The narrowing of the Holstein gene pool

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Without question, genomic selection is an exciting technology that is having a major impact on the genetics of the global Holstein breed – at least as much as previous technological advances such as A.I., progeny testing of bulls, and embryo transfer. However, those earlier technologies likely didn't alter dairy cattle genetics so dramatically in such a short period of time as has genomic selection. I was asked to provide this article to discuss consequences of genomic selection that have become controversial.

Many are unaware of the mechanics of genomic selection. The word "genomics" causes some to assume the methodology actually tracks the specific genes of animals from generation to generation. That's not really the case. Genomic selection is based on chromosome segments located between thousands of individual "markers" (SNP) scattered across the chromosomes of animals. The thousands of chromosome segments are compared with those of ancestors of young Holsteins that are included in the "reference population" for the breed. The most informative ancestors in the reference population are bulls with thousands of daughters. Genomic evaluation provides predicted transmitting abilities (PTA) based on the shared chromosome segments of young animals and their ancestors, and that information is integrated with the PTA of ancestors – especially ancestors that are well-represented in the breed's reference population.

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Consequently, to receive a very high PTA for a trait or index, a young Holstein must have ancestors that rank highly for PTA and are well-represented in the breed's reference population. What happens if the ancestors of a young Holstein aren't well-represented in the reference population? Logically, a high ranking for PTA becomes more difficult.

Because parents of the next generation of Holstein bulls can be chosen at a very young age based only on genomic PTA, the generation interval (average age of parents when offspring are born) has been dramatically shortened with genomic selection. In fact, the generational turnover of Holsteins, especially for the bulls provided by the breeding (A.I.) companies, is now occurring at warp speed, and almost all gain from genomic selection is explained by the shortened generation interval. Not surprisingly, the breeding companies are routinely breeding the highest-ranking genomic young bulls to the highest-ranking genomic young females as fast as they can. This approach may seem like the obvious thing to do, but it ignores concern about accumulation of genetic relationships within the Holstein breed (the narrowing of the gene pool). Without a limitation on the number of descendants of influential bulls and individual cow families, Holsteins will quickly become more related to each other with genomic selection.

In various forums, discussion about the narrowing of the Holstein gene pool is now common. Generally speaking, Registered Holstein breeders who track the pedigrees of the cows in their herds are struggling to find A.I. bulls that aren't closely related to the heifers and cows in their herds. Intuitively, Registered Holstein breeders wonder if this is a good thing. Also, geneticists who weren't directly involved in the development of genomic methodology and don't market Holstein genetics believe the rapid increase of genetic relationships among Holsteins is concerning in regard to the potential for the long-term genetic improvement of the Holstein breed. Breeders of Registered Holsteins who have successfully sold high-genomic breeding stock to the breeding companies may be pleased with the current situation and, therefore, lack concern about the accumulation of genetic relationships within the Holstein breed. On the other hand, some Registered Holstein breeders are now finding it difficult to maintain sales of breeding stock compared to the past.

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Understandably, the goal of breeding companies is to maintain market share and, historically, A.I. bulls have been marketed mostly based on their ranking for selection indexes such as Net Merit or TPI that combine the PTA across individual traits of bulls. However, some breeds of dairy cattle with large cow populations, such as numerous red dairy breeds in Scandinavia, France, and Germany, have heavily applied genomic selection (at least as heavily as the global Holstein breed) without an accompanying loss of genetic diversity. Actually, it is easy to implement methods to maintain genetic (pedigree) diversity within a breed despite heavy use of genomic selection by simply limiting the influence of individual bulls and females that rank highest in the breed at any point in time. Spreading the pedigrees of young bulls across more bull and cow families than has been done over the past decade for Holsteins will result in very little, if any, loss of actual genetic gain over the long term. In other words, it's possible to have "too much of a good thing" in regard to the influence of highest-ranking bulls and females.

Table 1. Five high-influence Holstein bulls and their GFI.

Bull	Birth year	Genomic Future Inbreeding (%)
Supersire	2010	11.2
O-Man	1998	10.9
Shottle	1999	10.5
Mogul	2010	10.0
Planet	2003	9.2

Source: Council on Dairy Cattle Breeding

Table 1 contains the short names, birth years, and average genomic future inbreeding of five Holstein bulls that permeate the pedigrees of most Holsteins in 2021. Registered Holstein breeders will be familiar with these high-influence bulls. Two (Supersire and Mogul) were born quite recently in 2010, so it's amazing the extent to which they have had such a tremendous impact on the entire breed. In fact, Supersire and Mogul often appear multiple times in both the male and female sides of the pedigrees of young Holsteins today. Also, the pedigrees of most Holsteins have many ties to O-Man, Shottle, and Planet that were each born about 20 years ago. It's interesting that Supersire is a grandson of Planet and a great-grandson of O-Man and Shottle, and Mogul is a great-grandson of O-Man. So, the five bulls in Table 1 are related to each other, too.

The first eight generations of Holstein pedigrees today overwhelmingly trace mostly to the five high-influence bulls in Table 1. Each of these five bulls must be regarded as a "genetic giant". However, regardless of how outstanding a bull may be for transmitting positive attributes to his descendants, he will also transmit some less-than-outstanding attributes, too. After all, no bull can rank highly for all traits.

Many dairy producers today use hormone intervention (not permitted as a routine practice in much of Europe) to achieve satisfactory fertility of their Holstein cows. Also, dairy producers complain that many Holstein cows today have rear legs that are too straight, have rear teats creeping up the inside of the rear quarters, and have teats that are too short in length. Three of the five high-influence bulls in Table 1 have substantially negative PTA for DPR (–2.3, –2.4, –2.9), and one is very negative for Livability (–3.1). Two of the five transmit very straight rear legs (–1.63, –2.07). Also, two of the five transmit close rear teats (+0.91, +1.35), and three of the five transmit short teats (–0.85, –1.50, –1.98). When a very small number of high-influence bulls are permitted to dominate a breed for future generations, the limitations of those high-influence bulls can become more difficult to grapple with over time.

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The topic of inbreeding is one that generates all sorts of observations by Holstein breeders. To begin with, “linebreeding” is simply inbreeding directed at a specific bull (usually) or cow. Therefore, linebreeding is actually a specialized form of inbreeding. There is no question that intentional inbreeding/linebreeding led to some high-impact bulls in Holstein history. Prior to routine DHI and the progeny testing of bulls, Registered Holstein breeders turned to intentional inbreeding/linebreeding to develop breeding stock that were potent in what they transmitted to their offspring. Most attempts at close inbreeding/linebreeding were major failures but, on occasion, they were very successful.

One of the most successful examples of inbreeding is found in the pedigree of Round Oak Rag Apple Elevation (RORAE). His sire was Tidy Burke Elevation that resulted from breeding a bull (Wis Burke Ideal) to his own daughter. When highly-inbred Tidy Burke Elevation (inbreeding of 25%) was mated with Round Oak Ivanhoe Eve (unrelated to him), RORAE was the incredible result. However, it’s important to keep in mind that RORAE himself had zero inbreeding, because he was the result of mating a highly inbred bull to a completely outcross cow. Today, how many Holstein females are unrelated to a highly-inbred Holstein bull?

So, yes, some of the high-impact Holstein bulls and cows from the 1930s and 1940s resulted from inbreeding/linebreeding. However, inbreeding in that era involved a very large number of alternative inbred lines of Holsteins that could be crossed with each other for commercial milk production. What we are experiencing in the 2020s is essentially the entire Holstein breed becoming a single inbred line. These are completely different concepts!

Table 2. Average inbreeding by birth year of Holstein females

Birth year	Inbreeding (%)	Annual increase (%)	
2000	4.5		
2001	4.6	+0.1	+0.12%
2002	4.8	+0.2	
2003	4.9	+0.1	
2004	5.0	+0.1	
2005	5.1	+0.1	
2006	5.2	+0.1	
2007	5.3	+0.1	
2008	5.4	+0.1	
2009	5.5	+0.1	
2010	5.7	+0.2	
2011	5.8	+0.1	
2012	5.9	+0.1	
2013	6.1	+0.2	+0.25%
2014	6.3	+0.2	
2015	6.6	+0.3	
2016	6.9	+0.3	
2017	7.3	+0.39	+0.43%
2018	7.7	+0.43	
2019	8.2	+0.46	
2020	8.7	+0.48 (first 80%)	
2021	9.0	+0.33 (first 10%)	

Bull mated to own daughter has inbreeding of 25%.
Inbreeding increases during a year.
Source: Council on Dairy Cattle Breeding

Inbreeding is measured by an “inbreeding coefficient”, which estimates the percentage of locations on the pairs of chromosome at which the two genes are identical because they descend from the same ancestor. When a bull is bred to his own daughter or a cow is mated with her own son, the inbreeding coefficient is 25% (as was the case for Tidy Burke Elevation). Therefore, most breeders will regard 25% as the upper limit of inbreeding (and not 100% as some may assume). Based on historical research at land-grant universities, geneticists have recommended average inbreeding shouldn’t surpass about 6.25% for commercial livestock production in order to avoid inbreeding depression for traits related to fertility, health, and mortality. There is nothing magical about 6.25%, but it is a goalpost for awareness that average inbreeding may be reaching a level that warrants attention.

Average inbreeding of U.S. Holstein females increased about 0.1% per year leading up to the past decade. That annual increase was modest and sustainable, and it was maintained until about 2013 when broad application of genomic selection (without pedigree restrictions) by the breeding companies took hold. Table 2 summarizes average inbreeding of Holsteins by birth year of females. Heifer calves born in 2014 (they are 7-year-old cows in 2021) were the first to have average inbreeding that surpassed 6.25%. The average birth year of Holstein cows that are currently milking in herds is probably 2017 with average inbreeding of 7.3%, which is only 1% above 6.25%.

However, the **annual increase of average inbreeding** of Holsteins has increased from **+0.12%** (for birth years 2000 to 2012) to **+0.25%** (for 2013 to 2016) to **+0.43%** (for 2017 to 2019). This documents a major acceleration of annual increase of average inbreeding of Holsteins. It's important to realize that average inbreeding goes up during a year. The first 80% of Holstein females entering the evaluation system for 2020 average 8.7% inbreeding (a +0.48% increase from 2019). The very first 10% of Holstein females entering the evaluation system for 2021 have average inbreeding of 9.0%. Almost certainly, average inbreeding of Holstein females born in 2021 will surpass 9.2% when the full year of females are included in the data. Some have argued that average inbreeding of Holsteins shouldn't be a problem until it surpasses 10.0%. That should happen for Holstein heifer calves in about two years.

Generally speaking, breeding companies seem unconcerned about the very high level of average inbreeding that Holstein cows will need to contend with as we move forward into the 2020s. Some believe the very strong selection being applied within the Holstein breed will eliminate most recessive genes that cause inbreeding depression. Also, there is hope that random mutation is continuously providing a large amount of new genetic diversity for the Holstein breed. Perhaps, these observations are correct – time will tell.

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However, the loss of genetic diversity (narrowing of the gene pool) of Holsteins is probably a more important concern than the potential negative effects of inbreeding depression. The limited opportunity for alternative bloodlines in the breed beyond the five high-influence bulls in Table 1 could hinder long-term genetic improvement of Holsteins, because maintaining genetic (pedigree) diversity is essential for the long-term genetic improvement of a breed. At the moment, most selection emphasis is placed on short-term genetic gain, especially for marketing purposes. Genetic theory tells us short-term genetic gain should always be balanced alongside the potential for long-term genetic gain when developing strategies for genetic improvement of a breed.

What recommendations can be offered to Registered Holstein breeders? Breeders could advocate that more attention be paid to genetic (pedigree) diversity by those responsible for Holstein breed improvement. Also, bulls that are somewhat less related to the breed (measured by lower GFI) but rank reasonably high for a selection index (Net Merit or TPI) could be chosen to breed heifers and cows to potentially improve long-term opportunities to market Holstein genetics by Registered Holstein breeders.