Comparison of 2-breed crossbred cows sired by Montbeliarde and Viking Red compared with pure Holstein cows during first lactation in high-performance Minnesota dairy herds

A DISSERTATION
SUBMITTED TO THE FACULTY OF THE
UNIVERSITY OF MINNESOTA
BY

Amy Renae Loeschke

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Dr. Leslie B. Hansen, Adviser

December 2017

ACKNOWLEGEMENTS

This dissertation has been supported by a large team of advisers, mentors, partners, and colleagues and I am eternally grateful for their help and encouragement during the 10 years of this project. My most sincere gratitude goes to the owners/managers of the dairy herds for their participation in this study and for providing data on the cows in their herds. I have appreciated all of our discussions at your farms, whether related to crossbreeding or otherwise. These relationships have taught me so much! I also wish to thank Kim DeFrang and Neal Grotsun and Minnesota Select Sires Co-op Inc. for their contributions of mating individual heifers and cows with AI bulls and the scoring of BCS and conformation traits. Funding for this project was provided by Coopex Montbéliarde (Roulans, France), Viking Genetics (Randers, Denmark), Creative Genetics of California (Oakdale, CA), Select Sires Inc. (PlainCity, OH), and Minnesota Select Sires Co-op Inc. (St. Cloud, MN). I have greatly enjoyed the relationships I've built with our partners in these companies, and especially the input provided by Stephane Fitamant, Sara Wiklert Petersson, Mike Osmundson, Chuck Sattler, and others throughout the project.

Thank you to my adviser, Les Hansen, who has invested extraordinary time and dedication to mentoring me personally and advising this project. I have learned so much from you over the years and I am very grateful that you have provided an environment to set a solid foundation for my future career. I am especially appreciative of the many opportunities I've had to travel and obtain further education both at conferences and in the field. I also wish to express appreciation to my committee members: Brad Heins,

Marcia Endres, and Kota Minegishi. Your mentorship as members of my degree committee has been invaluable during my time in the Animal Science program.

Chapters 2 and 3 of this dissertation have been previously published in the Journal of Dairy Science (Hazel et al., 2017a,b). I wish to especially thank co-authors Brad Heins and Les Hansen for their influence and contributions to both publications.

Many others have given me indirect support, and have made my Ph.D program possible and enjoyable. Thank you to my former office mates, Brad Heins, Stefan Blöttner, Jenn Becker, Mike Donnelly, and current grad student co-workers, Brittany Shonka-Martin and Eric Houdek, for your friendship, support, and excellent scientific debates and assistance over the years. I'd also like to thank the many other Minnesota grad students for providing your support and friendship, and some good times at after-work functions! My family has been such a blessing in my life, and I thank my parents, Brian and Judy Hazel, and siblings, Amber and Adam Hazel, for supporting my education, goals, and providing encouragement during this atypically long road to my finish line! Most importantly, I thank my husband, Nick, for putting up with my late nights at the office, travel time away from home, and being my sounding board. I will always appreciate the fact that you are supportive of my career and have been willing to put your career in the back seat to support mine. I love you so much for making that sacrifice.

But the LORD stood with me and gave me strength. 2 Timothy 4:17

ABSTRACT

Background

Dairy producers have interest in crossbreeding because crossbred cows have enhanced fertility and survival compared to Holstein (**HO**) cows, leading to more profitability. This research study was designed to compare the phenotypic performance of Montbeliarde (**MO**) × Holstein and Viking Red (**VR**) × HO crossbred cows with pure HO cows in large, high-performance dairy herds.

Methods

All cows were either 2-breed crossbred or pure HO cows that calved for the first time from December 2010 to April 2014. Best Prediction was used to calculate 305-d milk, fat, and protein production as well as SCS, and 513 MO × HO, 540 VR × HO, and 978 HO cows were analyzed for production during first lactation. Body condition score (**BCS**) and conformation were subjectively scored once during early lactation by trained evaluators. The analysis of survival to 60 d in milk included 536 MO × HO, 560 VR × HO, and 1,033 HO cows during first lactation. Cows analyzed for other fertility, survival, and conformation traits had up to 13% fewer cows available for analysis.

Results

Age at first calving was similar for breed groups, and the herds calved both crossbred ($\overline{x}$ = 23.8 mo) and HO ($\overline{x}$ = 23.9 mo) cows at young ages. The MO × HO crossbred cows had +3% higher production of 305-d fat plus protein production (actual basis, not mature equivalent) than the HO cows during first lactation, and the VR × HO were similar to the HO cows for fat plus protein production. Breed groups did not differ for SCS during first lactation. The VR-sired 3-breed crossbred calves (from MO × HO dams) were similar to pure HO calves for calving difficulty (**CD**) at first calving; however, MO-sired male calves born to VR × HO dams had a mean score that was +0.5 points higher for CD than pure HO male calves. The 3-breed crossbred calves from both MO × HO (4%) and VR × HO (5%) first-lactation dams had much lower stillbirth (**SB**) rates compared with pure HO calves (9%) from first-lactation dams. The first service conception rate of the crossbred cows (both types combined) increased 7%, as did the conception rate across the first 5 inseminations, compared with the HO cows during first lactation. Furthermore, the combined crossbred cows (2.11 ± 0.05) had fewer times bred than HO cows (2.30 ± 0.05) and 10 fewer d open compared with their HO herdmates. Across the herds, breed groups did not differ for first-lactation survival to 60 d in milk; however, the superior fertility of the crossbred cows allowed an increased proportion of the combined crossbreds (71 ± 1.5%) to calve a second time within 14 mo compared with the HO cows (63 ± 1.5%). For survival to second calving, the combined crossbred cows had 4% superior survival versus the HO cows. The MO × HO and VR × HO crossbred cows both had increased BCS (+0.50 ± 0.02 and +0.25 ± 0.02, respectively), but shorter stature and less body depth than HO cows during first lactation. The MO × HO cows had less set to the hock and a steeper foot angle than the HO cows, and the VR × HO had more set to the hock with a similar foot angle to the HO cows. The combined crossbred cows had less udder clearance from the hock than HO cows, more width between teats both front and rear, and longer teat length than the HO cows; however, the frequency of first-lactation cows culled for udder conformation was uniformly low (< 1%) across the breed groups.

Conclusions

The high-performance herds in this study experienced superior fertility and survival with no loss of production during first lactation for 2-breed crossbreds compared to pure HO cows. The fertility and survival of cows are very influential on lifetime profitability. The first-lactation results from this study suggest MO × HO and VR × HO 2-breed crossbred cows may have increased lifetime profit than pure HO cows in high-performance dairy herds. A comparison of the lifetime profitability and, also, profitability of the subsequent generations of crossbred cows for this rotational crossbreeding system versus pure HO cows warrants further examination.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 3

LIST OF FIGURES

CHAPTER 2

CHAPTER 1

Introduction

1.1 Background and justification

The commercial dairy industry in the United States has been dominated by pure Holstein (**HO**) dairy cattle for the last 50 yr because the pure HO breed has experienced a large response to selection for milk production. Volume of fluid milk and, later, milk volume plus fat and protein content was the only selection criteria until 1994 within United States (**US**) dairy breeds (VanRaden, 2017). However, selection on these criteria caused significant decline in fertility of cows, and fertility has a documented negative genetic and phenotypic relationship with production. Furthermore, other functional traits such as health and survival of HO cows have experienced deterioration. Numerous research studies have documented crossbreeding may provide benefits for functional traits compared to purebreeding, and those studies are described later in this chapter.

Selection within a closed population inevitably leads to increased mean inbreeding (Falconer and MacKay, 1996); therefore, some increase of mean inbreeding in the HO breed is anticipated with time. However, HO cows born during the first half of 2017 have mean inbreeding of 7.1% from pedigree. Both this absolute level of inbreeding and the accelerated annual increase in mean inbreeding in recent years because of genomic selection are alarming. Crossbreeding of unrelated genetic lines or breeds offers the opportunity to reduce or eliminate the impact of high levels of inbreeding.

The deterioration of functional traits and recent rise of mean inbreeding are the primary reasons some producers have interest in crossbreeding (Weigel and Barlass, 2003). Crossbreeding certainly is not a new concept, and it has been widely adopted by the commercial beef, pig, and poultry industries globally. Since the 1990's, most US producers, as well as US researchers, have focused on various backcrosses or rotational crossbreeding of HO, Jersey, and Brown Swiss. For some production environments, the Jersey breed, especially, may offer advantages to some crossbreeding schemes; however, for many high-performance confinement herds with adequate stall sizes for HO cows, the Jersey breed may not be optimal.

Alternative breeds of dairy cattle from Western Europe have been considered for crossbreeding by US dairy producers since 2000. In particular, the Montbeliarde (**MO**) breed from France and the Viking Red (**VR**) breed from Sweden, Finland, and Denmark have experienced increased use for crossbreeding in high-performance US dairy herds. Few studies have examined the results of a rotational crossbreeding system of the MO, VR, and HO breeds in comparison with pure HO cows, and those that have done so have been observational in nature (i.e., no balanced mating design) or examined cows in a variety of environments, such as combinations of high-input, low-input, grazing, or organic management systems. Therefore, the motivation of this research was to compare crossbred cows of MO, VR, and HO with pure HO cows from a designed experiment with high-performance, confinement herds in Minnesota.

1.2 Literature Review

1.2.1 History and selection among breeds of US dairy cattle

Domesticated dairy cattle have been an important part of human history and, perhaps, human survival. Historians believe dairy cattle were imported to the US with colonial settlers as early as 1611; however, records suggest imports of dairy cattle began in 1783 with Shorthorn cows from Great Britain (Hodgson, 1986). Many breeds of dairy cattle have been recognized in the US throughout history, but 8 distinct breeds have had meaningful breeding programs with herdbook societies in the US (Table 1.1). Since the 1970's, the commercial dairy industry in the US has seen a majority shift toward the HO breed, and over 90% of the dairy cows in the US enrolled in DHI consisted of HO cows in 2008 (Dechow, 2015). Only during the past decade has the Jersey breed experienced growth and now comprises about 8.3% of the US national herd; however, HO cows make up 85% of the national population for cows enrolled in DHI testing (Dechow, 2015). Only about 47% (4.4 million) of the 9.3 million dairy cows in the US are enrolled in milk recording (Council on Dairy Cattle Breeding, 2017b; USDA-ERS, 2017); therefore,

Table 1.1 Distinct breeds of dairy cattle with organized breeding programs in the United States

Breed	Country of origin	Year of herdbook society formation
Ayrshire	Scotland	1863
Brown Swiss	Switzerland	1880
Dutch Belted[1]	Netherlands	1886
Guernsey	Isle of Guernsey (UK)	1878
Holstein[2]	Netherlands	(ca)1871
Jersey	Isle of Jersey (UK)	1868
Red Danish[3]	Denmark	(ca)1935
Shorthorn	Great Britain	1915

Adapted from Hodgson (1986).
[1] Oklahoma State University (2017).
[2] Hodgson, 1986; Lush et al., 1936.
[3] USDA-ARS (1962).

breed composition of the other 53% of dairy cows is unknown. During most of the 20th century, dairy producers have increased profit by increasing milk production per cow; therefore, the majority of the genetic advancement of dairy cattle was focused on within-breed selection for increased milk production.

Selection indices in the US. The US Department of Agriculture (**USDA**) began collection of milk and fat records around 1895 (Council on Dairy Cattle Breeding, 2017c). In 1971, USDA introduced the first economically-based selection index in the US called Predicted Difference dollars, and this index had 52% of selection emphasis on milk volume and 48% on fat pounds (VanRaden, 2017). The USDA has continued to calculate economic-based selection indices, most recently referred to as lifetime net merit (**NM$**), and NM$ has undergone 9 revisions since its inception. The most noteworthy additions to NM$ included the traits of longevity and SCS in 1994; body size (negative emphasis), udder composite, and feet and leg composite in 2000; cow fertility in 2003; calving ability in 2006; and livability (death) in 2017 (VanRaden, 2017).

The Total Performance Index (**TPI**) for the HO breed in the US was first published by Holstein Association USA in 1976 and included only milk production and final score for conformation (VanRaden, 2002). The TPI has historically emphasized conformation to a larger extent than NM$, and final score for conformation has had between 10 and 40 percent of the emphasis in TPI over time (Funk, 2006). Furthermore, the conformation categories of body size, udder, and feet and leg composites have had varying degrees of emphasis, and some health and fertility traits were included in recent years (VanRaden, 2002; Holstein USA, 2017). Unlike NM$, which is an economic index calculated using revenue and expense assumptions for commercial dairy cows, TPI consists of traits and their relative weights determined by the genetic advancement committee and the board of directors of Holstein USA comprised primarily of registered HO breeders.

Global selection indices of dairy cattle. Miglior et al. (2005) studied 17 national HO selection indices used in 15 countries in 2003, and they reported selection in most countries shifted from heavy emphasis on production toward emphasis on durability (longevity and conformation) and fertility and health. For example, the Danish S-Index had emphasis of 34% production, 29% durability, and 37% fertility and health, and authors (Miglior et al., 2005) cited reasons for the shift may include quota-based milk marketing, increase in labor costs, and producer and consumer concerns regarding the deterioration of health and fertility of cows. However, many countries continue to ignore selection for functional traits.

Impact of selection for production in the HO breed. Genetic trends for traits of pure HO cows were documented by USDA from national data (Council on Dairy Cattle Breeding, 2017a), and USDA reported an increase in phenotypic milk production of 6,869 kg for HO cows in DHI born in 2014 versus those born in 1957. The genetic trend of cows for milk production was almost linear from 1970 to 2016 and averaged about +125 kg per year. Simultaneously, the genetic trend for fertility was negative, and phenotypic daughter pregnancy rates for pure HO cows dropped from 39% in the early 1960s to a low of 24% in 2000 (Council on Dairy Cattle Breeding, 2017a). Lucy (2001) also documented a decrease in reproduction over time, and cows with the most milk production also had more incidence of infertility.

To document the impact of selection for milk production of HO cows over time, the University of Minnesota initiated a selection experiment in 1964 (Hansen, 2000). The designed study established a control line of cows that were continuously mated to HO AI bulls. The AI sires for the control line were near the breed mean for PTA milk (kg) in 1964. The selection line was mated to the 4 highest bulls for PTA milk on an annual basis. In later years, selection criterion was altered to PTA protein production (kg). During 34 yr of the experiment, phenotypic milk production for the selection line increased dramatically compared with the control line (10,959 kg versus 6,454 kg, respectively). Furthermore, selection-line cows had +282 kg more fat plus protein production than control-line cows with similar SCS. In the same experiment, changes of linear type scores (on a 50-point scale) were documented in 1986 and again in 1999. For the traits measured, the increase in dairy form (+19 points), body size (+10 to +12 points), and rear udder (+10 to +13 points) were most profound. The health care costs for selection-line cows were $25 more during first lactation and $49 more across the first five lactations compared with control-line cows. Hansen (2000) concluded that emphasis on angularity in addition to production may result in increased predisposition to metabolic problems.

At Iowa State University, a similar selection experiment commenced in 1968 and included a HO base generation, split by genetic potential of milk production, with the successive generation of cows sired by high or average milk production AI bulls for the high-genetic and low-genetic lines, respectively (Shanks et al., 1978). After only 6.5 yr of the project, cows selected for high genetic potential based on milk production had significantly more milk production, but they also had 9% more digestive disorders, 5% more foot rot, 14% more skin and skeletal disorders, 11% more udder edema, and 2% more clinical mastitis, resulting in 250% and 101% increased health cost for the base- and first-generation cows, respectively (Shanks et al., 1978). A review by Rauw et al. (1998) identified over 100 studies in which undesirable metabolic, reproductive, or health effects were found when domestic livestock species were selected for high production efficiencies. Furthermore, increased occurrences of metabolic diseases, impaired fertility, and reduced survival resulted in compromised animal welfare (Rauw et al., 1998; Oltenacu and Broom, 2010).

1.2.2 Inbreeding in HO dairy cattle

Inbreeding, by definition, is the mating of 2 individuals that are related to each other by ancestry (Falconer and MacKay, 1996). The degree to which these 2 individuals are related is commonly measured by the inbreeding coefficient (***F***), which is the probability that 2 randomly chosen genes at any locus in an individual are identical by descent (Falconer and MacKay, 1996). Selection within a closed population typically results in inbreeding, because effective selection dictates some members of a population will have more offspring than others (Young, 1984). Tracking and controlling the level of inbreeding in breeds of dairy cattle is important for 2 reasons: 1) the detrimental effects caused by high levels of inbreeding have economic consequence for commercial dairy production, and 2) maintaining genetic diversity provides genetic alternatives for animal breeders to alter breeding goals and for selection to begin for traits of economic or biological importance that are newly identified.

Average F of HO cows in the US. Researchers at the Council of Dairy Cattle Breeding (2017d) have tracked the level of pedigree *F* of HO cows in milk recording using cows born in 1960 as the genetic base. Lush et al. (1936) provided a review of the founding members of the HO breed in the US beginning in the 1880s and estimated the HO breed had about 4% *F* by 1931. With the 1960 genetic base, the average of HO cows in the US surpassed 2% *F* in 1988 and has increased to 7.14% for cows born in early 2017. Furthermore, varying amounts of annual increase of *F* have been observed during the last 30 yr (Table 1.2). The rate of annual increase has not been linear through time for HO cows in the US (Table 1.2). Leroy (2014) suggested change in *F* may be a more

Table 1.2. Inbreeding coefficient (*F*) and annual increase of *F* for Holstein cows in the United States born from 1988 to 2017, relative to a 1960 genetic base

Birth year(s)	Number of cows (millions)[1]	Average pedigree *F*	Average annual increase in pedigree *F*
		-------------- %	---------------
2017[2]	0.57	7.14	+0.28
2016	1.61	6.86	+0.29
2015	1.76	6.57	+0.21
2014	1.91	6.36	+0.23
2013	2.02	6.13	+0.22
2008 - 2012	1.92	5.68	+0.11
2003 - 2007	1.63	5.13	+0.12
1998 - 2002	1.32	4.53	+0.17
1993 - 1997	1.15	3.69	+0.23
1988 - 1992	1.16	2.52	+0.20

Adapted from Council on Dairy Cattle Breeding (2017d).

[1] Cows consisted of only those enrolled in milk recording.

[2] Average pedigree *F* and average annual increase are based only on calves born early in the year, and *F* is expected to increase once all cows born in 2017 are included.

important estimator of inbreeding because change in *F* with respect to time or generation may overcome the challenges of incomplete pedigree information.

Effective population size. At the population level, genetic diversity can be assessed for conservation purposes by effective population size (**N_e**), which represents the number of distinct breeding individuals of a closed population (Wright, 1931). A N_e of 500 is required to retain long-term evolutionary potential; however, populations that fall below $N_e = 50$ may be in danger of extinction due to drift (Harmon and Braude, 2010) and are subject to short-term inbreeding depression (Howard et al., 2017). Others have concluded that N_e ranging from 50 to 100 is viable long-term (Meuwissen, 2009). The N_e of the HO breed is estimated to be no larger than 100, and Sørensen et al. (2005) reported N_e of 49 for Danish HO born 14 yr ago. The N_e varies across the genome, and may be as small as 40 for areas of the genome that correspond with traits under intense selection but as large as 250 for regions experiencing random segregation (Jiménez-Mena et al., 2016). Collectively, this evidence suggests ongoing genetic stewardship of the HO breed is warranted to maintain its viability as a pure breed.

The levels of *F* and the N_e for the HO breed do not elucidate the entire problem with inbreeding, because commercial dairy producers have concern regarding the availability of high-ranking HO AI bulls to breed to cows currently in their herds. The balance between choosing bulls with high genetic merit and diversity of pedigree has become more difficult with time. For example, Miglior and Beavers (2014) reported 9 bulls sired 50% of the young bulls that entered AI in North America in 2015, and only 18 bulls sired 50% of young bulls internationally in the same year. Among the top 100 proven bulls with official evaluations from the Council on Dairy Cattle Breeding in April 2017, 80% of them are sons or grandsons of only 3 bulls (Mountfield SSI Dcy Mogul-ET, Roylane Socra Robust-ET, and Ensenada Taboo Planet-ET). Two other bulls, O-Bee Mandred Justice-ET and Picston Shottle-ET, had major representation as sires of sons in the early 2000's and they are represented as grandsires or great-grandsires for 18 of the 20 other top-100 proven bulls, in addition to having similar representation among the 80 Mogul, Robust, and Planet sons and grandsons. The rapid rise of inbreeding is, therefore, easily acknowledged because almost all of the breed's proven top-ranked bulls trace heavily to these 5 major-impact bulls. A similar exercise on the breed's top 100 unproven bulls would have similar results because, of those, 51 are sons of Bacon-Hill Pety Modesty-ET or S-S-I Montross Jedi-ET.

Inbreeding and genomic selection. The acceleration of annual increase in inbreeding during the past 5 years is mostly a result of reliance on genomic selection, which was implemented into US dairy evaluations in 2008. Despite the increased rate of genetic progress observed after the implementation of genomic selection (García-Ruiz et al., 2016), the annual rate at which inbreeding has increased among HO cows has been of commensurate proportion (Pryce, 2017). Possibilities exist to use genomic data to select AI bulls with more diversity of genome (Howard et al., 2017); however the observed increase of F in recent years may outweigh the economic gains made for highly-heritable traits because lowly-heritable traits, collectively, have large economic importance (Miglior and Beavers, 2014). Some studies (García-Ruiz et al., 2016) have suggested genomic selection is even more beneficial for lowly-heritable traits versus the highly heritable traits like milk production; however, these theoretical gains have not been realized in commercial dairy herds, which have observed improvements in fertility primarily due to management improvements but continue to experience phenotypically low levels of conception rates (Norman et al., 2015b) and livability (Council on Dairy Cattle Breeding, 2017a) of HO cows.

Phenotypic impacts of inbreeding. Inbreeding depression reduces the rate of response when selection is imposed and also increases the rate of deterioration for negatively correlated traits (Falconer and Mackay, 1996). Therefore, health and fertility of cows may further deteriorate, and at a more rapid rate, for pure HO cows in the future, because genetic trends for milk production, angularity, and body size continue to increase (VanRaden et al., 2014). Numerous studies have documented decreased production of milk, fat, and protein among inbred cows (Miglior et al., 1995; Smith et al., 1998; Thompson et al., 2000; Mc Parland et al., 2007; Rokouei et al., 2010; Bjelland et al., 2013; Dezetter et al., 2015), but the amount of lost production does not appear to have large economic impact, even at moderate levels of inbreeding. Conversely, inbreeding depression tends to have largest impact on fitness traits, especially fertility and viability (Falconer and Mackay, 1996).

A study by Wall et al. (2003) demonstrated increases in calving interval and decreases in BCS when inbreeding levels surpassed 10%. Adamec et al. (2006) observed increases in dystocia of cows (+0.42% and +0.30% for cows birthing male and female calves, respectively) and for SB (+0.25% and +0.20% for male and female calves, respectively) per each 1% increase in inbreeding. Sewalem et al. (2006) reported HO cows in Canada had 1.14 and 1.25 increased odds of culling at moderate ($6.25 < F < 12.5\%$) and high ($12.5 < F < 18.25\%$) inbreeding.

The loss of lifetime profit is also affected by inbreeding, and Croquet et al. (2006) observed €6.13 loss of lifetime income per 1% increase in inbreeding; however, that study ignored the effects of fertility, longevity, and health. Smith et al. (1998) estimated a 6-d decrease in longevity, a 177 kg lifetime milk loss, an 11.5 kg fat plus protein loss, and a $22 to $24 income loss for every 1% increase of inbreeding coefficient among US HO cows. These and other estimates of economic impact are likely conservative because the impact on economic return is a multiplicative combination of single traits (Kristensen and Sørensen, 2005), and these studies ignore some of the single traits that affect total profit. Furthermore, many highly-inbred females never enter the data for the estimation of effects of inbreeding because they may fail to survive to full-term pregnancies or may be stillborn. Lastly, studies on inbreeding in the US using national data lack accuracy because large numbers of cows do not have complete pedigree information (Cassell et al., 2003), and the rate at which incorrect parents are assigned is high (Wiggans et al., 2012).

Genetic recessive disorders. Some researchers have suggested that the biological basis of inbreeding depression is an accumulation of mildly deleterious alleles in the genome, that accrue among individuals who are more homozygous across many loci (Howard et al., 2017). For this reason, inbreeding is generally regarded as a negative phenomenon and, from a population perspective, poor-performing individuals will leave herds more quickly and provide a purging of inbreeding depression (Mc Parland et al., 2009). However, the purging is at considerable cost to commercial dairy producers in the short term, and relying on purging of inbreeding depression is not economically viable.

In the last 30 yr, increases in *F* have allowed lethal deleterious recessives (e.g., BLAD, CVM, and DUMPS) to surface and to be identified in the HO breed from the heavy use of AI and embryo transfer. Within the past 9 years, genomic tools have allowed researchers to uncover additional lethal recessive loci and haplotypes (e.g., Brachyspina, Cholesterol Deficiency, and 5 affecting fertility) by inspecting matings of carriers of suspected haplotypes that generated no homozygous progeny (VanRaden et al., 2011). Therefore, more deleterious recessives generated by mutations are able to be identified and purged from a breed with higher average level of inbreeding (Kearney et al., 2004; Kristensen and Sørensen, 2005). Methods have been suggested to manage deleterious recessive genotypes (Cole, 2015) but cost of genotyping and development and adaption of capable software remains a challenge for the commercial industry.

1.2.3 Heterosis

The equal and opposite effect of inbreeding depression is heterosis, which is expressed fully for matings among unrelated individuals (Falconer and MacKay, 1996). Heterosis is measured as the deviation of the mean of offspring from the mid-parent value for a trait of interest. Heterosis is affected by 2 genetic components: additive and nonadditive genetic effects (Swan and Kinghorn, 1992). The additive component is simply the average merit of the 2 parental lines (or the weighted mean of all parental genotypes, adjusted for their average contribution). The nonadditive portion is the heterosis, which is made up of genetic interaction between alleles at single loci (dominance) as well as genetic interaction between alleles at different loci (epistasis).

The effects of dominance are usually meaningful for crossbred animals because, by nature, crossbreeding creates more heterozygosity for many loci because one allele comes from each of 2 parental breeds at each loci. Epistasis is usually negative and of secondary importance to dominance. Epistasis is typically a positive genetic effect for animals within a breed because, over many generations of selection and drift, desirable interactions between loci have developed and become fixed within purebred populations. When these favorable interactions are potentially broken up by crossbreeding, epistasis may be reduced—termed recombination loss. Recombination loss is more likely to be expressed when a third or fourth breed is introduced following the cross of 2 breeds because more of the potentially favorable interactions across loci that are present within a single breed may be disrupted. In practice, recombination loss is not necessarily negative and may result in recombination gain (VanRaden and Saunders, 2003).

Heterosis is meaningful when breeds are more distantly related (Mäki-Tanila, 2007); however, breeds must have suitability to the environment in which they are evaluated (Sørensen et al., 2008). Heterosis is highest for lowly-heritable traits, such as fertility, health, and survival in dairy cattle (Young et al., 1969). Sørensen et al. (2008) comprehensively reviewed estimates of expected heterosis for individual traits of importance for dairy producers during the first generation of crossbreeding (Table 1.3).

Table 1.3. Guidelines for dairy producers on expected F_1 heterosis to be obtained for important traits

Trait	Expected heterosis (%)
Production	3
Fertility	10
Calving difficulty (direct)	−10 to 15
Calving difficulty (maternal)	10 to 15
Stillbirth (direct)	−5 to 10
Stillbirth (maternal)	5 to 10
Longevity	10 to 15
Total merit	≥ 10

Adapted from Sørensen et al. (2008).

Globally, the beef, pig, and poultry industries have embraced heterosis for decades for commercial production to capitalize on the documented gains for growth, fertility, health, and profitability; furthermore, heterosis has been expressed as improved feed efficiency of animals selected for carcass growth (Rolfe et al., 2011). A study by L. M. Winters (1935) at the University of Minnesota on crossbreeding in swine was the most important, widely-implemented research in pig breeding. The Winters study documented 1) crossbred pigs could perform as profitable breeding sows, and 2) that a continuous rotational cross for sows was a viable breeding strategy. However, up to that point, only purebred parents were utilized as breeding stock to generate crossbred market pigs (Winters, 1935). The work of Winters et al. (1935) was highly controversial because purity of breeds and species was the convention in livestock husbandry in the 1930’s.

Economic merit is likely the most important trait for which crossbred dairy cows should be evaluated today. Several researchers have estimated heterosis for profitability measures in dairy cattle, and these studies were reviewed by Sørensen et al. (2008). Touchberry (1992) compared crosses of Guernsey and pure HO, and heterosis for income per cow per year was 11.4%. Crossbreds of Ayrshire and Holstein exhibited heterosis for lifetime milk production of 16.6% and 20.6% for annual net income (McAllister et al., 1994). In New Zealand, Lopez-Villalobos et al. (2000) simulated profit for crosses between HO, Jersey, and Ayrshire in a grass-based system, and the estimates of heterosis for profit per hectare were 17-22% for F_1 crossbreds and 27% for 3-breed crossbred cows. A Danish experiment that ended in 1985 reported heterosis for F_1 crossbreds of 21% and heterosis for a 3-breed rotation of 30.4% (Sørensen et al., 2008). Prendiville et al. (2011) studied JH cows compared to pure HO and Jersey cows in an institutional grazing herd in Ireland, and reported an impressive 69% heterosis for profit per hectare, because the F_1 cows (€1,392) out-performed the pure HO (€938) and Jersey (€711) cows by wide margins. Sørensen et al. (2008) concluded heterosis of at least 10% should be expected for total economic merit of both F_1 and 3-breed crossbred cows across environments.

H×E interaction. Environment has been shown to influence the expression of heterosis, and this may add additional complications to the estimation of crossbred performance (Barlow, 1981). The potential heterosis × environmental interaction (**H×E**) for important traits should be documented because, if heterosis varies for a specific combination of breeds across environments, dairy producers may determine alternative combinations of breeds or crossbreeding schemes are better suited to their herd environment. Furthermore, presence of large H×E would suggest that sires within breed may rank differently for different environments (Bryant et al., 2007a) and could either be ranked for optimal performance within herd conditions or for robustness across environments (Norberg et al., 2014).

Penasa et al. (2010a) studied 2 strains of HO cows and their crosses in the Netherlands and observed increased heterosis for production in low-production environments and the largest negative (favorable) heterosis for SCS in the high-production environment; however, no difference in heterosis was found for age at first calving across the 3 environmental groups. Contrarily, Bryant et al. (2007b) reported crossbred cows in the lowest environment for milk solids production expressed almost no heterosis, and those in the intermediate environment had the most heterosis for production. A similar result was reported from national data in Denmark by Kargo et al. (2012) for strains of Jersey, which were divided among 5 environmental levels. However, Norberg et al. (2014) used a reaction-norm model to analyze the same data as Kargo et al. (2012) and found the model with H×E effect showed the highest heterosis for high-level environments. Subsequently, Norberg et al. (2014) used a reaction norm model with both H×E and genotype × environment effects, and that analysis found no difference in heterosis across environments. The authors concluded that the genotype × environment effect captured the scaling effects of increasing protein yield with environmental level (Norberg et al., 2014). Neither de Haas et al. (2013) nor Walsh et al. (2008) observed H×E for crossbred and purebred contemporaries in contrasting herd environments.

Genotype × environment interaction has been analyzed for studies in which only pure HO cows were available for comparison with crossbred cows. Therefore, results from these observational studies do not allow for conclusions regarding heterosis, but may provide conclusions about the performance of crossbreds vs a pure HO “control” in contrasting environments. Hazel et al. (2014) reported MO-sired crosses that averaged ¼ Jersey and ¼ HO content had improved performance in a grazing herd than they did in a confinement herd relative to MO × HO crossbreds and HO cows. At an institutional herd in the United Kingdom, JH and pure HO cows were compared in high-input confinement versus low-input grazing systems and significant interaction existed for milk production but not for solids yield or SCS (Vance et al., 2012). Vance et al. (2013) compared JH and pure HO cows across 3 supplementation levels in a grazing environment, and genotype × environment interaction was not observed for fluid milk production, fat plus protein production, or SCS. Very little research has been conducted on H×E or genotype × environment interaction using crossbreds for traits other than production, but Washburn (2009) suggested that poor survival of HO cows in pasture-based herds may be the driving factor for the increased use of crossbreeding among grazing herds in the US.

1.2.4 Previous studies on crossbreeding

A review by Touchberry (1992) stated the first documented studies of crossbreeding in dairy cattle were conducted because researchers observed variation for production between herds (and among cows within herds), but researchers disagreed whether inheritance of production was affected by only a few or many segregating loci. Furthermore, questions remained regarding the impact of environment and genotype × environment (Touchberry, 1992). Therefore, the first crossbreeding experiments were conducted beginning in the mid-20th century, mostly among HO, Jersey, Ayrshire, and

Guernsey breeds to answer questions about the viability of crossbreeding for commercial dairy production (McDowell, 1982; Touchberry, 1992; McAllister et al., 1994). Although results of these studies were favorable for crossbred cows, adoption of crossbreeding did not result. Instead, producers widely chose to convert from milking cows of other breeds (Jersey, Guernsey, Ayrshire, and Brown Swiss in the US) to HO cows. Perhaps, progress of the HO breed for milk production was viewed as superior to gains from heterosis.

Producer surveys on crossbreeding. Crossbreeding has become more commonplace since about 2000 as a result of the previously discussed decline in fertility, health, and survival of HO cows (Funk, 2006). Fifty US dairy producers responded to a survey about crossbreeding conducted in the early 2000's (Weigel and Barlass, 2003). Dairy producers who responded had been crossbreeding for an average of 8.9 yr, and the majority of dairy producers were milking crossbreds consisting of HO, Jersey, and Brown Swiss. Weigel and Barlass (2003) reported producers sought increased component percentages in milk, improvement in fertility, less CD, and more longevity. Many producers also expressed concern about inbreeding depression and had interest in heterosis. Disadvantages of crossbreeding included difficulty marketing replacements, lack of uniform size among cows in the milking herd, and potentially lower milk volume for crosses of some breeds.

Crossbreeding with Jersey and Brown Swiss. In the US, as well as many other areas of the world, modern crossbreeding research (c.a. 2000) began using Jersey and Brown Swiss bulls to breed HO dams. These matings were logical because Jersey and

Brown Swiss were the most common breeds of US cows after HO at the time.

A 2-breed reciprocal crossbreeding study began in 2002 using HO and Jersey, and the experiment was a shared design with 3 cooperating universities: Virginia Tech, the University of Kentucky, and North Carolina State University (Olson et al., 2009). The F_1 calves did not differ from the 2 pure breeds for gestation length; however, pure Jersey and JH calves had much less CD and decreased SB than HO calves (Olson et al., 2009). Furthermore, researchers found no differences for binary incidence of pregnancy at 150 DIM, ketosis, or displaced abomasum; however crossbreds tended to have less metritis than HO, and similar (JH) or more (HO × Jersey) mastitis than HO herdmates (Olson et al., 2011). Differences for disease were difficult to detect because cows were only evaluated during the first 100 DIM of first lactation, disease was recorded as binary incidence, and the sample size was small.

At the University of Minnesota, crossbreeding commenced in 2000 with Jersey AI bulls, which were used on half of the HO cows in a high-input confinement dairy with TMR feeding, and a low-input grazing herd. The JH cows were bred to MO for subsequent years. The JH cows had similar fat production (kg) but with lower protein production (kg) and milk volume than the HO cows during first lactation. During second and third lactations, JH cows had significantly less fat plus protein production (Heins et al., 2011). The SCS was similar for breed groups during first and second lactations; however, JH had increased SCS in third lactation with lower clinical mastitis compared to the HO cows (Heins et al., 2011). The JH had −23 fewer days open (**DO)** during first lactation (Heins et al., 2008) and also −42 fewer DO during both second and third lactations (Heins et al., 2012b). For body traits, the JH had decreased body weight (**BW**), increased BCS, less udder clearance (**UC**), and wider front teat width (**FTW**) than the HO cows during all 3 lactations (Heins et al., 2011). The JH cows had similar survival to second calving and increased survival to third calving (+15%) than HO cows (Heins et al., 2012b). Despite some positive attributes for fertility and survival of the JH cows, the authors concluded that JH cows may not be suited to high-input production systems because of decreased production and increased culling for udder conformation during later lactations. The phenotypic results for traits of importance may be highly variable between environments, and this may explain the success and growth of crossbreeding with Jersey in New Zealand (LIC and DairyNZ, 2015).

A similar conclusion was reported by Bjelland et al. (2011), who compared backcross HO × Jersey (n = 319) cows (¾ HO and ¼ Jersey content on average) with pure HO cows (n = 648) in a high-input Wisconsin institutional herd. All sires of cows were either unproven F_1 Jersey × HO crossbred AI bulls or unproven pure HO AI bulls; therefore, highly variable results were anticipated in both breed groups. The backcross cows had decreased production and also did not have advantages for health and fertility compared to the HO cows; therefore, this study provided confirmation of the recommendation that a 3-breed rotation of breeds may be most appropriate, with bulls chosen based on high merit for a national index within breed.

Crossbreeding between Brown Swiss **(BS**) and Holstein were investigated in the US by Dechow et al. (2007) using national data. The BS × HO crossbreds (n = 256) were superior for daily fat production, similar for protein production, and lower for fluid milk volume than the pure HO cows (n = 2,125). Across lactations, BS × HO were similar for milk and fat, but with increased protein across lactation on a mature equivalent basis (Dechow et al., 2007). Furthermore, BS × HO had −14 fewer DO and lower SCS than the HO cows. Pure BS (n = 926) and BS backcross (¾ BS and ¼ HO; n = 105) were available for the estimation of heterosis and recombination, and Dechow et al. (2007) found heterosis of 5.0 to 7.3% for production traits, 8.0% for DO, and 7.8% for SCS, and 2.1% for age at first calving.

In a German institutional herd, a designed crossbreeding study of BS × HO (n = 55) compared with pure HO (n = 51) for phenotypic traits commenced in 2005 (Blöttner et al., 2011a). The BS × HO cows were bred to HO AI bulls for first calving and to Fleckvieh AI bulls for second and third calving. The BS and Fleckvieh are distantly-related breeds that originated in the Alps regions of Germany, Switzerland, and Austria; therefore, the results for longer gestation lengths of BS × HO cows at both first calving (+2 d) and at multiparous calvings (+6 d) were anticipated when compared to HO cows bred to HO AI bulls. The BS × HO cows did not differ from pure HO cows for birth weight of their HO-sired calves during first calving; however, Fleckvieh-sired calves were heavier (+6 kg) than HO calves at second and third calvings. The heavier birth weights of Fleckvieh-sired calves did not result in increased dystocia, and this was similar to the result of Heins et al. (2010) for MO-sired calves. Both studies collectively refuted conventional thought that heavier birth weight of calves has a linear and positive relationship with increased dystocia; however, other factors such as the shape of crossbred calves may influence dystocia. The BS × HO cows analyzed by Blöttner et al.

(2011a) had fewer days to first breeding only during second lactation and similar DO to HO cows. BS × HO cows had more body weight with more backfat thickness than the HO cows. They had similar stature but had wider chest width; therefore, the use of BS for crossbreeding did not provide a reduction in body size compared with pure HO cows. Furthermore, BS × HO cows had more compact, steeper foot conformation, which resulted in fewer hoof disorders for multiparous cows (Blöttner et al., 2011a). Production was similar for breed groups during all lactations (Blöttner et al., 2011b); but milking speed was slower for the BS × HO cows. Furthermore, udder clearance was less for the BS × HO cows during first lactation versus the HO cows, and the udders of BS × HO became even closer to the ground as cows aged to second lactation (Blöttner et al., 2011b). This result was different from those observed for udder clearance by Hazel et al. (2014), because MO-sired cows in that study had udders that became closer to the ground with age at the same rate as HO cows. Blöttner et al. (2011a,b) had a small sample size of cows; however, results indicated BS × HO were competitive with pure HO for many traits of importance.

Breed differences and heterosis were compared for crossbreds and purebreds among the traditional US dairy breeds from national data in a study by VanRaden and Sanders (2003). The F_1 crossbreds of BS with HO had heterosis ranging from 3.2 to 5.6% for production traits and crossbreds of Jersey with HO had heterosis of 1.6 to 7.5% across production traits. As a result, these 2 types of crossbred cows had similar or increased fat and protein production (kg) than HO cows. Heterosis for SCS was less than 1% and unfavorable. Heterosis for productive life was low (1.2%), and this differs from most other research results on longevity; however, the productive life analysis was heavily influenced by production and conformation traits and was not a direct measure of herd life or livability (VanRaden and Wiggans, 1995). Economic values from Net Merit (August 2000) were used to conduct an economic analysis of the breed groups, and both Jersey × HO and BS × HO crossbreds had higher net merit and cheese merit dollars than pure HO cows. VanRaden and Saunders (2003) concluded crossbreds of HO with BS and Jersey may be profitable for US dairy producers, especially those that sell milk for production of cheese and other processed products.

1.2.5 *Rotational crossbreeding and ProCROSS.*

The ProCROSS breeding scheme. A trademarked mating plan called ProCROSS was established in 2014 as a partnership between Viking Genetics and Coopex Montbeliarde (ProCROSS, 2017). This mating scheme is a continuous rotation of 3 breeds: MO, VR, and HO. The rotation usually starts with pure HO cows, because most herds interested in crossbreeding have HO cows. The HO cows are bred to either MO or VR AI bulls to create MO × HO or VR × HO F_1 crossbred cows, which are then bred to the third breed of the rotation in the next generation. The 3-breed crossbred cows are bred to HO AI bulls to create HO-sired ProCROSS cows in the third generation, and the rotation of purebred AI bulls continues into subsequent generations. The goal of ProCROSS is to develop a genetic brand for crossbreeding of dairy cattle, globally.

Three-breed rotational crossbreeding. The idea of rotating 3 breeds is often endorsed by geneticists over other types of crossbreeding rotations because this approach allows for a relatively high level of mean heterosis (Table 1.4). At stabilization, heterosis is calculated as: $(2^n - 2)/(2^n - 1) \times 100$, where n represents the number of breeds, and all breeds in the rotation are used in equal proportion.

Table 1.4. Mean proportion of maximum possible heterosis (100%) for successive generations of a 2-, 3-, and 4-breed rotation using purebred sires

Generation	2 breeds	3 breeds	4 breeds
	-------------------------	%	-------------------------
1	100.0	100.0	100.0
2	50.0	100.0	100.0
3	75.0	75.0	100.0
4	62.5	87.5	87.5
5	68.8	87.5	93.8
6	65.6	84.4	93.8
7	67.2	85.9	93.8
At stabilization	66.7	85.7	93.3

Mean heterosis at stabilization is only 67% of maximum for 2-breed crossbreeding. Furthermore, the second generation has only 50% of the maximum heterosis, and the second generation may be especially disappointing (e.g., Bjelland et al., 2011). However, when 3 breeds are rotated, the lowest mean heterosis occurs in the third generation at 75% of maximum (Table 1.4). For ProCROSS, the third generation will typically be a HO-sired crossbred and this breed is probably best suited for this generation in which heterosis is lowest because production is the strong suit of the HO breed. When 4 breeds are rotated, the mean heterosis at stabilization (93%) is higher than for a 3-breed rotation (86%); however, choosing 4 distinct breeds of dairy cattle that are well-suited for an individual management system may be difficult. Also, the additional +7% mean heterosis that is experienced after the necessary generations into the 4-breed rotation is usually not enough of a marginal difference to justify the use of a fourth breed, which may not be as well-suited to the environment as the first 3 breeds. Furthermore, managing semen inventory and mating plans for a fourth breed adds logistical complication for dairy producers.

The MO breed for crossbreeding. The MO breed originated in France, specifically in the Franche-Comté region, and is known as an Alpine breed because of its historic genetic ties with the Fleckvieh and BS breeds. Today, the states of Doubs and Jura in France have the highest concentration of MO cows, and the breed had 670,000 cows (440,000 enrolled in milk recording) in 2016 (O. S. Montbeliarde, 2017). The MO is a growing breed in France and has increased from about 12% of the French national herd to 17.5% over the past 20 years. The MO is the second most popular French dairy breed after HO. The breed has a strong selection program and progeny tests about 180 bulls annually. The AI organizations in France currently screen 2,160 males annually via genomic testing, and this is a higher proportion of the breed than other dairy breeds in France (O. S. Montbeliarde, 2017).

The MO cows in France average 8,520 kg milk, with 3.91% fat and 3.31% protein for 331 DIM lactations (O. S. Montbeliarde, 2017), and Dezetter et al. (2015) reported that MO cows had 16% lower production of milk solids than HO cows in France for 2000-2013. This may seem like a low milk production level compared to production of HO cows in the US; however, almost all dairy producers with MO cows sell their milk for the manufacture of specialty cheeses with protected designation of origin. Both Comté and Mobier cheese must be made with milk only from MO cows, the MO cows must receive access to pasture, and they are not allowed to consume fermented feeds.

The dietary restrictions placed on MO cows in France are the likely reason for lower production of the breed and perhaps not because they are genetically limited for milk output. No direct comparisons of purebred MO and HO cows in a high-input system like those commonly found in the US are available in the literature; however, early comparisons of MO × HO cows and pure HO have concluded the MO breed provides a high level of additive genetics for production, large heterosis with HO, or both (Heins et al., 2012a; Malchiodi et al., 2014b; Hazel et al., 2014; Hazel et al., 2017b).

The MO breed has been developed primarily for cheese production since 1889 and has aggressively selected for components of milk, but the breed did not ignore the importance of concurrent selection for fertility and health traits during the past 50 yr like the HO breed, globally. The MO national index in France is called ISU and emphasizes the traits of milk solids production (45%), fertility (18%), udder health (14.5%), conformation (12.5%), longevity (5%), and milking speed (5%). Furthermore, the MO breeders in France have historically had a profitable market for sales of fattened cull cows and Charolais × MO feeder calves and, for this reason, have selected for BCS and muscularity. For crossbreeding, the attributes of the MO breed may be complementary with HO because the HO breed has selected for health and fertility traits only recently (VanRaden, 2017); however, the HO breed has failed to dampen a strong genetic trend for increased body size and more angularity (i.e., decreased BCS; VanRaden et al., 2014). Finally, the MO breed has been mostly developed independent of HO influence; therefore, geneticists believe heterosis levels for crosses of MO and HO are likely larger than with other dairy breeds for which HO has been introduced more broadly (e.g., Norwegian Red and Danish Red).

The VR breed for crossbreeding. The VR breeding program was formed in 2008 from the consolidated breeding programs of Swedish Red, Danish Red, and Finnish Ayrshire. The goal of the consolidation was to gain efficiency to the separate breeding programs. The VR breed has 240,000 cows on milk recording across the 3 countries and is the second most popular breed of the region behind HO. Average production of VR cows in 2016 was 9,009 kg milk, 4.30% fat, and 3.46% protein (Viking Genetics, 2017). Across the 3 countries, 3,000 bulls are genomically tested annually and 150 are progeny tested. The Viking Genetics AI organization places a high priority on genetic diversity to prevent a rapid rise of inbreeding; therefore, the breed uses at least 100 progeny-test bulls as sires of sons for the subsequent generation.

The VR cows are often found in mixed-breed herds with HO cows in Denmark, Finland, and Sweden; however, dairy producers generally keep both breeds pure within their herds and receive subsidized genomic testing and other genetic services for doing so. Nonetheless, crossbreeding is of interest to dairy producers in those countries in recent years. Unlike the dairy economies of France and Italy especially, the 3 Nordic countries do not have large amounts of specialty cheeses, but most milk is manufactured and, therefore, high solids content of milk has been under selection in the VR breed for decades. Additionally, the VR breed is characterized by their small body size, ease of calving, and high fertility, and these traits were under selection as early as 1972—over 20 years earlier than most other breeding programs globally. The VR breed has also concentrated on lowering mortalities and culling, and the breed is superior to the HO breed for these traits (Alvåsen et al., 2012). Lastly, joint national planning for hoof health recording commenced in 2003 and was included in genetic evaluation by 2011 (Viking Genetics, 2017).

The three countries with VR have shared a joint evaluation since 2002 and also share a joint breeding goal (Kargo et al., 2014). Nordic Total Merit (Nordic Cattle Genetic Evaluation, 2016) is the national index of the VR breed, and the index places emphasis on production (36%), health (17%), conformation (15%), longevity and survival (10%), fertility (9%), calving traits (7%), milking speed (3%), and temperament (1%). Most VR AI bulls currently marketed have less than 12.5% HO content, which is gradually being reduced with time. More HO influence was present for Danish Red cows in the late 1900's and early 2000's. At this point, VR has limited genetic ties with contemporary Holstein bulls, and any limitation on expression of heterosis may be small. The VR offers advantages for crossbreeding because the breed has reduced body size, superior calving ability, high fertility and excellent health compared to the HO breed.

Crossbreeding studies with MO and VR. Several studies have been conducted in recent years comparing MO- and VR-sired crossbred versus HO cows, and they are in Table 1.5. Collectively, these studies suggest the MO and VR breeds are viable candidates for a complementary crossbreeding rotation along with HO, because results show advantages of the crossbreds for traits that are most concerning in the HO breed: fertility, longevity, and health. Without exception, these studies (Table 1.5) had one or more of the following design limitations: 1) Observational data in which dams of cows studied were not paired for equivalent genetic merit, 2) No criteria for selection of service sires for equivalent merit, 3) Institutional herd data with small numbers of cows that precludes broad interpretation, 4) National data with assumption of average herd environment, or 5) performance of cows only for the F_1 generation. The premise of the current research study is to circumvent these limitations via a designed study with large, commercial dairy herds that have high herd performance. Furthermore, crossbred cows of multiple generations and pure HO cows will be evaluated concurrently for a lengthy period of time.

Table 1.5. Summary of studies from the literature that reported phenotypic or genetic results for lactating crossbred cows sired by Montbeliarde or Viking Red

Author(s)	Country[1]	Year(s)	Sire breed[2]	N[3]
Christensen and Pedersen, 1988 (via Sørensen et al., 2008)	DNK	1972-1985	VR	850
Ericson et al., 1998	SWE	1979-1983	VR	11,455
Heins et al., 2006a	USA	2001-2004	MO	370
			NR	264
Heins et al., 2006b	USA	2002-2004	MO	694
			NR	457
Heins et al., 2006c	USA	2002-2005	MO	494
			NR	328
Heins and Hansen, 2012	USA	2002-2009	MO	503
			NR	321
Heins et al., 2012a	USA	2002-2009	MO	503
			NR	321
Swalve, 2007	DEU	2003-2007	VR	110
Walsh et al., 2007	IRL	2001-2005	MO	96
Walsh et al., 2008	IRL	2001-2005	MO	60
Penasa et al., 2010b	IRL	2002-2006	MO	208
Schaeffer et al., 2011	CAN	2005-2011	VR	76
de Haas et al., 2013	NLD	2003-2009	MO	352
Hazel et al., 2013	USA	2005-2007	MO	57
Mendonça et al., 2013	USA	2009-2010	MO	47
Hazel et al., 2014	USA	2005-2012	MO	150
Mendonça et al., 2014	USA	2009-2010	MO	52
Piccardi et al., 2014	ARG	2008-2010	VR	98
Malchiodi et al., 2011	ITA	2008-2011	MO	71
			VR	41
Malchiodi et al., 2014a	ITA	2007-2011	MO	253
			VR	581
Malchiodi et al, 2014b	ITA	2013	MO	165
			VR	169
Jönsson, 2015	SWE	1990-2012	VR	59,274
Dezetter et al., 2015	FRA	2000-2013	MO	5,016

[1] DNK = Denmark, SWE = Sweden, USA = United States, DEU = Germany, IRL = Ireland, CAN = Canada, NLD = Netherlands, ARG = Argentina, ITA = Italy, and FRA =France.

[2] VR = Viking Red (or Swedish Red, Danish Red, or Finnish Ayrshire independently), MO = Montbeliarde, NR = Nordic Red (Swedish Red and Norwegian Red combined).

[3] N = number of crossbred cows. For studies where number of cows varied for multiple traits, N was for the trait with the most cows.

1.3 Objectives and hypotheses

The overall objective of this research was to compare phenotypes of MO × HO and VR × HO cows during first lactation with pure HO cows in high-performance dairy herds in Minnesota with a designed study. Specific objectives for Chapter 2 were to compare the 2 types of crossbred cows with pure HO cows during first lactation for production, SCS during the first 305 d of first lactation, and calving traits at first calving. Specific objectives for Chapter 3 were to compare 2-breed crossbreds to HO cows for fertility, survival, and conformation during first lactation.

Crossbred cows were anticipated to be similar to HO cows for production and SCS but superior to HO cows for SB, fertility, and survival. Variable results were anticipated between breed groups for conformation traits, but crossbred cows were expected to have increased BCS, decreased stature, and less-desirable scores for udder traits.

CHAPTER 2

Production and calving traits of Montbeliarde × Holstein and Viking Red × Holstein cows compared with pure Holstein cows during first lactation in 8 commercial dairy herds

2.1 Introduction

Crossbreeding of dairy cattle has not been common for commercial milk production during the late 20th century, and this is contrary to the routine use of crossbreeding for commercial production of beef, swine, and poultry. However, the use of crossbreeding in dairy cattle is currently on the rise globally. Among cows enrolled in milk recording in the US, crossbreds have had a 9-fold increase from 0.5% in 2003 to 4.5% in 2014 (VanRaden and Sanders, 2003; Norman et al., 2015a). Crossbreeding of Holstein-Friesian and Jersey has become prevalent in New Zealand, where crossbreds were 46% of cows in 2014 (LIC and DairyNZ, 2015). In Ireland, crossbreds were 10.6% of dairy cattle births in 2015 (Department of Agriculture, Food and the Marine, 2015). Interest in crossbreeding for commercial milk production has grown over the past 20 yr because dairy herd owners desire robust dairy cows that are healthier, fertile, and long-lived compared to purebreds (Weigel and Barlass, 2003). Another reason for heightened interest in crossbreeding is growing concern about the accelerated increase in mean inbreeding of Holstein (**HO**) cows, because inbreeding has incrementally negative effects on performance and profitability of cows (Dezetter et al., 2015). During the past 5 yr, the annual increase of mean inbreeding coefficient doubled from +0.1 to +0.2% in the US and is mostly the consequence of shortened generation intervals that have accompanied genomic selection (Dechow, 2014). Dezetter et al. (2015) recently studied inbreeding depression in HO cows, and the 6.8% average inbreeding of US pure HO females born in 2016 (Council on Dairy Cattle Breeding, 2016) results in an estimated loss of −279 kg of milk, −12 kg of fat, and −9 kg of protein production per 305-d lactation.

Comparisons of crossbreds with HO cows in exclusively high-input environments (Blöttner et al., 2011a; Heins et al., 2012a; Heins and Hansen, 2012) and from national data with various levels of inputs (VanRaden and Sanders, 2003; Dechow et al., 2007; Dezetter et al., 2015) have documented the need for further evaluation of crossbreds compared to HO cows for high-performance confinement herds. In particular, a 3-breed rotation including MO from France, VR from the Nordic countries, and HO may be well suited to high-performance environments. The VR breed resulted from combining the genetic improvement programs of the Swedish Red, Finnish Ayrshire, and Danish Red breeds, which have historically shared genetic material and applied similar selection criteria with emphasis on the functional traits of cows. Several studies have reported results of Montbéliarde × Holstein crossbred (**MO × HO**) compared with HO cows (Walsh et al., 2008; Malchiodi et al., 2014b; Dezetter et al., 2015) as well as Viking Red × Holstein crossbred (**VR × HO**) compared with HO cows (Ericson et al., 1988; Swalve, 2007; Sørensen et al., 2008) in various environmental settings. Most research on crossbreeding of dairy cattle has reported results from analysis of field data, which has often had very unbalanced numbers of cows per breed group, little regard for genetic merit of cows within breed, breed groups of cows not reared in the same environment, or a small number of herds. The present long-term study overcomes these challenges by the careful assignment of the "foundation" pure HO cows to the base generation for each breed group and by maintaining control over the successive generations of matings. Eventually, this research will study data for lifetimes of cows from multiple generations of a 3-breed rotation of MO, VR, and HO. The objective of this research was to analyze phenotypes for 305-d production, SCS, and calving traits from the first lactations of MO × HO and VR × HO crossbred cows compared with pure HO cows in a 10-yr designed study.

2.2 Materials and methods

2.2.1 Experimental design

Description of Herds and Cows Enrolled. Pure HO females in 8 dairy herds were offered by herd owners as "foundation" females for a 10-yr genetic study from March to September of 2008. Across the 8 herds, 3,550 nulliparous heifers as well as cows (primarily first or second lactation) were enrolled. The 8 herds are located in southeastern, southwestern, and central Minnesota and are elite herds for production. Cows in all herds were housed in a 4- or 6-row freestall confinement facility and fed a TMR during lactation. In May 2016, the herds ranged in size from 295 to 1,932 cows with a mean herd size of 791 cows and weighted mean production across the 8 herds of 13,918 kg of milk, 510 kg of fat, and 430 kg of protein with 3 times daily milking. The mean production level across the 8 herds placed them among the 94th percentile for mean milk, fat, and protein production for Minnesota herds enrolled in milk recording in June of 2016 (Dairy Records Management System, Raleigh, NC, personal communication). The herds exceeded many benchmarks for well-managed dairy herds when the study was initiated. However, interest of the herd owners in the study was driven by a desire to reduce labor costs, to lessen the need for health treatment, and to minimize hormonal synchronization for fertility. The herds co-mingled the crossbred and HO cows at all times, and they grouped cows only by age, stage of lactation, and fertility status. Also, the herds applied the same management criteria across all breed groups, including criteria for health treatment and culling.

Mating Design. The authors assigned the foundation HO females offered by the herd owners to either the crossbred or the HO breed groups. The foundation HO heifers and cows were grouped for assignment to breed groups based on age and sire for heifers, and on lactation number, sire, and projected mature equivalent (**ME**) milk production for cows. Dams of HO and crossbred cows in this study had mean lactation number of 0.63 and 0.67, respectively, at time of enrollment because many females were virgin heifers. Furthermore, only 34% of cows in this study had dams with a 305-d ME milk production record, and dams of HO (12,274 kg) and crossbred (12,562 kg) cows did not differ (P = 0.10) at time of enrollment. All herds offered a minimum of 250 foundation pure HO females, of which at least 150 were mated to HO bulls through successive generations and at least 100 were mated to either MO or VR bulls to initiate the 3-breed rotation. Within the 2 crossbred groups, the resulting F_1 crossbred progeny were mated via AI to the third breed (i.e., MO × HO cows were mated to VR bulls and the VR × HO cows were mated to MO bulls) to create 3-breed crossbred cattle. In many cases, herd owners chose to enroll more than 250 foundation pure HO heifers and cows, and they designated to which breed group (crossbred or HO) the additional animals were enrolled. Across the herds, approximately 56% of the foundation HO females were mated to either MO or VR bulls with exactly half mated to bulls from each of the 2 breeds. The other approximately 44% of the foundation HO cattle were bred to HO bulls. Heifers and cows were assigned individually to AI bulls for mating by 2 genetic advisors employed by Minnesota Select Sires Co-op Inc. (St. Cloud, MN). Both crossbred and HO cows were correctively mated for conformation, and heifers were correctively mated based on the conformation scores of their dam when possible. Additionally, inbreeding protection was provided for matings of HO bulls to HO cows and heifers. Some of the herds mated cows on fifth and later services to unproven AI bulls or natural service bulls, but the resulting progeny were excluded from the study. Only proven AI bulls with very high rank for genetic merit from each of the 3 breeds were selected to breed the heifers and cows in the study. Herd owners chose the AI bulls for each breed in consultation with the 2 professional genetic advisors. For MO and VR bulls, all semen was imported to the US by Creative Genetics of California (Oakdale, CA). The bulls ranked highly among those available in the US based on the French ISU index (O. S. Montbéliarde, 2016) and the Nordic Total Merit index (Nordic Cattle Genetic Evaluation, 2016), which are the national selection indices for the MO and VR breeds, respectively. All HO bulls were proven AI bulls marketed by Select Sires Inc. (Plain City, OH), and herd owners were asked to select bulls that ranked among the top 10% of available bulls for the Net Merit index (VanRaden and Cole, 2014). The MO, VR, and HO breeds apply selection indices with, respectively, 45, 36, and 43% emphasis on production, 42.5, 49, and 41% emphasis on functional traits, and 12.5, 15, and 16% emphasis on conformation traits. However, the MO and VR breeds have a much longer history of selection for fertility and health traits compared with the HO breed, and this could improve their complementarity with HO for crossbreeding. Sires of cows in this study were selected from 2008 to 2011, which was 5 to 8 yr before the analysis of data from this study. The most frequent sires of cows in this study are reviewed in Table 2.1, which reports the sires of 75% of cows for each breed and reflects the bulls used most heavily during the first 4 yr of the study. The remaining 25% of cows were sired by 9 MO bulls, 10 VR bulls, and 45 HO bulls. The weighted mean birth year for sires of cows was 1999 for both the MO × HO and VR × HO cows, but it was 4 yr younger (2003) for the HO cows. Therefore, the sires of the pure HO cows in this study likely had an advantage for genetic level respective to breed.

Table 2.1. Most frequent sires of cows that comprised 75% of the cows in each breed group of first lactation cows

Pure Holstein (n = 978)			Montbeliarde × Holstein (n = 513)			Viking Red × Holstein (n = 540)		
n	Name	Registration no.	n	Name	Registration no.	n	Name	Registration no.
117	Michael	USA133389654	112	Plumitif	FRA7045598076	95	Orraryd	SWE91433
97	Million	USA61547476	93	Patinage	FRA2541872822	91	B Jurist	SWE91011
74	Moscow	USA132582764	75	Micmac	FRA196014411	74	O Brolin	SWE91804
52	Elias	USA134603522	66	Papayou	FRA4240303647	67	Peterslund	SWE91213
47	Plato	USA62297905	53	Redon	FRA2529434146	56	Sörby	SWE91716
45	Colby	USA60697343				46	Gunnarstorp	SWE92104
40	Plus	USA133186916						
35	Cadet	USA60182858						
35	Morpheous	USA62169176						
28	Alexander	USA61133837						
26	Graybil	USA50747059						
26	Roland	USA136278496						
25	Richman	USA62030417						
25	Durable	USA136747211						
22	Planet	USA60597003						
22	Bogart	USA135257546						
20	Gabor	USA60845420						

2.2.2 Initial data editing

Table 2.2 summarizes the initial editing of cows within each breed group. Calvings of cows that had gestation length (**GL**) less than 260 d were considered an abortion and were removed from the analysis. After initial editing, 1,105 crossbred and 1,101 HO cows with normal first calvings remained for analysis. Table 2.3 provides a summary of the number of cows by year of calving, herd, and breed group.

Table 2.2. Editing of cows by breed group

Edit	Pure Holstein	Montbeliarde × Holstein	Viking Red × Holstein
	-------------------------	n	-------------------------
Viable females born[1]	1,351	633	642
Left prior to first calving	194	81	58
Calved after April 2014	23	4	1
Initiated first lactation with abortion	33	9	17
Remained for analysis	1,101	539	566

[1] Females with opportunity to calve for a first time from December 2010 to April 2014 and to milk 305 d into their first lactation.

The design of the study ensured breed groups would have sufficient size for comparison within each year and within each herd. However, 2013 and 2014 were transition years of first calving between generations because the last of the F_1 crossbreds (MO × HO and VR × HO) calved for the first time and the majority of crossbreds that calved for the first time had shifted to the 3-breed crossbreds. Similarly, few of the first-generation HO cows calved during 2013 and 2014 and, instead, most the HO cows used for comparison shifted to the second generation of HO cows. Therefore, the number of crossbreds calving in 2014 was smaller than the number of HO cows, and this difference for generation of the breed groups likely gave the HO cows an advantage for genetic level within breed.

Table 2.3. Distribution of cows calving for the first time from December 2010 to April 2014 by year and breed group and by herd and breed group

	Breed group			
Year	Pure Holstein	Both crossbred groups	Montbeliarde × Holstein	Viking Red × Holstein
2011[1]	362	461	215	246
2012	321	399	198	201
2013	326	214	111	103
2014	92	31	15	16
Herd				
A	157	87	41	46
B	126	57	30	27
C	85	96	52	44
D	213	183	91	92
E	163	298	148	150
F	132	202	100	102
G	110	71	30	41
H	115	111	47	64
Total	1,101	1,105	539	566

[1] Includes 5 pure Holstein, 2 Montbeliarde × Holstein, and 1 Viking Red × Holstein cows that calved in December 2010.

2.2.3 Trait descriptions

Production and SCS. Analysis of 305-d production of first-lactation milk, fat, and protein as well as SCS used test-day records from milk recording (DHI). Test days occurred monthly for 5 herds and at least 8 times per year for the other 3 herds. Individual test days of cows with fewer than 4 DIM were excluded, and each test day was required to have an observation for milk, fat, and protein production. Test-day milk weight was required to be at least 4.54 kg, fat percentage was required to be at least 1.0% but no more than 9.0%, and protein percentage was required to be at least 1.0% but no more than 6.0%. Lactations were required to have at least 2 test days to project 305-d production and SCS for cows that left herds before 305 DIM.

Daily milk, fat, and protein production and SCS were calculated with Best Prediction (**BP**; Cole and VanRaden, 2009), which is routinely used for genetic evaluation in the US. The BP adjusted lactational records for age at first calving and projected daily production records to 305 d for records less than 305 d. The 305-d SCS for each cow was the mean of predicted daily SCS. The BP was applied separately to each of the 8 herds in this study, and herd-specific lactation curves were used to calculate 305-d production (actual basis, not mature equivalent). Fat and protein percentages for each cow were calculated by dividing the 305-d fat and protein production (kg), respectively, by 305-d milk production (kg). All 8 herds routinely milk most of their cows 3 times daily; however, 4% of test-day observations were for cows milked 2 times per day on specific test days. A chi-squared test indicated the crossbreds did not differ from HO cows for percentage of observations that were from 2-times-daily versus 3-times-daily milking.

Calving Traits. The incidence of twinning (**TW**), GL, CD, and SB were recorded for calving events from December 2010 to April 2014. Owners or employees of herds recorded all of the calving traits except GL. Neither calf weight nor BW of dams were available. The TW was recorded by herds in a binary manner as either a single birth or twins, and no cows gave birth to more than 2 calves. The GL was calculated by subtracting the date of conception from the calving date. A 5-point scale was used uniformly across herds to score CD, with 1 = no assistance and less than 2 h in labor, or calving was unobserved; 2 = slight difficulty and more than 2 h in labor but no assistance was provided; 3 = needed assistance, such as a hand pull; 4 = difficult pull, such as obstetrical chains were used with significant force; 5 = extreme difficulty, such as a mechanical puller was used or cesarean section was performed. The SB was recorded in a binary manner as either living or dead within 24 h of birth.

2.2.4 Final editing and analysis

Production and SCS. Lactations of cows without 2 test days (46 crossbred and 64 HO cows) were removed from the analysis for production and SCS. Cows were assigned to a herd-year-season (**HYS**) of first calving, and HYS was defined as 4-mo periods (January to April, May to August, and September to December) within each herd; therefore, each herd had up to 11 HYS of first calving across the years of the study. The HYS were further edited to permit valid comparison of crossbreds to HO cows within each HYS. First, HYS were required to contain at least 3 crossbred (MO × HO and VR × HO breed groups combined) and 3 HO cows, and this requirement resulted in the removal of 6 crossbred and 59 HO cows across all HYS. Subsequently, the HYS that contained fewer than 3 of either MO × HO or VR × HO were combined with the adjacent HYS within herd that had the fewest cows in a breed group. This criteria was satisfied by combining 2 HYS in all cases, except 1 instance where 3 HYS were combined. After edits, the number of cows analyzed for production and SCS included 1,053 crossbred (513 MO × HO and 540 VR × HO) and 978 HO cows. Independent variables for the statistical analysis of age at first calving, 305-d milk, fat, and protein production (kg), 305-d fat plus protein production (kg), and SCS included the fixed effects of HYS, breed of cow (crossbred or HO), and breed group (MO × HO nested within crossbred or VR × HO nested within crossbred versus HO cows). Additionally, sire nested within breed group was a random variable. The MIXED procedure of SAS (release 9.4, SAS Institute Inc., Cary, NC) was used to conduct the ANOVA and to obtain solutions. Orthogonal contrasts between least squares means of production traits were performed for the effects of breed of cow and breed group. The *P*-values for the comparison of breed groups were subjected to the Bonferroni correction and used HO as the control to account for multiple comparisons with HO cows. Subsequently, the *P*-value for the comparison of MO × HO with VR × HO cows was subjected to the Bonferroni correction with no control breed group designated.

Calving Traits. Herds were asked to follow the prescribed matings for the first 4 services and were permitted to use a nonprescribed AI bull or natural service bull on fifth and later services. Furthermore, some virgin heifers were mistakenly bred to a bull other than prescribed. Therefore, 6% of first lactation cows (90 crossbred and 47 HO) gave birth to calves that did not conform to the design of the study and the calving records of these cows were eliminated. Cows were assigned to HYS for all calving traits in the same manner as production traits. For the analysis of TW, the HYS edit removed 9 crossbred and 82 HO cows, and a total of 1,004 crossbreds (496 MO × HO and 508 VR × HO cows) and 971 HO cows remained. For the analysis of GL, CD, and SB, the twin births in each breed group (3 MO × HO, 4 VR × HO, and 6 HO cows) were removed. Subsequently, the HYS edit was applied to data for GL, CD, and SB and the HYS requirement removed 9 crossbred and 86 HO cows. The number of cows analyzed for

GL, CD, and SB was 997 crossbred (493 MO × HO and 504 VR × HO) and 961 HO cows.

The TW was evaluated with a chi-squared test (SAS) to determine probability of significant difference between breed groups. For the analysis of GL, CD, and SB, the fixed effects included HYS of first calving, sex of calf, breed of calf (crossbred versus HO), breed group of calf (MO × VR/HO or VR × MO/HO nested within crossbred vs. HO), the interaction of breed of calf and sex of calf, and the interaction of breed group and sex of calf. Finally, sire of calf nested within breed group of calf was a random variable. The MIXED procedure of SAS was used to conduct the ANOVA and obtain solutions for GL and CD. Because SB was a binary trait, the MIXED procedure of SAS was used to obtain least squares means but the GLIMMIX procedure (SAS) was used to assess statistical significance of variables. Orthogonal contrasts were evaluated in the same manner as the production traits and employed the Bonferroni correction for comparisons between breed groups as well as the interaction of sex of calf with breed group.

2.3 Results and discussion

Results for combined crossbred breed groups are compared with the HO cows; however, results are also provided separately for MO × HO and VR × HO compared with HO cows (and for MO × HO versus VR × HO crossbred cows when significant). The collective examination of both types of crossbreds provides a better reflection of the experience of herds initiating a 3-breed rotation using MO and VR bulls in a pure HO herd.

2.3.1 Production and SCS

Most herds had aggressive goals to calve cows the first time at 22 or 23 mo of age, and the effect of HYS was highly significant (*P* < 0.01) for age at first calving. Herd E (Table 2.3) had especially low mean age at first calving (22.2 mo). On the other hand, herd C preferred to calve cows at a substantially older age than the other 7 herds (27.5 mo). The combined crossbred (23.8 mo) and pure HO cows (23.9 mo) were very similar for age at first calving (Table 2.4). Pure MO cows in France usually have older age at first calving than pure HO cows in the US, but the reason for this difference is not likely because of genetics for growth, maturity, or fertility of the 2 breeds. Hazel et al. (2014) reported similar age at first calving for MO-sired crossbreds compared with HO cows in a single high-input confinement herd; however, MO-sired crossbreds calved 0.9 mo earlier than HO cows in a grazing herd in the same study. A Swedish study (Ericson et al., 1988) found heterosis for age at first calving of +1.2%, but reported only a 0.12-mo difference, phenotypically, for VR × HO compared with HO cows. Results from this study indicate both MO × HO and VR × HO crossbred heifers can be managed together with pure HO heifers without concern for difference in age at first calving between breed groups.

The effect of HYS was highly significant (*P* < 0.01) for milk, fat, protein, and fat plus protein production as well as SCS during first lactation. Production of fluid volume of milk (kg) was significantly lower (*P* = 0.04) for the combined crossbred cows (−2%) than the HO cows (Table 2.4); however, the difference resulted from the VR × HO cows (−4%) producing significantly less fluid volume of milk than the HO cows because the

Table 2.4. Least squares means and standard errors for age at calving and 305-d production (actual basis, not mature equivalent) for both crossbred groups (pooled), Montbeliarde × Holstein crossbreds, and Viking Red × Holstein crossbreds compared with pure Holstein cows for first lactations

	Pure Holstein		Both crossbred groups		Montbeliarde × Holstein		Viking Red × Holstein	
Trait	LSM	SEM	LSM	SEM	LSM	SEM	LSM	SEM
Cows (n)	978		1,053		513		540	
Age at calving (mo)	23.9	0.08	23.8	0.08	23.8	0.12	23.7	0.12
Milk (kg)	10,970	73	10,745*	84	10,954	122	10,537**	114
Fat (kg)	408	2.7	415[†]	3.1	417	4.5	413	4.2
% Fat	3.74	0.023	3.88**	0.029	3.83	0.042	3.93**	0.039
Protein (kg)	333	1.9	339*	2.1	343**	3.1	336	2.9
% Protein	3.05	0.010	3.17**	0.013	3.14**	0.019	3.19**	0.017
Fat + Protein (kg)	741	4.2	755*	4.7	760*	6.8	749	6.4
Somatic cell score	2.10	0.047	2.16	0.052	2.17	0.074	2.14	0.070

[†] Tendency for significant difference ($P < 0.10$) from pure Holsteins.
* Significant difference ($P < 0.05$) from pure Holsteins.
** Significant difference ($P < 0.01$) from pure Holsteins.

MO × HO cows were not different from the HO cows. Furthermore, the contrast of MO × HO with VR × HO cows indicated that the VR × HO cows produced less (*P* = 0.04) fluid volume of milk than the MO × HO cows. Fluid volume of milk has historically been an important barometer for measuring productivity of cows and continues to be used for day-to-day management of cow health. However, fat and protein production have become more commonplace as gauges for economic productivity of cows. Furthermore, a vast majority of herds in the US are paid only for the solids (kg) that milk contains. Predictions of future milk price are used in the US to assign weights on traits in the Net Merit selection index (VanRaden and Cole, 2014), and those authors estimated a slightly negative weight (−$0.006/PTA unit) should be assigned to fluid volume of milk based on milk price forecasts for 2015 to 2019. Therefore, most dairy producers in the US should compare productivity of breed groups of cows based on solids (kg) production instead of on fluid volume of milk.

The combined crossbred cows in this study tended (*P* = 0.09) to produce more (+2%) fat (kg) than the HO cows, and this resulted from the numerically increased fat production of both of the MO × HO (+9 kg) and the VR × HO (+5 kg), collectively, versus the HO cows (Table 2.4). Fat percentage was +0.14% more (*P* < 0.01) for the combined crossbred cows than the HO cows. The VR breed is known for its high fat content of milk, and the VR × HO cows (3.93%) had increased fat content (*P* < 0.01) compared with the 3.74% of the HO cows during first lactation.

The advantage (+2%) of the combined crossbred cows versus HO cows for protein production (kg) was similar to the results for fat production (kg); however, the significance was greater (*P* = 0.02) because the standard errors for protein production were smaller than those for fat production (Table 2.4). Both crossbred groups had numerically higher protein production (+10 kg and +3 kg for MO × HO and VR × HO, respectively); however, only the comparison of MO × HO (+3%) to HO cows was highly significant (*P* < 0.01). Both crossbred groups had significantly higher (*P* < 0.01) protein percentage (+0.10 and +0.16% for MO × HO and VR × HO, respectively) than the HO cows. These results agree with previous reports that pure MO and VR cows were superior to HO cows for protein percentages in milk (Dezetter et al., 2015; Jönsson, 2015).

For production of fat plus protein (kg), the combined crossbreds were significantly (*P* = 0.03) higher than the HO cows (+2%) during first lactation (Table 2.4). The MO × HO cows had +3% more fat plus protein production than HO cows; however, the VR × HO cows were statistically similar to their HO herdmates for fat plus protein production because of the higher percentages of fat and protein in their milk despite lower fluid volume of milk. Our analysis of the production traits did not adjust for pregnancy status (i.e., days open) of cows; however, a chi-squared test of the percentage of cows pregnant by 150 DIM indicated that significantly more (*P* < 0.02) of the MO × HO (76%) and VR × HO (74%) cows were pregnant at 150 DIM compared with the HO cows (68%). Consequently, the increased proportion of HO cows that were open at 150 DIM may have provided them with a reduced effect of pregnancy (i.e., more late-lactation production) versus the crossbred cows during first lactation.

Results for 305-d production of fat and protein production (kg) in this study differed somewhat from other recent comparisons of MO × HO and VR × HO with HO cows. Least squares means of fat, protein, and fat plus protein production were −2 to −4% for MO × HO compared with HO cows in studies by Heins et al. (2006c), Walsh et al. (2008), Heins and Hansen (2012), Hazel et al. (2014), and Dezetter et al. (2015). However, Heins and Hansen (2012) pointed out the MO sires that had the most daughters in their study had comparatively low ranking within breed for production. On the other hand, Malchiodi et al. (2014b) found MO × HO had +5% increased fat production (kg) and equal protein production (kg) to HO cows for first lactation. Other studies compared production of VR × HO with HO cows during first lactation (Heins et al., 2006c; Heins and Hansen, 2012; Malchiodi et al., 2014b), and they reported the VR × HO cows ranged from −1 to −7% for fat and protein production (kg) compared with HO cows. Conversely, Swalve (2007) found VR × HO produced +6% more fat (kg) and +8% more protein (kg) than HO cows for a lower-production organic herd. These previous studies were often observational in nature or included a small number of cows. Therefore, perhaps, the more favorable results for production of the crossbreds in the current study can be explained by the use of high-ranking sires within all of the breed groups. Also, field data on crossbred cows could contain biases because herd owners may assign service sires based on phenotype of the dam (e.g., HO cows with poor fertility were bred to non-Holstein bulls, HO cows with large body size were bred to VR bulls, or HO cows with poor leg conformation were bred to MO bulls) or herd owners may intentionally breed their best cows to HO bulls, whereas lower-ranking HO cows are bred to bulls from a different breed. Differential mating of this nature was not possible in this study because of the meticulous assignment of foundation HO dams of cows by age or lactation number, sire, and production level within sire. Results from this study provide evidence that crossbreeding may be well-suited for herds at high production levels in addition to those with low production levels. The first-lactation crossbred cows in this study met the production expectations of these high-performance herds. Kargo et al. (2012) grouped more than 1,700 Jersey herds in Denmark into 5 environmental categories according to level of protein production (kg), and they found heterosis for production traits was independent of level of production for crosses of Danish and US strains of Jersey cows. The 8 herds in the current study varied little for mean fat (kg) and protein (kg) production during first lactation (Figure 1), and the range from lowest to highest herd mean was slightly more than 100 kg of fat plus protein (kg) production. Figure 1 reveals the combined crossbred cows had no loss of milk solids production (kg) compared with HO cows during first lactation in any of the 8 herds. Each herd had similar selection criteria for AI bulls, but the bulls used were not identical across herds unlike the 2-herd study of Hazel et al. (2014). Consequently, the AI bulls used within each herd, combined with herd-level management factors, influenced the degree of difference between the crossbred and HO breed groups for the 8 herds.

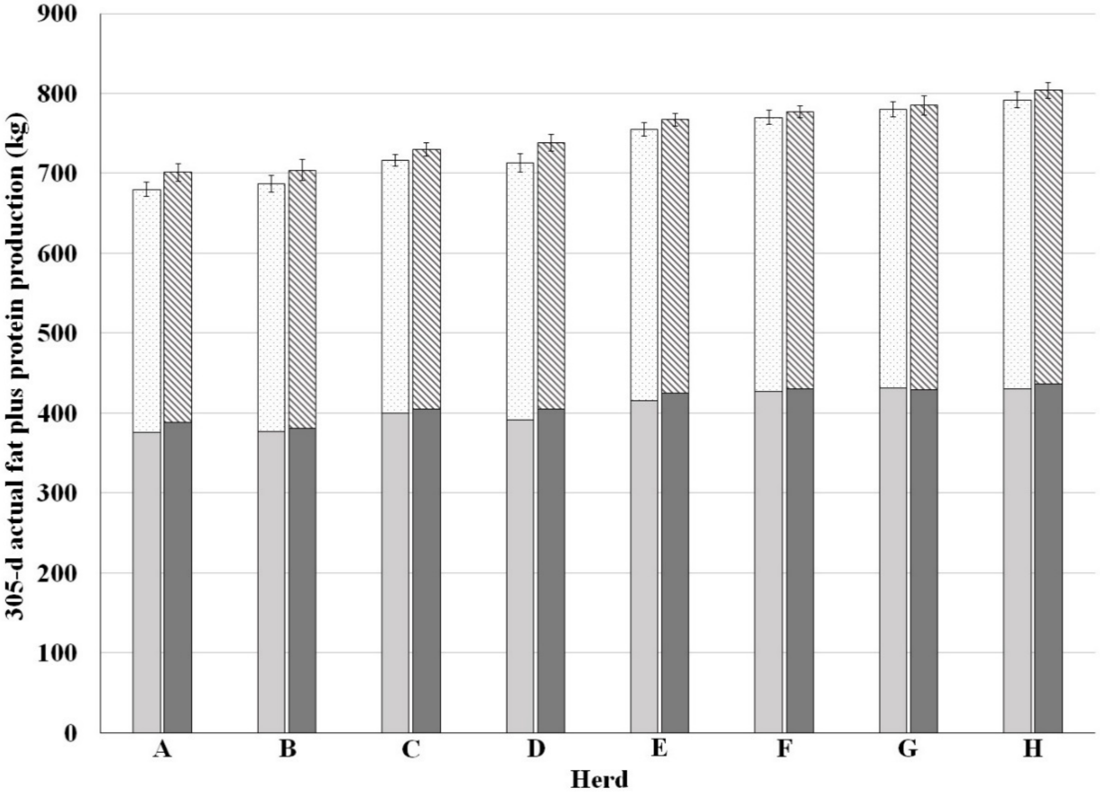

Figure 2.1. Least squares means of 305-d fat production (kg) of pure Holstein (light gray bars) and both crossbred groups (dark gray bars), protein production (kg) of pure Holstein (dotted bars) and both crossbred groups (diagonal striped bars), and SEM of fat plus protein production (kg) for 8 Minnesota herds during first lactation.

The SCS did not differ for combined crossbreds compared with HO cows during first lactation, and SCS was uniformly low for the breed groups (Table 2.4). Other studies that compared MO- and VR-sired crossbred with HO cows during first lactation had a range of results for SCS. Comparisons of MO × HO with HO cows by Walsh et al. (2008), Hazel et al. (2014), and Malchiodi et al. (2014b) found no difference in SCS during first lactation; however, Dezetter et al. (2015) reported MO × HO cows (3.41) had lower SCS across lactations than HO cows (3.62), and Heins and Hansen (2012) found lower SCS in first lactation for MO × HO crossbreds (2.45) compared with HO cows

(2.73). Studies of Norwegian Red × HO crossbreds (Cartwright et al., 2012; Ezra et al., 2016), which share genetic similarity to VR × HO crossbreds, reported no difference for SCS between the crossbred and HO cows. However, Heins and Hansen (2012) reported lower SCS for both VR-sired and Norwegian Red-sired crossbreds (2.53) compared with HO cows (2.73) in first lactation from a field study, and Malchiodi et al. (2014b) also observed lower SCS for VR × HO compared with HO cows (2.35 vs. 2.88, respectively) during first lactation. Contrarily, Swalve (2007) reported VR × HO cows had SCS of 3.18, which was higher than the HO cows (2.75) for a German low-production organic herd. Problems with subclinical mastitis typically become more prevalent for cows in later lactations (Heins and Hansen, 2012), so the lack of difference between the crossbred and HO cows during first lactation in the current study was not surprising.

2.3.2 Calving traits

No difference was detected between combined crossbred (0.7%) and HO cows (1.0%) for TW at first calving (Table 2.5). First-lactation cows tend to have low rates of TW compared with older cows, and a summary of TW studies by Wiltbank et al. (2000) reported only 0.7 to 1.3% TW at first calving. Fricke (2001) reported variation for TW may result from differences in breed composition of cows; however, production level of cows, hormonal treatments for infertility, or other management practices (all of which may vary for breed groups) could also affect TW. Multiple lactations of crossbred and HO cows must be compared to assess the extent these risk factors affect TW among crossbred versus HO cattle.

Table 2.5. Least squares means and standard errors for twinning rate, gestation length, calving difficulty score (1-5 scale), and stillbirth rate for both crossbred groups (pooled), Montbeliarde × Holstein crossbreds, and Viking Red × Holstein crossbreds compared with pure Holstein cows for first calving

	Pure Holstein (HO service sire)		Both crossbred groups (MO or VR service sire)		Montbeliarde × Holstein (VR service sire)		Viking Red × Holstein (MO service sire)	
Trait	LSM	SEM	LSM	SEM	LSM	SEM	LSM	SEM
Cows (n)	971		1,004		496		508	
Twinning rate (%)	1.0	0.3	0.7	0.3	0.6	0.3	0.8	0.4
Cows (n)	961		997		493		504	
Gestation length (d)	276	0.3	279**	0.4	279**	0.6	280**	0.6
Calving difficulty	1.5	0.05	1.6*	0.05	1.6	0.07	1.7*	0.07
Females	1.4	0.06	1.4	0.06	1.4	0.08	1.3	0.08
Males	1.6	0.06	1.9**	0.06	1.7	0.08	2.1**	0.08
Stillbirth rate (%)	9	1.1	5**	1.2	4*	1.5	5[†]	1.7
Females (%)	6	1.3	2*	1.4	2	1.9	3	2.0
Males (%)	11	1.3	8	1.4	7	1.9	8	2.0

[†] Tendency for significant difference (*P* < 0.10) from pure Holsteins.

* Significant difference (*P* < 0.05) from pure Holsteins.

** Significant difference (*P* < 0.01) from pure Holsteins.

The effect of HYS significantly (*P* < 0.01) explained variation of GL and CD, but was not significant for SB. Sex of calf explained significant variation (*P* < 0.01) for GL, CD, and SB. Across breed groups, male calves had longer GL (+2 d), higher CD score (+0.4), and increased SB (+6%) compared with female calves. This result was anticipated because pure HO male calves had +1.2 d longer GL compared with pure HO female calves for Norman et al. (2009b), and MO-sired and pure HO male calves had longer GL (+1.2 and +2.0 d, respectively) than females studied by Heins et al. (2010). Results of this study are in accordance with the literature for CD and SB with male calves having more CD and increased SB than female calves (Lombard et al., 2007).

Both the MO × HO cows (bred to VR bulls) and the VR × HO cows (bred to MO bulls) had significantly (*P* < 0.01) longer GL (+3 and +4 d, respectively) than the HO cows bred to HO bulls (Table 2.5). The interaction of sex of calf with breed group was not significant, which indicated the 3-breed crossbred calves had longer GL than HO calves regardless of sex of calf. The GL of cows is primarily influenced by the genetics of the calf, and the 3-breed crossbred calves averaged either 25 or 50% MO content. The MO breed, like its related breeds of Brown Swiss and Fleckvieh, has significantly longer GL than the other major breeds of dairy cattle. Norman et al. (2009b) reported Brown Swiss cows had +9 d longer GL than HO cows calving for the first time, and the MO breed has +7 d longer GL than the HO breed in France (Ledos and Moureaux, 2013). The GL of the HO cows was 276 d, which is 2 d shorter than the GL reported by Norman et al. (2009b) for HO first-calf heifers (278 d). However, Norman et al. (2009b) also observed a 0.8-d shorter GL for heifers conceiving at young (<14 mo) versus old (>20 mo) ages, and cows in the current study conceived and calved at very young ages.

The combined crossbred cows in this study had significantly (*P* = 0.05) more CD than HO cows (1.6 vs. 1.5, respectively) when evaluated subjectively on a 1 (no assistance) to 5 (extreme difficulty) scale. However, statistical tests of the interaction of sex of calf with breed group revealed the numerically small, but significant, difference between breeds (one-tenth of 1 score) for CD was due entirely to the significantly increased CD for male MO-sired calves that were born to VR × HO first-calf dams (Table 2.5). The heifer calves of the same breed group actually had the numerically lowest CD (1.3) among all the combinations of sex and breed groups. Contrasts between the 2 crossbred breed groups for CD were not significant for both sexes combined, nor for female calves independently; however, the male MO-sired calves (2.1) had more CD (*P* = 0.03) than the male VR-sired crossbred calves (1.7). Results for CD in this study were contrary to those found in the field study of Heins et al. (2006a), who reported significantly fewer difficult births for MO × HO cows (7.2%) and VR × HO (3.7%) compared with HO cows (17.7%); however, the cows in that study were bred to various breeds of AI bulls with no mating design. Birth weights of calves were not available for the current study; however, a possible explanation for the increased CD of male MO-sired calves could be a significant (*P* < 0.01) positive correlation between GL and CD, which may have potentially resulted from increased birth weights. The Pearson correlations between GL and CD were 0.09 for HO calvings and 0.20 for combined crossbred calvings, and they are lower than the 0.27 correlation of sire EBV for GL and CD from Danish national data of HO calvings (Hansen et al., 2004).

Differences for SB between the breed groups were highly significant ($P < 0.01$) and favored the MO × HO and VR × HO crossbreds (4 and 5%, respectively) compared with pure HO (9%) at first calving (Table 2.5). Contrary to results for CD, the 2 interactions involving sex of calf with the breed groups were not significant, and this indicated the crossbred calves had less SB than HO calves regardless of sex of calf. Typically, CD has a positive relationship with SB within the HO breed (Lombard et al., 2007); however, the MO × VR/HO bull calves (8%) did not have more SB than the pure HO bull calves (11%) despite the increased CD of the MO × VR/HO bull calves.

Direct heterosis (due to the genetics of the calf) of CD and SB was negative (unfavorable) in the literature reviewed by Sørensen et al. (2008), and they estimated −10 to −15% direct heterosis for CD and −5 to −10% direct heterosis for SB. On the other hand, maternal heterosis (due to the genetics of the cow) for CD and SB was opposite in sign (positive) and of similar magnitude (Sørensen et al., 2008). Besides this, breeds are expected to differ for additive genetic effects for CD and SB. For the breeds included in this study, pure VR cows had 18% lower CD and 36% less SB at first calving than HO cows evaluated in Sweden (Jönsson, 2015); therefore, the numerical superiority for CD and SB of VR-sired 3-breed calves compared with the MO-sired 3-breed calves in this study was anticipated. Both CD and SB are economically important traits because cows experiencing CD require extra labor, and moderate to severe CD necessitates high costs of health treatments for cows giving birth.

Herd owners are accustomed to SB in excess of 8% for pure HO calves born to first lactation dams (Lombard et al., 2007; Sørensen et al., 2008), and some published studies estimate SB to be more than 12% for first calving (Ettema and Santos, 2004; Heins et al., 2006a). VanRaden and Cole (2014) estimated the lost revenue for each SB calf at $300 for the calculation weights for the Net Merit index; therefore, the extent of economic loss from SB calves was substantially lower for crossbred versus HO calves in this study.

The revenue from milk production (volume, component, and SCC pay adjustments), the labor cost associated with dystocia, as well as the value of live calves born, will eventually contribute to a comprehensive analysis of the profitability of the MO × HO and VR × HO versus HO cows in this study on a lifetime basis. Previous studies on crossbreeding in dairy cattle have usually been limited to comparisons of performance for routinely measured traits (e.g., production traits, SCS, fertility, and survival), and most of the studies reported traits divided into single parities. An exception is the study of Heins et al. (2012a), which reported lifetime profitability and profit per day in the herd for crossbred cows (+5.3 and +3.6% for MO × HO and VR × HO, respectively) compared with HO cows. More studies of this nature are needed because the comparisons of individual traits ignores any potential antagonism between traits, relies heavily on intuition to assign economic value to the traits, and considers only the value of outputs without regard to inputs. Furthermore, the welfare of dairy cattle is of increasing concern to consumers, and measures of profitability may be more reflective of animal well-being than some measures of performance, especially milk production

(Oltenacu and Broom, 2010). The effect of health costs of cows on lifetime profitability has not been considered in most research of crossbreeding, and the 8 herd owners in this study (and likely most other dairy producers) place high value on the economic effects of cow health.

2.4 Conclusions

Potential loss of production is often mentioned as a reason to avoid crossbreeding in dairy cattle. Concerns about lost production may be legitimate when heterosis in not fully exploited (either by rotating only 2 breeds or by using breeds which are genetically similar), inappropriate breeds are used out of familiarity or convenience, or when AI bulls of low genetic rank are selected. This study was designed and implemented to mitigate those concerns by focusing on 8 high-performance Minnesota herds that used a 3-breed rotational crossbreeding system with the use of high-ranking AI bulls from the MO, VR, and HO breeds. Furthermore, most estimates of the negative effects of inbreeding are dated and, perhaps, recent selection practices in the pure HO breed has exacerbated the potential effect of inbreeding depression. The 2-breed crossbreds in this study met the production expectations of the 8 participating dairy herds. In fact, the MO × HO and VR × HO crossbreds, collectively, had increased production of milk solids (kg) in first lactation with similar SCS compared with their pure HO herdmates. The CD of the VR-sired 3-breed crossbred calves was similar to pure HO; however, the male MO-sired calves out of VR × HO dams had somewhat more CD than male HO calves. The SB rate of crossbred calves was one-half that of the pure HO calves, and this is a major advantage for both profitability and animal welfare. In the future, the lifetime performance and profitability of the crossbred versus pure HO cows in this study will be compared, including the costs of health treatments, fertility, and survival.

CHAPTER 3

Fertility, survival, and conformation of Montbeliarde × Holstein and Viking Red × Holstein crossbred cows compared with pure Holstein cows during first lactation in 8 commercial dairy herds

3.1 Introduction

Breeding goals of dairy cattle throughout the world have heavily emphasized production traits. However, a negative genetic correlation between production and fertility has been documented (Philipsson et al., 1994; Berry et al., 2014). Phenotypically, Holstein (**HO**) cows have deteriorated for fertility commensurate with increases in production (Walsh et al., 2011). Therefore, fertility and longevity have gradually received more emphasis over time in selection indices around the world (Miglior et al., 2005).

A steep decline in phenotypic fertility for HO cows may have plateaued at a low level during the early 2000's (Berry et al., 2014), but the explanation for the plateau may be mostly because of environmental intervention rather than a reversal of the genetic trend for HO cows (VanRaden et al., 2014). Norman et al. (2015b) reported decreases in days open (**DO**) and calving interval from 2004 to 2014 among pure HO cows in the US; however, the results were not caused by increased conception rate (**CR**), which was only 34% for first services in 2014. Also, a continual increase of the mean inbreeding coefficient may have impeded phenotypic improvement for fertility, because inbreeding is more detrimental for functional traits, such as fertility, health, and survival than other traits (Falconer and Mackay, 1996). The average inbreeding coefficient of HO females born early in 2017 in the US was 7.14% (Council on Dairy Cattle Breeding, 2017d). Heterosis results when distinct breeds of cattle are crossed; therefore, some commercial dairy producers have turned to crossbreeding to improve fertility (Walsh et al., 2008). Sørensen et al. (2008) summarized the heterosis for fertility traits of 2-breed crosses including HO and concluded about 10% heterosis should be expected for fertility traits when other breeds are crossed with HO cows. Furthermore, the marked advantage in fertility for crossbred cows over HO cows may be due to additive genetic effects of non-HO breeds (Sørensen, 2007; Norman et al., 2009a; Dezetter et al., 2015) in addition to heterosis.

Culling decisions for individual cows are heavily impacted by production, fertility status, age, health status, stage of lactation, cull value of cows, value of replacements, or the combination of these factors (Gröhn et al., 2003). Diseases of cows have a major impact on longevity, and Kyntäjä (2013) documented fewer health treatments for VR cows than HO cows in Finland. Dairy producers have recorded health treatments, including lameness, for many years in France (Bourrigan et al., 2016) and the Nordic countries (Emanuelson, 2013). Therefore, selection for improved health was possible for the MO and VR breeds and, as a result, these breeds may be well-suited for crossbreeding with the HO breed.

The MO cows in France had approximately 13% less mortality than French HO cows in 2005 (Raboisson et al., 2011), and VR cows had 22% less mortality than HO cows in Sweden (Alvåsen et al., 2012). Advantages for additive genetic effects of the MO and VR breeds for mortality combined with 10 to 15% heterosis for longevity from crossbreeding (Sørensen et al., 2008) has resulted in interest in 3-breed rotational crossbreeding using the MO, VR, and HO breeds. Despite the global prominence of the HO breed over the past 30 yr, pure HO cows rank poorly for survival compared to other dairy breeds (Hare et al., 2006), and this has generated interest by dairy producers in crossbreeding. Cow survival is a growing concern of the general public for animal welfare.

The HO breed has been heavily selected for large frame size over time and the genetic trend for increased stature, strength, and body depth of HO cows continues (VanRaden et al., 2014) despite a negative weight on frame size since 2000 in the US Net Merit index (VanRaden and Cole, 2014). The continuous increase of mean body size of HO cows is concerning because larger body size of cows results in increased costs for health treatments (Becker et al., 2012), reduced feed efficiency because of increased maintenance requirements of large-framed cows (VandeHaar et al., 2016), and reduced survival of cows (Hansen et al., 1999; VanRaden and Cole, 2014). Selection for angularity of HO cows via selection for final score type has resulted in reduction of BCS (Hansen, 2000), and the phenotypic relationship of low BCS and poor fertility and health in HO cows is well documented (Roche et al., 2009; Walsh et al., 2011).

The MO and VR breeds may complement the HO breed for crossbreeding because the selection goals of these 2 breeds have included fertility and health alongside production of milk solids; meanwhile, the HO breed focused more on production at the expense of fertility and health. The VR breed ignored body condition and the MO breed selected for increased body condition in their selection programs over time. The MO ×

HO crossbred cows evaluated by Hazel et al. (2013, 2014) had similar stature to their pure HO herdmates. Also, VR × HO cows may have reduced body size compared with HO cows because pure VR cows are 6.5 cm shorter than HO cows in Denmark, Finland, and Sweden (H. Stålhammar, VikingGenetics, Skara, Sweden, *personal communication*). Advantages of crossbred cows over HO cows for fertility and survival may have resulted from the increased BCS of crossbreds (Pryce and Harris, 2006; Walsh et al., 2008; Hazel et al., 2014). Studies of pure HO cows have found negligible relationships between rump, leg, and udder conformation with metabolic and reproductive diseases (Zwald et al., 2004), but HO cows with shallower udders are superior for udder health (Zwald et al., 2004; Carlström et al., 2016a).

The objective of this study was to compare phenotypes of fertility, survival, and conformation from first lactations of MO × HO and VR × HO crossbred cows with pure HO cows in a designed study. The same 2-breed crossbreds were previously compared with pure HO cows for production and calving traits during first lactation (Hazel et al., 2017b).

3.2 Materials and methods

The descriptions of herds and cows enrolled as well as the mating design were described in Chapter 2, and data for these analyses originated from the same group of cows as in Chapter 2.

3.2.1 Trait descriptions

Fertility. Reproductive protocols varied from herd to herd as well as over time within herds and were not recorded for this study. However, herd owners were requested to manage cows in the same manner at all times across breed groups. All the herds had a large number of cows and used group housing; therefore, reproductive protocols were likely applied uniformly across breed groups. The days to first breeding (**DFB**) was the number of d from calving to first insemination. First-service CR (**FSCR**) was the proportion of cows that became pregnant after a single insemination divided by the cows that were bred for the first time. Pregnancy status was ascertained by a subsequent insemination, by palpation or ultrasound, or by subsequent calving. The overall CR consisted of the proportion of successful inseminations divided by the total number of inseminations during first lactation, including cows that did not conceive by the end of the study. However, only the first 5 inseminations that occurred from 45 DIM to 305 DIM were considered in order to eliminate individual cows that may have been treated preferentially by herd owners. Times bred was the number of inseminations, and the maximum number of inseminations was set to 5 for cows with more than 5 inseminations. The final fertility trait was DO, which was defined as the number of days from first calving to pregnancy.

Survival. Survival was recorded as a binary trait and was defined as survived or not for each of 4 time intervals. Survival to 60 DIM was the proportion of cows that survived in the herds to 60 DIM divided by the total cows that calved a first time. Subsequent calving within 14 mo and subsequent calving within 17 mo were the proportion of cows that calved a second time within 14 or 17 mo, respectively, divided by all cows that calved a first time. Survival to second calving was the proportion of cows that calved a second time divided by the total number of cows that calved for a first time.

BCS and Conformation. The BCS and conformation were evaluated once during first lactation from 2 to 110 DIM and cows were mostly scored during early lactation (32 ± 0.5 DIM) by the 2 genetic advisors across the years of the study. The BCS was subjectively assigned on a 1-to-5 scale (1 = thin and 5 = obese) in increments of 0.25 (Ferguson et al., 1994). The 10 conformation traits included stature (**STA**; height at the withers), body depth (**BD**), strength (**STR**), rump angle (**RA**), leg set (**LS**; side view), foot angle (**FA**), udder clearance (**UC**, relative to hock), front teat width (**FTW**), rear teat width (**RTW**), and teat length (**TL**; front teats). Conformation traits were scored from 1 to 9 in increments of 1, and scores were assigned independent of age or stage of lactation (Select Sires, Inc., Plain City, OH). Linear scores were subjectively assigned; however, definitions of scores for some linear traits corresponded with a measurement objective.

Table 3.1. Descriptions of minimum, intermediate, and maximum score for linear conformation traits

	Linear score		
Trait[1]	1	5	9
Stature	Short (≤ 129 cm)	Intermediate (140 cm)	Tall (≥ 150 cm)
Body depth	Shallow	Proportionate to body length	Deep
Strength	Narrow	Intermediate	Wide
Rump angle	Reverse slope (pins 13 cm higher than hips)	Level pins and hips	Slope (pins 13 cm lower than hips)
Leg set	Posty	Slight set	Sickle
Foot angle	Low (≤ 25 degrees)	Intermediate (45 degrees)	Steep (≥ 65 degrees)
Udder clearance	Low (≥ 5 cm below hocks)	Intermediate (5 cm above hocks)	High (≥ 15 cm above hocks)
Front teat width	Wide	Central	Close
Rear teat width	Wide	Central	Close
Teat length	Short (≤ 3 cm)	Intermediate (6 cm)	Long (≥ 8 cm)

[1] All traits were subjectively scored; however, measurement goals are provided for stature, rump angle, foot angle, udder clearance, and teat length.

Descriptions of the scales used for conformation traits is described in Table 3.1. For all conformation traits, a score of 5 was the biological mid-point and did not necessarily represent a mean score.

3.2.2 Final editing and analysis

Fertility. The number of cows analyzed varied for each of the 5 fertility traits because edits were applied separately to each trait. For DFB, cows that were first bred before 45 DIM (n = 2), cows that left the herd prior to first insemination (n = 116), and cows bred by a natural service bull (n = 3) were removed. Cows retained were assigned to herd-year-season (**HYS**) of first calving, and HYS was defined as 4-mo periods (Jan-Apr, May-Aug, and Sept-Dec) within each herd that likely best reflected climatic conditions in Minnesota. Each herd had up to 11 HYS of first calving across the years of the study. The data were further edited to permit a valid comparison of crossbreds and HO cows within each HYS, and those edits were conducted separately for each trait. To remain in the data, each HYS was required to contain at least 3 crossbred (MO × HO and VR × HO breed groups combined) and 3 HO cows; therefore, a total of 6 combined crossbred and 63 HO cows that did not meet this criterion were removed from the analysis for DFB. Other HYS with small numbers of cows in the MO × HO or VR × HO breed group were combined within herds. The HYS that contained fewer than 3 of either MO × HO or VR × HO cows were combined with adjacent HYS. After edits, the number of cows analyzed for DFB included 1,046 crossbred (both types combined) and 970 HO cows.

For FSCR, 2 HO cows with a first insemination before 45 DIM were removed, but these 2 cows had subsequent inseminations after 45 DIM and were included for overall CR. All other edits were identical for FSCR and overall CR, and they included the removal of cows that did not remain in the herd to be bred or to be verified for pregnancy after a first service (n = 132), the removal of cows that were bred to a natural service bull or to an AI bull that did not conform to the mating design of the study (n = 22), and the removal of cows in HYS that had fewer than the 3 crossbred and 3 HO contemporaries (n = 75). A total of 1,027 crossbred cows were compared with 948 (for FSCR) and 950 (for overall CR) HO cows.

The cows removed from the analysis of times bred included cows first bred before 45 DIM (n = 2), cows that did not remain in the herd to a first insemination (n = 116), cows bred to a natural service bull or an AI bull that did not conform to the mating design prior to fifth service (n = 17), and cows calving in HYS with fewer than 3 crossbred and 3 HO cows (n = 69). Following these edits, 1,043 crossbred and 959 HO cows were compared for times bred.

For DO, cows exceeding 250 d (n = 217) were set to 250 d (VanRaden et al., 2004), which is the method used for genetic evaluation in the US. Also, DO were required to be at least 50 DIM, and 18 crossbred and 3 HO cows with DO of 45 to 49 d were set to 50 d. Cows were required to complete 250 DIM to be included in the analysis (VanRaden et al., 2004) and, therefore, 103 crossbred and 132 HO cows were removed. Cows bred by natural service bulls prior to 250 DIM (n = 11) and cows calving in HYS with less than 3 crossbred and 3 HO cows (n = 65) were removed. To provide an example of the distribution of crossbred and HO cows across herds, the number of cows analyzed for DO within each of the herds by breed group are in Table 3.2.

Table 3.2. Distribution of cows analyzed for days open by herd

Herd	Pure Holstein	Montbeliarde × Holstein	Viking Red × Holstein
A	127	36	40
B	85	28	23
C	73	45	42
D	182	84	88
E	136	130	139
F	113	90	88
G	97	25	41
H	88	42	53
Total	901	480	514
Mean (SE)	113 (12)	60 (13)	64 (13)

The analysis of DFB, FSCR, overall CR, times bred, and DO included the fixed effects of HYS of first calving, breed of cow (crossbred or HO), and breed group (MO × HO nested within crossbred, VR × HO nested within crossbred, or HO). Sire of cow nested within breed group was a random effect. Additionally, FSCR and overall CR included the random effect of service sire nested within breed group of sire (i.e., MO or VR sire nested within crossbred). The MIXED procedure of SAS (release 9.4, SAS Institute Inc., Cary, NC) was used to obtain least squares means and to conduct the ANOVA for DFB, times bred, and DO. Because conception is a binary trait, the GLIMMIX procedure of SAS was used to determine probability of significance for contrasts between breed of cow and between breed groups for FSCR and overall CR. The *P*-values for the comparison of breed groups were subjected to the Bonferroni correction to account for multiple comparisons. Firstly, HO was designated the control to correct the *P*-values that compared MO × HO and VR × HO with HO cows. Secondly, no control group was designated in order to correct the 3 *P*-values that included the comparison of MO × HO with VR × HO cows.

Survival. For survival to 60 DIM, the cows sold for dairy purposes (n = 4) during the first 60 d of first lactation were removed from the analysis. Also, the HYS of first calving were edited in the same manner as they were for fertility for all survival traits, and cows (n = 73) that calved during HYS without at least 3 crossbred and 3 HO cows were removed. After all edits, 1,096 crossbred and 1,033 HO cows were analyzed for survival to 60 DIM.

For analysis of subsequent calving within 14 mo, cows sold for dairy purposes during the first 14 mo of first lactation (n = 30) were removed from analysis. In total, 1,082 crossbred and 1,021 HO cows were available for analysis of subsequent calving within 14 mo. The edits for subsequent calving within 17 mo were identical to subsequent calving within 14 mo, except 2 additional crossbred cows were sold for dairy purposes between 14 and 17 mo after first calving. For survival to second calving, cows sold for dairy purposes during first lactation were removed (n = 32). Also, 8 HO cows completed at least 17 mo of their first lactation but had not yet completed their entire first lactation at the time of this analysis (mean DIM was 647 ± 42 d). These cows were removed from analysis because their final status for survival to second lactation was unknown.

The analysis of all survival traits included the fixed effects of HYS of first calving, breed of cow (crossbred or HO), and breed group of cow (MO × HO nested within crossbred, VR × HO nested within crossbred, or HO). Furthermore, the random effect of sire of cow nested within breed group was included. Least squares means were obtained from the MIXED procedure of SAS, and the significance of contrasts were obtained from the GLIMMIX procedure of SAS because survival is a binary trait. Orthogonal contrasts for each type of 2-breed crossbred versus HO cows were evaluated in the same manner as fertility traits and employed the Bonferroni correction for comparisons between breed groups.

BCS and Conformation. Across breed groups, 134 cows were excluded from analysis of BCS because they either left the herd prior to scoring or did not have BCS recorded. Cows were assigned to HYS of first calving for both BCS and conformation in the same manner as fertility and survival traits. The same criteria was used for editing and combining of HYS of first calving. A total of 1,040 crossbred and 956 HO cows were analyzed for BCS. The edits were identical for all 10 conformation traits. In total, 95 cows that calved for a first time were not scored for conformation. The analysis of conformation traits included 1,051 crossbred and 983 HO cows after all edits.

The uniform model used for the analysis of BCS and conformation included the fixed effects of HYS of first calving, breed of cow (crossbred or HO), and breed group of cow. Furthermore, the effect of DIM at scoring was included as a class variable, and the 4 DIM classes consisted of 2 to 19 d, 20 to 39 d, 40 to 59 d, and 60 to 110 d. Finally, the random effect of sire nested within breed group was included. The MIXED procedure of SAS was used to obtain the least squares means and to perform the ANOVA. A

Bonferroni correction was used to evaluate orthogonal contrasts between breed groups as previously described.

3.3 Results and discussion

3.3.1 Fertility

The effect of HYS of first calving was highly significant for DFB, FSCR, overall CR, and times bred; however, HYS did not differ for DO. The crossbred cows (both types combined) were superior ($P < 0.01$) to the HO cows for all 5 of the fertility traits during first lactation (Table 3.3). The combined crossbred cows (69 ± 0.4 d) were bred 2 d sooner ($P < 0.01$) after first calving than their pure HO herdmates (71 ± 0.4 d). Most first inseminations resulted from enrollment in a timed AI protocol, and this may explain the small differences of the least squares means between breed groups and the small standard errors for DFB.

The combined crossbred cows had increased ($P < 0.01$) FSCR and overall CR (45 ± 1.7% and 45 ± 1.4%, respectively) compared with the HO cows (38 ± 1.7% and 38 ± 1.3%, respectively; Table 3.3). The VR × HO crossbred cows bred to MO bulls (47 ± 2.4%) had 9% increased ($P < 0.01$) FSCR than the HO cows; however, the MO × HO cows bred to VR bulls were similar to HO cows for FSCR. Potential differences between the 2 types of crossbreds were inconsequential for FSCR or overall CR because the 2 types of crossbreds did not differ ($P > 0.98$) for either trait. Differences between crossbreds and HO cows for FSCR in the current study were similar to those reported by Heins et al. (2006b) from a California field study, in which MO × HO (31 ± 3.0%) had increased ($P < 0.05$) FSCR. For both Heins et al. (2006b) and the current study, the

Table 3.3. Least squares means and standard errors for days to first breeding (DFB), first-service conception rate (FSCR), overall conception rate (CR), times bred (up to 5), and days open (DO) for both crossbred groups (pooled), Montbeliarde × Holstein crossbreds, and Viking Red × Holstein crossbreds compared with pure Holstein cows during first lactation

	Pure Holstein			Both crossbred groups			Montbeliarde × Holstein			Viking Red × Holstein		
Trait	n	LSM	SEM	n	LSM	SEM	n	LSM	SEM	n	LSM	SEM
DFB (d)	970	71	0.4	1,046	69**	0.4	507	69*	0.6	539	70	0.5
FSCR (%)	948	38	1.7	1,027	45**	1.7	499	43	2.4	528	47**	2.4
Overall CR (%)	950	38	1.3	1,027	45**	1.4	499	46**	1.9	528	43[†]	1.9
Times bred	959	2.30	0.05	1,043	2.11**	0.05	506	2.07**	0.06	537	2.15	0.06
DO (d)	901	125	2.1	994	115**	2.0	480	113**	2.8	514	117*	2.8

[†] Tendency for significant difference ($P < 0.10$) from pure Holsteins.

* Significant difference ($P < 0.05$) from pure Holsteins.

** Significant difference ($P < 0.01$) from pure Holsteins.

crossbred cows had advantages from both the heterosis of the cows and the heterosis of their embryos compared with the pure HO cows and their pure HO embryos.

The times bred for the combined crossbred cows (2.11 ± 0.05) were fewer ($P < 0.01$) than the times bred of the HO cows (2.30 ± 0.05) during first lactation (Table 3.3). The difference was from the MO × HO cows being inseminated fewer times ($P < 0.01$), because the VR × HO were not different ($P = 0.12$) from their HO herdmates for times bred. Results in this study concur with those of Malchiodi et al. (2014a), who found MO × HO (2.02) and VR × HO (2.14) had fewer times bred than first-lactation HO cows (2.53).

For DO, the combined crossbred cows (115 ± 2.0 d) had 10 fewer DO than the HO cows (125 ± 2.1 d) during first lactation. The MO × HO (−12 d) and VR × HO (−8 d) crossbred cows did not differ ($P = 0.84$) from each other for DO; however, both types of crossbreds had decreased ($P < 0.02$) DO compared with the HO cows in first lactation (Table 3.3). VanRaden et al. (2004) reported that 14% of DO records exceeded 250 d in a national evaluation of HO cows enrolled in DHI, and this is very similar to the 13% of records set to 250 d for the pure HO cows in this study. However, a Chi-squared test indicated fewer ($P < 0.05$) crossbred cows (10%) surpassed 250 DO than HO cows; therefore, imposing the maximum of 250 DO provided an advantage for mean DO to the HO cows in this study. The differences between the crossbred and HO cows in this study were not nearly as extreme as those found by Malchiodi et al. (2014a), who reported 25 fewer DO for MO × HO versus HO cows in first lactation. Piccardi et al. (2014) observed a 30-d advantage in fewer DO for VR × HO compared with HO cows in first lactation. Malchiodi et al. (2014a) reported VR × HO cows had 13 fewer DO than pure HO cows in first lactation. Also, Heins and Hansen (2012) observed 17 and 14 fewer DO for MO × HO and Nordic Red × HO crossbreds, respectively, versus pure HO cows in first lactation for high-performance commercial herds in California. Reports for DO of pure HO from other recent studies ranged from 122 to 124 d across multiple lactations (Bastin et al., 2010; Norman et al., 2015b) and are similar to the 125 DO of the first-lactation HO cows in this study. The 125 DO of the HO cows in this study is reasonable by many standards; however, the 10-d advantage in DO for the combined crossbred cows may provide an economic advantage of $14 to $51 during first lactation over HO cows (Groenendaal et al., 2004; De Vries, 2006). The difference in economic advantage may result from decreased re-synchronization, less culling for fertility, and a faster return to peak production at second calving.

The fertility traits of cows in this study were not adjusted for the production level of cows. Production of these cows was reported previously by Hazel et al. (2017b), and the combined crossbred cows produced 2% more 305-d fat plus protein (kg) production (actual basis, and not mature-equivalent) compared with the HO cows. Some have suggested crossbred cows will produce less milk than pure HO cows, and this must be tolerated in order to capitalize on the advantages for fertility and other functional traits from crossbreeding (Walsh et al., 2008; Piccardi et al., 2014). However, that was not the outcome for the MO × HO and VR × HO crossbreds compared to pure HO cows in this study. Researchers have hypothesized HO cows have been selected to preferentially partition energy to production over fertility (Sundrum, 2015). The crossbreds in this study apparently overcame physiological challenges of this sort more readily than the HO cows because they produced at least as much milk solids as the pure HO cows (Hazel et al., 2017b) and also were superior for fertility. Malchiodi et al. (2014a) suggested crossbred and HO cows may have physiological differences that allow crossbred cows to better respond to the metabolic demands of production, health, and fertility, which all occur concurrently in early lactation.

The biological reason for the superior fertility of the crossbred cows compared to the pure HO cows in this study may be partially due to the difference in BCS between them. Researchers (Dechow et al., 2002; Roche et al., 2009; Walsh et al., 2011) have reported HO cows that had more BCS at the time of calving or less loss in BCS after calving had increased reproductive success. Reasons for the reproductive advantages of the 2-breed crossbred cows in this study may be the advantage of the MO and VR breeds for fertility compared to the HO breed (Sørensen, 2007; Dezetter et al., 2015) and a 10% expected heterosis for fertility when 2 unrelated pure breeds of dairy cattle are crossed (Sørensen et al., 2008).

3.3.2 Survival

The effect of HYS of first calving was not significant for survival to 60 DIM and subsequent calving within 14 mo, but HYS tended to be significant for subsequent calving within 17 mo ($P = 0.09$) and survival to second calving ($P = 0.08$). The combined crossbreds did not differ ($P = 0.48$) from HO cows for survival to 60 DIM, and 96 ± 0.6% of both the crossbred and HO cows calving for a first time survived to 60 DIM (Table 3.4). The first 60 d after calving is a period in which cows are most at risk for health disorders (Donnelly et al., 2016) that results in removal from herds. For first-lactation cows, Dechow and Goodling (2008) found 5% of HO cows were removed from herds during the interval from 21 d before first calving to 60 d after first calving, and this was similar to the 4% of both crossbred and HO cows that left herds. However, Heins et al. (2012a) analyzed survival in first lactation from calving to the first test day for milk recording (4 to 30 DIM for most cows) and, despite the much shorter interval of time, only 91% of HO cows compared to an increased percentage of MO × HO (98%) and Nordic Red × HO (98%) survived to a first test day. An explanation for the superior early-lactation survival of HO cows in this study compared with Heins et al. (2012a) could be the increased CD of HO cows in comparison to the crossbreds in that study (Heins et al., 2006a). The crossbred cows (1.6 ± 0.05) in this study differed from HO cows (1.5 ± 0.05) by only a tenth of a score (on a 5-point scale) for CD at first calving (Hazel et al., 2017b).

More ($P < 0.01$) of the combined crossbred cows (71 ± 1.5%) had a subsequent calving within 14 mo after their first calving (Table 3.4) compared with the HO cows (63 ± 1.5%). At 17 mo after first calving, the combined crossbreds (82 ± 1.5%) continued to surpass ($P < 0.01$) the HO cows (76 ± 1.4%) for subsequent calving. Traits such as subsequent calving within 14 and 17 mo and survival to second calving revealed the more rapid speed at which the crossbreds returned to peak production than did the HO cows. The MO × HO and VR × HO did not differ for any measure of survival.

For survival to second calving, 4% more of the combined crossbred cows commenced a second lactation compared with HO cows (Table 3.4). This result was

Table 3.4. Least squares means and standard errors for survival of both crossbred groups (pooled), Montbeliarde × Holstein crossbreds, and Viking Red × Holstein crossbreds compared with pure Holstein cows during first lactation

	Pure Holstein			Both crossbred groups			Montbeliarde × Holstein			Viking Red × Holstein		
Trait	n	LSM	SEM	n	LSM	SEM	n	LSM	SEM	n	LSM	SEM
Survival to 60 DIM (%)	1,033	96	0.6	1,096	96	0.6	536	96	0.8	560	97	0.8
Calved again within 14 mo (%)	1,021	63	1.5	1,082	71**	1.5	530	72**	2.1	552	70*	2.0
Calved again within 17 mo (%)	1,021	76	1.4	1,080	82**	1.5	529	83**	2.1	551	81†	2.0
Survival to second calving (%)	1,014	80	1.5	1,080	84*	1.5	529	84	2.2	551	83	2.1

† Tendency for significant difference (*P* < 0.10) from pure Holsteins.

* Significant difference (*P* < 0.05) from pure Holsteins.

** Significant difference (*P* < 0.01) from pure Holsteins.

similar to those of Norman et al. (2016), who analyzed US national data and reported 77% of crossbred cows compared to 74% of HO cows in first lactation calved for a second time.

3.3.3 BCS and Conformation

The HYS of first calving was significant for the analysis of BCS and all 10 of the conformation traits. Similarly, class of DIM at the time of scoring was significant for all traits except for STA ($P = 0.16$), LS ($P = 0.11$), and FA ($P = 0.17$). Cows scored at later DIM had increased BD, decreased STR, RA with less slope, increased LS, closer FTW and RTW, and longer TL. A directional pattern for class of DIM at scoring was not observed for STA, FA, or UC. The combined crossbred cows (3.58 ± 0.02) had 0.38 increased ($P < 0.01$) BCS than the HO cows (3.20 ± 0.02) because both the MO × HO (+0.50) and VR × HO (+0.25) had increased BCS than HO cows (Table 3.5). Additionally, the MO × HO (3.70 ± 0.02) had increased ($P < 0.01$) BCS than VR × HO cows (3.45 ± 0.02). Hazel et al. (2014) reported MO × HO cows had +0.49 more BCS across lactations than HO cows. Walsh et al. (2008) had +0.23 more BCS for MO × HO versus HO cows, but the magnitude of the difference was smaller in the grazing environment of that study compared with the high-performance, confinement environment of the current study. The association of low BCS with impaired fertility of cows is well documented (Roche et al., 2009; Bastin et al., 2010), and the increased BCS of crossbred cows in this study may explain some of the 10-d advantage for DO and the fewer times bred compared with HO cows. A documented close biological relationship between BCS and fertility (Dechow et al., 2002; Roche et al., 2009) precludes the use of one variable to explain variation of the other. The BCS of cows in this study was only scored once during early lactation; therefore, this study did not provide information about potential differences among the breed groups for BCS at calving, BCS at its lowest during lactation, or rate or amount of BCS lost during the transition period of lactation. The combined crossbreds had shorter STA ($P < 0.01$) than the HO cows (Table 3.5), and the mean scores convert to 138 cm for the combined crossbred cows and 141 cm for the HO cows (Select Sires, Inc., Plain City, OH). Also, the VR × HO (137 cm) had shorter STA ($P < 0.01$) than both the MO × HO and pure HO cows. The combined crossbred cows (4.3 ± 0.09) had shallower BD ($P < 0.01$) compared with their HO herdmates (5.2 ± 0.08) during first lactation. The taller STA and deeper BD of the HO cows may be detrimental to the health of cows (Becker et al., 2012), and this may reduce survival compared to cows with smaller body size (Hansen et al., 1999). The combined crossbred cows in this study had more STR ($P < 0.01$) compared to the HO cows (+0.7 points), but the difference was completely due to the more STR of the MO × HO (+1.5 points) compared with HO cows, whereas the VR × HO cows had similar STR to the HO cows.

Both MO × HO (7.0 ± 0.12) and VR × HO (6.6 ± 0.11) had more slope ($P < 0.01$) from hips to pins for RA than HO cows (6.1 ± 0.07), and the slope was steeper ($P = 0.02$) for the MO × HO than the VR × HO cows. For LS, the combined crossbred cows tended ($P = 0.06$) to have less set to the hock; however, the 2 types of crossbreds were different from each other because MO × HO (4.6 ± 0.14) had less set to the hock than HO cows (5.6 ± 0.09), while the VR × HO crossbreds had more set to the hock than their HO

Table 3.5. Least squares means and standard errors for body condition score (1 to 5 scale) and conformation scores (1 to 9 scale) for both crossbred groups (pooled), Montbeliarde × Holstein (MO × HO), and Viking Red × Holstein (VR × HO) cows compared with pure Holstein cows during first lactation

Trait	Pure Holstein		Both crossbred groups		Montbeliarde × Holstein		Viking Red × Holstein		Probability from contrast of MO × HO and VR × HO
	LSM	SEM	LSM	SEM	LSM	SEM	LSM	SEM	
Cows (n)	956		1,040		502		538		
Body condition score	3.20	0.02	3.58**	0.02	3.70**	0.02	3.45**	0.02	< 0.01
Cows (n)	983		1,051		510		541		
Stature (9=taller)	5.4	0.10	4.2**	0.12	4.6**	0.17	3.8**	0.15	< 0.01
Body depth (9=deeper)	5.2	0.08	4.3**	0.09	4.2**	0.13	4.5**	0.12	0.21
Strength (9=wider)	5.3	0.09	6.0**	0.11	6.8**	0.16	5.2	0.15	< 0.01
Rump angle (9=more slope)	6.1	0.07	6.8**	0.09	7.0**	0.12	6.6**	0.11	0.02
Leg set (9=more sickle)	5.6	0.09	5.3†	0.10	4.6**	0.14	6.1**	0.13	< 0.01
Foot angle (9=steeper)	5.6	0.08	6.0**	0.09	6.6**	0.12	5.4	0.12	< 0.01
Udder clearance (9=shallower)	6.9	0.08	5.9**	0.10	5.5**	0.14	6.2**	0.13	< 0.01
Front teat width (9=closer)	5.5	0.10	4.8**	0.11	4.5**	0.16	5.1*	0.15	0.06
Rear teat width (9=closer)	6.5	0.10	5.7**	0.12	5.4**	0.17	5.9**	0.16	0.12
Teat length (9=longer)	3.9	0.11	4.3*	0.13	4.6**	0.18	4.0	0.16	0.08

† Tendency for significant difference (*P* < 0.10) from pure Holsteins.

* Significant difference (*P* < 0.05) from pure Holsteins.

** Significant difference (*P* < 0.01) from pure Holsteins.

herdmates. The combined crossbred cows (6.0 ± 0.09) had steeper FA ($P < 0.01$) than the HO cows (5.6 ± 0.08), but the difference was entirely due the MO × HO cows with a 1.0-point advantage over the HO cows. The FA of VR × HO (5.4 ± 0.12) and HO cows (5.6 ± 0.08) was not different ($P = 0.29$).

For udder traits, the combined crossbred cows (5.9 ± 0.10) had less UC ($P < 0.01$) from the hock than the HO cows (6.9 ± 0.08), and the MO × HO cows (5.5 ± 0.14) had less UC ($P < 0.01$) than the VR × HO cows (6.2 ± 0.13). The scores for UC corresponded to udders about 7.5 cm above the hock for the combined crossbreds and about 10 cm above the hock for the HO cows during first lactation for a difference of about 2.5 cm (Select Sires, Inc., Plain City, OH). The difference between the crossbred and HO cows for UC may partially be a reflection of the 3 cm difference for STA. Cows with shorter STA likely have shorter rear legs, which provides for less UC above the hock. The actual depth of the udders (distance from the body wall to the udder floor) may differ little between breed groups. The results from this study agree with those of Hazel et al. (2014), who objectively measured UC from the ground to the udder floor of MO × HO versus HO cows and the MO × HO cows had 2.6 cm less UC than HO cows across 5 parities. In that study, udders became deeper with increasing parity at approximately the same rate in each breed group. The standard errors of UC scores for both the crossbred and HO cows in the current study were small (0.10 and 0.08, respectively), which suggested very few cows had extreme scores for UC during first lactation. Cows that carry udders closer to the ground may experience more functional problems while milking or may have more contact with bedding in stalls (Hansen et al., 1999). Carlström et al. (2016a) reported cows with less UC had increased SCS; however, the 2-breed crossbred cows in this study did not differ from HO cows for SCS during first lactation (Hazel et al., 2017b).

The FTW was wider (*P* < 0.01) for the crossbred (4.8 ± 0.11) than the HO cows (5.5 ± 0.10). Close FTW is generally regarded as favorable for functional milking. Also, RTW was wider (*P* < 0.01) for the crossbred (5.7 ± 0.12) than the HO cows (6.5 ± 0.10). The mean RTW of the first lactation HO cows in this study was +1.5 points closer than the 5-point intermediate optimum, and close RTW is especially problematic for automated milking systems. Ontario farmers reported the attachment sensor for automated milking systems may consider the 2 rear teats as a single teat when cows have close RTW, and this problem resulted in up to 3% additional culling (Rodenburg, 2002). Therefore, the wider RTW of the crossbred cows versus the HO cows in this study may have functional advantages for milking.

The TL was longer (*P* < 0.01) for the crossbred cows (4.3 ± 0.13) versus their HO herdmates (3.9 ± 0.11), and the difference was entirely due to the longer TL of the MO × HO cows (4.6 ± 0.18), because the VR × HO cows did not differ from the HO cows. Historical selection for shorter TL was motivated by a desire for faster milking speeds, but very short TL may be a problem for teat cup attachment (Carlström et al., 2016b). Based on the conversion of linear scores to a metric scale, the mean TL of HO cows in this study was 5 cm, and TL of the crossbred cows were 0.5 cm longer than those of the HO cows. Furthermore, 16% of HO cows had very short TL (score of 1 on a 9-point scale) compared with fewer (*P* < 0.03) of the MO × HO cows (11%). A Chi-squared test indicated the proportion of cows culled for udder conformation during first lactation in this study did not differ (P = 0.87) between the crossbred (7 of 1,080 cows) and HO cows (6 of 1,014 cows); therefore, differences between breed groups for udder traits during first lactation may not have practical consequence.

3.3.4 Implications for the industry

The results of this study are informative for high-performance dairy herds that seek improvement of fertility and survival of their cows without loss of production. A limitation of this study may be results are from cows managed only in high-performance dairy herds in the upper Midwest of the US. Results may be different for cows provided lower management levels or located in other environments, globally.

The 2-breed crossbred cows in this study had shorter STA and shallower BD than their HO herdmates, and this may have provided benefits for cow health and production efficiency. In the future, cows in this study will contribute to a comprehensive economic comparison of the crossbred versus HO cows in the 8 herds that will include revenues and expenses from production, salvage value of cows, value of calves, costs of replacements, feed intake, fertility, and cost of health disorders. The first generation of crossbred cows examined in this designed study are only a single generation at the initiation of a rotational crossbreeding program. Therefore, subsequent generations of crossbred cows must be studied to assess the long-term consequences of 3-breed rotational crossbreeding.

BIBLIOGRAPHY

Adamec, V., B. G. Cassell, E. P. Smith, and R. E. Pearson. 2006. Effects of inbreeding in the dam on dystocia and stillbirths in US Holsteins. J. Dairy Sci. 89:307-314.

Alvåsen, K., M. Jansson Mörk, C. Hallén Sandgren, P. T. Thomsen, and U. Emanuelson. 2012. Herd-level risk factors associated with cow mortality in Swedish dairy herds. J. Dairy Sci. 95:4352-4362. http://dx.doi.org/10.3168/jds.2011-5085.

Barlow, R. 1981. Experimental evidence for interaction between heterosis and environment in animals. Anim. Breed. Abstr. 49:715-737.

Bastin, C., S. Loker, N. Gengler, A. Sewalem, and F. Miglior. 2010. Genetic relationships between body condition score and reproduction traits in Canadian Holstein and Ayrshire first-parity cows. J. Dairy Sci. 93:2215-2228. http://dx.doi.org/10.3168/jds.2009-2720.

Becker, J. C., B. J. Heins, and L. B. Hansen. 2012. Costs for health care of Holstein cows selected for large versus small body size. J. Dairy Sci. 95:5384-5392. http://dx.doi.org/10.3168/jds.2012-5344.

Berry, D. P., E. Wall, and J. E. Pryce. 2014. Genetics and genomics of reproductive performance in dairy and beef cattle. Animal 8:105-121. http://dx.doi.org/10.1017/S1751731114000743.

Bjelland, D. W., K. A. Weigel, P. C. Hoffman, N. M. Esser, W. K. Coblentz, and T. J. Halbach. 2011. Production, reproduction, health, and growth traits in backcross Holstein × Jersey cows and their Holstein contemporaries. J. Dairy Sci. 94:5194-5203.

Bjelland, D. W., K. A. Weigel, N. Vukasinovic, and J. D. Nkrumah. 2013. Evaluation of inbreeding depression in Holstein cattle using whole-genome SNP markers and alternative measures of genomic inbreeding. J. Dairy Sci. 96:4697-4706.

Blöttner, S., B. J. Heins, M. Wensch-Dorendorf, L. B. Hansen, and H. H. Swalve. 2011a. Brown Swiss × Holstein crossbreds compared with pure Holsteins for calving traits, body weight, backfat thickness, fertility, and body measurements. J. Dairy Sci. 94:1058–1068.

Blöttner, S., B. J. Heins, M. Wensch-Dorendorf, L. B. Hansen, and H. H. Swalve. 2011b. Short communication: A comparison between purebred Holstein and Brown Swiss × Holstein cows for milk production, somatic cell score, milking speed, and udder measurements in the first 3 lactations. J. Dairy Sci. 94:5212-5216.

Bourrigan, X., S. Mattalia, C. Bouissel, R. Dremaux, M. Dupres, J. J. Evard, X. Gouraud, M. Legay, L. Maurin, B. Schmitt, J. M. Gautier, P. Roussel, and G. Blériot. 2016. French health recording systems: possible new valorizations of events recorded by farmers. Pages 177-182 in Proc. 40th ICAR Biennial session, Puerto Varas, Chile. ICAR, Rome, Italy.

Bryant, J. R., N. López-Villalobos, J. E. Pryce, C. W. Holmes, D. L. Johnson, and D. J. Garrick. 2007a. Environmental sensitivity in New Zealand dairy cattle. J. Dairy Sci. 90:1538–1547.

Bryant, J. R., N. López-Villalobos, J. E. Pryce, C. W. Holmes, D. L. Johnson, and D. J. Garrick. 2007b. Short communication: Effects of environment on the expression of breed and heterosis effects for production traits. J. Dairy Sci. 90:1548–1553.

Carlström, C., E. Strandberg, K. Johansson, G. Pettersson, H. Stålhammar, and J. Philipsson. 2016a. Genetic associations of in-line recorded milkability traits and udder conformation with udder health. Acta Agric. Scand. A Anim. Sci. 66:84-91. http://dx.doi.org/10.1080/09064702.2016.1260154.

Carlström, C., E. Strandberg, G. Pettersson, K. Johansson, H. Stålhammar, and J. Philipsson. 2016b. Genetic associations of teat cup attachment failures, incomplete milkings, and handling time in automatic milking systems with milkability, temperament, and udder conformation. Acta Agric. Scand. A Anim. Sci. 66:75-83. http://dx.doi.org/10.1080/09064702.2016.1260153.

Cartwright, S. L., L. R. Schaeffer, E. B. Burnside, and B. A. Mallard. 2012. Adaptive immune response, survival, and somatic cell score between postpartum Holstein and Norwegian Red × Holstein first-calf heifers. J. Anim. Sci. 90:2970–2978.

Cassell, B. G., V. Adamec, and R. E. Pearson. 2003. Effect of incomplete pedigrees on estimates of inbreeding and inbreeding depression for days to first service and summit milk yield in Holsteins and Jerseys. J. Dairy Sci. 86:2967-2976.

Christensen, L. G., and J. Pedersen. 1988. Crossbreeding of Dairy Cattle. 650th report from the National Institute of Animal Science. Landhusholdningsselskabets forlag, København, Denmark. (in Danish with English subtitles and summary).

Cole, J. B. 2015. A simple strategy for managing many recessive disorders in a dairy cattle breeding program. Genet. Sel. Evol. 47:94.

Cole, J. B., and P. M. VanRaden. 2009. A manual for use of BESTPRED: A program for estimation of lactation yield and persistency using best prediction. Release 2.0 rc 6. Animal Improvement Programs Lab, USDA, Beltsville, MD.

Council on Dairy Cattle Breeding. 2016. Trend in inbreeding coefficients of cows for Holstein or Red & White. Accessed Feb. 8, 2017. https://www.uscdcb.com/eval/summary/inbrd.cfm.

Council on Dairy Cattle Breeding. 2017a. Bovine genetic trends for Holstein of Red & White. Accessed Nov. 3, 2017. https://queries.uscdcb.com/eval/summary/trend.cfm.

Council on Dairy Cattle Breeding. 2017b. DHI participation as of January 1, 2017—DHI report K-1. Accessed Jul.27, 2017. https://queries.uscdcb.com/publish/dhi/current/partx.html.

Council on Dairy Cattle Breeding. 2017c. History of USDA dairy evaluations. Accessed Jul. 31, 2017. https://www.uscdcb.com/aipl/history/hist_eval.htm.

Council on Dairy Cattle Breeding. 2017d. Trend in inbreeding coefficients of cows for Holstein or Red & White. Accessed Aug. 17, 2017. https://www.uscdcb.com/eval/summary/inbrd.cfm.

Croquet, C., P. Mayeres, A. Gillon, S. Vanderick, N. Gengler. 2006. Inbreeding depression for global and partial economic indexes, production, type, and functional traits. J. Dairy Sci. 89:2257-2267.

de Haas, Y., E. A. A. Smolders, J. N. Hoorneman, W. J. Nauta, and R. F. Veerkamp. 2013. Suitability of cross-bred cows for organic farms based on cross-breeding effects on production and functional traits. Animal 7:655-664.

De Vries, A. 2006. Determinants of the cost of days open in dairy cattle. Pages 1114-1115 in 11th International Symposium on Veterinary Epidemiology and Economics, Cairns, Australia.

Dechow, C. D. 2014. Options exist to confront inbreeding. Page 218 in Hoards Dairyman. Mar. 25, 2014. W. D. Hoard and Sons, Fort Atkinson, WI.

Dechow, C. D. 2015. U.S. breed composition has been slowly shifting. Page 469 in Hoards Dairyman. July 15, 2015. W. D. Hoard and Sons, Fort Atkinson, WI.

Dechow, C. D., and R. C. Goodling. 2008. Mortality, Culling by sixty days in milk, and production profiles in high- and low-survival Pennsylvania herds. J. Dairy Sci. 91:4630-4639. http://dx.doi.org/10.3168/jds.2008-1337.

Dechow, C. D., and G. W. Rogers, and J. S. Clay. 2002. Heritability and correlations among body condition score loss, body condition score, production and reproductive performance. J. Dairy Sci. 85:3062-3070. http://dx.doi.org/10.3168/jds.S0022-0302(02)74393-2.

Dechow, C. D., G. W. Rogers, J. B. Cooper, M. I. Phelps, and A. L. Mosholder. 2007. Milk, fat, protein, somatic cell score, and days open among Holstein, Brown Swiss, and their crosses. J. Dairy Sci. 90:3542–3549.

Department of Agriculture, Food and the Marine. 2015. AIM bovine statistics report 2015. Accessed Jun. 2, 2016. http://www.agriculture.gov.ie/animalhealthwelfare/animalidentificationmovement/cattle/.

Dezetter, C., H. Leclerc, S. Mattalia, A. Barabat, D. Boichard, and V. Ducrocq. 2015. Inbreeding and crossbreeding parameters for production and fertility traits in Holstein, Montbéliarde, and Normande cows. J. Dairy Sci. 98:4904–4913.

Donnelly, M. R., A. R. Hazel, B. J. Heins, and L. B. Hansen. 2016. Health treatment costs of pure Holsteins in 8 high-performance Minnesota dairies. J. Dairy Sci. 99 (E-Suppl. 1):1242. (Abstr.)

Emanuelson, U. 2013. Validation of the Nordic disease databases. Pages 101-107 in ICAR technical series no.17, Aarhus, Denmark. ICAR, Rome, Italy.

Ericson, K., B. Danell, and J. Rendel. 1988. Crossbreeding effects between two Swedish dairy breeds for production traits. Livest. Prod. Sci. 20:175–192.

Ettema, J. F., and J. E. P. Santos. 2004. Impact of age at calving on lactation, reproduction, health, and income in first-parity Holsteins on commercial farms. J. Dairy Sci. 87:2730–2742.

Ezra, E., M. Van Straten, and J. I. Weller. 2016. Comparison of pure Holstein to crossbred Holsteins with Norwegian Red cattle in first and second generations. Animal 10:1254–1262.

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. 4th ed. Longman House, Harlow, Essex, UK.

Ferguson, J. D., D. T. Galligan, and N. Thomsen. 1994. Principal descriptors of body condition score in Holstein cows. J. Dairy Sci 77:2695-2703. http://dx.doi.org/10.3168/jds.S0022-0302(94)77212-X.

Fricke, P. M. 2001. Twinning in dairy cattle. Accessed Feb. 8, 2017. https://host.cals.wisc.edu/dairyscience/wp-content/uploads/sites/40/2013/11/Fricke-Twinning.pdf.

Funk, D. A. 2006. Major advances in globalization and consolidation of the artificial insemination industry. J. Dairy Sci. 89:1362-1368.

García-Ruiz, A., J. B. Cole, P. M. VanRaden, G. R. Wiggans, F. J. Ruiz-López, and C. P. Van Tassell. 2016. Changes in genetic selection differentials and generation intervals in US Holstein dairy cattle as a result of genomic selection. Proc. Natl. Acad. Sci. USA 113:E3995–E4004. https://doi.org/10.1073/pnas.1519061113.

Groenendaal, H., D. T. Galligan, and H. A. Mulder. 2004. An economic spreadsheet model to determine optimal breeding and replacement decisions for dairy cattle. J. Dairy Sci. 87:2146-2157. http://dx.doi.org/10.3168/jds.S0022-0302(04)70034-X.

Gröhn, Y. T., P. J. Rajala-Schultz, H. G. Allore, M. A. DeLorenzo, J. A. Hertl, and D. T. Galligan. 2003. Optimizing replacement of dairy cows: modeling the effects of diseases. Prev. Vet. Med. 61:27-43. http://dx.doi.org/10.1016/S0167-5877(03)00158-2.

Hansen, L. B. 2000. Symposium: Selection for milk yield. Consequences of selection for milk yield from a geneticist's viewpoint. J. Dairy Sci. 83:1145-1150. http://dx.doi.org/10.3168/jds.S0022-0302(00)74980-0.

Hansen, L. B., J. B. Cole, G. D. Marx, and A. J. Seykora. 1999. Productive life and reasons for disposal of Holstein cows selected for large versus small body size. J. Dairy Sci. 82:795-801. http://dx.doi.org/10.3168/jds.S0022-0302(99)75298-7.

Hansen, M., M. S. Lund, J. Pedersen, and L. G. Christensen. 2004. Gestation length in Danish Holsteins has weak genetic associations with stillbirth, calving difficulty, and calf size. Livest. Prod. Sci. 91:23–33.

Hare, E., H. D. Norman, and J. R. Wright. 2006. Survival rates and productive herd life of dairy cattle in the United States. J. Dairy Sci. 89-3713-3720. http://dx.doi.org/10.3168/jds.S0022-0302(06)72412-2.

Harmon, L. J., and S. Braude. 2010. Conservation of small populations: Effective population size, inbreeding, and the 50/500 rule. Pp.125-138 in: An Introduction to Methods and Models in Ecology and Conservation Biology. Edited by: S. Braude, and S. B. Low. Princeton University Press, New Jersey.

Hazel, A. R., B. J. Heins, and L. B. Hansen. 2017a. Fertility, survival, and conformation of Montbeliarde × Holstein and Viking Red × Holstein crossbred cows compared with pure Holstein cows during first lactation in 8 commercial dairy herds. J. Dairy Sci. 100:9447-9458. https://dx.doi.org/10.3168/jds.2017-12824.

Hazel, A. R., B. J. Heins, and L. B. Hansen. 2017b. Production and calving traits of Montbéliarde × Holstein and Viking Red × Holstein cows compared with pure Holstein cows during first lactation in 8 commercial dairy herds. J. Dairy Sci. 100:4139-4149. http://dx.doi.org/10.3168/jds.2016-11860.

Hazel, A. R., B. J. Heins, A. J. Seykora, and L. B. Hansen. 2013. Montbéliarde-sired crossbreds compared with pure Holsteins for dry matter intake, production, and body traits during the first 150 days of first lactation. J. Dairy Sci. 96:1915-1923. http://dx.doi.org/10.3168/jds.2012-5667.

Hazel, A. R., B. J. Heins, A. J. Seykora, and L. B. Hansen. 2014. Production, fertility, survival, and body measurements of Montbéliarde-sired crossbreds compared with pure Holsteins during their first 5 lactations. J. Dairy Sci. 97:2512–2525. http://dx.doi.org/10.3168/jds.2013-7063.

Heins, B. J., and L. B. Hansen. 2012. Short communication: Fertility, somatic cell score, and production of Normande × Holstein, Montbéliarde × Holstein, and Scandinavian Red × Holstein crossbreds versus pure Holsteins during their first 5 lactations. J. Dairy Sci. 95:918–924. http://dx.doi.org/10.3168/jds.2011-4523.

Heins, B. J., L. B. Hansen, and A. De Vries. 2012a. Survival, lifetime production, and profitability of crossbreds of Holstein with Normande, Montbéliarde, and Scandinavian Red compared to pure Holstein cows. J. Dairy Sci. 95:1011–1021. http://dx.doi.org/10.3168/jds.2011-4525.

Heins, B. J., L. B. Hansen, A. R. Hazel, A. J. Seykora, D. G. Johnson, and J. G. Linn. 2010. Birth traits of pure Holstein calves versus Montbéliarde-sired crossbred calves. J. Dairy Sci. 93:2293–2299.

Heins, B. J., L. B. Hansen, A. R. Hazel, A. J. Seykora, D. G. Johnson, and J. G. Linn. 2012b. Short communication: Jersey × Holstein crossbreds compared with pure Holsteins for body weight, body condition score, fertility, and survival during the first three lactations. J. Dairy Sci. 95:4130-4135.

Heins, B. J., L. B. Hansen, and A. J. Seykora. 2006a. Calving difficulty and stillbirths of pure Holsteins versus crossbreds of Holstein with Normande, Montbéliarde, and Scandinavian Red. J. Dairy Sci. 89:2805–2810. http://dx.doi.org/10.3168/jds.S0022-0302(06)72357-8.

Heins, B. J., L. B. Hansen, and A. J. Seykora. 2006b. Fertility and survival of pure Holsteins versus crossbreds of Holstein with Normande, Montbeliarde, and Scandinavian Red. J. Dairy Sci. 89:4944-4951. http://dx.doi.org/10.3168/jds.S0022-0302(06)72545-0.

Heins, B. J., L. B. Hansen, and A. J. Seykora. 2006c. Production of pure Holsteins versus crossbreds of Holstein with Normande, Montbéliarde, and Scandinavian Red. J. Dairy Sci. 89:2799–2804.

Heins, B. J., L. B. Hansen, A. J. Seykora, A. R. Hazel, D. G. Johnson, and J. G. Linn. 2011. Short communication: Jersey × Holstein crossbreds compared with pure Holsteins for production, mastitis, and body measurements during the first 3 lactations. J. Dairy Sci 94:501-506.

Heins, B. J., L. B. Hansen, A. J. Seykora, D. G. Johnson, J. G. Linn, J. E. Romano, and A. R. Hazel. 2008b. Crossbreds of Jersey × Holstein compared with pure Holsteins for production, fertility, and body and udder measurements during first lactation. J. Dairy Sci. 91:1270-1278.

Hodgson, R. E. 1986. Dairy production research by the United States Department of Agriculture, 1895 to 1980: A historical review. USDA Misc. Pub. No. 1447.

Holstein USA. 2017. Sire summaries April 2017. Holstein Association USA, Inc., Brattleboro, VT.

Howard, J. T., J. E. Pryce, C. Baes, and C. Maltecca. 2017. Invited review: Inbreeding in the genomics era: Inbreeding, inbreeding depression, and management of genomic variability. J. Dairy Sci. 100:6009-6024. http://dx.doi.org/10.3168/jds.2017-12787.

Jiménez-Mena, B., F. Hospital, and T. Bataillon. 2016. Heterogeneity in effective population size and its implications in conservation genetics and animal breeding. Conserv. Genet. Resour. 8:35–41.

Jönsson, R. 2015. Estimation of heterosis and performance of crossbred Swedish dairy cows. MS Thesis. Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Uppsala.

Kargo, M., L. Hjortø, M. Toivonen, J. A. Eriksson, G. P. Aamand, and J. Pedersen. 2014. Economic basis for the Nordic Total Merit Index. J. Dairy Sci. 97:7879-7888.

Kargo, M., P. Madsen, and E. Norberg. 2012. Short communication: Is crossbreeding only beneficial in herds with low management level? J. Dairy Sci. 95:925–928.

Kearney, J. F., E. Wall, B. Villanueva, and M. P. Coffey. 2004. Inbreeding trends and application of optimized selection in the UK Holstein population. J. Dairy Sci. 87:3503-3509.

Kristensen, T. N., and A. C. Sørensen. 2005. Inbreeding—Lessons from animal breeding, evolutionary biology and conservation genetics. Anim. Sci. 80:121–133.

Kyntäjä, J. 2013. Health data recording in Finland. Pages 83-85 in ICAR technical series no. 17, Aarhus, Denmark. ICAR, Rome, Italy.

Ledos, H., and S. Moureaux. 2013. Durée de gestation pour les principales races de l’espéce bovine: Moyenne et variabilité. Accessed Jul. 12, 2016. http://idele.fr/?eID=cmis_download&oID= workspace://SpacesStore/6e1935c2-3970-4fb3-9320-30f29165866e.

Leroy, G. 2014. Inbreeding depression in livestock species: review and meta-analysis. Anim. Genet. 45:618–628.

LIC and Dairy NZ. 2015. New Zealand dairy statistics 2014–15. Accessed Jun. 29, 2016. http://www.dairynz.co.nz/media/3136117/new-zealand-dairy-statistics-2014-15.pdf.

Lombard, J. E., F. B. Garry, S. M. Tomlinson, and L. P. Garber. 2007. Impacts of dystocia on health and survival of dairy calves. J. Dairy Sci. 90:1751–1760.

Lopez-Villalobos, N., D. J. Garrick, C. W. Holmes, H. T. Blair, and R. J. Spelman. 2000. Profitabilities of some mating systems for dairy herds in New Zealand. J. Dairy Sci. 83:144-153.

Lucy, M. C. 2001. Reproductive loss in high-producing dairy cattle: Where will it end? J. Dairy Sci. 84:1277-1293.

Lush, J. L., J. C. Holbert, and O. S. Willham. 1936. Genetic history of the Holstein-Friesian cattle in the United States. J. Hered. 27:61-72.

Mäki-Tanila, A. 2007. An overview on quatitative and genomic tools for utilizing dominance genetic variation in improving animal production. Agric. Food Sci. 16:188-198.

Malchiodi, F., A. Cecchinato, and G. Bittante. 2014a. Fertility traits of purebred Holsteins and 2- and 3-breed crossbred heifers and cows obtained from Swedish Red, Montbéliarde, and Brown Swiss sires. J. Dairy Sci. 97:7916-7926. http://dx.doi.org/10.3168/jds.2014-8156.

Malchiodi, F., A. Cecchinato, M. Penasa, C. Cipolat-Gotet, and G. Bittante. 2014b. Milk quality, coagulation properties, and curd firmness modeling of purebred Holsteins and first- and second-generation crossbred cows from Swedish Red, Montbéliarde, and Brown Swiss bulls. J. Dairy Sci. 97:4530–4541.

Malchiodi, F., M. Penasa, F. Tiezzi, and G. Bittante. 2011. Milk yield traits, somatic cell score, milking time, and age at calving of pure Holstein versus crossbred cows. Agric. Conspec. Sci. 76:259-261.

Mc Parland, S., F. Kearney, and D. P. Berry. 2009. Purging of inbreeding depression within the Irish Holstein-Friesian population. Genet. Sel. Evol. 41:16.

Mc Parland, S., J. F. Kearney, M. Rath, and D. P. Berry. 2007. Inbreeding effects on milk production, calving performance, fertility, and conformation in Irish Holstein-Friesians. J. Dairy Sci. 90:4411-4419.

McAllister, A. J., A. J. Lee, T. R. Batra, C. Y. Lin, G. L. Roy, J. A. Vesely, J. M. Wauthy, and K. A. Winter. 1994. The influence of additive and nonadditive gene action on lifetime yields and profitability of dairy cattle. J. Dairy Sci. 77:2400-2414.

McDowell, R. E. 1982. Crossbreeding as a system of mating for dairy production. Southern Coop. Series Bull. No. 259, Louisiana Agricultural Experiment Station, Baton Rouge, LA.

Mendonça, L. G. D., C. C. Abade, E. M. da Silva, N. B. Litherland, L. B. Hansen, W. P. Hansen, and R. C. Chebel. 2014. Comparison of peripartum metabolic status and postpartum health of Holstein and Montbéliarde-sired crossbred dairy cows. J. Dairy Sci. 97:805-818.

Mendonça, L. G. D., N. B. Litherland, M. C. Lucy, D. H. Keisler, M. A. Ballou, L. B. Hansen, and R. C. Chebel. 2013. Comparison of innate immune responses and somatotropic axis components of Holstein and Montbéliarde-sired crossbred dairy cows during the transition period. J. Dairy Sci. 96:3588-3598.

Meuwissen, T. H. E. 2009. Genetic management of small populations: A review. Acta Agric Scand. A Anim. Sci. 59:71–79.

Miglior, F., and L. Beavers. 2014. Genetic Diversity and Inbreeding: Before and after Genomics. Accessed Aug. 1, 2017. http://www.progressivedairy.com/topics/a-i-breeding/genetic-diversity-and-inbreeding-before-and-after-genomics.

Miglior, F., E. B. Burnside, and B. W. Kennedy. 1995. Production traits of Holstein cattle: Estimation of nonadditive genetic variance components and inbreeding depression. J. Dairy Sci. 78:1174-1180.

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

Norberg, E., P. Madsen, G. Su, J. E. Pryce, J. Jensen, and M. Kargo. 2014. Short communication: Heterosis by environment and genotype by environment interactions for protein yield in Danish Jerseys. J. Dairy Sci. 97:4557-4561.

Nordic Cattle Genetic Evaluation. 2016. NTM-Nordic Total Merit. Accessed Jun. 6, 2016. http://www.nordicebv.info/en/ntm-nordic-total-merit-2/.

Norman, H. D., L. M. Walton, and J. Dürr. 2015a. Reasons that cows in dairy herd improvement programs exit the milking herd (2014). Accessed Feb. 9, 2017. https://www.uscdcb.com/publish/dhi/dhi15/cullall.html.

Norman, H. D., L. M. Walton, and J. Dürr. 2015b. Reproductive status of cows in dairy herd improvement programs and bred using artificial insemination (2014). Accessed Mar 2, 2017. https://www.uscdcb.com/publish/dhi/current/reproall.html.

Norman, H. D., L. M. Walton, and J. Dürr. 2016. Reasons that cows in dairy herd improvement programs exit the milk herd (2015). Accessed Mar 2, 2017. https://www.uscdcb.com/publish/dhi/current/cullall.html.

Norman, H. D., J. R. Wright, S. M. Hubbard, R. H. Miller, and J. L. Hutchison. 2009a. Reproductive status of Holstein and Jersey cows in the United States. J. Dairy Sci. 92:3517-3528. http://dx.doi.org/10.3168/jds.2008-1768.

Norman, H. D., J. R. Wright, M. T. Kuhn, S. M. Hubbard, J. B. Cole, and P. M. VanRaden. 2009b. Genetic and environmental factors that affect gestation length in dairy cattle. J. Dairy Sci. 92:2259– 2269.

Oklahoma State University. 2017. Breeds of livestock – Dutch Belted (Lakenvelder) cattle. Accessed Jul. 31, 2017. http://www.ansi.okstate.edu/breeds/cattle/dutchbelted/index-2.html.

Olson, K. M., B. G. Cassell, M. D. Hanigan, and R. E. Pearson. 2011. Short communication: Interaction of energy balance, feed efficiency, early lactation health events, and fertility in first-lactation Holstein, Jersey, and reciprocal F_1 crossbred cows. J. Dairy Sci. 94:507-511.

Olson, K. M., B. G. Cassell, A. J. McAllister, and S. P. Washburn. 2009. Dystocia, stillbirth, gestation length, and birth weight in Holstein, Jersey, and reciprocal crosses from a planned experiment. J. Dairy Sci. 92:6167-6175.

Oltenacu, P. A., and D. M. Broom. 2010. The impact of genetic selection for increased milk yield on the welfare of dairy cows. Anim. Welf. 19(Suppl. 1):39–49.

O. S. Montbéliarde. 2016. The Unique Synthesis Index (ISU), the steering tool of the Montbéliarde selection. Accessed May 4, 2016. http://www.montbeliarde.org/en-428.html.

O. S. Montbéliarde. 2017. Montbeliarde Association. Accessed Aug. 9, 2017. http://www.montbeliarde.org.

Penasa, M., M. De Marchi, R. Dal Zotto, G. de Jong, G. Bittante, and M. Cassandro. 2010a. Heterosis effects in a black and white dairy cattle population under different production environments. Livest. Sci. 131:52–57.

Penasa, M., N. López-Villalobos, R. D. Evans, A. R. Cromie, R. Dal Zotto, and M. Cassandro. 2010b. Crossbreeding effects on milk yield traits and calving interval in spring-calving dairy cows. J. Anim. Breed. Genet. 127:300-307.

Philipsson, J., G. Banos, and T. Arnason. 1994. Present and future uses of selection index methodology in dairy cattle. J. Dairy Sci.77:3252-3261. http://dx.doi.org/10.3168/jds.S0022-0302(94)77266-0.

Piccardi, M., D. Pipino, G. A. Bó, and M. Balzarini. 2014. Productive and reproductive performance of first lactation purebred Holstein versus Swedish red & white × Holstein in central Argentina. Livest. Sci. 165:37-41. http://dx.doi.org/10.1016/j.livsci.2014.04.025.

Prendiville, R., L. Shalloo, K. M. Pierce, and F. Buckley. 2011. Comparative performance and economic appraisal of Holstein-Friesian, Jersey, and Jersey×Holstein-Friesian cows under seasonal pasture-based management. Irish J. Agri. Food Res. 50:123-140.

ProCROSS. 2017. Ground breaking ProCROSS take-off. Accessed Aug. 8, 2017. http://www.procross.info/news/Ground-breaking-procross-take-off.

Pryce, J. E. 2017. The effect of genomic selection on dairy cow populations. J. Dairy Sci. 100(E-Suppl. 2):63 (abstr.).

Pryce, J. E., and B. L. Harris. 2006. Genetics of body condition score in New Zealand dairy cows. J. Dairy Sci. 89:4424-4432. http://dx.doi.org/10.3168/jds.S0022-0302(06)72490-0.

Raboisson, D., E. Cahuzac, P. Sans, and G. Allaire. 2011. Herd-level and contextual factors influencing dairy cow mortality in France in 2005 and 2006. J. Dairy Sci. 94:1790-1803. http://dx.doi.org/10.3168/jds.2010-3634.

Rauw, W. M., E. Kanis, E. N. Noordhuizen-Stassen, and F. J. Grommers. 1998. Undesirable side effects of selection for high production efficiency in farm animals: a review. Livst. Prod. Sci. 56:15-33.

Roche, J. R., N. C. Friggens, J. K. Kay, M. W. Fisher, K. J. Stafford, and D. P. Berry. 2009. *Invited review:* Body condition score and its association with dairy cow productivity, health, and welfare. J. Dairy Sci. 92:5769-5801. http://dx.doi.org/10.3168/jds.2009-2431.

Rodenburg, J. 2002. Robotic milkers: What, Where…and how much!! ?? Pages 1-18 in Proc. Ohio Dairy Management Conf., Columbus, OH. Ohio State University Extension, Columbus.

Rokouei, M., R. Vaez Torshizi, M. Moradi Shahrbabak, M. Sargolzaei, and A. C. Sørensen. 2010. Monitoring inbreeding trends and inbreeding depression for economically important traits of Holstein cattle in Iran. J. Dairy Sci. 93:3294-3302.

Rolfe, K. M., W. M. Snelling, M. K. Nielsen, H. C. Freetly, C. L. Ferrell, and T. G. Jenkins. 2011. Genetic and phenotypic parameter estimates for feed intake and other traits in growing beef cattle, and opportunities for selection. J. Anim. Sci. 89:3452-3459.

Schaefer, L. R., E. B. Burnside, P. Glover, and J. Fatehi. 2011. Crossbreeding results in Canadian dairy cattle for production, reproduction, and conformation. Open Ag. Journ. 5:63-72.

Sewalem, A., G. J. Kistemaker, F. Miglior, and B. J. Van Doormaal. 2006. Analysis of inbreeding and its relationship with functional longevity in Canadian dairy cattle. J. Dairy Sci. 89:2210-2216.

Shanks, R. D., A. E. Freeman, P. J. Berger, and D. H. Kelley. 1978. Effect of selection for milk production on reproductive and general health of the dairy cow. J. Dairy Sci. 61:1765-1772.

Smith, L. A., B. G. Cassell, and R. E. Pearson. 1998. The effects of inbreeding on the lifetime performance of dairy cattle. J. Dairy Sci. 81:2729-2737.

Sørensen, A. C., M. K. Sørensen, and P. Berg. 2005. Inbreeding in Danish dairy cattle breeds. J. Dairy Sci. 88:1865-1872.

Sørensen, M. K. 2007. Crossbreeding—An important part of sustainable breeding in dairy cattle and possibilities for implementation. Pages 29-40 in Crossbreeding of dairy cattle: The science and the impact. 4th Biennial W. E. Petersen Symposium, St. Paul, MN. Department of Animal Science, University of Minnesota, St. Paul.

Sørensen, M. K., E. Norberg, J. Pedersen, and L. G. Christensen. 2008. *Invited review:* Crossbreeding in dairy cattle: A Danish perspective. J. Dairy Sci. 91:4116-4128. http://dx.doi.org/10.3168/jds.2008-1273.

Sundrum, A. 2015. Metabolic disorders in the transition period indicate that the dairy cows' ability to adapt is overstressed. Animals 5:978-1020. http://dx.doi.org/10.3390/ani5040395.

Swalve, H. H. 2007. Crossbreeding in dairy cattle: International trends and results from crossbreeding data in Germany. Lohmann Inf. 42:38–46.

Swan, A. A. and B. P. Kinghorn. 1992. Symposium: Dairy Crossbreeding: Evaluation and exploitation of crossbreeding in dairy cattle. J. Dairy Sci. 75:624-639.

Thompson, J. R., R. W. Everett, and N. L. Hammerschmidt. 2000. Effects of inbreeding on production and survival in Holsteins. J. Dairy Sci. 83:1856-1864.

Touchberry, R. W. 1992. Crossbreeding effects in dairy cattle: The Illinois experiment, 1949 to 1969. J. Dairy Sci. 75:640-667.

USDA-ARS. 1962. Dairy cattle breeds. Farmers' Bulletin No. 1443. Superintendent of documents, Washington, D.C.

USDA-ERS. 2017. Milk cows and production by state and region (Annual). Accessed Nov. 3, 2017. https://www.usda.ers.gov/webdocs/DataFiles/48685/milkcowsandprod_1_.xlsx?v=42866.

Vance, E. R., C. P. Ferris, C. T. Elliott, H. M. Hartley, and D. J. Kilpatrick. 2013. Comparison of the performance of Holstein-Friesian and Jersey × Holstein-Friesian crossbred dairy cows within three contrasting grassland-based systems of milk production. Livest. Sci. 151:66-79.

Vance, E. R., C. P. Ferris, C. T. Elliott, S. A. McGettrick, and D. J. Kilpatrick. 2012. Food intake, milk production, and tissue changes of Holstein-Friesian and Jersey × Holstein-Friesian dairy cows within a medium-input grazing system and a high-input total confinement system. J. Dairy Sci. 95:1527-1544.

VandeHaar, M. J., L. E. Armentano, K. Weigel, D. M. Spurlock, R. J. Templeman, and R. Veerkamp. 2016. Harnessing the genetics of the modern dairy cow to continue improvements in feed efficiency. J. Dairy Sci. 99:4941-4954. http://dx.doi.org/10.3168/jds.2015-10352.

VanRaden, P. 2002. Selection of dairy cattle for lifetime profit. Presentation at 7th World Congress on Genetics Applied to Livestock Production, August 2002. Accessed Aug. 1, 2017. http://aipl.arsusda.gov/publish/present.htm#2002.

VanRaden, P. M. 2017. AIP Research Report NM$6: Net merit as a measure of lifetime profit: 2017 revision. Accessed Jun. 16, 2017. https://www.aipl.arsusda.gov/Reference/nmcalc-2017.htm.

VanRaden, P. M., and J. B. Cole. 2014. AIP Research Report NM$5: Net merit as a measure of lifetime profit: 2014 revision. Accessed Jun. 6, 2016. http://aipl.arsusda.gov/reference/nmcalc-2014.htm.

VanRaden, P. M., K. M. Olson, D. J. Null, and J. L. Hutchison. 2011. Harmful recessive effects on fertility detected by absence of homozygous haplotypes. J. Dairy Sci. 94:6153-6161.

VanRaden, P. M., and A. H. Sanders. 2003. Economic merit of crossbred and purebred US dairy cattle. J. Dairy Sci. 86:1036–1044.

VanRaden, P. M., A. H. Sanders, M. E. Tooker, R. H. Miller, H. D. Norman, M. T. Kuhn, and G. R. Wiggans. 2004. Development of a national genetic evaluation for cow fertility. J. Dairy Sci. 87:2285-2292. http://dx.doi.org/10.3168/jds.S0022-0302(04)70049-1.

VanRaden, P. M., M. E. Tooker, J. R. Wright, J. B. Cole, D. J. Null, and T. J. Lawlor. 2014. AIP Research Report BASE3: Genetic base changes for December 2014. Accessed Jul 26, 2016. http://aipl.arsusda.gov/reference/base2014.htm.

VanRaden, P. M., and G. R. Wiggans. 1995. Productive life evaluations: Calculation, accuracy, and economic value. J. Dairy Sci. 78:631-638.

Viking Genetics. 2017. About VikingRed. Accessed Aug. 9, 2017. http://www.vikinggenetics.com/dairy/vikingred/about-vikingred.

Wall, E., S. Brotherstone, J. F. Kearney, J. A. Wolliams, and M. P. Coffey. 2003. Effect of including inbreeding, heterosis and recombination loss in prediction of breeding values for fertility traits. Interbull Bull. 31:117-121.

Walsh, S., F. Buckley, D. P. Berry, M. Rath, K. Pierce, N. Byrne, and P. Dillon. 2007. Effect of breed, feeding system, and parity on udder health on milking characteristics. J. Dairy Sci. 90:5767-5779.

Walsh, S., F. Buckley, K. Pierce, N. Bryne, J. Patton, and P. Dillon. 2008. Effects of breed and feeding system on milk production, body weight, body condition score, reproductive performance, and postpartum ovarian function. J. Dairy Sci. 91:4401-4413. http://dx.doi.org/10.3168/jds.2007-0818.

Walsh, S. W., E. J. Williams, and A. C. O. Evans. 2011. A review of the causes of poor fertility in high milk producing dairy cows. Anim. Reprod. Sci. 123:127-138. http://dx.doi.org/10.1016/j.anireprosci.2010.12.001.

Washburn, S. P. 2009. Lessons learned from grazing dairies. Pages 57-68 in Proc. 46th Florida Dairy Prod. Conf., Gainesville, FL. Univ. of Florida, Gainesville.

Weigel, K. A., and K. A. Barlass. 2003. Results of a producer survey regarding crossbreeding on US dairy farms. J. Dairy Sci. 86:4148-4154.

Wiggans, G. R., T. A. Cooper, P. M. VanRaden, K. M. Olson, and M. E. Tooker. 2012. Use of the Illumina Bovine3K BeadChip in dairy genomic evaluation. J. Dairy Sci. 95:1552-1558.

Wiltbank, M. C., P. M. Fricke, S. Sangsritavong, R. Sartori, and O. J. Ginther. 2000. Mechanisms that prevent and produce double ovulations in dairy cattle. J. Dairy Sci. 83:2998–3007.

Winters, L. M., O. M. Kiser, P. S. Jordan, and W. H. Peters. 1935. A six years' study of crossbreeding swine. Minn. Agr. Exp. Stn. Bull. 320, St. Paul, MN.

Wright, S. 1931. Evolution in mendelian populations. Genetics 16:97-159.

Young, C. W., W. J. Tyler, A. E. Freeman, H. H. Voelker, L. D. McGilliard, and T. M. Ludwick. 1969. Inbreeding investigations with dairy cattle in the North Central region of the United States. Minn. Agr. Exp. Stn., North Central Regional Research Publication 191, St. Paul.

Young, C. W. 1984. Inbreeding and the gene pool. J. Dairy Sci. 67:472-477.

Zwald, N. R., K. A. Weigel, Y. M. Chang, R. D. Welper, and J. S. Clay. 2004. Genetic selection for health traits using producer-recorded data. II. Genetic correlations, disease probabilities, and relationships with existing traits. J. Dairy Sci. 87:4295-4302. http://dx.doi.org/10.3168/jds.S0022-0302(04)73574-2.