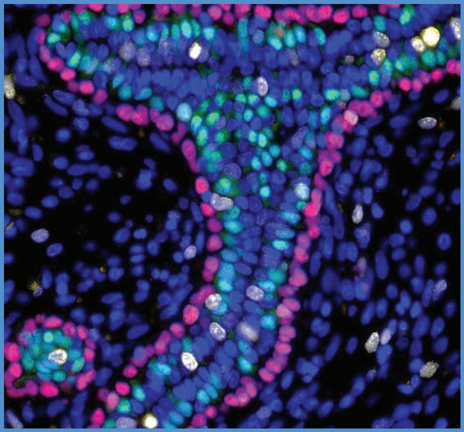
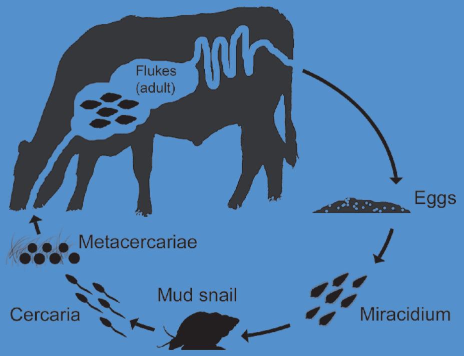
Large Dairy Herd Management

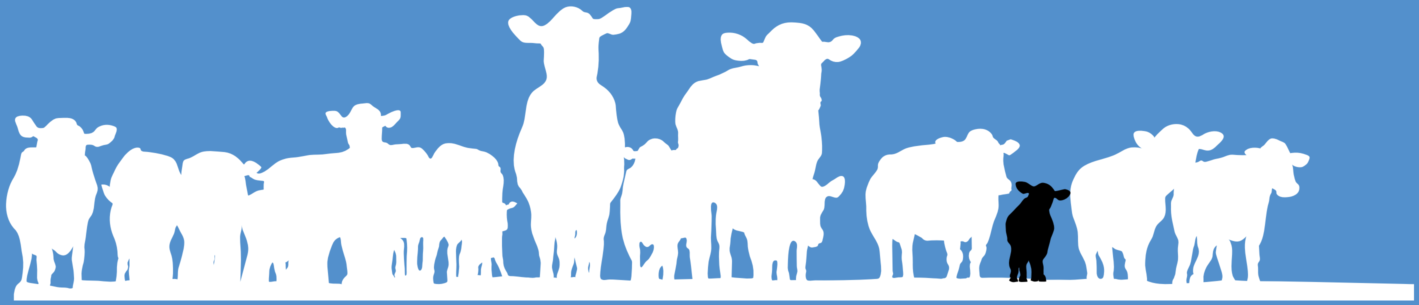
Third edition

Section 5: Genetic Selection Programs and Breeding Strategies





Edited by David K. Beede



Abbreviations

The following abbreviations may be used without definition in the book.

AA	amino acid
ACTH	adrenocorticotropin
ADF	acid detergent fiber
ADG	average daily gain
ADL	acid detergent lignin
ADIN	acid detergent insoluble nitrogen
AI	artificial insemination
BCS	body condition score
BHB	β-hydroxybutyrate
BLUP	best linear unbiased predictor
BSA	bovine serum albumin
bST	bovine somatotropin
BTA	*Bos taurus* autosome
BUN	blood urea nitrogen
BW	body weight
CI	confidence interval
CLA	conjugated linoleic acid
CN	casein
CNS	coagulase-negative staphylococci
CoA	coenzyme A
CP	crude protein
CV	coefficient(s) of variation
DCAD	dietary cation-anion difference
DHI(A)	Dairy Herd Improvement (Association)
DIM	days in milk
DM	dry matter
DMI	dry matter intake
DNA	deoxyribonucleic acid
EAA	essential amino acid
EBV	estimated breeding value
ECM	energy-corrected milk
ELISA	enzyme-linked immunosorbent assay
ETA	estimated transmitting ability
FAME	fatty acid methyl esters
FCM	fat-corrected milk
FSH	follicle-stimulating hormone
GnRH	gonadotropin-releasing hormone
h^2	heritability
HTST	high temperature, short time
IFN	interferon
Ig	immunoglobulin
IGF	insulin-like growth factor
IL	interleukin
IMI	intramammary infection
LA	α-lactalbumin
LG	β-lactoglobulin
LH	luteinizing hormone
LPS	lipopolysaccharide
LSD	least significant difference
LSM	least squares means
mAb	monoclonal antibody
ME	metabolizable energy
MIC	minimum inhibitory concentration
MP	metabolizable protein
mRNA	messenger ribonucleic acid
MUFA	monounsaturated fatty acids
MUN	milk urea nitrogen
NAN	nonammonia nitrogen
NDF	neutral detergent fiber
NDIN	neutral detergent insoluble N
NEAA	nonessential amino acid
NE_{G}	net energy for gain
NE_{L}	net energy for lactation
NE_{M}	net energy for maintenance
NFC	nonfiber carbohydrates
NPN	nonprotein nitrogen
NRC	National Research Council
NSC	nonstructural carbohydrates
OM	organic matter
PCR	polymerase chain reaction
$\text{PGF}_{2\alpha}$	prostaglandin $\text{F}_{2\alpha}$
PMNL	polymorphonuclear leukocyte
PTA	predicted transmitting ability
PUFA	polyunsaturated fatty acids
QTL	quantitative trait loci
r	correlation coefficient
R^2	coefficient of determination
RDP	rumen-degradable protein
REML	restricted maximum likelihood
RIA	radioimmunoassay
RNA	ribonucleic acid
RUP	rumen-undegradable protein
SARA	subacute ruminal acidosis
SCC	somatic cell count
SCS	somatic cell score
SD	standard deviation
SDS	sodium dodecyl sulfate
SE	standard error
SEM	standard error of the mean
SFA	saturated fatty acids
SNP	single nucleotide polymorphism
SPC	standard plate count
TDN	total digestible nutrients
TMR	total mixed ration
TS	total solids
UF	ultrafiltration, ultrafiltered
UFA	unsaturated fatty acids
UHT	ultra-high temperature
USDA	United States Department of Agriculture
UV	ultraviolet
VFA	volatile fatty acids

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Cover images

Top left: *Example of immunofluorescent staining in prepubertal bovine mammary tissue. The cross section of the developing duct shows the expression of p63 (red), which indicates myoepithelial nuclei, estrogen receptor (green), about 50% of the epithelial cells, and Ki67 (yellow), a marker for cell proliferation; DAPI staining (blue) is a general DNA stain that labels all cell nuclei.*
[Chapter 9-59: Mammary development in calves and heifers; Figure 4D]

Top center: *The daily trail to (and from) milking.*
[Chapter 10-67: Mastitis control in pasture and seasonal systems; Figure 3]

Top right: *Cow brushes are clearly a valued resource as they are used voluntarily by cows and are required by some voluntary assurance programs. Photo credit: DeLaval, Tumba, Sweden.*
[Chapter 11-71: Assuring and verifying dairy cattle welfare; Figure 2]

Bottom left: *The bedding material commonly recommended for controlling environmental mastitis is washed sand.*
[Chapter 10-65: Practical approaches to environmental mastitis control; Figure 3]

Bottom center: *Life cycle of a liver fluke.*
[Chapter 12-81: Parasite control in large dairy herds; Figure 2]

Bottom right: *Studies have shown that positive handling is correlated with cows having low fear responses to people and higher milk production. Some animal welfare standards now include a standardized test of avoidance distance to people as a way of screening for appropriate handling and good human–animal relationships on farms. Photo credit: University of British Columbia (UBC) Animal Welfare Program.*
[Chapter 11-71: Assuring and verifying dairy cattle welfare; Figure 3]

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Section 5: Genetic Selection Programs and Breeding Strategies

Note

This section is an excerpt from *Large Dairy Herd Management*, third edition. As such, links within these chapters to other sections of the book are not functional. Other sections of the book are available for purchase at https://ldhm.adsa.org/. The front matter and index of the complete book are available as free downloads.

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Improving production efficiency through genetic selection

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SUMMARY

Genetic selection has been a very effective tool for achieving lasting gains in animal production and efficiency. Prediction of the genetic merit of animals for a variety of traits occurs through the integration and analysis of multiple types of data, including genotypes that describe variation in DNA sequences among animals. These data are gathered, maintained, and analyzed through the efforts of multiple organizations working together in the dairy industry. The success of this genetic evaluation program is evidenced by improvements in the genetic merit and actual performance of cows for milk, fat, and protein yields. Although these production traits will continue to be important to US dairies in the future, interest in the ability to select animals for improved efficiency of production has increased in recent years. Estimation of genetic merit for feed intake, feed efficiency traits, or both will likely be added to US genetic evaluation programs in the future.

INTRODUCTION

The goal of dairy cattle breeding is to increase productivity and efficiency by means of genetic selection. This is possible because related animals share some of their DNA, and we can use statistical models to predict the genetic merit of animals based on the performance of their relatives. Historically, production goals focused on the amount of milk, butterfat, and protein produced. Although these traits remain an important part of most selection strategies, other traits, such as longevity and fertility, have increased in importance. A substantial amount of research now focuses on production efficiency, often calculated as a function of individual feed intake or greenhouse gas emissions. Interest in selection for production efficiency, rather than total production of milk, fat and protein, is increasing because of greater competition for feed and water, as well as growing demand for animal protein from the growing global middle class.

The goals of this chapter are to describe how genetic and genomic selection programs work, and to demonstrate how these tools are being used to produce dairy cattle that are efficient producers of food for human diets.

GENETIC SELECTION AND GENOMIC PREDICTION

Genetic gains differ from those due to improvements in an animal's environment (e.g., housing or feeding) because they are cumulative and can be transmitted from parents to offspring. Selection programs are designed to identify the animals in a population with the highest genetic merit. The animals with highest genetic merit may then be selected as the parents of the next generation, resulting in genetic improvement of the population.

Genes Versus Environment

An animal's performance for a trait of interest (its phenotype) is influenced by the genes it inherited from its parents, as well as the environment in which it is placed. Records from all animals in a population can be used to estimate the amount of variation in the trait, and that variation can be broken down into portions due to genetics and to the environment (Falconer and MacKay, 1996). Traits that are influenced mostly by environment are said to have low heritabilities, and traits with large genetic components are said to have high heritabilities. In general, traits with higher heritabilities respond more rapidly to genetic selection because genetic merit for highly heritable traits can be estimated more accurately than that for lowly heritable traits. Table 1 shows heritabilities for traits included in the lifetime net merit economic index (**NM$**), which represents a broad array of phenotypes. The traits in

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Table 1. The heritability of traits in the lifetime net merit economic index, which range from 0.01 (heifer conception rate) to 0.40 (body size composite); the emphasis placed on each trait in the index is a function of its heritability and economic value[1]

Trait	Heritability
Milk yield	0.20
Fat yield	0.20
Protein yield	0.20
Somatic cell score	0.12
Productive life	0.08
Udder composite	0.27
Feet/legs composite	0.15
Body size composite	0.40
Daughter pregnancy rate	0.04
Heifer conception rate	0.01
Cow conception rate	0.02
Sire calving ease	0.086
Daughter calving ease	0.048
Sire stillbirth	0.030
Daughter stillbirth	0.065

[1] Data from VanRaden and Cole (2014).

NM$ have heritabilities ranging from 1% for heifer conception rate to 40% for body size composite. Generally, traits associated with physical shape and size have high heritabilities (≥40%), traits related to milk and solids yield have moderate heritabilities (15 to 30%), and traits associated with health and fertility have low heritabilities (≤10%). If there is no variation in a trait attributable to genetics, such as for sire conception rate, then population performance cannot be improved using genetic selection.

How Does Genetic Selection Work?

Genetic selection works by improving the average genetic merit of animals in the population each generation. In dairy cattle, this is accomplished by selecting bulls that have high genetic merit for traits of interest as sires of the next generation of cows. The breeder's equation, shown in Equation [1], describes how different aspects of traits under selection affect the rate of genetic gain in the population (see, e.g., Bourdon, 1999):

$$\Delta G_{year} = \frac{\sqrt{reliability} \times selection\ intensity \times \sqrt{genetic\ variance}}{generation\ interval}. \quad [1]$$

In this equation, ΔG_{year} is the annual rate of genetic change in the population, *reliability* is a measure of the precision with which genetic merit is estimated, *selection intensity* is a measure of how selective we are when choosing the parents of the next generation, *genetic variance* is the variation among animals in the population that is attributable to genetic differences, and *generation interval* is the average age of parents when their offspring are born. Reliability and genetic variance differ from trait to trait, whereas selection intensity and generation interval are generally properties of a population and do not depend directly on the trait under selection. The use of genomic information allows us to increase the rate of gain by computing high-reliability genetic evaluations early in an animal's life, affecting both the reliability and the generation interval.

Calculation of Breeding Values

For many years, dairy cattle genetic improvement programs have been based on the mixed model methodology developed by Henderson (1984). In a simple mixed model analysis, the phenotype is modeled as a function of fixed (e.g., sex) and random (e.g., genetic) effects:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}, \quad [2]$$

where $\mathbf{y}$ is a vector of phenotypes; $\mathbf{X}$ and $\mathbf{Z}$ are matrices that link observations to fixed and random effects; $\mathbf{b}$ is a vector of values for fixed effects; $\mathbf{u}$ is a vector of random animal breeding values; and $\mathbf{e}$ is a vector of residual error effects. This equation describes the phenotype measured on an animal as a combination of genetic and environmental effects, as well as unknown effects that we cannot measure individually (error). When these equations are solved, each animal in the pedigree receives an estimate of genetic merit known as a *predicted transmitting ability* (**PTA**), which is the estimated animal breeding value from $\mathbf{u}$ divided by 2. The animal model used for most traits in the United States (VanRaden and Wiggans, 1991) is more complex than the example described above, and includes sophisticated contemporary groups, herd-by-sire, and cow permanent environmental effects.

Genomic Prediction

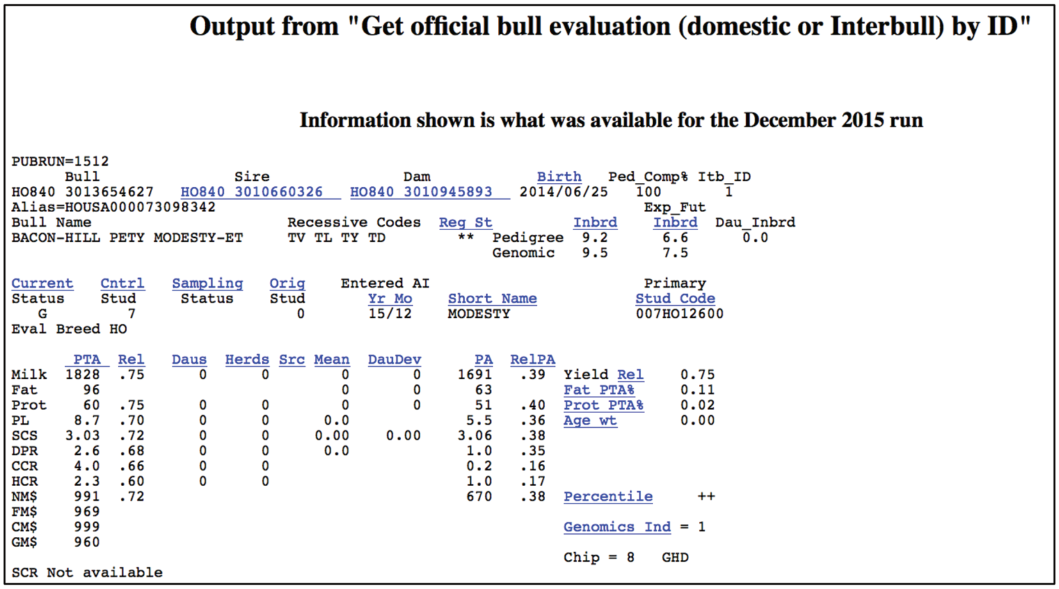
Genomic prediction occurs when information about an animal's DNA is used along with its performance and pedigree data for the estimation of genetic merit. Genotypes describe DNA inherited from each parent at specific markers known as *single nucleotide polymorphisms* (SNP). Each SNP represents a position in the DNA sequence that has only 2 possible variants. Genotypes at these SNP can be read in large numbers at low cost, and they describe which variant(s) at each SNP an animal has inherited. These genotypes provide information about an animal's genetic composition that is not influenced by the environment, thus improving the accuracy with which genetic merit is estimated.

Genotyping Chips

When the initial sequencing of the bovine genome was completed in 2009, an international consortium of government, university, and industry cooperators worked with Illumina Inc. (San Diego, CA) to develop a set of SNP to be included on a genotyping chip for cattle. This resulted in a set of 54,001 SNP included on the Illumina BovineSNP50 BeadChip, which became publicly available in December 2007. Genotypes were pooled from the Beltsville Agriculture Research Center (Maryland), University of Missouri (Columbia), and University of Alberta (Edmonton, AB, Canada) to identify SNP useful for genomic evaluation. Markers were excluded from genomic evaluation for many reasons, such as low call rates (genotypes frequently could not be determined), low minor allele frequencies (variants occurred too rarely), or high correlations with adjacent SNP (markers added little new information). In addition to computing genomic breeding values, the SNP also are used to identify and correct pedigree errors. As of June 2016, 1,418,194 genotypes from 21 different chips are included in the National Dairy Database, including low-density (6,000 to 9,000 SNP), medium-density (30,000 to 60,000 SNP), and high-density (77,000 to 777,000 SNP) chips. The majority of the genotyped animals are young females that do not yet have completed lactation records. This represents the largest database of genotyped animals in the world, but most of the ~9 million cows in the national herd do not receive genomic tests.

Genomic PTA

Effects of alternative SNP variants associated with traits of interest are estimated using phenotypes, pedigrees, and genotypes from a group of animals with high-reliability PTA, known as the *predictor population*. Once these SNP effects have been estimated, genomic PTA can be computed for animals that have genotypes but no available phenotypes. The marker effects must be periodically re-estimated, so phenotypes must be collected continuously. The final genomic predictions combine 3 terms using selection index procedures: (1) direct genomic predictions based on the SNP effects; (2) parent averages (**PA**) or PTA computed from genotyped ancestors using traditional relationships; and (3) traditional PA or PTA computed using pedigree and phenotype information. Reliabilities of genomic predictions are approximated using the genomic relation of each animal to the predictor population and the reliability of the predictor evaluation. The official evaluation for the bull Bacon-Hill Pety Modesty-ET (HO84003013654627), the top-ranked bull for lifetime net merit in the December 2015 evaluation, is shown in Figure 1 as an example of the results from the evaluation system.



Output from "Get official bull evaluation (domestic or Interbull) by ID"

Information shown is what was available for the December 2015 run

```
PUBRUN=1512
      Bull               Sire               Dam            Birth   Ped_Comp% Itb_ID
HO840 3013654627   HO840 3010660326   HO840 3010945893   2014/06/25   100       1
Alias=HOUSA000073098342                                                Exp_Fut
Bull Name                      Recessive Codes  Reg St         Inbrd    Inbrd  Dau_Inbrd
BACON-HILL PETY MODESTY-ET     TV TL TY TD        **  Pedigree  9.2      6.6      0.0
                                                      Genomic   9.5      7.5

Current   Cntrl   Sampling   Orig    Entered AI                        Primary
Status    Stud     Status    Stud       Yr Mo    Short Name           Stud Code
   G         7                  0       15/12    MODESTY              007HO12600
Eval Breed HO

       PTA  Rel   Daus  Herds Src Mean  DauDev      PA  RelPA
Milk  1828  .75      0      0        0       0    1691   .39  Yield Rel    0.75
Fat     96                           0       0      63        Fat PTA%     0.11
Prot    60  .75      0      0        0       0      51   .40  Prot PTA%    0.02
PL     8.7  .70      0      0      0.0             5.5   .36  Age wt       0.00
SCS   3.03  .72      0      0     0.00    0.00    3.06   .38
DPR    2.6  .68      0      0      0.0             1.0   .35
CCR    4.0  .66      0      0                      0.2   .16
HCR    2.3  .60      0      0                      1.0   .17
NM$    991  .72                                    670   .38  Percentile     ++
FM$    969
CM$    999                                                    Genomics Ind = 1
GM$    960
                                                              Chip = 8   GHD
SCR Not available
```

Figure 1. December 2015 official bull evaluation for the Holstein sire Bacon-Hill Pety Modesty-ET (HO84003013654627). Source: Council on Dairy Cattle Breeding (https://www.uscdcb.com/cgi-bin/general/Qpublic/proc.Q.cgi?qname=getbull&single&id=HO840003013654627).

THE US DAIRY GENETIC EVALUATION SYSTEM

Input Data

Selection programs make use of many types of information about the animals in the population, including phenotypes, pedigrees, and genotypes. *Phenotypes* are measurements of individual animal performance, such as a test-day milk yield or breeding record. *Pedigrees* describe genetic relationships among animals in the population. *Genotypes* describe the DNA inherited from each parent using SNP markers. The information provided by records can vary considerably. For example, a record for a trait with high heritability, such as milk yield, provides more information about an animal's genetic potential than a record from a trait with a low heritability, such as conception rate. Pedigrees differ in their quality (error rate) and completeness, with scientific studies reporting error rates of 15 to 20%. These errors introduce bias into genetic evaluations and can reduce rates of genetic gain. Genotypes can provide varying amounts of information based on the number of markers on the chip, but this can be accounted for using a process called *imputation*.

The most familiar phenotypes are those related directly to cow productivity, such as milk, butterfat, and protein yields. In typical milk recording programs, those yields are recorded on a monthly basis under the supervision of a technician using certified meters to ensure accurate observations. Milk samples taken during the test are sent to a laboratory for measurement of fat and protein contents and somatic cell score. The test-day milk yield and composition information are then sent to a dairy records processing center, where the observations are adjusted to a mature-equivalent basis. Corrections are also applied to account for differences in lactation length and milking frequency so that production records from animals in different environments are comparable. This is similar in principle to comparing feed properties on a dry matter basis. Finally, lactation yields are estimated from test-day observations using best prediction (VanRaden, 1997). Schmidt et al. (1988) cover these topics in much greater detail, including many worked examples.

The US Genetics Industry

The Council on Dairy Cattle Breeding (**CDCB**; https://www.uscdcb.com/) is responsible for receiving data and computing and delivering genetic evaluations for US dairy cattle, a role that it assumed from the Animal Improvement Program (**AIP**; http://aipl.arsusda.gov/) of the USDA's Agricultural Research Service in December 2015. The Council has 3 voting board members from each of the 4 major sectors of the dairy improvement industry. The Purebred Dairy Cattle Association (**PDCA**; http://www.purebred-dairycattle.com/) represents the national dairy breed registries, such as the American Jersey Cattle Association and Holstein Association USA. The National Association of Animal Breeders (**NAAB**; http://www.naab-css.org/) represents the individuals and organizations that produce semen for use in AI. The dairy records processing centers (**DRPC**) receive data from farms and milk recording laboratories, use those data to provide herd management tools, and forward data to other organizations, such as CDCB and PDCA, on behalf of their customers. The national Dairy Herd Information Association (**DHIA**) represents all of the organizations involved in dairy production recording, including the DRPCs, maintains national standards for data recording, and certifies devices for use in milk recording programs. Other industry groups, such as genotyping laboratories, have nonvoting representation on the CDCB Board of Directors.

Evaluation Releases

Official genetic evaluations are released 3 times each year (April, August, and December). In addition to providing authoritative genomic PTA for all animals evaluated in the United States, these releases include information from the multiple-trait across-country evaluations computed by the International Bull Evaluation Service (Interbull; Uppsala, Sweden). Additional information, such as animal rankings for the lifetime net merit, cheese merit, fluid merit, and grazing merit indices (VanRaden and Cole, 2014), are provided when new official releases are published. Monthly genomic evaluations for young bulls are provided to the organization that nominated each animal for genotyping, and evaluations for females are sent to the respective breed associations. These evaluations include genomic PTA, reliabilities, and genomic inbreeding values. Recently received genotypes are processed each week to generate approximate genomic evaluations for new animals, but those releases include only approximated reliabilities and genomic inbreeding because of computational limitations. Animals with genotypes that became usable since the previous weekly evaluation (e.g., because of corrected pedigrees) also receive weekly evaluations. The goal of this release schedule is to provide animal owners with accurate information for decision making as quickly as possible.

SELECTION FOR INCREASED PRODUCTION

Response to Selection

The production of milk, fat, and protein by cows in the US dairy herd has increased dramatically in the past 75 years. During this time, the number of cows in the national herd has decreased from 23.67 million in 1940 to 9.26 million in 2014, whereas average annual milk yield has increased from 2,097 to 10,092 kg over the same time period (Figure 2a,b). The average Holstein in 2014 produced almost 5 times as much milk as cows in 1940, and much of this improvement in productivity is due to genetic selection. The genetic improvement for milk yield averaged 65.9 kg per year between 1960 and 2013, accounting for roughly half of the total improvement in milk yield observed over the same period. Similarly, genetic improvement for fat yield averaged 2.3 kg per year from 1960 to 2013, whereas that for protein was 2.1 kg per year between 1970 and 2013. The rate of genetic improvement has remained similar for cows and bulls. Although the emphasis placed on milk yield in selection indices has decreased over time [from 52% in the 1977 PD$ (Predicted Difference Dollars) index to 1% in 2014 NM$], milk volume remains important in some markets (Florida and Southeast marketing areas) and the emphasis on milk solids has remained largely consistent (48% in PD$ and 42% in NM$). Even though milk receives relatively little emphasis in NM$, genetic merit for volume continues to increase due to its correlations with the other traits in the index (Table 2).

The CDCB publishes 4 selection indices to account for differences in how farmer are paid for their milk, fat, and protein (VanRaden and Cole, 2014). The net merit index (NM$) is based on the average value of

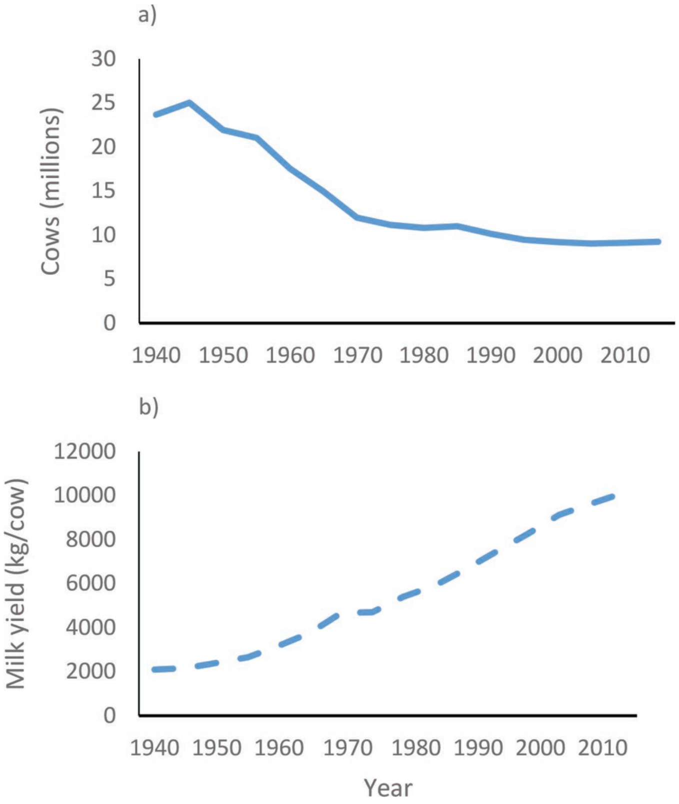


Figure 2. The number of cows in the US national dairy herd (a) and the average milk yield per cow per year (b) between 1940 and 2014. Source: Milk Production, Disposition, and Income Annual Summary (http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1105) .

Table 2. Correlations of predicted transmitting abilities (PTA) for individual traits in the lifetime net merit (NM$), cheese merit (CM$), fluid merit (FM$), and grazing merit (GM$) indices with the overall index, and the expected genetic response of those traits to selection on the index per year and decade[1]

	Correlation of PTA with index				Expected genetic progress from NM$	
Trait	2014 NM$	2014 CM$	2014 FM$	2014 GM$	PTA change/year	Breeding value change/decade
Protein yield	0.62	0.60	0.64	0.56	4.7	94
Fat yield	0.70	0.69	0.69	0.65	7.2	144
Milk yield	0.46	0.38	0.62	0.39	134	2,679
Productive life	0.68	0.68	0.64	0.70	0.64	13
Somatic cell score	−0.44	−0.46	−0.36	−0.43	−0.04	−0.75
Udder composite	0.09	0.09	0.08	0.11	0.04	0.75
Feet/legs composite	0.11	0.11	0.09	0.11	0.05	1.04
Body size composite	−0.20	−0.20	−0.20	−0.19	−0.09	−1.80
Daughter pregnancy rate	0.35	0.37	0.29	0.49	0.22	4.4
Heifer conception rate	0.15	0.14	0.15	0.23	0.10	2.0
Cow conception rate	0.34	0.35	0.31	0.48	0.34	6.7
Calving ability dollars[2]	0.37	0.36	0.36	0.41	2.8	57

[1] Data from VanRaden and Cole (2014; http://aipl.arsusda.gov/reference/nmcalc-2014.htm).

[2] Calving ability dollars is a weighted average of sire and daughter calving ease and stillbirth.

milk and components across marketing orders, but the fluid merit (**FM$**) and cheese merit (**CM$**) indices provide tools for farmers whose milk is used principally for bottling or cheese manufacturing, respectively. The grazing merit index is useful for pasture-based dairies who often want greater emphasis on fertility in the bulls they use. Purebred dairy cattle associations also have their own selection indices for ranking animals, such as Holstein Association's Total Performance Index and the American Jersey Cattle Association's Jersey Performance Index. Rankings are generally similar across indices, but the top animals for each index sometimes differ, as shown in Table 3 for NM$, FM$, and CM$ (grazing merit is not included Table 3 because sorted bull lists are not currently published for that index). For example, 6 bulls appear in the top 10 for both NM$ and FM$, but they are ranked differently. Most of these sires are young bulls with genomic evaluations but no daughters. Before the introduction of genomics, semen was not offered for sale until a bull completed progeny testing, with the objective of obtaining performance data from about 100 milking daughters.

Genetic Lag

Cows on commercial dairies typically have lower genetic merit than elite cows used to breed young sires and bull dams, and this difference is referred to as *genetic lag*. This lag is often easy to see when PTA for bulls and cows are plotted together, such as in Figure 3, which shows the genetic trend for Holsteins born between 1957 and 2014. It seems intuitive to many people to conclude that routine genomic testing of all heifer calves would provide a one-time increase in average genetic merit but that the trend would not change. However, this is not true. The routine use of genomic testing provides better information than traditional PTA about an animal's true genetic merit because it tracks the chromosomes actually inherited from each parent, rather than assuming that hypothetical "average" chromosomes were inherited. Genomic selection, as anticipated, is producing changes in the parameters in the breeder's equation. The first major change was to the reliability term in the numerator of Equation [1] (VanRaden et al., 2009). García-Ruiz et al. (2016) also recently documented large changes in the selection intensity term in the numerator, particularly for lowly heritable traits such as fertility, and the generation interval in the denominator of Equation [1]. This means that the slopes of the genetic trend lines are changing, as well as their heights, and that PTA for bulls and cows both are improving faster under genomic selection than traditional selection.

Table 3. The name and predicted transmitting abilities of the top 10 available Holstein bulls for lifetime net merit (NM$), fluid merit (FM$), and cheese merit (CM$) from the December 2015 genetic evaluations; bulls have similar rankings across different indices[1]

Lifetime net merit		Fluid merit		Cheese merit	
Bull name	NM$	Bull name	FM$	Bull name	CM$
BACON-HILL PETY **MODESTY**-ET	991	BACON-HILL PETY **MODESTY**-ET	969	BACON-HILL PETY **MODESTY**-ET	999
SEAGULL-BAY **SUPERSIRE**-ET	936	SEAGULL-BAY **SUPERSIRE**-ET	928	SEAGULL-BAY **CHARISMATIC**-ET	944
SEAGULL-BAY **CHARISMATIC**-ET	934	SEAGULL-BAY **CHARISMATIC**-ET	912	SEAGULL-BAY **SUPERSIRE**-ET	938
MR MOGUL **DELTA** 1427-ET	903	S-S-I MONTROSS **JEDI**-ET	877	TRIPLECROWN **GATEDANCER**-ET	935
MR **MEGA-DUKE** 54608-ET	901	MR MOGUL **DELTA** 1427-ET	874	MR PRE **DIRECTOR** 57512-ET	932
TRIPLECROWN **GATEDANCER**-ET	900	MR OAK **DELCO** 57279-ET	871	MR **MEGA-DUKE** 54608-ET	921
S-S-I MONTROSS **JEDI**-ET	898	SEAGULL-BAY **COMANCHE**-ET	868	MR MOGUL **DELTA** 1427-ET	915
MR PRE **DIRECTOR** 57512-ET	887	MR **MEGA-DUKE** 54608-ET	853	NO-FLA **BARCLAY**	905
NO-FLA **BARCLAY**	886	ABS **RAIDEN**-ET	852	S-S-I MONTROSS **JEDI**-ET	905
BRANDVALE STOIC 266-ET	883	NO-FLA **ALTAFIREUP**	849	BRANDVALE STOIC 266-ET	897

[1] Data from Bull Lists by Breed–Sorted by Merit Index, December 2015 (https://www.uscdcb.com/dynamic/sortnew/current/index.shtml).

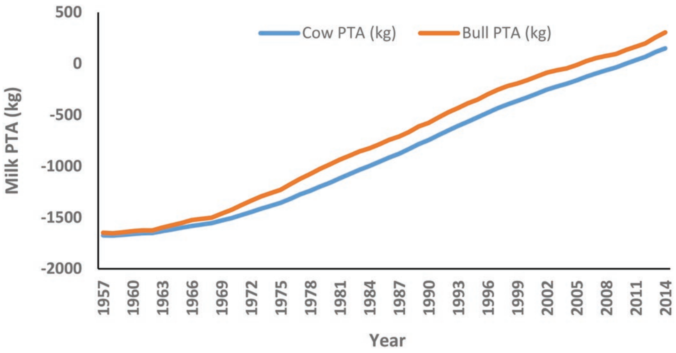


Figure 3. The change in average predicted transmitting ability (PTA) for milk yield of US Holstein bulls (red line) and cows (blue line) between 1957 and 2014. Source: Trend in Milk BV for Holstein or Red & White Calculated April 2016 (https://www.uscdcb.com/eval/summary/trend.cfm).

Selection for Low-Heritability Traits

The total merit genetic indices used for ranking animals in most countries have evolved substantially over time (Egger-Danner et al., 2015). Selection objectives originally focused on yield and conformation traits, which have relatively large heritabilities, meaning that a substantial amount of the variation between animals can be attributed to genetic differences among animals. However, emphasis is increasingly being placed on low-heritability traits, particularly those related to animal health and fitness. Genetic progress is generally slower for low-heritability traits but can still be substantial when genomic evaluations can be used to reliably identify the animals in the population with the best genetic merit for those traits. In traditional progeny test programs, hundreds of daughter records are needed to obtain breeding values with high reliabilities, but genomic evaluations can provide similar accuracy based only on the genotype.

Genetic Diversity

Although genetic selection is a very powerful tool for changing populations, it is not without pitfalls. One of the most important of these is genetic variability. In any population of a limited size, even one including several million animals, there is a loss of genetic diversity over time. This is most commonly measured using the *coefficient of inbreeding*, which is the probability that 2 alleles are identical because they originated in the same ancestor (e.g., Young and Seykora, 1996). The coefficient of inbreeding has increased by 0.11% per year since 1960 in US Holsteins (Figure 4) and currently averages 6.42, 7.04, 7.40, 6.57, 7.54, and 6.02% for US Ayrshire, Brown Swiss, Guernsey, Holstein, Jersey, and Milking Shorthorn cows born in 2015. The negative effects of inbreeding are most pronounced for health and fitness traits, but effects are undesirable for most traits, including production traits (Table 4). For example, a 1% increase in inbreeding is associated with decreases of 28.88, 1.07, and 0.85 kg in PTA for milk, fat, and protein production, respectively.

Table 4. Changes in predicted transmitting abilities associated with a 1% increase in inbreeding for several traits included in the lifetime net merit economic index[1]

Trait	Effect
Milk yield (kg)	−28.88
Fat yield (kg)	−1.07
Protein yield (kg)	−0.85
Somatic cell score	0.00
Productive life (mo)	−0.27
Daughter pregnancy rate (%)	−0.13
Heifer conception rate (%)	−0.12
Cow conception rate (%)	−0.16

[1] Data from December 2015 Across Breed Base Adjustment Parameters (https://www.uscdcb.com/eval/summary/Bmean_bases_het.cfm).

Another consequence of a decrease in genetic diversity is an increase in the rate at which recessive disorders are discovered in the population. This may appear at first to be undesirable, but if a recessive disorder is known, it can be tracked and managed in the population. If a popular bull is a carrier of a harmful recessive, then harmful alleles can spread rapidly through the population, as was the case with bovine leukocyte adhesion deficiency (BLAD), which was traced back to the popular bull Osborndale Ivanhoe (HOUSA000001189870). Ivanhoe sired 10,194 daughters and 267,158 granddaughters, and 137 of his sons and 934 of his grandsons entered AI service. Any recessive that results in the death of calves following their birth and

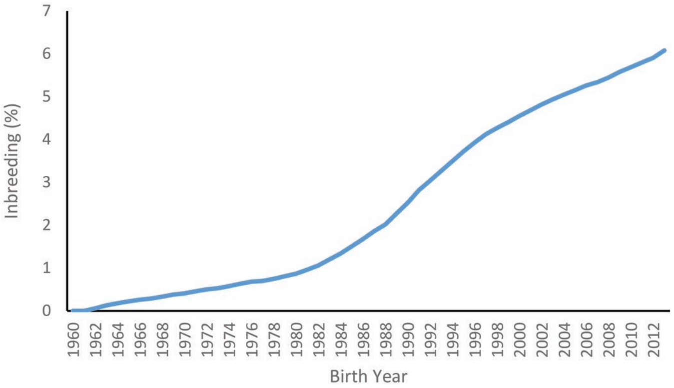


Figure 4. The change in inbreeding in the US Holstein population between 1960 and 2012. Source: Trend in Inbreeding Coefficients of Cows for Holstein or Red & White Calculated December 2015 (https://www.uscdcb.com/eval/summary/inbrd.cfm).

early rearing period is particularly problematic because the economic impact is much greater than that of recessives that cause early embryonic loss. Recessives that cause loss later in gestation are also expensive if the cow is culled or the next lactation delayed. The CDCB currently is using haplotype and SNP tests to track 25 recessives, including several haplotypes that result in early embryonic loss (Cole et al., 2013).

Undesirable Correlations

Modern selection programs attempt to balance selection for many traits against one another to produce profitable cattle. This can be difficult when antagonistic correlations exist among traits in the selection objective. For example, the phenotypic and genetic correlations of milk with daughter pregnancy rate (**DPR**) are −0.10 and −0.23, respectively, and fat and protein have undesirable correlations with fertility. These correlations imply that selection programs that place substantial emphasis on yield will select for poorer fertility (Pryce et al., 2004). It is possible to identify animals that have favorable PTA for both yield and fertility, which means that large populations have an advantage over smaller ones because the likelihood of identifying an individual that has desirable genetic merit for 2 unfavorably correlated traits is higher in the larger population.

SELECTION FOR EFFICIENCY GAINS

The dairy industry as a whole has become more efficient because the cost of maintaining the national cow herd has decreased with the decline in number of animals needed to meet the demand for dairy products. This increase in efficiency has been largely due to genetic and management advances focused on increasing milk production. Although this has led to a dramatic increase in efficiency of dairy operations, strategies to more directly improve feed efficiency (the efficiency with which individual cows convert feed to milk) may be necessary to maintain improvements in production efficiency (and profitability) in the future (VandeHaar et al., 2012).

Feed costs of lactating cows represent a significant portion of input costs for dairies. Although the ability to select cows capable of maintaining milk production with reduced feed intake requirements would be beneficial, feed intake has not been included in traditional genetic evaluation programs because of a lack of individual cow feed intake data. Although research herds often monitor feed intake on individual cows, this is a time- and labor-intensive endeavor that often relies on the use of specialized equipment. Thus, PTA for feed intake and related traits have not yet been computed on a regular basis in the United States.

Several AI and breed organizations have recently developed selection indices to describe production efficiency. Although these indices differ across organizations, in general production traits are rewarded whereas expected feed intake is penalized. In the absence of actual feed intake data, these indices assume feed intake is proportional to the amount of feed needed to support milk production and maintenance requirements, and maintenance requirements are estimated from the body size composite score. Additional traits are included in the efficiency index by some organizations to further reward cows with the ability to be efficient producers across multiple lactations. These indices currently provide a tool to producers wanting to include production efficiency in their selection goals. However, they are limited by assumptions that intake requirements to support a given level of milk production, and intake requirements to support a given body size are the same across all cows.

To more directly address genetic differences among cows for feed efficiency, a multi-institutional project including international collaboration began in 2011. A goal of this federally funded project is to measure feed intake on thousands of Holstein cows to investigate the genetic regulation of feed intake and efficiency. These phenotypic data, along with genotypes from the same animals, provide the predictor population data needed for genomic prediction of PTA for feed intake and efficiency traits. In this way, the power of genomic prediction is combined with phenotypic data from research herds to estimate the genetic merit of animals for feed efficiency based on their genotypic profiles. It is anticipated that PTA for feed intake and efficiency traits will be available in the United States in the near future. Other traits, such as those related to cow longevity, are also related to cow efficiency and will be discussed in other chapters.

CONCLUSIONS, IMPLICATIONS, AND THE FUTURE

The rapid acceptance of new genetic and reproductive technologies by the dairy industry has been essential to the success of modern genetic selection programs (e.g., Nicholas, 1996). The most notable example of this is the widespread adoption of AI using frozen semen in the 1950s, which allowed genetically superior bulls to sire many more daughters than was possible using natural service. In vitro fertilization and embryo transfer, ovulation synchronization and timed AI, and sexed semen are also used frequently to increase the rate of genetic progress. The recent rapid adoption of genomic selection (Wiggans et al., 2011) demonstrates the continued interest in technologies that support faster rates of genetic improvement, but a continued willingness to adopt new technologies is essential to ensure that US dairy producers remain competitive as the global marketplace changes.

Production efficiency will continue to grow in importance as demand for animal protein and competition for resources such as feed and water increases. Predictions from the Food and Agriculture Organization of the United Nations suggest that overall food production must be increased by 70% between 2005 and 2050 to meet the nutritional needs of a human population of 9.1 billion (FAO, 2009), which includes a doubling of agricultural production in developing countries. This will require that all aspects of livestock production systems become more efficient. The use of genomic selection has resulted in a doubling of the rate of genetic gain in the US dairy cattle population, but that alone is not sufficient to meet future demands for animal-based food in human diets. It also is necessary that cows be provided with the environment to support such levels of productivity, which will be challenging as global climate change puts new pressure on feed and water resources and transportation costs rise. The most efficient dairy animal for the future may look very different from today's elite cow.

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