AI) studs on the L achieved. Total L of the four selection paths was reduced by 55% from 29.2 years in 1980 to 13.2 years in 2016 in the Holstein breed. Substantial reductions in total L were also observed in the Ayrshire, Jersey, and Brown Swiss populations between 1980 and 2016. Unlike progeny year of birth, housing system, agricultural region in Québec (region) – as well as their interaction – were not important on realised L of sires and dams used on Canadian dairy farms. There were significant variations among herds and AI studs on the age of sires and dams used for breeding. The considerable variations in realised L among herds and AI studs offer opportunities to increase the annual rate of genetic progress in the four Canadian dairy cattle populations.

Keywords: generation interval, Holstein, herd, dairy, Ayrshire.

6.2 INTRODUCTION

The annual rate of genetic progress (ΔGy) for economically important traits in any livestock population hinges on four key factors: selection intensity (i), accuracy of estimated breeding values (r_{EBV}), genetic standard deviation of traits (σg), and generation intervals (L).

$$\Delta G_y = i.r_{EBV}.\sigma_g/L$$

Although r_{EBV} and σg of traits might be costly and difficult to change or alter in an attempt to maximise the ΔGy, i and L are relatively easier to manipulate by livestock farmers. Generation interval, being the average age of parents when their offspring are born, is the only factor that is extremely easy to change by farmers, using for example younger animals for breeding or sexed semen for heifer and cow inseminations. Generation interval has the greatest impact on ΔGy (Decker 2014; Wiggans et al. 2017). All things being equal, a decrease in L will increase the ΔGy in selected traits in a given population.

The continuous research and genetic improvement in the Canadian dairy industry have contributed to the important stature the nation has on the global dairy industry (Blayney et al. 2006). The genetic improvement in the national population per generation is due to genetic selection, whereas the annual rate of genetic improvement is due partly to the genetic selection applied for breeding objective traits and partly to the realised L. This suggests that L is vital in determining how fast genetic progress is being made in a population. The introduction of genomic selection in some national breeding programs in developed countries has greatly reduced L (García-Ruiz et al. 2016), which has been predicted to significantly increase the rate of genetic progress (Schaeffer 2006). Generation intervals have been studied in beef cattle (Gutiérrez et al. 2003; Mc Parland et al. 2007), sheep (Joakimsen 1969; Mokhtari et al. 2014), and goat (Rashidi et al. 2015) populations. There have also been few studies on genetic selection and L in dairy cattle

(Burnside et al. 1992; Maiwashe et al. 2006; García-Ruiz et al. 2016). Rapitta et al. (1988) also studied L of young Holstein sires in Canadian artificial insemination (AI) studs. Most of these studies have only examined L at the population level with no report of L achieved in individual herds.

Though AI centres are the most important key players in national animal breeding programs, individual producers also play an important role in the final annual genetic gains attained in national programs, as they are many in numbers and influence the sires of cows and dams of cows' pathways by their selection decisions.

The objectives of this study were to determine realised L in four Canadian dairy cattle breeds (Holstein, Ayrshire, Jersey, and Brown Swiss) over time and the variabilities among herds or AI studs in the L achieved in sires and dams used for breeding.

6.3 MATERIALS AND METHOD

6.3.1 Data

Data for this study were the April 2018 EBV for Canadian Holstein, Ayrshire, Jersey, and Brown Swiss bulls and cows provided by the Canadian Dairy Network, and dairy herd recording information by Valacta, Québec. The EBV files contained information on animal identifications, dates of birth, sire and dam identifications, and dates of birth of sire and dams. The herd information on the other hand included herd identification, agricultural region, and milking system from which the housing systems (HS) were deduced (Table 6.1).

Before editing the data files, there were records of 203 696 bulls and 6 204 898 cows for the Holstein breed. For the Ayrshire breed, there were records of 10 187 bulls and 251 793 cows, whereas there were records of 20 478 bulls and 210 941 cows for Jersey breed and 6 292 bulls and

Table 6.1 Groups of agricultural regions in Québec, milking system, and housing systems in Québec, Canada.

Factor	Classes
Agricultural region	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 parlour, robot
Housing system	Tie stall, free stall

44 135 cows for the Brown Swiss breed. The bull and cow files of respective breeds were merged to produce the data sets for the computations of L for the sires of bulls (SB), dams of bulls (DB), sires of cows (SC), and dams of cows (DC). As part of the editing process, records of all bulls born before 1950 and cows born before 1960 were removed. The pedigree completeness by year of birth (YOB) of cows and bulls was computed as the percentage of known parents and grandparents of cows and bulls using the approaches of Van Doormaal et al. (2005) and Stachowicz et al. (2011). Cow or bull records with missing sires or dams were removed as we needed to have the dates of birth of both progeny and their parents to compute L. In addition, progeny born before 1980 were removed from the data sets irrespective of whether their sires and dams were born before or after 1950 and 1960, respectively. This was done so that we can report on the population L from 1980 onwards and not before 1980, as many current herd owners may not have been owning and managing their herds 40 years ago and thus, may not be interested in the L during that period. The

number of records for each selection pathway for the four dairy breeds studied, after data editing, are presented in Table 6.2.

Table 6.2 Number of records in each selection path (SB, SC, DB, and DC).

Breed	[1]SB	SC	DB	DC
Holstein	77 059	2 064 528	44 810	1 975 923
Ayrshire	1 562	90 313	1 277	89 629
Jersey	7 574	38 671	3 721	38 026
Brown Swiss	1 752	10 433	1 189	9 668

[1]SB – sires of bulls; SC – sires of cows; DB – dams of bulls; DC – dams of cows

6.3.2 Generation intervals

Realised L were computed as the difference between the dates of birth of cows or bulls and their sires or dams birth dates, expressed in years (Van Tassell and Van Vleck 1991). The mean L per progeny birth year were computed for the SB, DB, SC, and DC selection pathways for each of the four dairy cattle breeds.

6.3.3 Statistical analyses

The L for each of the four selection pathways were analysed using the high performance mixed procedure of SAS version 9.4 (SAS Institute Inc., Cary, NC, USA). For the SC and DC pathways, L were analysed using model 6.1 below

$$L_{ijkmn} = \mu + YOB_i + HS_j + Region_k + Herd_{jkm} + Herd*YOB_{ijkm} + HS*YOB_{ij} + Region*YOB_{ik} + HS*Region_{jk} + e_{ijkmn}$$ **[Model 6.1]**

where L_{ijkmn} is the generation interval of SC or DC; μ is the overall mean effect; YOB_i is the fixed effect of the ith progeny birth year (i =1980, …, 2016); HS_j is the fixed effect of the jth housing system (j = Tie stall, Free stall); $Region_k$ is the fixed effect of the kth agricultural region (Table 6.1); $Herd_{jkm}$ is the random effect of herd nested within the jth HS and the kth agricultural region ~ $N(0, \sigma^2_{herd})$; $Herd*YOB_{ijkm}$ is the random interaction of the mth herd nested within the jth HS and the kth agricultural region by the ith YOB ~ $N(0, \sigma^2_{herd*YOB})$; $HS*YOB_{ij}$ is the fixed effect of the interaction between the jth HS and the ith YOB; $Region*YOB_{ik}$ is the fixed effect of the interaction between the kth agricultural region and the ith YOB; $HS*Region_{jk}$ is the fixed effect of the interaction between the jth HS and the kth agricultural region; and e_{ijkmn} is the random residual ~ $N(0, \sigma^2_e)$.

The model used to analyse L of the SB and DB paths is presented as model 6.2 below

$$L_{ijk} = \mu + YOB_i + Stud_j + Stud*YOB_{ij} + e_{ijk} \qquad \textbf{[Model 6.2]}$$

where L_{ijk} is the generation interval of SB or DB; μ is the overall mean; YOB_i is the fixed effect of the ith progeny birth year (i = 1980, …, 2016); $Stud_j$ is the random effect of the jth AI centre ~ $N(0, \sigma^2_{stud})$; $Stud*YOB_{ij}$ is the random interaction between the jth AI stud and the ith YOB ~ $N(0, \sigma^2_{stud*YOB})$; and e_{ijk} is the random residual ~ $N(0, \sigma^2_e)$.

Models 6.1 and 6.2 were subsequent modified and written where one random effect was dropped at a time and the difference in Bayesian Information Criterion (BIC) values of models with and without one random factor were noted and used to determine whether a random factor was significant or not. A random factor was deemed significant when the difference in BIC value between the models with and without the random factor was greater than 8.

6.4 RESULTS AND DISCUSSION

6.4.1 Pedigree completeness

The pedigree completeness of the Holstein, Ayrshire, Jersey, and Brown Swiss populations is presented in Figure 6.1. The depth and completeness of pedigree are important factors which have effects on both estimated inbreeding coefficients and estimated L (Stachowicz et al. 2011). The percentages of animals born between 1950 and 1980 with known parents and grandparents range from 33 to 90% for the Holstein, 5 to 92% for the Ayrshire, 2 to 94% for the Jersey, and 6 to 83% in the Brown Swiss breeds. During this period (1950 to 1980), there were considerable variabilities in the pedigree completeness among the four breeds. However, for animals born between 1980 and 2016, which marks the study period we are reporting, the percentages of animals with known parents and grandparents were high and similar for all the breeds. The percentages range from 86 to 99% for the Holstein, 92 to 99% for the Ayrshire, 94 to 99% for the Jersey, and 78 to 98% for the Brown Swiss breeds (Fig. 6.1). The pedigree completeness of the Brown Swiss breed was slightly lower than those of the other breeds; however, the difference was not significant. The generally similar pedigree completeness of the Holstein, Ayrshire, Jersey, and Brown Swiss breeds makes it reliable to compare the realised L of the four breeds. The percentages of Holstein bulls and cows with known parents and grandparents in this study were similar to the reports of Van Doormaal et al. (2005).

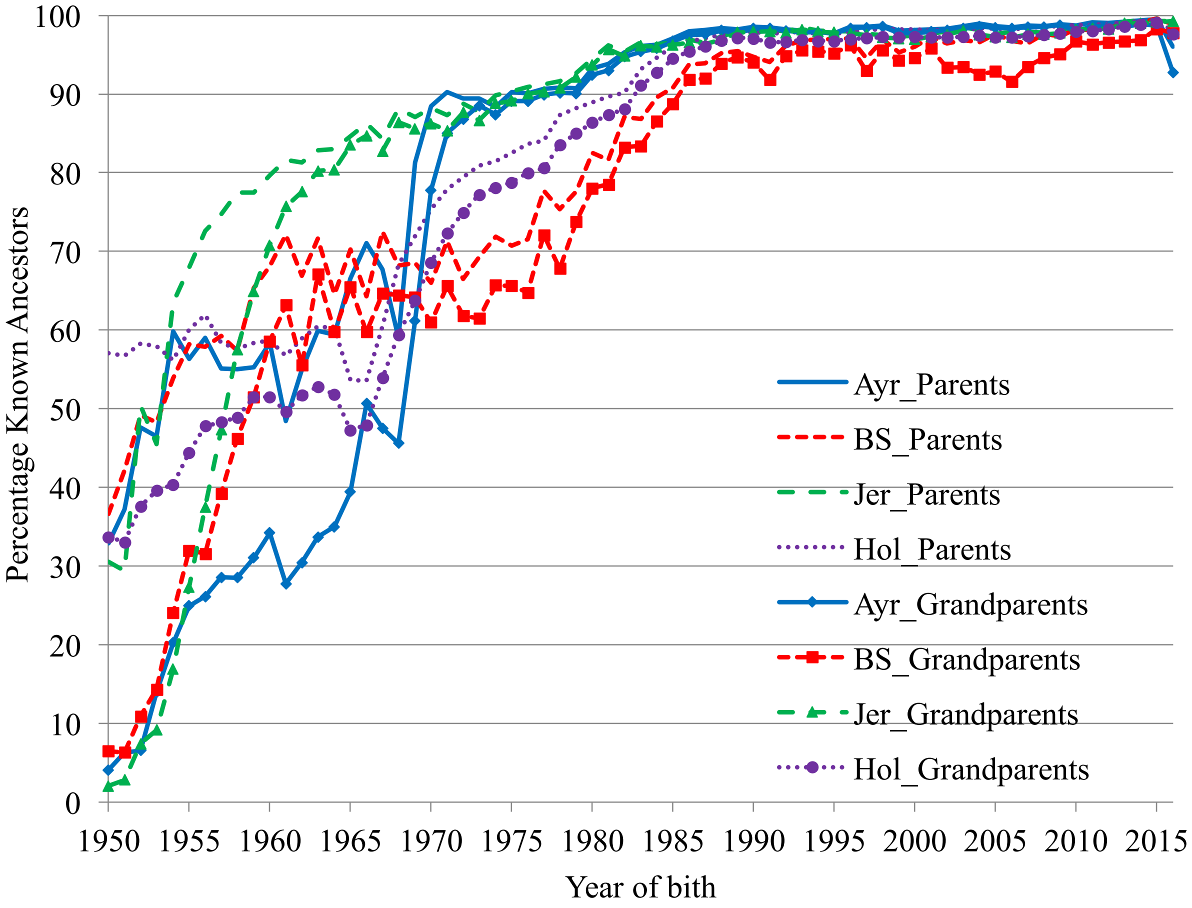

Figure 6.1 Completeness of pedigree by year of birth in the Holstein, Ayrshire, Jersey and Brown Swiss populations as defined as the percentage of known parents and grandparents.

6.4.2 Generation intervals

The mean realised L per YOB for the Holstein, Ayrshire, Jersey, and Brown Swiss breeds are presented in Figures 6.2 – 6.5, respectively. For the Holstein population, there has been gradual decline in L in the three most influential selection paths (SB, DB, and SC) between 1980 and 2009, being the period before the introduction of genomic selection (Fig. 6.2). Within this period, L has declined by 29%, 50%, 14%, and 10% in the SB, DB, SC, and DC paths, respectively. However, just about 8 years after the introduction of genomic selection in the Canadian Holstein population, L has declined substantially in the male pathways (SB and SC). There were 67% and 26%

reductions in L in the SB and SC paths, respectively, between 2009 and 2016. There was also an appreciable reduction in L in the DB (33%) with a marginal decline of 12% in the DC within the same period. Cumulatively, L reduced by 27% in all paths between 1980 and 2009, whereas there was a 38% reduction between 2009 and 2016. The large decline in L in the genomic era corroborates the findings of García-Ruiz et al. (2016). The total L of all four paths in 2016 (13.2 years) was similar to 13.5 years observed in the USA Holstein population in 2015 (García-Ruiz et al. 2016) but still higher than the 9.8 years proposed by Schaeffer (2006). Although Schaeffer predicted an L of 1.75 years for the SC path in the genomic era, Holstein dairy herds in Canada were still using relatively older AI bulls (4.62 years) for mating. Rapitta et al. (1988) reported mean L of 9.3 and 7.4 years for SB and DB, respectively, in Canadian AI studs prior to 1990. Currently, the mean L in the SB and DB paths are 2.3 and 2.5 years in the Canadian Holstein population signifying three to four times reduction in L of sires and dams used by AI centres. The high reduction in L in the SB and DB paths and the considerable reduction in L in the SC path signify that both AI centres and producers have embraced genomic testing and selection. The increased adoption of reproductive technologies such as in-vitro fertilization and embryo transfer among AI centres have largely contributed to the reduction in L of the DB path (Van Doormaal and Beavers 2019).

For the Ayrshire population, L declined gradually in the SB, DB, and SC paths from 1980 to 2016, whereas L has remained stable in the DC (Fig. 6.3). The mean L for SB, DB, SC, and DC in 1980 were 11.9, 7.4, 8.0, and 4.9 years, respectively. These L reduced by 57%, 41%, 34%, and 14% between 1980 and 2016 in the SB, DB, SC, and DC, respectively. The total L for all four paths have reduced by 41% within the 36 years' period. There was no substantial reduction in L in the genomic era for the Ayrshire population (Fig. 6.3) as was observed in the Holstein population. Generation intervals reduced by only 21, 11, 9, and 4 months in the SB, DB, SC, and DC, respectively, between 2009 and 2016. The low reduction in L observed in the Ayrshire population between 2009 and 2016 was due to the fact that genomic evaluation and selection in Ayrshire breed only started recently (2013) in Canada (www.cdn.ca) and the USA (2013) (Wiggans et al. 2017). Between 2013 and 2016, L reduced by 24.8%, 10.9%, and 4.8% in the SB, SC, and DC paths, respectively, but increased slightly (11.1%) in the DB path.

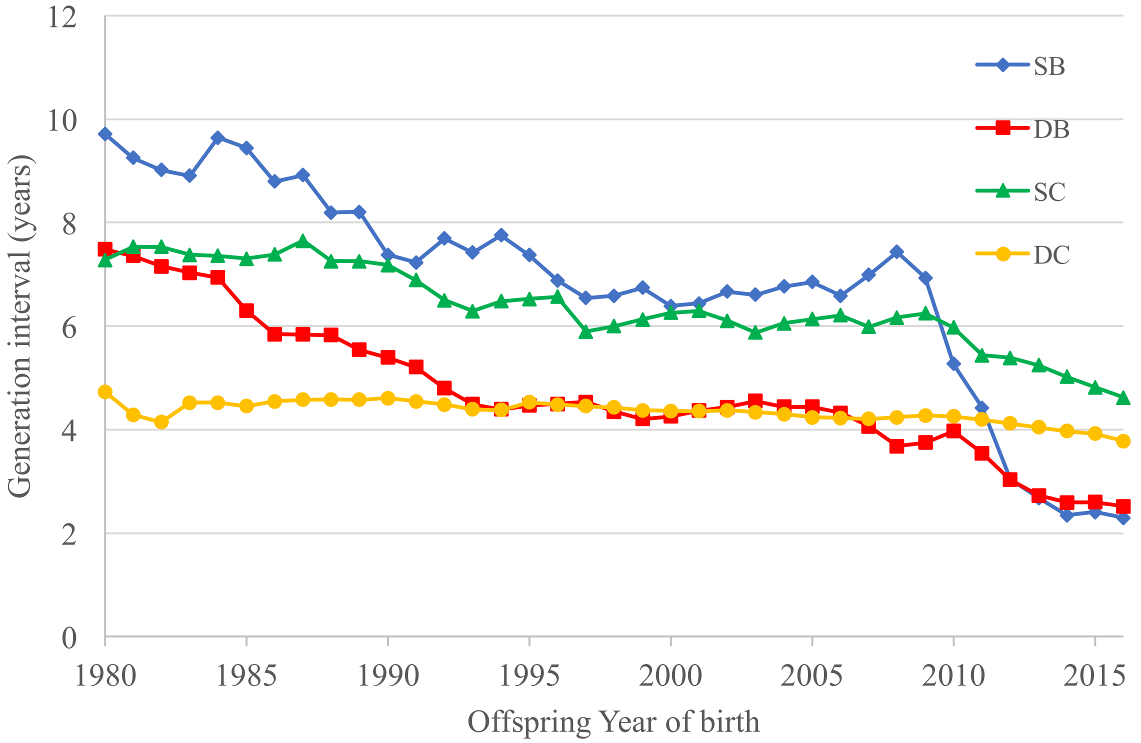

Figure 6.2 Generation intervals of the sire-to-bull (SB), sire-to-cow (SC), dam-to-bull (DB) and dam-to-cow (DC) by offspring birth year for the Holstein breed.

Generation intervals in the Jersey population have also reduced gradually in the SB and DB but not the SC and DC paths between 1980 and 2009 (Fig. 6.4). Generation intervals reduced by 36%, 25%, 3%, and 11% within this period (1980-2009) in the SB, DB, SC, and DC paths, respectively. Between 2009 and 2016, however, L reduced substantially in the SB and DB paths and slightly in the SC and DC paths. Generation intervals reduced by 55%, 40%, 13%, and 7% in the SB, DB, SC, and DC, respectively, for the Jersey breed in the genomic era. The large reduction in L within this period suggests that AI studs of the Jersey population were in recent times using younger bulls and dams due partly to more efficient progeny testing schemes and uptake of genomic testing and selection (Wiggans et al. 2017). The mean L of DB and DC in the USA registered Jersey (Nizamani and Berger 1996) was slightly lower than those observed in this study (6.4 and 4.8 years) between 1980 and 1990. However, the mean L of SB and SC in this study (8.9 and 6.6 years) were lower than the 9.3 and 7.6 years reported by Nizamani and Berger (1996) within the same period.

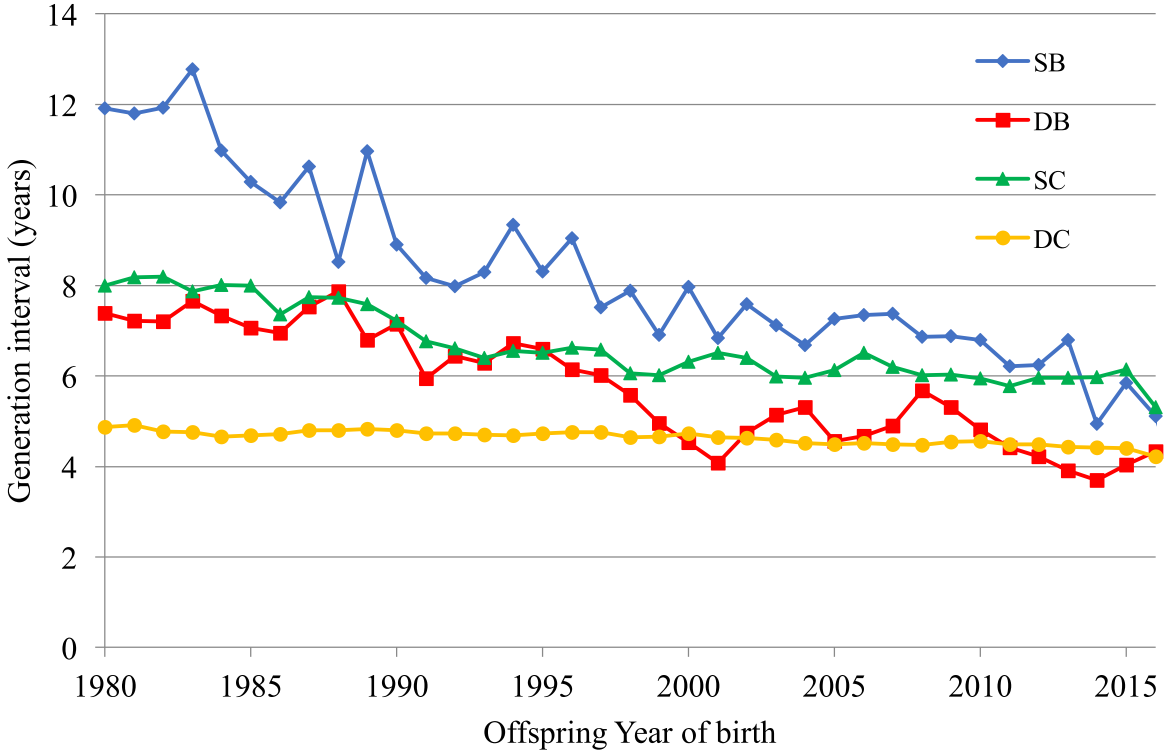

Figure 6.3 Generation intervals of the sire-to-bull (SB), sire-to-cow (SC), dam-to-bull (DB) and dam-to-cow (DC) by offspring birth year for the Ayrshire breed.

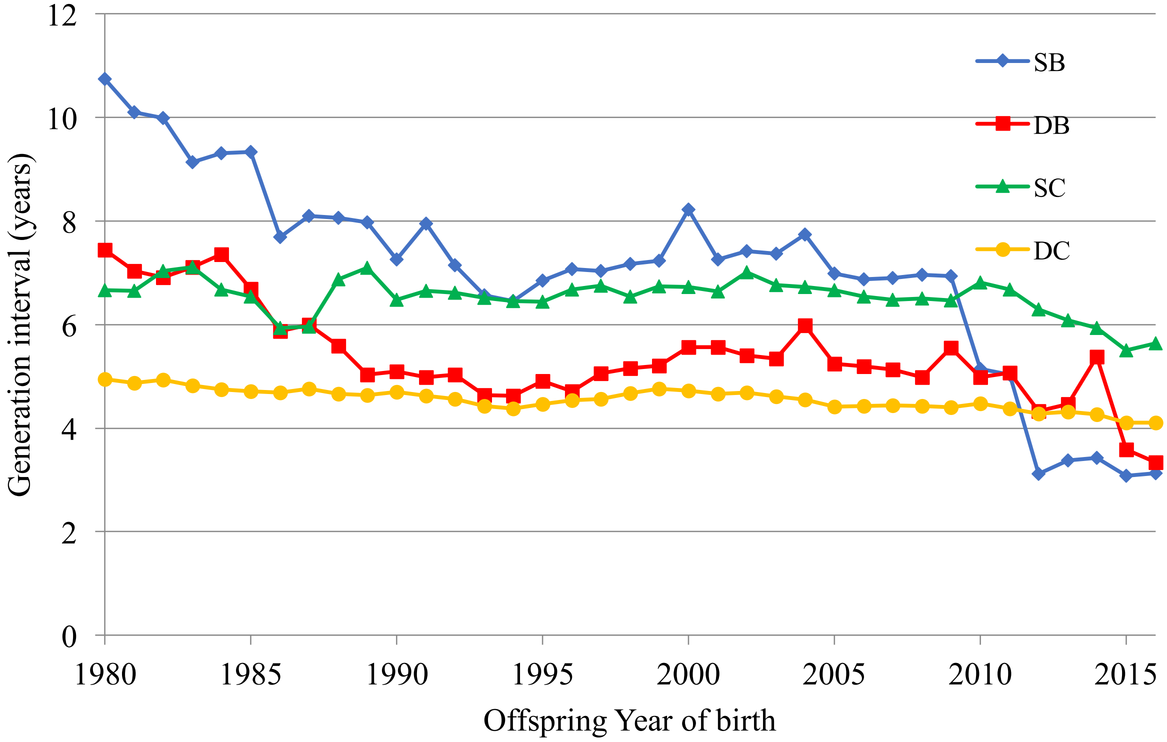

Figure 6.4 Generation intervals of the sire-to-bull (SB), sire-to-cow (SC), dam-to-bull (DB) and dam-to-cow (DC) by offspring birth year for the Jersey breed.

In the Brown Swiss population, L reduced gradually from 11.0, 7.7, and 7.5 years to 4.5, 4.8, and 5.2 years in the SB, DB, and SC paths, respectively, between 1980 and 2016 (Fig. 6.5). The DC path has, however, seen no change in L over that period. The SB, DB, and SC have cumulatively seen reductions of 59%, 37%, and 30%, respectively, within the 36 years' period. There were drastic reductions of 3.5 and 2.7 years between 2011 and 2016 in the SB and SC of the Brown Swiss population. This marked reduction in L could be attributed to genomic evaluation of young bulls which has resulted in the availability of young sires for breeding in the Brown Swiss population as genomic evaluations of the Brown Swiss breed started in 2009 (Wiggans et al. 2017).

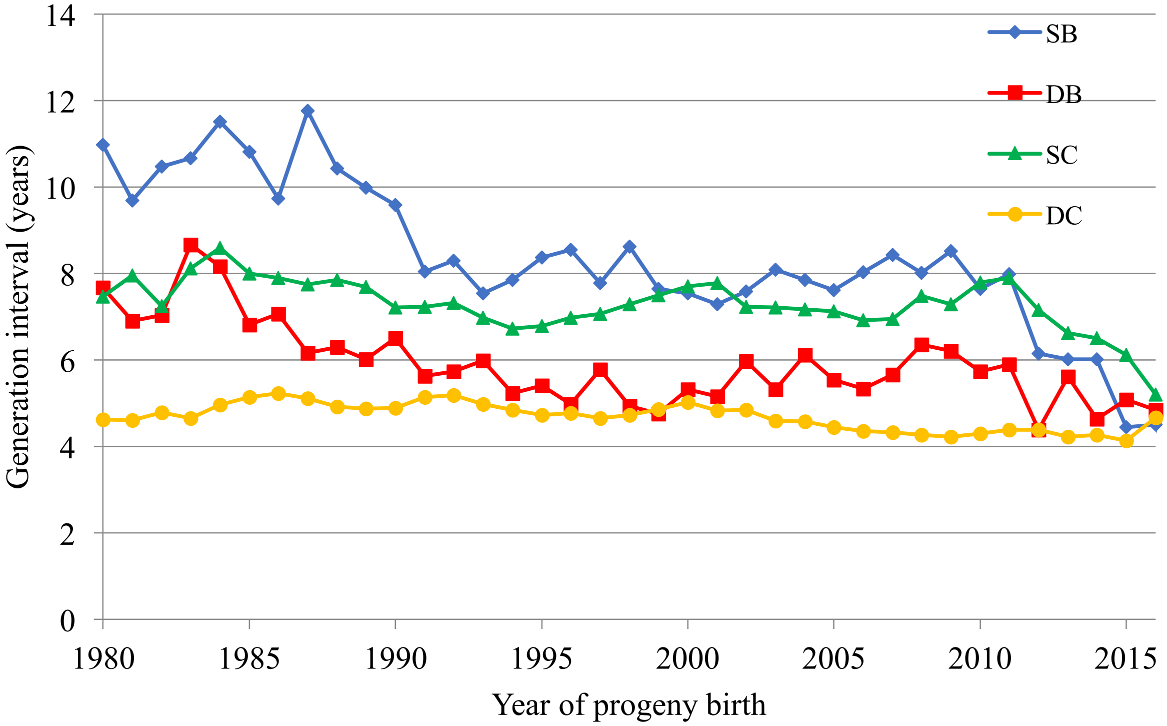

Figure 6.5 Generation intervals of the sire-to-bull (SB), sire-to-cow (SC), dam-to-bull (DB) and dam-to-cow (DC) by offspring birth year for the Brown Swiss breed.

In the Holstein breed, the L of the SB and DB paths appear to have reached their biological minimum (~ 2 years) 4 years after the introduction of genomic selection (Fig. 6.2). A similar pattern can be observed in the Jersey breed (Fig. 6.4), but it was slower than that of the Holstein as it has taken 6 years to obtain L of approximately 3 years in the SB and DB paths. In contrast, the biological minimum L has not been reached in the Ayrshire and Brown Swiss breeds in neither the SB nor the DB paths, as the L in the SB and DB are still beyond the 4 years' threshold.

6.4.3 Effects of non-genetic factors on realised L in the four selection pathways

Information is scanty on the effects of environmental factors on the realised L in all four paths of selection in the Holstein, Ayrshire, Jersey, and Brown Swiss populations. The P values for the effects of YOB, HS, region, HS*YOB, region*YOB, and HS*region on L achieved in all four pathways in the four dairy cattle populations have been presented in Tables 6.3 – 6.6. Year of birth had significant effect ($P < 0.05$) on L of SB, DB, SC, and DC pathways in all four cattle breeds (not shown in tables), except for the non-significant effect ($P > 0.05$) of YOB on L of the DC path of the Brown Swiss breed (Table 6.6). Both AI organizations and dairy farmers are heavily using younger bulls and dams for breeding in recent times due to improvements in the methods of genetically evaluating animals, such as genomic evaluation, which has resulted in increase in the accuracy of EBV of younger animals (Meuwissen et al. 2001). Genomic evaluation allows for the identification of superior animals at a much early age of about 3 months (Wiggans et al. 2017) or even less with high accuracy hence a lower L. Prior to genomic selection, AI organizations used progeny testing schemes to identify genetically superior animals which took a much longer time, resulting in the frequent use of older animals for breeding.

Table 6.3 Effects of housing system (HS), region, HS*YOB, region*YOB and HS*region on L in the SB, DB, SC, and DC selection paths (*P* values for the fixed effects) and the variance components of herd(HS*region), herd*YOB[3], and residuals for the Holstein breed.

	[1]Fixed effects					Variance components		
[2]Path	HS	Region	HS*YOB	Region*YOB	HS*Region	Herd	Herd*YOB	Residual
SB						0.6881	0.5377	3.4363
DB						0.8171	0.4483	3.6151
SC	0.1019	0.2258	<0.0001	<0.0001	0.1232	0.07336	0.07643	7.1912
DC	0.2301	0.1114	0.0001	<0.0001	0.0813	0.1207	0.09022	4.2838

[1] Fixed effects are statistically significant if $P<0.05$

[2] SB – sires of bulls; DB – dams of bulls; SC – sires of cows; DC – dams of cows

[3] YOB – Year of birth ($P < 0.001$ for all paths in the table).

Table 6.4 Effects of housing system (HS), region, HS*YOB, region*YOB and HS*region on L in the SB, DB, SC, and DC selection paths (*P* values for the fixed effects) and the variance components of herd(HS*region), herd*YOB[3], and residuals for the Ayrshire breed.

	[1]Fixed effects					Variance components		
Path	HS	Region	HS*YOB	Region*YOB	HS*Region	Herd	Herd*YOB	Residual
[2]SB						1.3441	0.2056	11.5879
DB						0.6494	0.2028	6.1826
SC	0.7385	0.7385	0.0424	0.0001	0.1315	0.5934	0.6710	11.5511
DC	0.9031	0.8376	0.0260	0.0039	0.2968	0.1290	0.08631	4.9071

[1] Fixed effects are statistically significant if $P<0.05$

[2] SB – sires of bulls; DB – dams of bulls; SC – sires of cows; DC – dams of cows

[3] YOB – Year of birth ($P < 0.001$ for all paths in the table).

The HS being used by dairy producers of all four breeds did not have a significant effect ($P > 0.05$) on the realised L of SC or DC except the effect of HS on realised L of DC of the Brown Swiss breed. In the Brown Swiss population, free stalls producers largely used younger dams in producing replacement cows than tie stall producers. Similarly, agricultural region did not have significant effects ($P > 0.05$) on realised L of SC and DC in all dairy breeds except for the significant effect ($P < 0.05$) of agricultural region on realised L of SC in the Brown Swiss breed (Table 6.6). Herds in Bas-Saint-Laurent, Chaudière-Appalaches, and Capitale-Nationale generally used younger aged sires for breeding replacement cows than herds located in agricultural regions such as Gaspésie-îles-de-la-Madeleine, Abitibi-Témiscamingue, and Lanaudière. The reasons for this observation are not clear.

Table 6.5 Effects of housing system (HS), region, HS*YOB, region*YOB and HS*region on L in the SB, DB, SC, and DC selection paths (*P* values for the fixed effects) and the variance components of herd(HS*region), herd*YOB[3], and residuals for the Jersey breed.

	[1]Fixed effects					Variance components		
[2]Path	HS	Region	HS*YOB	Region*YOB	HS*Region	Herd	Herd*YOB	Residual
SB						0.4786	0.2236	6.6102
DB						0.7860	0.2886	5.6429
SC	0.9685	0.4801	0.9926	0.0131	0.3131	0.5585	0.7731	10.7105
DC	0.4084	0.2355	0.4954	0.0126	0.6900	0.1580	0.09694	5.0664

[1]Fixed effects are statistically significant if $P<0.05$

[2]SB – sires of bulls; DB – dams of bulls; SC – sires of cows; DC – dams of cows

[3]YOB – Year of birth ($P < 0.001$ for all paths in the table).

Table 6.6 Effects of Year of birth (YOB), housing system (HS), region, HS*YOB, region*YOB and HS*region on L in the SB, DB, SC, and DC selection paths (*P* values for the fixed effects) and the variance components of herd(HS*region), herd*YOB, and residuals for the Brown Swiss breed.

	[1]Fixed effects						Variance components		
[2]Path	YOB	HS	Region	HS*YOB	Region*YOB	HS*Region	Herd	Herd*YOB	Residual
SB	0.001						0.7555	0.6984	8.4600
DB	0.001						0.3237	0.1557	7.1244
SC	0.001	0.3449	0.0429	0.0026	0.2743	0.0064	1.1419	1.2060	11.3079
DC	0.1113	0.0078	0.1778	0.2040	0.0963	0.7305	0.1604	0.1283	5.1118

[1]Fixed effects are statistically significant if $P<0.05$

[2]SB – sires of bulls; DB – dams of bulls; SC – sires of cows; DC – dams of cows

The effects of HS*YOB and region*YOB were significant ($P < 0.05$) on realised L of SC and DC in both the Holstein and Ayrshire populations. The significant interactions of HS*YOB and region*YOB on realised L of SC suggest that differences in L of SC between HS and amongst agricultural regions are not the same for all years. There has been increased acceptance of young genomic tested bulls among dairy producers in the USA (Schefers and Weigel 2012) and Canada where about 70% of all inseminations are done with semen from young genomic bulls between the ages of 1 and 4 years (Canadian Dairy Network 2017). For the Jersey population, only the interaction between region and YOB were significant ($P < 0.05$) on realised L of SC and DC, whereas the effect of HS*YOB was only significant ($P < 0.05$) for realised L of SC of the Brown Swiss population.

The interaction between HS and agricultural region was not significant ($P > 0.05$) on realised L in SC and DC in all four breeds except for L of SC in the Brown Swiss population. Apart from time, the other environmental factors studied were generally not important in the decision of age of sires or dams selected and used for breeding.

6.4.4 Variations among herds and herd*YOB on realised L in the four selection pathways

This study also sought to determine the variability among herds and AI studs keeping Holstein, Ayrshire, Jersey, and Brown Swiss breeds in their realised L during breeding. The variations due to herds and AI studs constituted between 1.0 and 16.7% of the total variation in realised L in the Holstein population. Among AI organizations, there were higher variations (14.8 – 16.7%) in the realised L of sires and dams used for breeding. This variability could be due to the different rates of adoption of genomic technology among AI organizations. In contrast, there was little variability among herds (1.0 – 2.7%) in the age of sire and dams used for breeding. Dairy farmers will generally use bulls with high EBV for breeding objective traits, and these bulls were often progeny-tested bulls of older and similar ages during the pre-genomic era. Artificial insemination organizations were, therefore, marketing the semen of bulls with high EBV for economic traits but of older ages to producers who were using them for breeding. Also in the genomic era, genomic young bulls of similar ages were being marketed to producers. These practices largely explain the small variations in L observed among herds in their usage of sires for breeding. The variation due to herd*YOB or stud*YOB also constituted between 1.0 and 11.5% of the total variation observed in age of sires and dams used for breeding (Table 6.3). Higher variabilities in realised L were observed among the AI organizations (9.2 – 11.5%) compared to dairy herds (1.0 – 2.0%). The low variabilities in realised L among herds indicate that there were relatively small differences in the ages of sires used for breeding by producers in any given year.

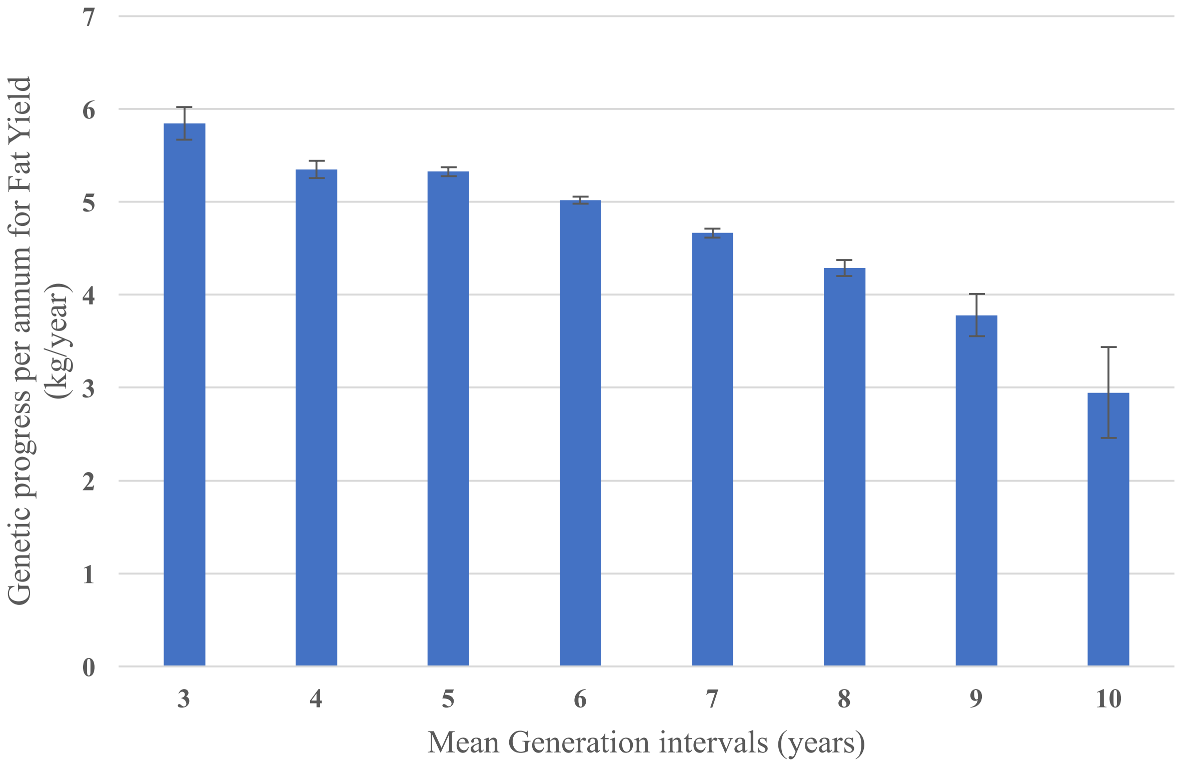

Figure 6.6 Relationship between realised generation intervals and annual genetic progress for fat yield (kg) between 2010 and 2015 in herds of the Holstein dairy cattle population.

For the Ayrshire, Jersey, and Brown Swiss populations, the variations in parental L attributed to herds or studs were 2.5 – 10.2%, 3.0 – 11.7% and 3.0 – 8.4%, respectively. Although the variations in realised L among studs were higher for the AI organizations of the Holstein population, the variations in realised L among herds of the minor dairy cattle breeds were slightly higher than those of the Holstein population. Variations in realised L due to herd were 2.5 – 4.6% for Ayrshire, 3.0 – 4.6% for Jersey, and 3.0 – 8.3% for Brown Swiss populations, respectively. This suggests that there are greater variabilities in the ages of sires or dams used for breeding among dairy producers of the minor dairy cattle breeds than the Holstein breed. All these variations were significant except for the herd*YOB on realised L in the DC of the Brown Swiss breed, probably due to the relatively small data size of the Brown Swiss breed.

The variation in realised L due to stud*YOB or herd*YOB range from 1.6 – 5.2%, 1.8 – 6.4%, and 2.1 – 8.8% for the Ayrshire, Jersey, and Brown Swiss breeds, respectively. Higher variations were observed for the SC and DC paths compared to the paths controlled by the AI organizations (SB and DB). This suggests that among herds of the minor dairy breeds, there were significant differences in sire and dam ages used for breeding of bulls and cows over time.

6.4.5 Relationship between a herd's realized L and rate of genetic progress

Generation interval is an important determinant of the ΔGy (Decker 2014) at both the population and herd levels. The use of young genomic bulls for breeding has been showed to increase profitability of breeding programs (König et al. 2009). We, therefore sought to observe the relationship between mean L and ΔGy for Holstein herds during the period of genomic evaluations. We present a couple of randomly selected example herds in the Ayrshire and Holstein populations in both pre-genomic and genomic eras. The mean realised L for each year from 1984 to 2015, marking both the pre-genomic and genomic eras, were computed for each of the example herds in the two populations. The mean EBV per year for each of the example herds in the Ayrshire and Holstein populations were also computed.

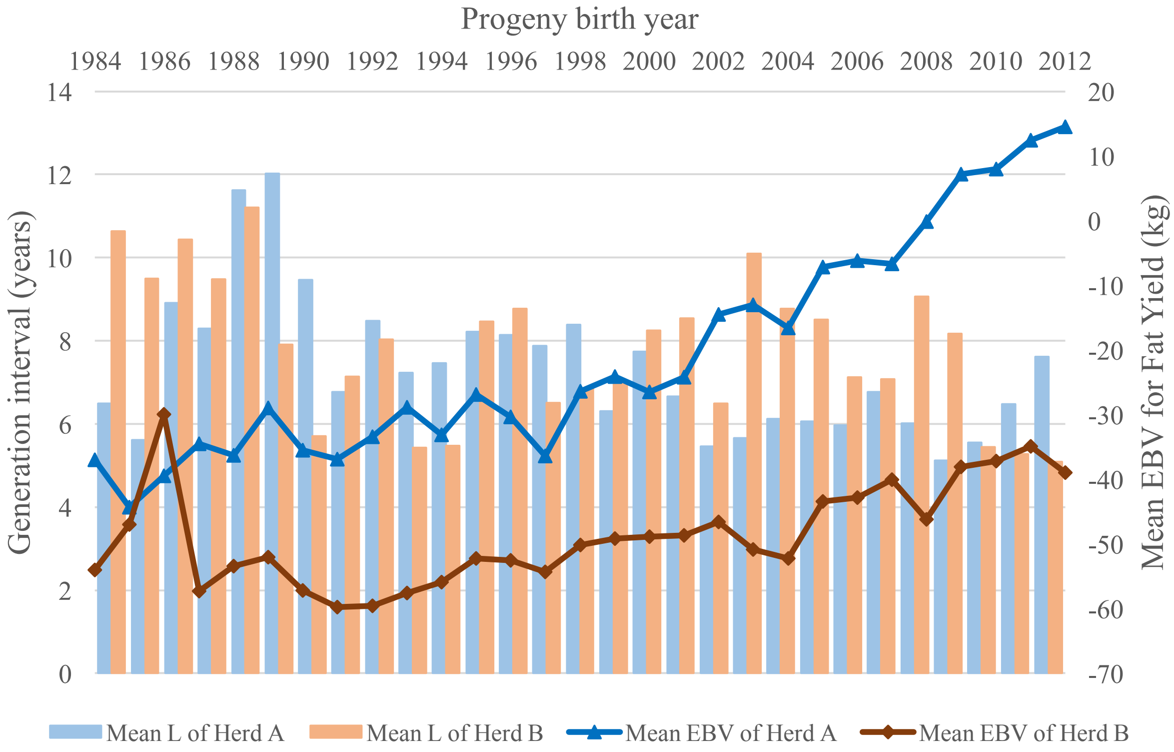

Figure 6.7 Mean generation interval and EBV for fat yield (kg) per year of birth of progeny for two randomly selected herds, A and B, in the Ayrshire population.

In addition, the mean realised L for all herds were classified into distinct year categories from 3 to 10 years for the period 2010 to 2015, and the generalized linear model procedure of SAS was used to analyse the effects of realised L on rate of genetic progress in the Holstein population. The relationship was illustrated using information from the SC pathway. Generation interval had a significant effect ($P < 0.05$) on the ΔGy in the Holstein population between 2010 and 2015 (Fig. 6.6). Lower realised L were significantly ($P < 0.05$) associated with higher estimated ΔGy. Thus, herds with lower mean realised L had higher rates of genetic progress. A couple of example herds were selected from both the Ayrshire and Holstein populations and their mean realised L per YOB and mean EBV per year were compared (Figs. 6.7 and 6.8).

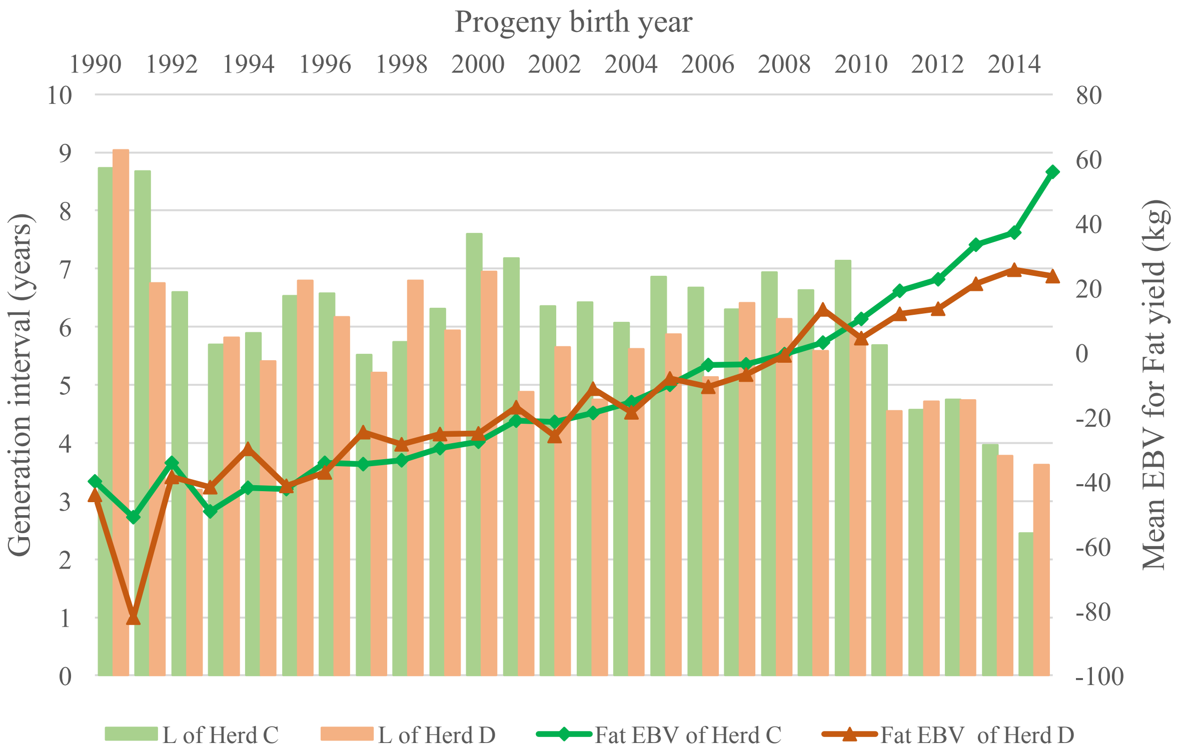

Figure 6.8 Mean generation interval and EBV for fat yield (kg) per progeny birth year for two randomly selected herds, C and D, in the Holstein population.

For the Ayrshire population, the mean realised L for herd A was largely lower than that of herd B especially between 1999 and 2009 progeny birth years. This period marked the greatest rate of change in EBV in herd A compared to herd B. For the Holstein population, the realised L of the two herds (C and D) were mostly similar with slightly higher mean realised L for herd C. There was not much difference in the rate of change of EBV in the two herds. This suggests that the ages of sires used for breeding in a herd affect the rate of change of genetic progress in a herd.

6.5 CONCLUSIONS

Realised L in the Canadian Holstein, Ayrshire, Jersey, and Brown Swiss dairy cattle breeds have been studied using the four-path selection model. There have been steady reductions in realised L from 1980 to 2009 in the three most influential pathways after which there were steep reductions in realised L in especially the SB and DB from 2009 to 2016 in the Holstein breed which is attributable to genomic selection by AI companies. The realised L of the DC remained fairly stable over the years with marginal reduction in recent times. The realised L in the minor dairy cattle breeds have also seen gradual but steady declines between 1980 and 2016 in the SB, DB, and SC paths. Generation interval in the DC path have remained steady over the period for all the minor dairy cattle breeds.

Year of birth had substantial influence on the realised L in all dairy cattle populations, whereas the other environmental factors studied were relatively less important on realised L in Canadian dairy cattle breeds. There were considerable variations among herds or AI studs on age of sires and dams used for breeding by both dairy herds and AI organizations. In addition, considerable variations in realised L due to herd*YOB or stud*YOB were observed in the four dairy cattle populations studied. The variations observed offer opportunity for increasing the ΔGy at both the herd and national population levels.

6.6 ACKNOWLEDGEMENTS

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CONNECTING STATEMENT

Generation intervals in four Canadian dairy cattle breeds were described along the 4-path selection model in chapter VI. In chapter VII, genetic and phenotypic parameters for milk production, SCS, lactation body weight, and profit indicator traits were estimated in first to fourth lactation Holstein cows. The estimated parameters for milk production and body weight were used to design a simple selection index; the aim of the index was to halt or slow down the positive genetic trends in cow body weight which have adverse effects on cow maintenance cost and reduction in margin over feed cost.

7 CHAPTER VII: Genetic parameter estimates for body weight and milk production traits in Canadian Holstein cows

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7.1 ABSTRACT

First to fourth lactation records of Québec Holstein cows born from 2008 were used to estimate heritabilities of milk production traits, lactation body weight (BWT), somatic cell score (SCS), cumulative milk value (MV), cumulative feed cost (FC), and margin over feed cost (MOFC) using mixed linear animal models. Genetic and phenotypic correlations among all the traits and across all four lactations were also studied. Heritability estimates for milk production traits and BWT were moderate in all four lactations ranging from 0.214 to 0.468. Heritabilities for milk production traits generally tend to decrease with increasing lactation numbers, whilst heritability estimates for BWT did not follow any regular pattern. Heritability estimates for SCS and FC were low (0.054 to 0.121) and moderate for MV and MOFC (0.161 to 0.368). Moderate to strong positive genetic correlations exist among the milk production traits, MV, FC, and MOFC. Somatic cell score has weak and positive genetic correlations with production, MV, FC, and MOFC in the first lactation, but correlations are mostly weak and negative in later lactations. Body weight has weak and mostly negative genetic correlations with milk production traits, MV, and MOFC, but moderately positive correlations with FC. Body weight has essentially weak and negative genetic correlations with SCS in first and third lactations, but not second (0.041) and fourth (0.087) lactations. Genetic correlations of the same traits in different lactations were very high (>0.80) for milk production, BWT, SCS, and FC and generally high (0.60 to 0.80) for MV and MOFC. The greatest correlations were found between adjacent lactations. There are positive genetic trends for BWT which suggest that cow size is genetically increasing and this could have implications on cow efficiency and profitability in the long term, as well as for other management aspects, such as stall dimensions.

Keywords: body weight, genetic correlation, heritability, milk value, margin over feed cost

7.2 INTRODUCTION

Dairy producers in Canada do not directly genetically select for body weight because first, estimated breeding values (EBVs) are not produced for bodyweight and secondly, the traits in the national selection index (Lifetime Performance Index) do not include body weight. There is, however, evidence that body weight has been increasing (Valacta annual reports (2015, 2016)) probably due to correlated response to selection for milk production (Ahlborn and Dempfle, 1992; Berry et al., 2003) and/or improved nutrition and cow management.

Cow body weights are important in dairy production as heavier cows are generally less efficient than smaller cows (Sieber et al., 1988; Yerex et al., 1988), consume more feed and demand high maintenance requirement (Groen et al., 1994) which is not commensurate to the increase in their level of milk production. Feed cost, being the largest variable cost for milk production, (Ho et al., 2013) will make bigger and heavier cows to be less profitable as the extra milk production from bigger cows has to pay for the increase in feed consumption brought about by the additional size or weight. VanRaden (1988) reported that smaller cows are more profitable than heavier cows because of their low maintenance requirement and lower feed intake. Smaller cows also stay longer in dairy herds (Hansen et al., 1999). The inclusion of body weight and milk production traits in selection index could increase the profitability of dairy herds through the increase in accuracy of estimating cow profitability (Ahlborn and Dempfle, 1992).

Many studies have estimated genetic parameters for milk production traits in Holstein dairy cattle under pasture-based systems (Ahlborn and Dempfle, 1992; Visscher and Goddard, 1995; Berry et al., 2003; Haile-Mariam et al., 2003) and concentrate-based feeding systems (Van der Werf and De Boer, 1989; Moore et al., 1991; Hoekstra et al., 1994; Jamrozik and Schaeffer, 1997). The heritability estimates for milk production traits in these studies range between 0.20 and 0.48. Heritability estimates for lactation body weights are moderate to high and range from 0.18 to 0.60 (Moore et al., 1991; Ahlborn and Dempfle, 1992; Veerkamp and Brotherstone, 1997; Parke et al., 1999; Veerkamp et al., 2000; Berry et al., 2003). There are several studies on heritability estimates for cow profit indicators with wide ranges (0.12 to 0.50) among these estimates (Gill and Allaire, 1976; Jairath et al., 1994; Visscher and Goddard, 1995; Pérez-Cabal and Alenda, 2002) due to differences in definitions of cow profit.

Genetic correlations between body weight and milk production traits have been estimated in dairy populations in the UK, New Zealand and Netherlands (Ahlborn and Dempfle, 1992; Veerkamp et al., 2000; Berry et al., 2003) and these estimates range from 0.01 to 0.39. Berry et al. (2003) reported an approximately zero genetic correlation between unadjusted body weight and milk production for pasture-fed multiparous Holstein-Friesian cows in Southern Ireland. There is little information on the genetic correlations between body weight and milk production, somatic cell score and cow profit indicators in the Canadian dairy population. It is important to periodically estimate the genetic correlations among these traits (milk production, body weight, milk value, feed cost, margin over feed cost) in the Canadian Holstein population to know what the effects of selection for production and other traits are having on cow BWT; which might suggest that present cow stalls might not be big enough if cows are getting bigger and heavier. Also, if the cows are bigger, then their maintenance costs are higher and this needs to be acknowledged in selection indices and economic values used in these selection indices.

The objective of this study was to estimate genetic parameters for milk production, body weight, somatic cell score, and cow profit indicators in Holstein dairy population in Québec, Canada.

7.3 MATERIALS AND METHODS

7.3.1 *Traits and trait definitions*

The traits studied were production, live weight, health, and measures for cow profitability related traits. These are namely 305-day milk yield (MY), 305-day fat yield (FY), 305-day protein yield (PY), lactation body weight (BWT), somatic cell score (SCS), cumulative milk value (MV), cumulative feed cost (FC), and margin over feed cost (MOFC). These traits were selected because we were interested in examining how cows' body weights during lactation relate with their production, health and indicators of cow profit during first and later lactations.

The 305-day milk, fat, and protein yields are cows' milk, fat, and protein yields expressed on a 305-day lactation basis. Lactation body weight is the live weight of a lactating cow taken during her lactation period. Lactation body weights were usually recorded in early lactation, at the first or second test-days in lactation with about 15% of the producers recording more than one body weight per lactation. For instance, in the first lactation records, about 65% of the body weights that were used for the analysis were recorded within the first 60 days after calving (Figure 7.1). The pattern of distributions in the later lactations were similar to that of the first lactation. Body weights were mostly measured using tape measure estimation (Heinrichs et al. 1992) or weighing scale. Approximately 15% of producers record body weights of lactating cows multiple times during their lactation period, e.g. monthly or bi-monthly. For this study, however, only one BWT was randomly selected per cow per lactation for the analysis as we were not using a test-day model and also not interested in estimating repeatability of BWT. Somatic cell score is the transformation of somatic cell count (SCC) onto a linear scale ranging from 0 to 10, and SCC is recorded on each test day. Cumulative milk value is the total dollar value of milk produced by a cow during her 305-day lactation period based on fat and protein contents in the milk and the current prices that are paid to producers. Cumulative feed cost is the total cost of feed, which includes grains, protein supplement, minerals, and forages, consumed by a lactating cow during her lactation. The feed cost is specific to a particular producer, test-day and feeds available. Both MV and FC are calculated by Québec Centre of Dairy Expertise, Lactanet. Margin over feed cost is the difference between the MV and the FC for a lactating cow, for a specific lactation.

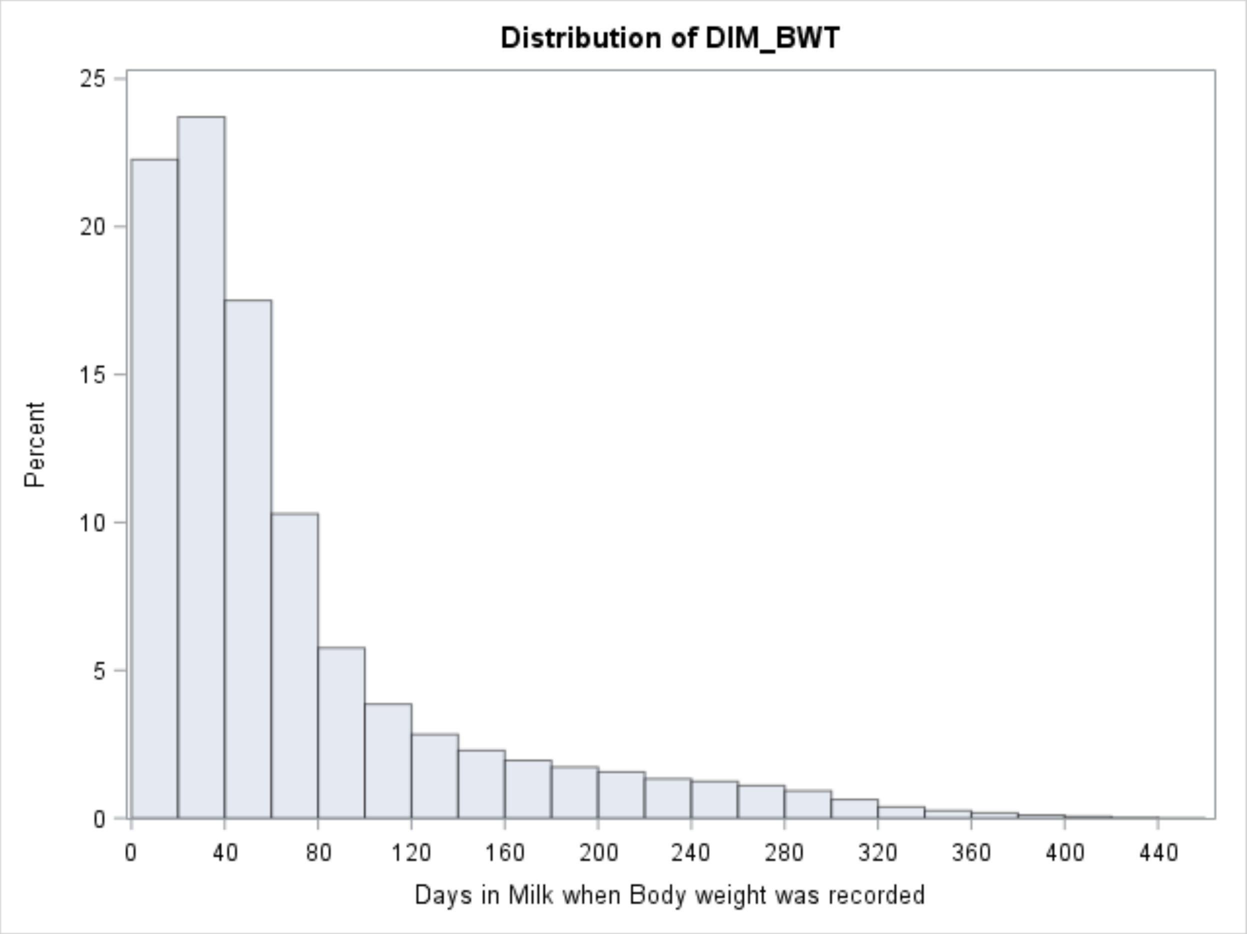

Figure 7.1 Distribution of Days in Milk when Body weight was recorded (DIM_BWT) during the first lactation.

7.3.2 *Data and editing procedures*

Data for this study comprise first, second, third, and fourth lactation records of Canadian Holstein cows born from 2008 in herds located in the province of Québec. Data before 2008 were not included for this study because prior to 2008, the body weight of cows were usually based on group averages rather than individually recorded body weight. The data were obtained from Lactanet. The number of animals in first, second, third, and fourth lactations which remained in only one herd in a given lactation during the study period were 441,042, 285,132, 162,701, and 77,957, respectively. Initial editing restricted the datasets to cows which had at least one lactation body weight record within the lactation period of a given parity. This resulted in 285,067, 166,308, 88,383, and 39,703 records of cows in the first, second, third, and fourth lactations, respectively. Further editing of datasets were carried out using various criteria to improve the quality of the data before analyses were done as presented in Table 7.1.

Table 7.1 Editing criteria and number of records and animals remaining after each edit for first, second, third, and fourth lactation datasets

Editing criteria	**Number of records remaining after each editing criteria**			
	Lactation 1	**Lactation 2**	**Lactation 3**	**Lactation 4**
Cows with body weight recorded within the lactation length	285,067	166,308	88,383	39,703
Removal of records outside of the mean MY ± 3σ and mean lactation length ± 3σ	278,988	163,306	87,092	39,342
Removal of records outside of the mean BWT ± 3σ for each week in milk (WIM)	276,900	162,148	86,424	39,055
Removal of records outside of the mean MY ± 3σ for each WIM	275,565	161,403	86,062	38,882
Removal of cow records with lactation length < 200 days or > 450 days	233,412	137,756	72,057	31,828
Exclusion of cow records with ages at calving outside of 22 – 34 months, 34 – 49 months, 46 – 64 months, and 58 – 79 months for 1st, 2nd, 3rd, and 4th lactations cows, respectively	227,583	122,680	69,587	30,896

Exclusion of lactation body weights outside of 400 – 800 kg, 500 – 850 kg, 550 – 880 kg, 570 – 900 kg for 1st, 2nd, 3rd, and 4th lactation cows, respectively	226,944	132,221	68,639	30,401
Retain only one BWT record per cow per lactation	182,750	109,618	57,415	25,325
Exclusion of Herd-Years of Calving (YOC) with < 5 records for 1st to 3rd lactations and < 2 records for 4th lactation	169,273	95,801	42,812	23,024
Exclusion of records of sires with <3 progeny in at least 3 herds	137,627	71,974	29,260	13,964
Removal of records outside of mean FY ± 3σ for each WIM	136,780	71,515	29,075	13,883
Removal of records outside of mean PY ± 3σ for each WIM	136,493	71,329	29,000	13,859
Removal of records outside of mean SCS ± 3σ for each WIM	135,308	70,928	28,895	13,823
Removal of records outside of mean MV ± 3σ for each WIM	135,052	70,783	28,827	13,799
Exclusion of records of FC outside of \$1000 – \$4000, \$1000 – \$4500, \$1000 – \$5000, and \$1000 – \$5000 for 1st, 2nd, 3rd, and 4th lactations, respectively	41,230	21,139	8,682	4,251

The remaining records in each of the datasets were subjected to sire connectedness by ensuring that each of the sires had at least three daughters in at least three herds. Also, all records without identifiable housing system and herd-year contemporary groups with less than five records were removed. The final edited datasets had 125,205, 62,155, 22,071, and 12,266 records for the first, second, third, and fourth lactations, respectively. For FC and MOFC, there were 38,697, 18,901, 6,801, and 3,861 records in the final datasets for first, second, third, and fourth lactations, respectively. The fewer number of records of FC and MOFC relative to the other traits is due to the fact that many herds do not keep records of feed information on their cows, therefore calculations of FC for these cows are not done. Subsequently, we could not compute the MOFC of cows with no information on FC. The final number of records in first, second, third, and fourth lactations were from 11,558, 6,949, 3,011, and 3,597 herd-year contemporary groups and 858, 461, 211, and 106 sires, respectively.

Besides the eight traits studied, the final datasets also contained information on cow, sire and dam registrations, cow birth year, herd identification, agricultural region (region), housing system (HS), year of calving (YOC), age at calving (Age), lactation length (LL), and days-in-milk when body weight was recorded (DIM_BWT). Lactation length is the number of days a cow was in lactation in a given lactation number. The editing criteria used for this study restricted the LL to from 200 to 450 days. Days-in-milk when body weight was recorded is the stage of lactation (in days) when the body weight of a lactating cow was recorded.

7.3.3 *Pedigree*

The pedigree records contained cow, sire and dam information. The pedigree was traced back three generations in the Canadian Holstein database. The initial number of animals in the pedigree files of the first, second, third, and fourth lactations and the editing procedures undertaken with related relations are presented in Table 7.2.

Table 7.2 Number of animals in pedigree files of first, second, third, and fourth lactations

Numbers of animals in each category	Lactation 1	Lactation 2	Lactation 3	Lactation 4
Animals before pruning of uninformative animals	303,629	172,653	72,716	44,438
Uninformative animals pruned	41,833	28,144	14,570	10,279
Animals remaining after pruning	261,796	144,509	58,146	34,159
Animals with unknown sires	5,467	3,405	1,690	1,063
Animals with unknown dams	49,343	31,877	15,503	10,558
Animals with both parents unknown	4,703	2,961	1,475	914
Animals with known paternal grand-sires	250,812	137,373	54,417	31,511
Animals with known paternal grand-dams	225,961	119,992	46,382	25,310
Animals with known maternal grand-sires	203,892	107,576	40,289	22,281
Animals with known maternal grand-dams	153,850	76,156	25,953	13,070
Animals with records	125,205	62,155	22,071	12,266

7.3.4 *Data analyses*

Before the analysis of the final datasets, records of some of the traits were rescaled to save computing space and ease analysis. Records of MY, MV, FC, and MOFC were divided by 10^3, whilst records of FY, PY, and BWT were divided by 10^2. The mixed model procedure of SAS version 9.4 (SAS Institute Inc., Cary, NC) was used to determine which fixed effects and covariates best described the data for each trait. Based on the significance of the fixed effects and covariates, different models best fitted the data for the different traits. The model for the MY, FY, PY, SCS, MV, FC, and MOFC contained the fixed effects of YOC, HS, region, herd, LL, and age of calving (Age). For BWT, the model contained fixed effects of YOC, HS, region, herd, age, and

DIM_BWT. A random effect of animal genetic effect was added for the estimation of the genetic parameters. The following were the models used for the traits studied:

$Y_{ijkmnpq} = HY_i + region_j + HS_k + LL_m + b_nAge + b_nAge^2 + animal_p + e_{ijkmnpq}$ **Model 7.1**

where $Y_{ijkmnpq}$ is the observation for a trait (MY, FY, PY, MV, or MOFC);

HY_i is the fixed effect of the ith Herd-Year (11,558, 6,949, 3,011, and 3,597 levels for first, second, third, and fourth lactations, respectively);

$region_j$ is the fixed effect of the jth agricultural region (17 levels);

HS_k is the fixed effect of the kth housing system (2 levels);

LL_m is the fixed effect of the mth lactation length (251 levels);

b_nAge is the fixed linear regression on age at calving (22 to 34, 34 to 49, 46 to 64, and 58 to 78 mo of age for first, second, third, and fourth lactation cows, respectively);

b_nAge^2 is the fixed quadratic regression on age at calving (22 to 34, 34 to 49, 46 to 64, and 58 to 78 mo of age for first, second, third, and fourth lactation cows, respectively);

$animal_p$ is the random additive genetic effect of animal $\sim N(0, A\sigma^2_a)$ where A is the additive genetic relationship matrix and σ^2_a is additive genetic variance;

and $e_{ijkmnpq}$ is the random residual associated with $Y_{ijkmnpq} \sim N(0, I\sigma^2_e)$ I is the identity matrix and σ^2_e is residual variance.

For lactation body weight, the model was as below:

$Y_{ijkmnpq} = HY_i + region_j + HS_k + DIM\_BWT_m + b_nAge + b_nAge^2 + animal_p + e_{ijkmnpq}$ **Model 7.2**

where DIM_BWT_m is the fixed effect of the mth days-in-milk when body weight was recorded; and all other fixed and random factors are as in model 7.1.

For somatic cell score, the model was as below:

$Y_{ijkmnpq} = HY_i + region_j + HS_k + b_mLL + b_mLL^2 + b_nAge + b_nAge^2 + animal_p + e_{ijkmnpq}$ **Model 7.3**

where b_mLL is the fixed linear regression on lactation length (251 levels);

b_mLL^2 is the fixed quadratic regression on lactation length (251 levels);

and all other fixed and random factors are as in model 7.1.

For cumulative feed cost, the model was as below:

$Y_{ijkmnpq} = HY_i + region_j + HS_k + LL_m + b_nAge + animal_p + e_{ijkmnpq}$ **Model 7.4**

where b_nAge is the fixed linear regression on age at calving (22 to 34, 34 to 49, 46 to 64, and 58 to 78 mo of age for first, second, third, and fourth lactation cows, respectively);

and all other fixed and random factors are as in model 7.1.

Univariate analyses were carried out with WOMBAT to obtain the univariate heritability, and genetic and phenotypic covariance estimates for each trait and these were used as the starting values for bivariate analyses using WOMBAT software (Meyer, 2007). Twenty-eight bivariate analyses were carried out for each lactation dataset, which produced heritabilities, and genetic and phenotypic covariance estimates for each pair of traits. In all, seven heritability estimates were obtained for each trait in each lactation and the average h^2 estimate for each lactation was calculated to obtain the final heritability estimate for a trait for that lactation. For each analysis, there were many (between 10 and 34) iterations of genetic and residual variance and covariance components before convergence was achieved, when the change in -2Log(likelihood) was less than 10^{-9}.

7.4 RESULTS

7.4.1 *Descriptive statistics*

The raw means and standard deviations for the traits studied in first, second, third, and fourth lactations are presented in Table 7.3. The mean values for the traits studied increased with increasing lactation numbers. The standard deviations of the traits also increased with increasing lactation numbers. The standard deviations for SCS were high whilst those for BWT were comparatively lower.

7.4.2 *Phenotypic variances and heritability estimates*

The phenotypic variances and heritability estimates for the traits studied in the first, second, third, and fourth lactations are presented in Table 7.4. The phenotypic variances of the production traits were generally larger in third and fourth lactations than first and second lactations. Similarly, the phenotypic variances for BWT, SCS, MV, FC, and MOFC in third and fourth lactations were comparatively higher than in first and second lactations. The heritability estimates for milk production traits across lactations were all moderate to high and ranged from 0.214 to 0.468. The heritability estimates for BWT were also moderate ranging from 0.300 to 0.428. The heritability estimates for SCS and FC were all low whilst those of MV and MOFC were moderate. The heritability estimates of SCS ranged from 0.102 to 0.121.

Table 7.3 Mean and standard deviation (sd) of traits studied in first, second, third, and fourth lactations in Holstein cows

	First lactation		Second lactation		Third lactation		Fourth lactation	
Traits[a]	Mean	sd	Mean	sd	Mean	sd	Mean	sd
MY, kg	9,369.9	1905.3	10,833.5	2,209.9	11,589.5	2,314.7	11,685.4	2,391.6

FY, kg	374.4	79.2	430.4	91.8	458.1	97.2	460.5	100.5
PY, kg	308.1	63.9	358.9	73.0	378.3	76.4	378.8	78.5
BWT, kg	618.1	56.1	670.7	58.4	706.1	59.8	720.5	60.7
SCS	2.037	1.259	2.400	1.361	2.667	1.437	2.849	1.526
MV, $	6,858.77	1,395.30	7,915.70	1,602.02	8,407.60	1,689.45	8,421.85	1,743.38
FC, $	2,168.41	430.56	2,404.36	472.34	2,508.58	488.06	2,524.16	510.51
MOFC, $	4,618.66	1,111.69	5,441.67	1,287.12	5,843.01	1,360.62	5,814.10	1,431.31

[a]MY – 305-day milk yield, FY – 305-day fat yield, PY – 305-day protein yield, BWT – lactation body weight, SCS – somatic cell score, MV – cumulative milk value, FC – cumulative feed cost, MOFC – margin over feed cost

Table 7.4 Estimates of phenotypic variances (σ_p^2) and average heritabilities (h^2) ± standard errors (SE) for study traits in first, second, third, and fourth lactation Holstein cows

	First lactation		Second lactation		Third lactation		Fourth lactation	
Traits[a]	σ_p^2	$h^2 \pm$ SE	σ_p^2	$h^2 \pm$ SE	σ_p^2	$h^2 \pm$ SE	σ_p^2	$h^2 \pm$ SE
MY	1.4236	0.468 ± 0.011	1.7942	0.329 ± 0.016	1.9576	0.280 ± 0.004	1.9425	0.214 ± 0.030
FY	0.2016	0.390 ± 0.011	0.3097	0.368 ± 0.018	0.3468	0.258 ± 0.025	0.3702	0.246 ± 0.039
PY	0.1056	0.321 ± 0.010	0.1543	0.289 ± 0.017	0.1715	0.257 ± 0.027	0.1750	0.237 ± 0.039
BWT	0.2015	0.300 ± 0.011	0.2442	0.423 ± 0.018	0.2669	0.378 ± 0.033	0.2820	0.391 ± 0.050
SCS	1.4551	0.102 ± 0.009	1.6672	0.121 ± 0.012	1.8698	0.119 ± 0.018	2.0683	0.119 ± 0.050
MV	0.5418	0.321 ± 0.011	0.9259	0.368 ± 0.017	0.9176	0.294 ± 0.022	1.1162	0.264 ± 0.033
FC	0.0314	0.098 ± 0.012	0.0358	0.081 ± 0.013	0.0388	0.055 ± 0.020	0.0394	0.054 ± 0.025
MOFC	0.4254	0.291 ± 0.019	0.6544	0.286 ± 0.028	0.7461	0.218 ± 0.040	0.7751	0.161 ± 0.049

[a]MY – 305-day milk yield, FY – 305-day fat yield, PY – 305-day protein yield, BWT – lactation body weight, SCS – somatic cell score, MV – cumulative milk value, FC – cumulative feed cost, MOFC – margin over feed cost.

[b]Phenotypic variances of MY, MV, FC, and MOFC were divided by 10^6

[c]Phenotypic variances of FY, PY, and BWT were divided by 10^4

7.4.3 *Phenotypic and genetic correlations*

The phenotypic correlations among the milk production traits across lactations were all high in all lactations ranging from 0.601 to 0.877 (Tables 7.5, 7.6, 7.7, and 7.8) with the highest correlations observed between MY and PY. The genetic correlations among the production traits were also moderate to high with PY having greater correlations with MY and FY. There are generally weak genetic correlations between BWT and all traits across all lactations except for FC. Strong positive genetic and phenotypic correlations exit between MV and MOFC across all lactations (Tables 7.5, 7.6, 7.7, and 7.8). Somatic cell score has weak genetic correlations with milk production, body weight and profit indicator (MV, FC, and MOFC) traits ranging from positive to negative.

High and positive genetic correlations and moderate to high phenotypic correlations existed between FC and milk production, and between FC and BWT. The genetic correlations of FC with milk production traits (0.662 to 0.986) were relatively higher than with BWT across all lactations. There were also strong and positive genetic and phenotypic correlations between MOFC and milk production traits. The highest genetic correlations were between MOFC and FY.

Table 7.5 Genetic (above) and phenotypic (below) correlations among 305-day milk, fat, and protein yields (MY, FY, and PY), somatic cell score (SCS), lactation body weight (BWT), cumulative milk value (MV), cumulative feed cost (FC), and margin over feed cost (MOFC) in first lactation Holstein cows

	MY	**FY**	**PY**	**BWT**	**SCS**	**MV**	**FC**	**MOFC**
MY		0.298	0.759	-0.006	0.024	0.592	0.815	0.620
FY	0.615		0.556	-0.008	0.131	0.906	0.803	0.927

PY	0.877	0.738		0.053	0.136	0.823	0.824	0.823
BWT	0.085	0.089	0.118		-0.049	-0.062	0.352	-0.049
SCS	-0.061	-0.050	-0.035	-0.002		0.139	0.056	0.099
MV	0.783	0.927	0.890	0.120	-0.047		0.850	0.996
FC	0.521	0.494	0.542	0.225	-0.036	0.548		0.817
MOFC	0.754	0.913	0.859	0.057	-0.048	0.974	0.265	

[1] Standard errors for genetic correlations ranged from 0.001 to 0.107; and for phenotypic correlations they range from 0.001 to 0.010

Table 7.6 Genetic (above) and phenotypic (below) correlations among 305-day milk, fat, and protein yields (MY, FY, and PY), somatic cell score (SCS), lactation body weight (BWT), cumulative milk value (MV), cumulative feed cost (FC), and margin over feed cost (MOFC) in second lactation Holstein cows

	MY	**FY**	**PY**	**BWT**	**SCS**	**MV**	**FC**	**MOFC**
MY		0.207	0.715	-0.021	0.049	0.499	0.707	0.481
FY	0.601		0.524	0.029	-0.053	0.915	0.763	0.912
PY	0.872	0.735		-0.012	0.020	0.807	0.764	0.775
BWT	0.003	0.020	0.030		0.041	0.057	0.503	-0.151
SCS	-0.113	-0.137	-0.102	0.040		-0.040	-0.161	-0.099
MV	0.770	0.930	0.888	0.039	-0.129		0.818	0.997
FC	0.521	0.495	0.544	0.168	-0.064	0.553		0.710
MOFC	0.739	0.919	0.860	-0.009	-0.136	0.981	0.293	

[1] Standard errors for genetic correlations ranged from 0.001 to 0.117; and for phenotypic correlations they range from 0.001 to 0.009

The genetic correlations between the same traits in different lactations were very high for MY, FY, PY, BWT, and FC (Table 7.9) and ranged from 0.860 to 0.989. The genetic correlations between MV and MOFC in different lactations were relatively lower than those of other traits and ranged from between 0.660 and 0.926. The lowest correlation was observed between MV in second and fourth lactations.

Table 7.7 Genetic (above) and phenotypic (below) correlations among 305-day milk, fat, and protein yields (MY, FY, and PY), somatic cell score (SCS), lactation body weight (BWT), cumulative milk value (MV), cumulative feed cost (FC), and margin over feed cost (MOFC) in third lactation Holstein cows

	MY	**FY**	**PY**	**BWT**	**SCS**	**MV**	**FC**	**MOFC**
MY		0.150	0.658	-0.017	0.010	0.460	0.758	0.501
FY	0.610		0.501	0.025	-0.055	0.899	0.662	0.935
PY	0.872	0.741		-0.017	0.107	0.805	0.747	0.827
BWT	-0.001	0.017	0.026		-0.004	0.063	0.702	-0.056
SCS	-0.113	-0.141	-0.088	0.056		0.001	-0.159	-0.073
MV	0.770	0.925	0.885	0.037	-0.130		0.718	0.997
FC	0.523	0.473	0.539	0.197	-0.075	0.537		0.600
MOFC	0.743	0.923	0.861	-0.026	-0.128	0.981	0.321	

[1] Standard errors for genetic correlations ranged from 0.016 to 0.196; and for phenotypic correlations they range from 0.001 to 0.016

Table 7.8 Genetic (above) and phenotypic (below) correlations among 305-day milk, fat, and protein yields (MY, FY, and PY), somatic cell score (SCS), lactation body weight (BWT), cumulative milk value (MV), cumulative feed cost (FC), and margin over feed cost (MOFC) in fourth lactation Holstein cows

	MY	**FY**	**PY**	**BWT**	**SCS**	**MV**	**FC**	**MOFC**
MY		0.150	0.599	0.019	-0.004	0.397	0.818	0.406
FY	0.632		0.463	-0.052	-0.238	0.910	0.726	0.944
PY	0.871	0.747		0.027	0.083	0.792	0.986	0.800
BWT	0.006	0.003	0.030		0.087	0.133	0.586	-0.311
SCS	-0.100	-0.139	-0.076	0.046		-0.157	-0.294	-0.387
MV	0.778	0.930	0.881	0.042	-0.112		0.778	0.997
FC	0.549	0.492	0.567	0.166	-0.086	0.551		0.578
MOFC	0.740	0.927	0.856	-0.076	-0.134	0.982	0.743	

[1] Standard errors for genetic correlations ranged from 0.021 to 0.315; and for phenotypic correlations they range from 0.001 to 0.020

Table 7.9 Genetic correlations among lactations within the same traits

	Genetic correlations					
Trait	1 – 2	1 – 3	1 – 4	2 – 3	2 – 4	3 – 4
MY	0.933	0.937	0.927	0.992	0.980	0.989
FY	0.942	0.946	0.921	0.991	0.986	0.986
PY	0.921	0.923	0.889	0.988	0.975	0.989
BWT	0.974	0.958	0.931	0.994	0.983	0.989
SCS	0.887	0.796	0.754	0.962	0.918	0.986
MV	0.779	0.665	0.670	0.787	0.660	0.926
FC	0.924	0.860	0.907	0.936	0.921	0.953

MOFC	0.758	0.681	0.790	0.754	0.697	0.838

[1] MY – 305-day milk yield; FY – 305-day fat yield; PY – 305-day protein yield; BWT – lactation body weight; SCS – somatic cell score; MV – cumulative milk value; FC – cumulative feed cost; MOFC –margin over feed cost

7.5 DISCUSSION

7.5.1 *Mean production, body weight, SCS, and profit indicator traits across lactations*

The mean first lactation MY, FY, and PY for the Holstein cows in Québec were slightly higher than the values reported by Martin et al. (2019) in Canadian Holstein cows that calved from 2000. The difference in mean production traits in this study and those of Martin et al. (2019) was that the first lactation cows in this study calved from 2010 and thus continuous selection emphases for production traits have changed the population means for the milk production traits. Also, the data for this study were from only herds in Québec whilst those of Martin et al. (2019) were Canadian Holstein cows. The first lactation mean BWT (618 kg) was significantly higher than 504 kg (Moore et al., 1992), and 533 kg (Parke et al., 1999) weight at calving for cows in herds enrolled in the Québec Dairy Herd Analysis Service (DHAS) program from 1979 to 1986, and from 1979 to 1991, respectively. This suggests that there might be direct or indirect selection for BWT over time in Holstein herds in Québec. The mean SCS were similar to the 2.01 and 2.14 reported in Canadian (Martin et al., 2019) and Québec (Do et al., 2018) herds, respectively. The mean first lactation MV and FC were higher than values reported by Moore et al. (1992) in a similar population between 1979 and 1986. First lactation FC represented 31.6% of the MV, and this is favourably less than the 36.9% reported earlier by Moore et al. (1992).

The mean second lactation MY, FY, and PY were 15 to 16% higher than the mean milk production traits at first lactation. A similar increase (14%) was observed in Japanese Holstein cows which calved between 2007 and 2011 (Yamazaki et al., 2019). Second lactation BWT and SCS also increased by 8.5% and 18% from the first lactation BWT and SCS, respectively. Second lactation MV, FC, and MOFC increased by between 11% to 18% of the first lactation values. Second lactation FC constituted 30.4% of the second lactation MV.

The third lactation trait means were all higher than those of the second lactation. The increases ranged from 5% to 11%. There were slight increases (0.1 to 6.8%) between third lactation trait means and the fourth lactation trait means except for MOFC (-0.5%). The feed costs of both third and fourth lactations constituted 30% of third and fourth lactations' MV similar to earlier lactations.

7.5.2 *Phenotypic variances and heritability estimates of traits across lactations*

The high phenotypic variations in the third and fourth lactations either partly suggest that there is a greater influence of the environment on the traits in later lactations or partly attributed to more random variability. The heritability estimate for first lactation MY (0.468) was higher than the 0.26 reported by Do et al. (2018) with a standard error of 0.07, but within the range of 0.410 to 0.518 in previous studies in Canadian Holstein cows (Muir et al., 2004; Miglior et al., 2007; Bilal et al., 2016). The difference in the estimates between Do et al. (2018) and this study could be attributed to differences in the sample sizes and statistical models used. Do et al. (2018) used a single trait animal model with 1,793 records and fitted the fixed effects of herd*parity group and a linear regression of DIM in their model. Miglior et al. (2007) also used a herd test-day animal model with 60,645 test-day records from 5,022 cows and reported a slightly higher estimate of 0.518 for MY. They fitted a classification fixed effect of herd-test day, fixed linear regressions of age, parity, and season of calving, and random regression effects of permanent environment and animal in their model. Swalve (1995), however, indicated that heritability estimates from test-day records were generally lower than from 305-day lactation records. The higher milk production levels in dairy cattle have been associated with higher heritability estimates for milk production (Hoekstra et al., 1994).

The first lactation heritability estimate of FY was similar to the value of 0.369 reported by Miglior et al. (2007), but higher than reports of other studies (Moore et al., 1992; Dematawewa and Berger, 1998; Kadarmideen et al., 2003; Stoop et al., 2008; Do et al., 2018). The heritability estimate of first lactation PY agrees with estimate (0.33) by Hoekstra et al. (1994) in Dutch Black and White dairy cows but was higher than estimates reported by Do et al. (2018), Dematawewa and Berger (1998), and Moore et al. (1992). Miglior et al. (2007) estimated a higher heritability of 0.423 for protein yield at first parity in Québec Holstein cows that calved between 2001 and 2004. Miglior et al. (2007) used a model which included random regression coefficients for permanent environmental effects. Among the production traits, PY had the lowest heritability estimate at first lactation. Similar findings have been reported by different authors (Moore et al., 1992; Hoekstra et al., 1994; Kadarmideen et al., 2003; Stoop et al., 2007; Stoop et al., 2008; Do et al., 2018). Heritability estimates for PY were also lowest in second and third but not fourth lactation. The heritability estimates for the milk production traits tended to decrease with increasing parities which agrees with studies in Swedish Holstein cows (Carlén et al., 2004). The increase in residual variances in later lactations mainly contributed to the decreasing heritabilities in the later lactations. The decreasing heritabilities with increasing lactation numbers could also partly be attributed to selection in first lactation. Miglior et al. (2007), however, reported higher heritabilities for third parity production traits compared with heritabilities in second parity.

The heritability estimates for BWT were moderate (0.300 to 0.423) and were similar to report by Parke et al. (1999), but higher than the 0.24 reported in Holstein-Friesian cows in New

Zealand (Ahlborn and Dempfle, 1992). The estimates tended to increase with increasing lactation numbers although the highest estimate was found in second lactation. The generally increasing heritabilities of BWT with lactation were mainly due to the effects of increasing additive genetic variances. The heritabilities for BWT in this study were higher than the 0.165 to 0.223 reported by Moore et al. (1992) for body weight at first test-day after calving in first lactation Holstein cows in Québec. Several studies have also reported higher estimates for body weight ranging from 0.44 to 0.60 (Veerkamp and Brotherstone, 1997; Veerkamp et al., 2000; Søndergaard et al., 2002; Berry et al., 2003). The differences in the heritability estimates of BWT could be due to the differences in population size, editing criteria, statistical models used, and trait definitions. Whilst the studies reviewed defined weight at calving as the first test-day body weight after calving, BWT in this study was the body weight of a cow taken between day zero and 450 DIM during her lactation (Figure 7.1). It should, however, be noted that most of the body weights were recorded within the first three test-days.

The heritabilities for SCS across lactations did not follow any regular pattern although the estimate for the first lactation was the lowest. This was contrary to reports by Miglior et al. (2007) and Samoré et al. (2008) who observed significant increases in heritabilities across parities. However, Carlén et al. (2004) reported decreasing heritabilities (0.14 to 0.10) with increasing parities in Swedish Holstein cows. They explained the decreasing heritabilities across parities as due to both increasing residual variances and decreasing genetic variances in some cases. In this study, the heritability estimates for SCS agrees with those of other studies ranging from 0.10 to 0.14 (Haile-Mariam et al., 2003; Carlén et al., 2004; Zavadilová et al., 2011; Do et al., 2018). Miglior et al. (2007), however, reported high estimates for second (0.27) and third (0.34) lactations using multi-trait random regression test-day models. These high estimates were explained as being probably due to inclusion of extreme values at the beginning and end of lactations in the computation of the heritabilities referred to as “end-of-range” problem (Zavadilová et al., 2011).

The moderate heritability estimates for MV were similar to the 0.245 and 0.323 reported by Moore et al. (1992) using bivariate analyses of milk value and four or five-trait selection index. The low heritability estimates for FC across lactations were below the values (0.157 to 0.174) reported by Moore et al. (1992) in first lactation cows. Generally, the heritability estimates of MV and FC decreased with increasing lactation numbers and these were mainly attributed to the effect of increasing residual variances rather than increasing or decreasing genetic variances. The moderate heritability estimates for MOFC were similar to the estimates of 0.255 for milk value less feed cost in Holstein cows in Québec herds (Moore et al., 1992). As with MV and FC, the heritabilities of MOFC decreased with increasing lactation numbers.

7.5.3 *Phenotypic and genetic correlations among and within traits across lactations*

The high phenotypic correlations between MY and PY corroborate the findings of Carlén et al. (2004). The genetic and phenotypic correlations among the milk production traits observed in this study were similar and within the ranges reported in other studies (Schutz et al., 1990; Van Dorp et al., 1998; Carlén et al., 2004). Miglior et al. (2007) and Dematawewa and Berger (1998) have, however, reported higher genetic and phenotypic correlations among milk production traits. The genetic correlations among the milk production traits decreased with increasing lactation numbers similar to other reported works (Schutz et al., 1990; Carlén et al., 2004). This could be explained by the fact that residual variances for the production traits increased with lactation, and an indication that the effects of environmental factors on milk production traits tend to increase with lactation (Zavadilová et al., 2011). However, the phenotypic correlations did not follow any regular trend.

The weak genetic correlations between BWT and milk production traits suggest that selection for milk production will have minimal effect on body weight of cows. The genetic correlations between BWT and milk production traits agree with the close to zero correlations (-0.03 to 0.03) between average unadjusted body weight and milk production traits in Holstein-Friesian cows in the south of Ireland (Berry et al., 2003) and -0.09 to 0.03 in Scotland (Veerkamp and Brotherstone, 1997). Ahlborn and Dempfle (1992) also reported moderate genetic correlations between subjectively assessed body weight and milk production traits in New Zealand Holstein-Friesian cows.

The weak genetic and phenotypic correlations of BWT with SCS and MV across lactations were significantly different from zero, especially the genetic correlations between BWT and MV in second, third, and fourth lactations. The moderate to strong genetic correlations (0.352 to 0.702) that existed between BWT and FC across lactations was not surprising as heavier cows have higher maintenance costs. The negative genetic correlations that exist between BWT and MOFC suggests that the national breeding programs could consider properly accounting for body weight as a cost in the national selection indices to increase or enhance cow profitability.

The weak and positive genetic correlations between milk production and SCS in first lactation were largely comparable to Schutz et al. (1990) and Rupp and Boichard (1999) estimates which ranged from 0.11 to 0.29. The weak but negative genetic correlations between FY and SCS in later lactations could be attributed to selection for milk production and culling of low producing cows with mastitis during first lactation (Banos and Shook, 1990). Schutz et al. (1990) and Miglior et al. (2007) have also reported mostly weak and negative genetic correlations between SCS and milk production traits in second and three lactations whilst low to medium genetic correlations (0.03 to 0.23) were observed across three lactations in Swedish Holstein cows (Carlén et al., 2004).

The phenotypic correlations between SCS and milk production traits across lactations were all weak and negative and agree with other findings (Banos and Shook, 1990; Schutz et al., 1990), indicating a decline in milk production with increasing SCS. The increasing genetic and phenotypic correlations between SCS and BWT in later lactations compared to first lactation could be due to selection on SCS in the first lactation.

Strong genetic correlations were found between MV and milk production traits across all lactations with the strongest correlations between MV and FY. The genetic correlation of MV with MY were relatively lower than with FY and PY. The lower correlations are due to the fact that milk yield *per se* is not important in the pricing of milk in Canada; milk prices at the farm-gate level are basically a function of fat yield and protein yield, with some other minor adjustments. The weak but positive genetic correlations between BWT and MV after the first lactation suggest that heavier cows may be a bit valuable in terms of their milk value; however, heavier cows have been reported to be less efficient than smaller cows (Sieber et al., 1988) since heavier cows have higher maintenance cost (Visscher et al., 1994). This was observed, in this study, through the moderate to strong genetic correlations (0.352 to 0.702) between BWT and FC across lactations in addition to the negative genetic correlations between BWT and MOFC (-0.049 to -0.311). This confirms that indeed heavier cows are less profitable as the maintenance costs of heavier cows are higher than smaller cows (Dempfle, 1986; Visscher et al., 1994) hence tend to reduce margin over feed cost.

The high genetic correlations that existed between MOFC and milk production traits suggest that MOFC could be improved by directly selecting for milk production traits, especially FY and PY. The strong positive genetic correlations between MV and MOFC across all lactations suggest that MV and MOFC are probably similar traits.

The largely weak genetic correlations of BWT with MY, FY, PY, and MOFC are favourable and indication that cow body weight could be included in a selection index that comprises BWT, milk production traits, FC, and MOFC. The moderate heritability of BWT will make it possible to reduce or stop the increase in cow body weight and feed cost thereby increasing cow profitability when all these traits are included in an index.

7.5.4 *Genetic correlations between the same trait at different lactations*

For the milk production traits, the high correlations between lactations in this study (0.889 to 0.992) were similar to Carlén et al. (2004), but higher than those of Miglior et al. (2007). The high correlations suggest that each of the milk production traits are the same traits in first and later lactations thus the same genes are controlling each of these traits in first and subsequent lactations. The genetic correlations between BWT in different lactations were also high and close to unity (0.931 to 0.989). This is an indication that lactation body weight in different lactations is the same trait and controlled by the same genes. In an attempt to produce relatively smaller and more efficient cows to increase cow profitability, cows with smaller weight could be selected in the first parity without necessarily putting more selection pressure on BWT in later lactations.

The genetic correlations among SCS in different lactations were similar to Carlén et al. (2004), but higher than reports in other studies (Jamrozik et al., 1998; Miglior et al., 2007). Other studies have also reported higher genetic correlations between SCS in different lactations (Liu et al., 2000; Zavadilová et al., 2011), although correlations between lactations 2 and 3 were similar to those observed in this study. The relatively low genetic correlations between SCS in lactations 1 and 2, 1 and 3, and 1 and 4 partly suggests that different genes may be controlling SCS in first and later lactations (Banos and Shook, 1990; Carlén et al., 2004). The correlations of adjacent lactations tend to be higher than distant lactations. The highest correlations were observed between lactations 2 and 3, and lactations 3 and 4 which suggest probably SCS in lactations 2 and 3, and 3 and 4 are the same or similar traits. The relatively higher genetic correlations between lactations 2 and 3 compared to lactations 1 and 2, and 1 and 3 corroborate findings of other studies (Liu et al., 2000; Carlén et al., 2004; Miglior et al., 2007).

The genetic correlations for MV and MOFC at different lactations were comparatively lower than the correlations of milk production, BWT, SCS, and FC in different lactations. The correlations for the SCS were also generally lower than the production traits. The correlations within MV ranged from 0.660 to 0.926 and those within MOFC ranged from 0.681 to 0.838. For both traits, correlations of adjacent lactations (1 – 2, 2 – 3, and 3 – 4) were mostly higher than distant lactations (1 – 3, 1 – 4, and 2 – 4). Besides the correlations between lactations 3 and 4 which were 0.926 and 0.838 for MV and MOFC, respectively, the relatively lower correlations within MV and MOFC indicate that MV and MOFC in first and later lactations are different, but correlated traits. Selection indices could therefore be developed to include first and later lactations of MV and MOFC as correlated traits to ultimately improve the overall cow profitability of Holstein cows.

7.5.5 *Phenotypic and genetic trends for lactation body weight*

The phenotypic and genetic trends for BWT across lactations are presented in Figures 7.2 and 7.3, respectively. Phenotypic trends of body weight of Québec Holstein cows are positive for all lactations. The annual rate of change ranges from 3.4 kg/year to 7.2 kg/year for first to fourth lactation body weights and these are similar to the 4 kg/year and 4.5 kg/year reported for heifer cows and multiparous cows in Québec, respectively (Quebec Evolution of Dairy Production, 2010 – 2018). The appreciable changes in phenotypic cow body weights can be attributed to both improvement in management and genetic changes. This is evident by the positive genetic trends of body weight across all lactations (Figure 7.3). The genetic trend for first lactation BWT was increasing at a rate of approximately 1.0 kg/year and showed no evidence of decline. For the later lactations, there were evidences of decline in the genetic trends in the later years. However, these declines might not be factual, but rather due to truncation of data since some cows in the second to fourth lactations did not have completed lactation records. The increasing genetic trends in BWT are indications that either producers were directly selecting for bigger and heavier cows or correlated responses in body weights were being realised from the selection for MV; this could have an adverse effect on efficiency of cows, hence affecting cow profitability, as selection for body size may reduce milk production and feed efficiency in the long term (Parke et al., 1999).

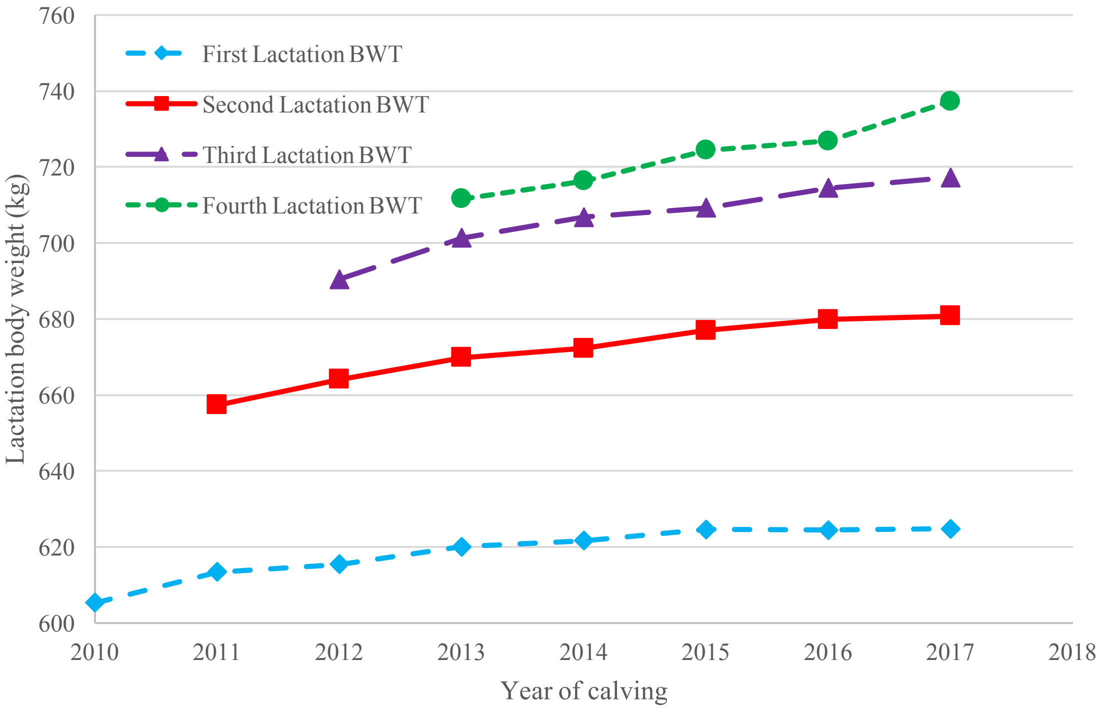

Figure 7.2 Phenotypic trends of lactation body weight (BWT) for first, second, third, and fourth lactations

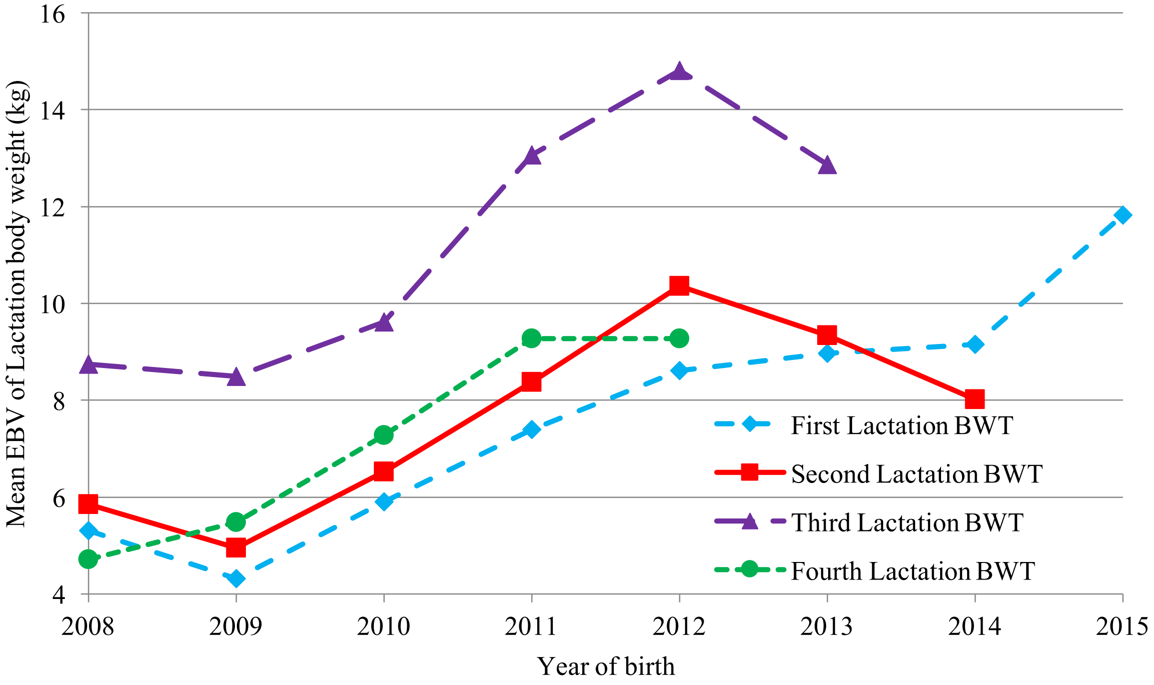

Figure 7.3 Genetic trends of lactation body weight (BWT) for first, second, third, and fourth lactations

7.5.6 *Simple selection index example*

An example of a small four-trait selection index was simulated using the genetic parameters estimated in this study to determine how the increasing genetic trends in body weight could be halted or slowed down by including BWT in an index of MY, FY, and PY. The weight of the traits in the index (b) is given below:

$b = P^{-1}Ga$

where P = phenotypic variance-covariance matrix

G = genetic variance-covariance matrix

a = vector of economic values of traits in the index

The initial economic values of the traits used in the selection index were from Vargas et al. (2002) who used a bio-economic model with a fixed milk-output. The economic values, phenotypic, and genetic variances for MY, FY, PY, and BWT are presented in Table 7.10. The index weights computed for MY, FY, PY, and BWT were -0.0498, 1.8111, 1.2270, and 0.0269, respectively.

Table 7.10 Economic values, phenotypic (σ_p^2), and genetic variances (σ_g^2) of 305-milk, fat, and protein yields (MY, FY, and PY) and body weight (BWT) used in the computation of the four-trait selection index

Trait	σ_p^2	σ_g^2	**Economic value**
MY	1423600	666244.80	-0.04
FY	2016	786.24	3.53
PY	1056	338.98	2.91
BWT	2015	604.50	0.51

Thus, the selection index, H, for any given cow is as below:

$$H = -0.0498(MY - \mu MY) + 1.8111(FY - \mu FY) + 1.2270(PY - \mu PY) + 0.0269(BWT - \mu BWT)$$

Where MY, FY, PY, and BWT are observations for 305-day milk, fat, protein yields, and lactation body weight of a cow, respectively; μMY, μFY, μPY, and μBWT are mean 305-day milk, fat, protein yields and lactation body weight, respectively; -0.0498, 1.8111, 1.2270, and 0.0269 are index weights, b for MY, FY, PY, and BWT, respectively.

The response to selection (R) on the index is given by the formular below:

$$R = i\sqrt{(b'Pb)}$$

Assuming a selection intensity (*i*) of 1.755 was applied, the expected response to selection on the index will be 3.84; and the expected change in BWT when selection was done on this index will be 33.47 kg/generation or 6.7 kg/year assuming average generation interval of 5 years. However, given that several studies have reported the economic values of body weight to be negative (Dempfle, 1986; Van Raden, 1998; Ahlborn and Dempfle, 1992), we decided to set the economic value of BWT to zero. The index weights were thus -0.0488 for MY, 1.8304 for FY, 1.1879 for PY, and -0.1268 for BWT. The expected response to selection on the index (3.83) will not see any significant change (-0.01) from the previous expected response, however, there will be a significant change in the expected response in BWT (-42.01 kg/generation or -8.40 kg/year) when we select on the index. The new index will thus be as given below:

$H = -0.0488\ (MY - \mu MY) + 1.8304\ (FY - \mu FY) + 1.1879\ (PY - \mu PY) - 0.1268\ (BWT - \mu BWT)$

This suggests that the inclusion of body weight and putting a negative weight on BWT could reverse the increasing trend in body weight. This would considerably reduce the maintenance cost of cows due to the medium to high genetic correlation between BWT and FC.

7.6 CONCLUSIONS

The estimates of heritability for milk production traits and BWT across lactations were moderate and agree with most literature values. The estimates for MY, FY, and PY generally decreased with increasing lactation numbers whilst for BWT, the estimates did not follow any regular pattern. Heritability estimates across lactations were low for SCS and FC but moderate for MV and MOFC. The observed positive genetic trends for BWT, coupled with the weak to moderately negative relationships between BWT and MOFC suggest that cow profitability is likely to be affected in the long-term if the positive genetic trends for BWT are not halted or reversed. In the future, cow BWT could be considered for inclusion in the national selection index by putting a negative weight on body weight. This, when done, will not only help sustain cow profitability, but also prevent the need to increase sizes of cow stalls in tie-stall operations at a high cost in order to accommodate larger size and heavier weight cows. The high genetic correlations (>0.9) between BWT in different lactations suggest that only first lactation BWT would be enough for inclusion in the selection index to still obtain appreciable responses in overall cow profitability.

7.7 DECLARATION OF COMPETING INTEREST

We certify that the authors have no conflict of interest with any financial organization regarding the material discussed in this manuscript.

7.8 ACKNOWLEDGEMENTS

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CONNECTING STATEMENT

Genetic and phenotypic paramters were estimated for milk production traits, lactation body weight, SCS, MV, FC, and MOFC. A simple selection index comprising lactation body weight and milk production traits has been proposed to slow down the rate of increase in cow body weight.

Chapter VIII sought to put all the pieces in chapters III, IV, V, and VI together. The information on GSDs for economically important traits and the generation intervals in the four paths of selection are put together to become more relevant to dairy producers and AI centers. A prototype software tool has been developed to monitor applied selection for 28 economically important traits in individual dairy herds. A number of benchmarks have been recommended for dairy producers to monitor applied selection in their herds with. Results can be presented in tabular or visualization forms and can be downloaded by producers or advisors for making both management and breeding decisions.

8 CHAPTER VIII: Expert system tool to monitor genetic selection differentials in animal improvement

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8.1 ABSTRACT

A prototype software tool was developed to allow a dairy producer and/or agricultural advisor to monitor the genetic selection differentials (GSD) that a dairy farm is making. Dairy producers seek to optimize genetic gains for economically important traits by genetic selection. It is important for producers and/or their advisors to regularly monitor selection practices to see if such selection is in harmony with the producer's breeding objectives. The objectives of this study were to develop a prototype software tool and visualization model to assist producers in monitoring the selection on their individual farm, and to compare their farm results with suitable benchmarks. Estimated breeding values (EBV) of 28 traits from four dairy cattle breeds in Canada, born between 1950 and 2018 were used to computed GSDs of bulls and cows. Average EBVs of all available bulls or cows on each day between 1980 and 2018 were computed. Parent GSD was then calculated as the EBV of the parent minus the average EBV of all bulls or cows at the time of conception of a progeny. Benchmark GSDs were computed and stored in flat files and individual producers could use these benchmark GSDs as reference goals to compare and visualize the selection they are making with. The developed software tool is updatable every time a new genetic evaluation list is produced (typically 3 times per year in Canada). The concept can be equally well applied to the other livestock species for which genetic evaluations are routinely computed (e.g. beef cattle, swine, sheep, goats). This methodology is not limited to the 28 traits, but can also be used for any new traits that are genetically evaluated. The prototype was initially developed using SAS (for rapidity and convenience in a University research environment); we have subsequently translated the prototype software using a variety of Open Source tools (R, Linux system tools, Fortran), for portability and easy use by breed societies and producers.

Keywords: Benchmark, dairy, estimated breeding values, Genetic selection differential, milk production

8.2 INTRODUCTION

Precision agriculture involves providing tailored advice and monitoring specific to the field, animal or individual farm; appropriate tools, thus, need to be developed to undertake such tasks. Precision dairy farming, in terms of precise selection decisions and regular monitoring of those decisions to align selection applied to the breeding objectives of producers, will improve the productivity and profitability of a dairy farm.

Genetic selection in dairy cattle has resulted in significant genetic gains in milk production in many countries (VanRaden, 2004; Oltenacu and Broom, 2010; Miglior et al., 2017). The genetic gains in animal productivity have a strong association with farm profitability (Thompson et al., 2015), making genetic selection an essential factor to a profitable animal farming business. Genetic trends have been used to monitor and demonstrate genetic gains in breeding programs by genetic evaluation organizations and breed societies such as, Lactanet, Charolais beef association, Animal Genomics and Improvement Laboratory (www.aipl.arsusda.gov).

Annual genetic trends depend upon genetic selection differentials ($EBV_{selected} - EBV_{average}$), accuracy of EBVs, and generation intervals in each of the four pathways of genetic improvement (Rendel and Robertson, 1950). The routine computation and monitoring of genetic selection in any livestock population, including dairy cattle, will therefore be important to farmers, advisors, and other sectors, e.g. Artificial Insemination (AI) centers. Reports of genetic trends and genetic lag in livestock show the realized results of selection, but not the cause of these results (i.e. amount of selection emphasis applied). Genetic trends do not also show the effects of selection in the four pathways of selection (Van Tassell and Van Vleck, 1991). In most dairy production systems, individual dairy producers control the selection made in the sire-to-cow (SC) and dam-to-cow (DC) pathways that is, the male-to-female and female-to-female pathways, respectively. On the other hand, AI centers control the sire-to-bull (SB) and dam-to-bull (DB) pathways, that is the male-to-male and female-to-male pathways, respectively. It is, therefore, important to show the selection realized in each pathway, so that both producers and AI organizations making selection decisions are properly informed about what selection they have been making.

In most national breeding programs, the genetic gains expected from breeding objective traits are often not commensurate to the selection thought to have been applied for these traits due to reasons such as selection emphases on traits other than the breeding objective traits, lack of opportunity for selection due to small herd size, involuntary culling, non-random mating (Van Tassell and Van Vleck, 1991; Burnside et al., 1992; García-Ruiz et al., 2016), and the absence of information and feedback on farmers' past selection activities. Annual genetic gains of between

2% to 3% of the trait mean are possible in national breeding programs when there are intense and accurate selection (Rendel and Robertson, 1950; Simm et al., 2004). To consistently attain this genetic gain and beyond, we will need appropriate tools to routinely measure and monitor selection applied in most animal herds. A deterministic program such as ZPLAN has been designed to optimize selection strategies in livestock breeding (Willam et al., 2008), but at the population level.

There is presently no tool available for individual dairy producers to measure and monitor the amount of selection emphases they are applying to breeding objective traits within their herds. Australian beef cattle breeders have some tools and reports for measuring genetic trends in individual herds (Johnston, 2007). In addition, Johnston (2007) reported that there were significant differences among herds in their sire selection differentials; however, there is no information as to whether such selection differentials are calculated on a routine basis for individual producers. In Canada, Lactanet is the institution responsible for genetic evaluations of dairy breeds. Lactanet publishes national and provincial genetic trends for 16 traits of all dairy cattle breeds (Holstein, Jersey, Ayrshire, Brown Swiss, etc.), but not realized selection in each of the 4 pathways of genetic improvement. Although genetic trends give an overview of the results of past selection practices in the entire national or provincial population, it does not give any information on selection emphases individual dairy producers are making. Monitoring and optimizing selection is important; if selection applied is less that what is possible, expected genetic gains will be less than optimal. Probably, one of the greatest limitations to achieving optimum genetic gains in individual dairy herds is the non-existence of a tool to measure and monitor selection pressures for selected traits. Precision agriculture needs to monitor what selection is being made and achieved, to be able to make decisions about which animals to use as parents of the next generation, to achieve the desired goals of the individual producer. Adequate data exist, but have not yet been exploited in ways to monitor selection in individual herds. It is important to have a decision support system (DSS) to assist producers and advisors to facilitate informed decision making and monitoring of selection. Upton et al. (2001) comment that “making it happen” is an essential component of genetic improvement, thus the measuring and monitoring of genetic selection differentials (GSD) will be important in making it happen.

The objectives of this study were to develop a precision animal agriculture GSD monitoring system built on genetic evaluations (EBVs) and herd recording information, to be used on a routine monitoring basis, by producers, advisors, and other managers of genetic improvement. This would enable producers to extract added value from the EBV data. The results were visualized to show longitudinal effects and/or comparisons amongst traits and allow a user to compare herd selection against user-selected benchmarks. Thus, the objective was to take the concepts outlined by Hagan and Cue (2018) and Hagan et al. (2020) and implement a prototype GSD visualization system.

8.3 MATERIALS AND METHODS

8.3.1 Data and animal

Data for this study were EBV files from the genetic evaluation runs which are routinely calculated for all dairy cattle breeds in Canada, and herd characteristics information from milk recording, both of which were provided by Lactanet (formerly the Canadian Dairy Network, and Valacta). The EBV files used in the development of this software suite contained information of about 30 trait EBVs, (such as 305-day milk yield EBV (MY), 305-day fat yield EBV (FY), 305-day protein yield EBV (PY), lifetime performance index EBV (LPI), etc.), animal, sire and dam identifications, animal date of birth, and herd identification as presented in Table 8.1. The herd information file contained herd identification, milking system, production system, and agricultural region in Quebec as presented in Table 8.2. The software suite has been developed as a complement to genetic evaluations, genetic trends produced by Lactanet, mating programs (e.g. PROGENIE) and Lactanet's software (e.g. COMPASS) which optimises breeding strategies in herds to maximise herds' profitability. The software has been deliberately developed in a modular manner, so as to make it easier to modify, update, and parallelized.

Table 8.1 Example of cow EBV file used as input for the development of the prototype software

Cow ID	Cow DOB	Herd ID	Sire ID	Dam ID	MY	FY	PY
CANF001	1990-12-01	00001A	CANM002	CANF003	34	12	8
CANF23X	1998-02-23	00235B	CANM123	CANF333	0	-5	2

[1]DOB – Date of birth; MY – 305-day milk yield; FY - 305-day fat yield; PY - 305-day protein yield

Table 8.2 Example of dairy herd information (DHI) file used as input for the development of the prototype software

Herd ID	Agricultural region	Milking system	Production system
00001A	Côte-Nord	Robot	Conventional
00235B	Laval	Milking parlour	Organic

The suite is logically divided into two parts; the 'back-end' portion which needs to be run once after each new genetic evaluation release (typically every 4 months) and the user-interface portion where the user (producer, advisor, etc.) selects the specific herd to view trait GSDs and benchmarks. The 'back-end' part of the suite is ideal for concurrent processing; for example, in the context of the 4 main dairy breeds in Canada that have been used (Holstein, Ayrshire, Jersey, and Brown Swiss), there are 28 trait EBVs for each breed and 4 pathways which corresponds to 4*28*4, totaling to 448 separate back-end calculations. All of these calculations can be run in parallel by making use of modern multi-core machines and/or a clustered system whereby concurrent processes can be spawning onto a cluster of computers.

8.3.2 Cows' and bulls' availability, average EBV of available bulls and cows, and computation of GSD of all sires and dams

The availability periods for all bulls and cows in the EBV files were determined. For each bull or cow that has been used for breeding (sire or dam), its first and last progeny dates of birth were taken from the bull or cow EBV file. From these, the dates of conception of the first and last progeny were calculated by subtracting 280 days, being the assumed gestation length of cows, from the dates of birth of progeny. For each sire or dam, the 1st and 99th percentile dates of conception of the sire's or dam's first and last progeny were used as the sire's or dam's first and last usage dates. The period between these two usage dates was the sire's or dam's availability period. The percentiles were used to exclude the odd outliers. For example, the use of frozen semen of a sire that is stored for 20 years after the sire has long died or been culled following its extensive usage of say 10 years. This indicates that the sire was not physically available during the 20 years after its extensive usage of 10 years. The 99th percentile will seek to remove this extreme value. For unused bulls (i.e. bulls that did not produce any offspring in their lifetime), the dates at which they attained 18 and 24 months were determined. The period between these two dates was deemed as the availability period of such unused bulls, for potential use in a young-sire testing program, with the assumption that an unused bull will be culled after two years. Similarly, for unused cows, the dates at which they attained 12 and 24 months were used as the period of their availability. Dates of conception that fall outside the 1st and 99th percentiles were deemed as outliers and were thus removed. In practice, these extreme outliers will be monitored constantly to ascertain as to whether they are sensible or not to be eligible for retention or flagged for omission. The average

EBVs of available bulls and available cows for each day from 1^{st} January, 1980 to date of release of the last genetic evaluations were computed.

The GSD for the sire of each cow was computed as the deviation of the sire's EBV from the mean EBV of all available sires and bulls on the day of conception of a cow. Similarly, the GSD of a dam is the dam's EBV minus the mean EBV of all available dams and cows on the day the dam was used for breeding. The GSDs computed were the GSDs of sires and dams at the time of mating and were thus the realized GSDs. Hagan et al. (2020) illustrated the computation of GSD of a sire in the data set and this has been reproduced in Figure 8.1 of this paper. New GSD for all sires and dams will be computed each time new genetic evaluations are released and these will be stored in a database or tables.

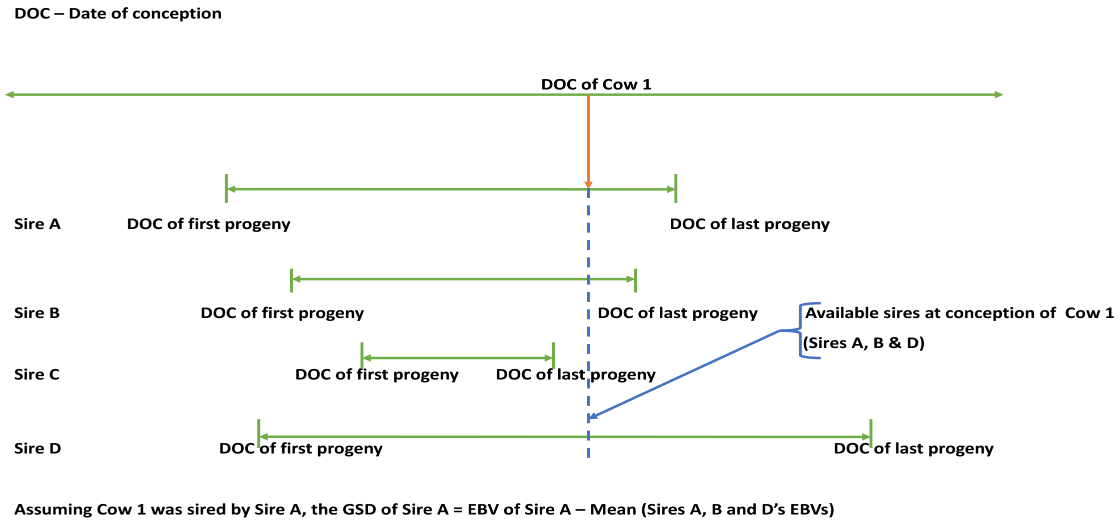

Figure 8.1 Illustration of the computation of genetic selection differential of a given sire (Sire A) from available sires (Sires A, B and D). Sourced from Hagan et al. (2020).

In Fig. 8.1, sire A produced cow 1 on the date of conception (DOC). At DOC of cow 1, the potential bulls that were available and could have been used to produce cow 1 were sires A, B and

D. The GSD of sire A will thus be the EBV of sire A minus the average of bulls A, B and D. Table 8.3 illustrates the data structure for the computation of GSD for each sire. Arbitrary animal identifiers and EBV figures have been used to illustrate the computations of sire GSD.

Table 8.3 Computation of genetic selection differentials for sires of given cows

Animal Id	DOB	DOC	Sire Id	Dam Id	Sire EBV	Mean EBV	GSD
Cow001	1990/12/30	1990/03/25	Sire001	Dam001	10.0	7.8	2.2
Cow003	2000/10/06	2000/01/01	Sire005	Dam007	5.0	8.5	-3.5

[1] DOB - date of birth; DOC - date of conception; EBV – estimated breeding value; GSD – genetic selection differential

8.3.3 Establishment of benchmarks

Appropriate benchmarks were established and calculated against which the mean GSD of individual herds can compared with. These benchmarks include the mean GSD of each of the 28 traits for each dairy cattle population, the mean GSD of the top and bottom 10% of sires of cows, dams of cows, sires of bulls and dams of bulls, mean GSD of top and bottom 10% of herds in the population and the mean GSD of top 10% available bulls and cows for each year of conception in the population. Other possible benchmarks are the mean GSD of each housing system (tie stalls and free stalls herds), mean GSD of herds of each agricultural region, and mean GSD of herds of each production system. The production system could be, for example, housing system (tie-stall vs free-stall), conventional production system or organic production, automatic milking system (i.e. robotic milking system), etc. We would expect herds with robotic milking system to put more selection pressure for udder conformation and teat placement. Also, free-stall herds are expected to place greater selection pressure on feet and legs than tie-stall herds.

8.3.4 Development of software suites

The concept of the software suite was initially developed using SAS software (as a Rapid Application Development environment in a research and university setting) to compute the average EBV of all available bulls or cows on each day and GSD of a sire or dam on a routine basis, and produce graphs for individual dairy herds and benchmarks (Hagan and Cue, 2018; Hagan et al., 2020). These computations were then translated to Open Source suite of programs for portability and for use where SAS™ is not available e.g. breed societies, milk recording organizations, etc. Initial Open Source development was attempted in R, but testing showed that some parts were very slow using R (e.g. calculating average EBV of available parents and calculation of the GSDs). These parts were thus re-written in Fortran (using the gfortran compiler for portability). Other parts used R, awk, and Linux command line tools, running under a bash shell. Development was in a Linux environment, but can be easily adapted to other environment; all codes and tools used Open Source software and are developed and coded with portability in mind. Data results were stored in data tables; however, any database could be used to store data results. Although some optimization was done by replacing 2 parts of the R code with custom-written Fortran code: CalcAveEBV and CalcSelectDiff, the objective was to develop and demonstrate a working prototype. However, we leveraged the power of R (lmerTest package) to estimate standard errors of the herd-year mean GSDs. The step by step process involved in the development of the software is illustrated in the flowchart in Figure 8.2 and explained below.

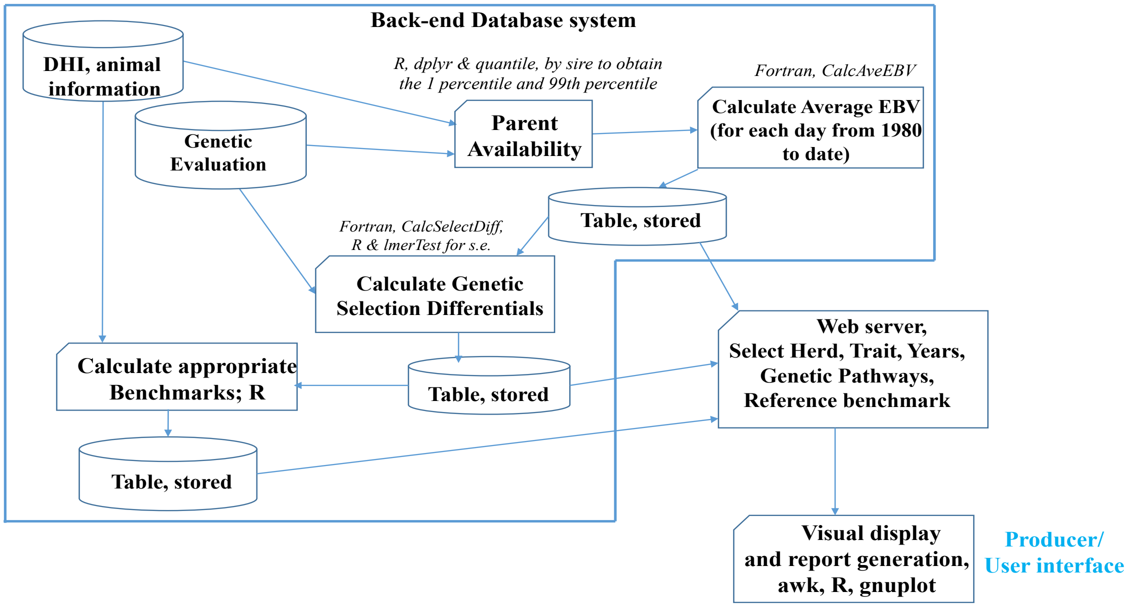

Figure 8.2 Flow chart of the procedures in the development of a prototype software

8.3.5 Back-end tasks

(I) Dairy herd information (DHI) together with the current run of genetic evaluations of cows and bulls (EBVs) were the input files used to determine the availability period of each parent (sire and dam). The dplyr package and the quantile function of R were used in determining the availability period of each cow or bull.

(II) The average EBV of all available bulls and cows on each day from 1st January, 1980 to date of release of last genetic evaluations were computed using a purpose-written Fortran program called “CalcAveEBV”. The average EBV of all available bulls and cows were repeated for each of the 28 traits in the EBV file for each breed and the results were stored in tables and flat files for subsequent use.

(III) The GSD of each sire or dam of any given cow or bull were computed for all the 28 traits in all 4 pathways of selection using purpose-written Fortran programs named “CalcSelectDiff”. The lmerTest package of R was used to compute the standard errors of the herd-year GSDs. All results were also stored in tables for use in steps V and VI. Since there are 448 jobs (being computation of GSDs of 28 traits in 4 pathways and 4 breeds) to be performed, multi-core and/or Cluster of Workstations (CoW) could be utilized.

(IV) A number of appropriate benchmarks of GSDs of the population were computed using R and stored in tables. Description of the types of benchmarks have been given in section 8.3.3. All computations in I to IV are back-end jobs and will be recomputed anytime new genetic evaluations are released.

8.3.6 Web-server

V) All the information on average EBV, GSDs, and benchmarks are fed into data tables (flat files were used). The information is delivered in a test web-server to allow individual producers to sign-in and access on-demand reports and graphs of their herds. The web-server uses cgi-bin and php to run user-selected scripts (carefully controlled and validated user-input for security) to deliver user choices. Although we have not implemented this, we have developed a prototype and it is envisaged that in an operational context one would implement user access control. The user access control can be any suitable control, e.g. user-id and password, all the way up to network information service (NIS) or active directory (AD). Access can be defined in various ways: e.g. an individual producer can be restricted to just his/her own herd and benchmarks, whereas an advisor to several producers could be restricted to only herds he/she is advising. Advisors can, however, display an individual herd (and benchmarks) at any given time.

8.3.7 User interface

(VI) On-demand visualization and reports were generated with Open Source software (e.g. awk, R, and gnuplot). A producer can select his/her herd (if the producer has only one herd identification, then only 1 choice is available to him/her). An advisor would have access to several herds (with producer permission), and therefore can select specific herd to review. Producer/advisor can select the breed (again, only actually a choice if more than 1 breed). Producers can also specify the years to display (e.g. 1980 to date, 2001 to date, etc.), the pathway (SC or DC), the trait, standard errors for herd-year mean GSDs, or whether the individual GSD data points should be displayed or not. The web-server will display PDF reports and graphs (comparable to the displayed output) and .csv files with the same information (for download and subsequent use). The downloadable files are to allow the use of the derived information in other subsequent tool-chains, e.g. we envisage that an agricultural economist might want to use these results as part of a whole-farm economic model to look at the whole-farm value of the genetic selection and its impact on farm productivity and profitability.

As indicated in the introduction, annual genetic improvement is both a function of GSD and generation interval (L). There are also 4 pathways of L (SB, DB, SC, and DC). It is possible to show the L for each animal in a producer's herd, together with the reference benchmark population proportions, to enable a producer to see if selection is coming at the expense of keeping breeding animals too long or using selected parents which are older than desirable. This will provide a visual indicator to a producer of the age of each parent animal.

8.4 RESULTS

8.4.1 Benchmarks

The mean population GSD of MY, FY, PY, and LPI for sires of cows in the Ayrshire breed are presented in Fig. 8.3. The mean GSDs for the three milk production traits and the LPI showed generally positive trends from 1989 to 2009. After 2009, the GSDs of all traits appear to be declining. The mean population GSDs serve as population benchmarks. They are useful for both describing past selection applied in the SC pathways in the Ayrshire population, and are suitable benchmarks that individual producers can compare their herds' realized selection with. Besides the population mean GSD for the SC pathways, there are also mean GSDs for the other three pathways of selection, SB, DB, and DC. Whilst dairy producers could use SC and DC benchmarks as comparable indicators to monitor their selection emphases for males and females, respectively; AI centres would use the population GSDs of the SB and DB pathways to monitor their selection emphases. Figure 8.4 presents the mean GSDs of SC of the top and bottom 10% of herds in the Ayrshire population and the top 10% available bulls in the population and these are other benchmarks that are available to producers for comparison with their herds. These benchmarks have also been produced for the other pathways of selection (SB, DB and DC).

8.4.2 Example of GSDs in two selected herds

We have presented mean GSD for FY of sires of cows in 2 selected Ayrshire herds against 3 benchmarks (average population GSD of FY, top and bottom 10% of herds) (Figure 8.5). The SC pathway has been presented here because it is the major pathway controlled by producers. Selection emphasis of Herd A appears similar to that of the population selection pressure for FY. Selection pressure of Herd B is similar to the bottom 10% of herds in the population. Could this be deliberate or accidental? Probably, the selection objective of Herd B was for some other trait other than FY. It is also possible that Herd B has not paid attention to the genetic merit of available sires and has fallen behind. This is where this expert system tool developed comes in handy for producers. This retrospective view cannot answer that question, but if used as an on-going monitoring tool, then we could ask the producer what she/he is doing.

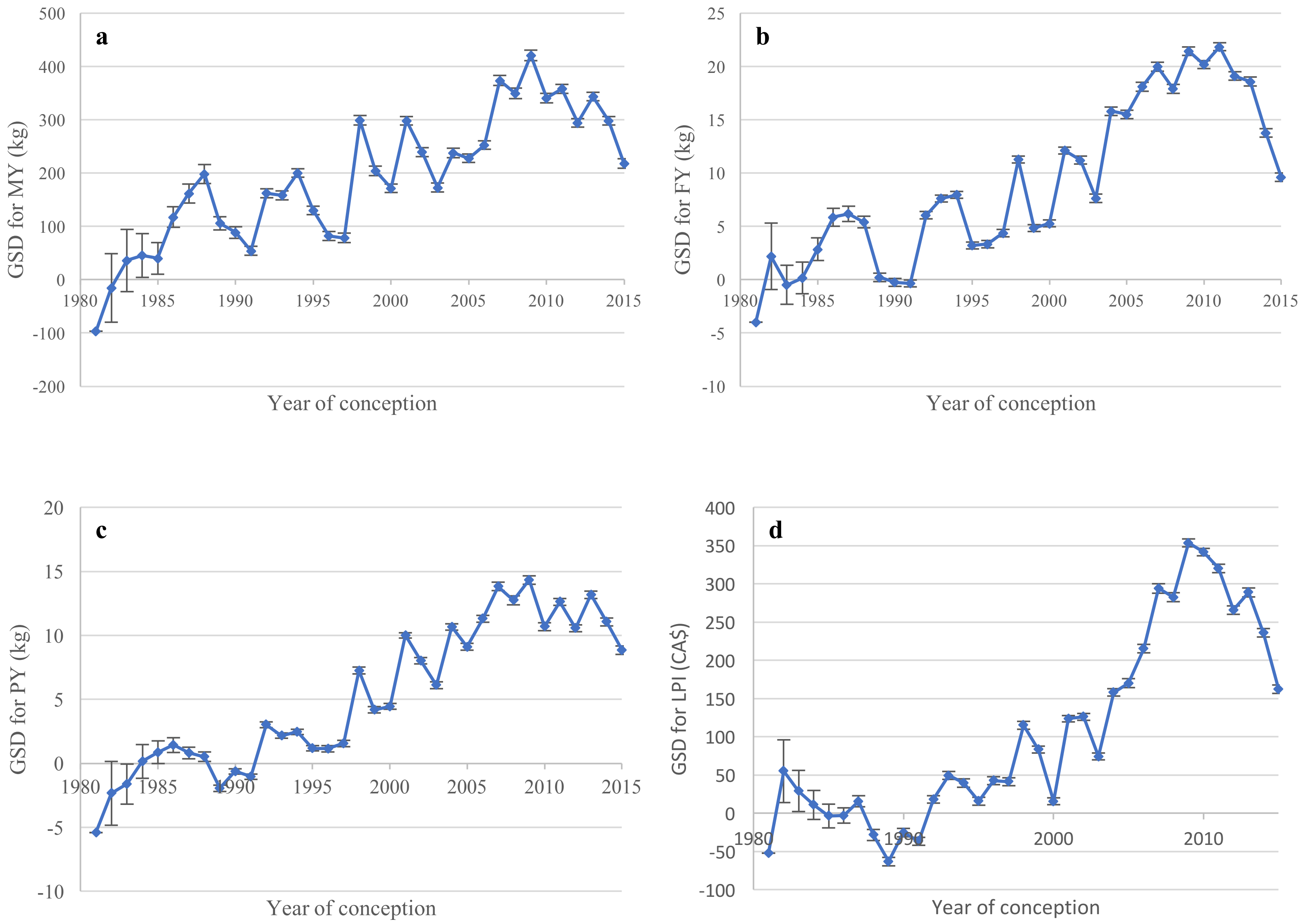

Figure 8.3a-d Population mean genetic selection differentials (GSD) for 305-day milk, fat, and protein yields (MY, FY, PY), and lifetime performance index (LPI) by year of conception for Ayrshire sires used for breeding between 1980 and 2015

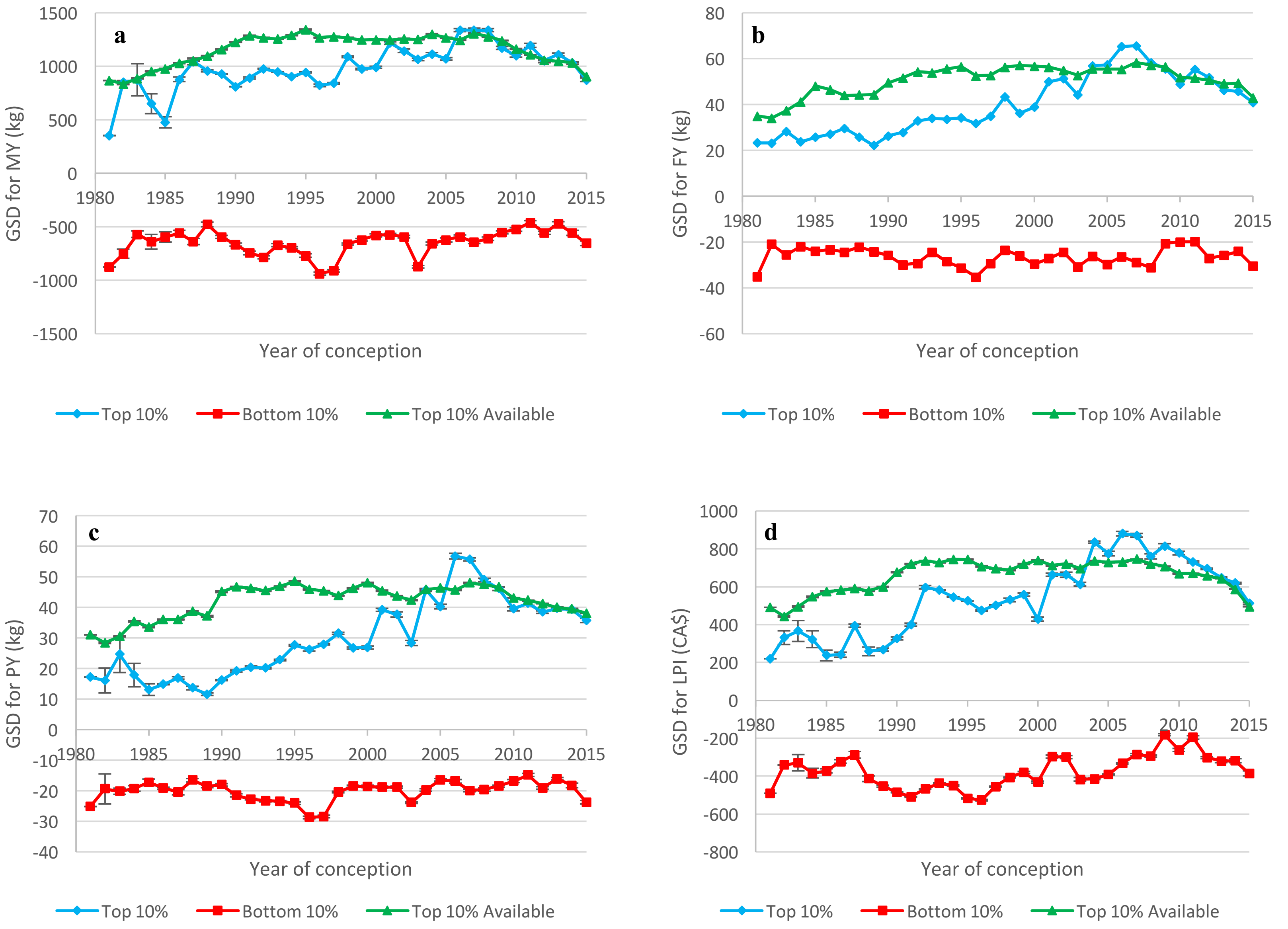

Figure 8.4a-d Mean genetic selection differentials (GSD) for top and bottom 10% sires and top 10% available bulls per year of conception for 305-day milk, fat and protein yields (MY, FY, PY) and lifetime performance index (LPI) for the Ayrshire dairy population

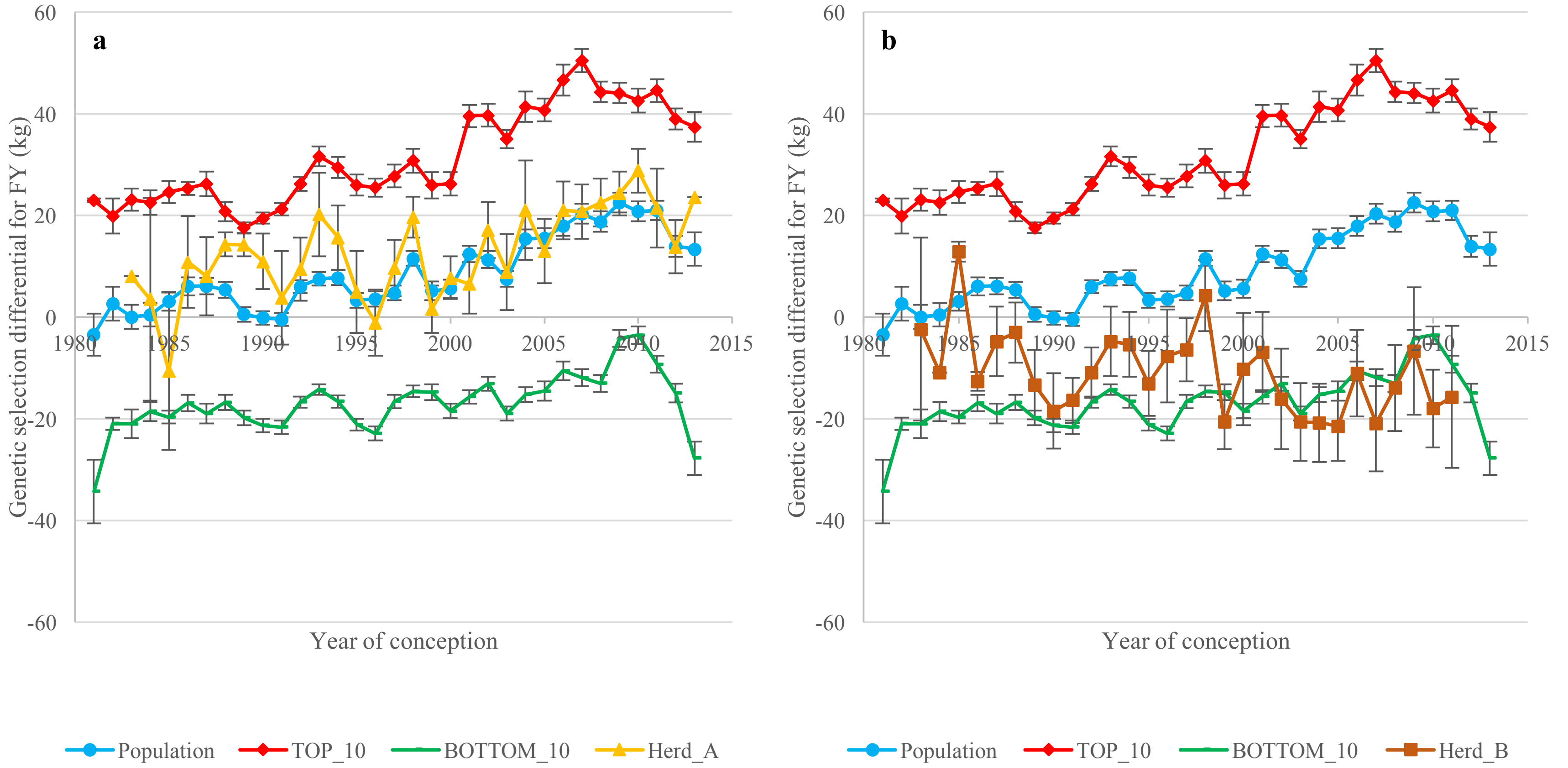

Fig. 8.5a-b Mean genetic selection differential (GSD) of 305-day fat yield (FY) for population, top and bottom 10% of herds and (a) Herd A and (b) Herd B by year of conception of progeny.

8.5 DISCUSSION

For precision dairy production, it is important for dairy producers to have knowledge of past selection applied on economically important traits so that producers can make changes if they are moving in unintended and undesirable directions. A prototype precision agriculture software has been developed to allow dairy producers monitor past selection applied and current selection being applied in their herds. The dairy industry on the whole will also find this software useful as the industry will need knowledge of past selection applied so that it can make changes in selection emphases when new traits gain prominence in their contribution to the profitability of the dairy production business. The benchmark population average GSDs in all 4 pathways provide update of the contributions of the 4 pathways to the total genetic trends for economically important traits. For instance, Van Vleck (1977) and McAllister (1980) indicated many years ago that the SB and DB pathways contributed between 71 and 76% of the total genetic gains for milk production in dairy cattle populations, whilst in more recent times (1990 to 2010), García-Ruiz et al. (2016) reported that the SB and SC pathways contributed between 73 and 90% of the total selection for milk production traits in the US Holstein population. In the Canadian Holstein population, born between 1980 and 2016, the SB and DB pathways contributed between 83 to 91% of the total selection for milk production traits. These are indications of the evolution of the contributions of the 4 pathways of selection to the genetic gains in milk production traits. The routine monitoring of the population benchmarks alone, of the 4 selection pathways, will give an indication or overview of the changing dynamics of the contribution of both producers and AI centres to the genetic gains or trends that are observed for economically important traits in the national population. Industry leaders could, thus, carry out extension activities to inform and educate industry players of their contributions to genetic improvement at any point in time and advise players as to whether they are relaxing their selection efforts or not.

Another use the benchmarks, top 10% sires and top 10% available bulls, could be put to is to monitor whether the dairy industry has optimised selection pressure for a trait in a given year. For instance, when the average GSD of the top 10% available bulls is greater than the average GSD of the top 10% sires used for breeding, it is an indication that selection was not maximised and that there was further opportunity to intensify selection. From the example benchmarks displayed in Figure 8.4, it can be seen that between 1981 and 2003, selection for MY, FY, PY, and LPI were not optimised as the average GSD of the top 10% available bulls were higher than the average GSD of the top 10% sires that were used for breeding.

The software tool detailed here will enable, for instance, producers of herds A and B to monitor their past selection for different traits and also visually or graphically compare their past selection pressures with appropriate benchmarks. Producers also have the opportunity to see the standard errors of their herd-year average GSD. The standard error bars in the graphs give indications of the variabilities in sire usage. The longer the standard error bars, the smaller the number of sires used for that year. Generally, there was greater variability in the choice of sires used in herd A compared with herd B, except for years 1993 to 1996 where herd A had higher standard errors of GSDs which is an indication that herd A was relatively less variable in its choice of AI bulls for breeding from 1993 to 1996. For instance, in 1994, herd A used 10 different sires for the 19 matings made in herd A with semen from one particular bull being used for inseminating 8 different replacement cows. On the other hand, 11 different sires were used for 18 matings in herd B during the same period. The display of the standard error bars could give a broad overview of the likelihood of inbreeding in a particular herd. Although this software tool is not meant for measuring or monitoring inbreeding in a herd, a herd with consistently high standard errors of GSDs from year to year might want to consider using appropriate tools to monitor inbreeding levels in that herd.

The computed average herd-year GSDs of traits can be expressed in standardized forms by dividing the average herd-year GSD by the standard deviation of each respective years' GSD. Once this is done, an individual producer could select the GSDs of several traits for within his/her herd and compare the realized selections he/she is making for each of the selected traits with respect to other traits. This will give the producer the opportunity to know where his/her selection focus has been and whether they align with his/her breeding objectives.

Some few limitations of this software are that EBV data are retrospective, therefore parents' availability (from 1st progeny to last progeny dates of conception) may not be exact as there may be some bulls and cows that were still available even after their last progeny has been born. Going forward, AI centres could be asked to specify when they use sires and indicate when sires are no longer available for use. For cows, information on the available of a cow for breeding purposes or otherwise could be recorded during milk recording. This is an example of a modification that could be incorporated to the appropriate module without having to change the whole tool-chain. When the appropriate modification is done with the incorporation of additional piece of information stipulated, we could calculate a more accurate average EBV of all available bulls or cows on each day and thus a more precise GSD of a sire or dam from the current EBVs (i.e. what is available and the current EBV when a mating is made), so that we obtain the actual GSD intended and not what was realized. In addition, if all breeders and producers provide comprehensive information on their herds' characteristics, such as production system (organic or conventional), housing system (free-stall or tie-stall), and age or educational level of producers, then more appropriate benchmarks could be produced and incorporated into the software from which producers could have varied and production specific-characteristic benchmarks to compare with. Some of these herd factors or characteristics have significant influences on the selection applied for economically important traits (Hagan et al., 2020). Brown and Cue (1992) reported that there were significant differences between selection differentials for type traits in officially milk recorded herds and owner-sampler herds.

This software is a relatively straight-forward by-product of already existing information, we are making use of synergy and presenting it. The concept of this software is equally applicable to other livestock species, e.g. beef cattle, sheep, goats, pigs, etc., for which genetic evaluations are produced.

8.6 CONCLUSIONS

A prototype software tool has been developed for monitoring past GSD realized by individual dairy herds and AI centres. With this tool, dairy farmers have the opportunity of monitoring their selection practices over the years and making changes to their selection decisions if producers are not moving in the right direction or decisions do not align with herds' breeding goals. Dairy producers will also have an idea of the best bulls and cows available in terms of bulls/cows' genetic superiority as compared to their available contemporaries in the short term (at least for the next 4 months before the release of new genetic evaluations) hence dairy producers can choose the best bulls available to optimise the genetic gains in the producers' herds. Although this prototype has been developed using dairy cattle breeds, it is equally applicable to other livestock breeds and species for which genetic evaluations are routinely calculated. This expert system tool is making use of genetic evaluations in other ways not typically of the original use of EBVs. With this software, the dairy industry has an additional tool to monitor the contribution of each selection pathways to the total genetic progress for economically important traits in the population.

8.7 ACKNOWLEDGEMENTS

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Declaration of Competing Interest

The authors have no conflict of interest to declare.

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9 Chapter IX: GENERAL DISCUSSION AND CONCLUSIONS

The main aim of this study was to define and determine genetic selection differentials (GSD) that are being realized in Canadian dairy cattle herds and explore the effects of environmental factors on selection realized for economically important traits. The information on realized GSD, which were computed using genetic evaluation data, will be used to develop a prototype software for monitoring selection realized within individual dairy herds and compare these realized selections against some benchmarks.

9.1 Determination of availability of cows and bulls in the datasets

Theoretically, GSD is computed as the EBV of a cow minus the mean EBV of the cow's year born cohorts. Although the computation of GSD in this way is correct and allows for the computation of genetic trends in national populations, we believe this definition of GSD might not be so useful to especially individual dairy producers who will often want to know whether the animals which producers are using for breeding today are the best animals available for their breeding objective traits. The availability of each cow or bull in the EBV files which were provided by CDN was computed. The mean EBV of available cows or bulls on each day between 1980 and the date of last release of genetic evaluations were computed. The year 1980 was used as the cut-off point because not many producers will be interested in knowing their selection history 30 to 40 years ago, or most herds were probably owned by other persons other than the current owners. The mean EBV each day are updatable each time new genetic evaluations are released. The mean EBV of available bulls and cows each day are important data source that can give a fair idea of the average gene pool for economically important traits on any specific day in retrospect, and can be available for use by advisors and the dairy industry at large. A few limitations about this dataset is that it requires lots of computing space for any one trait for some of the dairy breeds e.g. Holstein. For instance, the mean EBV of fat yield for each day between January 1, 1980 and December 31, 2017 took 77 GB of hard disk space.

In addition, some animals in the EBV files did not have information of trait EBV, hence, these animals were removed from the dataset during the editing process before the computation of the mean EBV of available bulls or cows on each day. The removal of these animals meant that they were technically not available on any day although they might be physically present.

Another important data resource that has been created from this study is the combined computed GSD and herd information files for each of the four dairy cattle populations and for each of the four pathways of selection. For each breed, the GSD for sires or dams for each year of conception together with their herd information which comprise herd identification, milking system, deduced housing system, and agricultural regions have been created. The combined dataset created, is only unique to the province of Québec because we had access to only herd information from the province of Québec. One important note on the milking systems of herds from which the HS were deduced is that the milking system for herds were recorded in only 2013 and 2015. The milking system of individual herds before those points were unknown from the herd information files used. It is possible that some herds might have changed milking systems during the period of the study. It will therefore be suggested that the milking system of each herd should be record during the routine milk recording each year. This will enable future studies on the effects of changes in milking systems and HS on selection emphases of herds to be explored more accurately.

9.2 Population genetic selection differentials and generation intervals

The computation of GSD of about 28 traits and selection indices in the Holstein, Ayrshire, Jersey, and Brown Swiss populations are the first comprehensive reports of applied and realized selection by both AI centers and dairy producers in Canada. This study also introduces the concept of year of conception (YOC) in the study of GSD rather than year of birth; because genetic materials are passed on from parents to offspring at the time of conception rather than at the time of birth. The mean GSD per YOC for each trait in each selection path are important benchmarks which both AI centers and dairy producers could measure their past and present selection pressures by. The comparison of all 4 selection pathways at any given time provides information on the contributions of both AI centers and dairy producers to the total selection being applied for economically important traits by the industry. In most of the traits studied, the mean realized GSD for the last 10 years of the data were greater than the overall mean realized GSD. This partly suggests that greater selection focus is being put on breeding objective traits by both AI centers and dairy producers in recent times, and also the introduction of genomic evaluations is having an influence on the selection being realized for economically important traits (García-Ruiz *et al.*, 2016). The importance of this knowledge base gives historical perspective of past selection applied on economically important in dairy cattle breeds in Canada and the evolution of breeding objectives in the Canadian dairy industry.

Information on generation intervals (L) of 4 Canadian dairy cattle populations is also important for the industry because it is a vital determinant of the annual genetic gains in these populations. Few studies on L in Canadian dairy cattle breeds exist (Rapitta *et al.*, 1988), therefore it is vital to update the information base on L in Canada. Population L could also give an idea of the rate of production of proven bulls by AI centers for sale to dairy producers. The inception of genomics has greatly contributed to reduction in population L (García-Ruiz *et al.*, 2016) as has long been anticipated or predicted in dairy populations (Schaeffer, 2006).

9.3 Factors influencing realized genetic selection differentials and generation intervals

Statistical analyses were performed to investigate which environmental or non-genetic factors have significant effect on realized GSDs and L. The objective of testing the environmental factors is to provide information about which specific benchmarks to create in the prototype software tool. For instance, a significant effect of HS on realized GSD would mean the creation of HS specific benchmarks would be needed for producers using a particular HS to compare the realized GSD in their herds with. Besides YOC, other environmental factors were largely not important on the realized GSD and L. Generally, HS had significant effect ($P<0.05$) on selection of type traits such as STA, ANG, RUMP, DS, CONF, and FL in the Holstein and Jersey populations; whereas agricultural region had significant effect ($P<0.05$) on selection of milk production traits (MY, FY, and PY) in Holstein cows. Realized GSD for FL in tie stall herds were greater than in free stall herds and this could probably explain the reason why there is higher number of FL events in free stalls compared with tie stall in Québec dairy herds (Delgado, 2015). Paakala *et al.* (2018) also reported significant effect of HS on selection preference for conformation traits in Finnish Ayrshire AI bulls in Finland.

Significant variations in realized GSD due to herd and herd*YOC observed for all 4 dairy cattle populations are indications that selection emphases for breeding objective traits varies among producers. This could partly suggest that the breeding objectives of some producers do not align with that of AI centers or the dairy industry. Likewise, significant variations in generation intervals were observed among herds and herd*YOB. Knowledge of variations in realized GSD and L among producers could urge individual producers to want to find out what selection they have been making or are making in their herds, and the average ages of sires or dams individual producers are using or have been using for breeding. As an African adage goes, “to know where you are going, you must first know where you are coming from". Thus, once producers have good knowledge of what selection emphases they have been making in the past, producers could make changes if they are not moving in the right or intended direction.

It is suggested that in future, other important factors worth recording for inclusion in the herd information file are the ages of the producers or herd owners, educational level, family size, etc. This will enable future studies to comprehensively investigate a lot of the non-genetic factors that are likely to influence the amount of selection emphases producers put on economically important traits.

9.4 Development of the prototype software

Apart from the documented reasons that affect the expected genetic gains of national breeding programs from being attain: selection emphases on traits other than breeding objective traits, non-random mating, low selection intensity of sires of bulls due to smaller population sizes, and longer generation intervals in the SB and DB paths of genetic improvement (Van Tassell and Van Vleck, 1991), one key reason which is often forgotten or ignored is lack of monitoring of past selection emphases in both individual herds and national populations.

A prototype software for monitoring GSD in individual herds against set benchmarks was developed by using combination of trait EBVs and dairy herd information. The main input data for the development of the prototype software tool were EBV for all traits and herd information. Major computations that need to be updated each time new genetic evaluations are released are determination of bulls and cows' availability, average EBV of available bulls and cows on each day, GSD of sires and dams, and GSD benchmarks. The average EBV per day, benchmarks, and GSD of sires and dams are stored in tables and they can be viewed as downloadable reports or visual displays on the user-interface. Herd identification number associated with sires or dams can be used to retrieve mean GSD of a trait for any given herd in the form of visual displays and reports.

Whilst this software has been developed for dairy producers and AI centers to make both breeding and management decisions, dairy advisors and agricultural or livestock economists could also use outputs from a group of herds analyses for advisory and on-farm economic decision making. The developed prototype software serves as an additional tool for the dairy industry to monitor genetic improvements and the causes of these genetic improvements in both national populations and individual herds. We are of the opinion that if this tool is adopted and regularly used by dairy producers and AI organizations, producers and AI centers can in the future optimize the genetic gains in their herds. Producers could also constantly ensure that their future selection align with the breeding objectives of individual producers' herds and the industry. The use of this developed prototype tool by individual dairy producers will help both producers and advisors to select and bargain or pay for realistic prices for the semen producers acquire from AI organizations which producers subsequently use for inseminating their replacement cows.

In conclusion, the findings from the studies presented in this thesis demonstrated that: i) significant selection were realized for economically important traits by both producers and AI centers of the Canadian Holstein, Ayrshire, Jersey, and Brown Swiss dairy breeds between 1980 and 2016; ii) considerable variations exist among herds in their realized GSD for economically important traits; iii) YOC significantly influenced the GSD realized by producers and AI centers; iv) the average ages of sires and dams of bulls and cows in four Canada dairy populations have been declining and variations exist among herds in the ages of sires and dams that herds used for breeding; v) estimated genetic parameters for milk production and BWT can be used to develop a simple selection index to slow down or halt the positive genetic trend of BWT of Québec Holstein cows; and vi) a developed prototype software could be used to monitor realized GSDs for economically important traits in individual dairy herds against benchmark GSDs.

9.5 REFERENCES

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