



Invited review: Beef-on-dairy—The generation of crossbred beef × dairy cattle

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ABSTRACT

Because a growing proportion of the beef output in many countries originates from dairy herds, the most critical decisions about the genetic merit of most carcasses harvested are being made by dairy producers. Interest in the generation of more valuable calves from dairy females is intensifying, and the most likely vehicle is the use of appropriately selected beef bulls for mating to the dairy females. This is especially true given the growing potential to undertake more beef × dairy matings as herd metrics improve (e.g., reproductive performance) and technological advances are more widely adopted (e.g., sexed semen). Clear breed differences (among beef breeds but also compared with dairy breeds) exist for a whole plethora of performance traits, but considerable within-breed variability has also been demonstrated. Although such variability has implications for the choice of bull to mate to dairy females, the fact that dairy females themselves exhibit such genetic variability implies that “one size fits all” may not be appropriate for bull selection. Although differences in a whole series of key performance indicators have been documented between beef and beef-on-dairy animals, of particular note is the reported lower environmental hoofprint associated with beef-on-dairy production systems if the environmental overhead of the mature cow is attributed to the milk she eventually produces. Despite the known contribution of beef (i.e., both surplus calves and cull cows) to the overall gross output of most dairy herds globally, and the fact that each dairy female contributes half her genetic merit to her progeny, proxies for meat yield (i.e., veal or beef) are not directly considered in the vast majority of dairy cow breeding objectives. Breeding objectives to identify beef bulls suitable for dairy production systems are now being developed and validated, demonstrating the financial benefit of using such breeding objectives over and above a focus on dairy bulls or easy-calving, short-gestation beef bulls. When this approach is

complemented by management-based decision-support tools, considerable potential exists to improve the profitability and sustainability of modern dairy production systems by exploiting beef-on-dairy breeding strategies using the most appropriate beef bulls.

Key words: beef × dairy, carcass, genetics

INTRODUCTION

“Dairy-beef” is a term used to describe meat that originated directly or indirectly from dairy herds; this could be in the form of cull cows and surplus calves that directly leave the farm for processing or are raised on another premises before processing. Dairy-beef is not a new concept, and scientific publications evaluating the credentials of beef from the dairy herd date back to at least the 1960s (Beanaman et al., 1962; Henderson, 1969). Nonetheless, the results from these studies are now dated and may not bear much resemblance to the populations of today. This is particularly true in light of the holsteinization of many dairy herds worldwide, concurrent with aggressive selection for milk production. Although information is lacking about the effect of selection for milk production on beef merit in dairy cattle, a negative relationship has been suggested between milk production and both carcass fat and conformation (McGee et al., 2005a).

The contribution of the dairy herd to the total beef output of many countries can be substantial, often surpassing the contribution of the respective national beef herd. In New Zealand, 65% of beef output by volume originates directly or indirectly from dairy herds (Morris, 2008). Beef from dairy herds (including dairy animals and cull cows) represents 20.5 to 22.7% of US beef production (DeCurto et al., 2017). Sixty percent of the beef produced in Sweden is either in the form of cull dairy cows or their progeny (Federation of Swedish Farmers, 2019) and 80% of the beef produced in Finland originates from dairy herds (Niemi and Ahlstedt, 2013). In Russia, 87% of beef meat originates from young dairy bulls and cull dairy cows (Legoshin and Sharafeeva, 2013). It is very likely that the contribution to the overall national beef output originating from dairy versus beef herds may further diverge in the

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future as the gap in profitability between dairy and beef enterprises widens in most countries. Beef herds may be under a further threat, because they tend to be less competitive in terms of land use, and they reside predominantly on marginal land; countries may come under ever-increasing pressure to use such land as a vehicle for carbon sequestration to realize their carbon targets as set out in the Paris Agreement on climate action and any future such treaties. Overall, given the large and growing contribution of the dairy herd to beef output in many countries, the most critical decisions about the genetic merit of animals being harvested for the beef industry are being made by dairy producers, and beef merit does not rank highly in their selection decisions for parents of the next generation.

Although beef is often viewed as a byproduct of the dairy herd, it remains a cash-flow source in dairy herds. On average, the value of male calves born in dairy herds from beef sires is greater than those born from dairy sires (Dal Zotto et al., 2009; Mc Hugh et al., 2010; Berry et al., 2018). Cook (2014) reported that beef (i.e., cull cows, bulls, and calves) contributes 6% of the total dairy farm income in New Zealand. Although somewhat dated now, especially given that the exercise was undertaken during a period when the European Union (EU) imposed a milk quota (although some sort of a quota may be reimposed in the future), van der Werf et al. (1998) stated that 10 to 20% of the gross income for Dutch dairy farms was from the sale of calves and cull cows. Using representative survey data from Irish dairy

herds over a single calendar year (2012), O'Brien et al. (2015) reported that "livestock plus forage revenue" contributed 2.7% of gross revenue per hectare, on average; therefore, this is an upper limit for the contribution of livestock sales to Irish dairy producers, although the extent of forage sales is small. The monetary benefit of a beef-sired versus a dairy-sired calf from a dairy dam, in price per liter of milk equivalent, is a function of the differential in calf price (after considering rearing costs) between a beef \times dairy calf and a dairy \times dairy calf, the prevailing milk price, and the mean yield per cow (Table 1). For the same yield per cow, the greater the differential in calf price between a dairy \times dairy or a beef \times dairy calf, the greater the equivalent price per liter (Table 1). Similarly, for the same price differential between the 2 genotypes of calves, the lower the yield per cow, the greater the price per liter of milk equivalent from a beef \times dairy animal. Therefore, the contribution of beef \times dairy crosses to the gross output per liter is, on average, greater in lower-yielding herds and when a greater price differential exists between beef \times dairy calves versus dairy \times dairy calves.

Interest in beef-on-dairy production is intensifying, especially more recently, due to a combination of factors, including the following: (1) improving reproductive performance of the dairy herd globally (Berry et al., 2014a; García-Ruiz et al., 2016), resulting in a reduced requirement for dairy female graduates to the mature herd; (2) exploiting potential heterosis effects in the embryo or fetus from beef-on-dairy matings, further

Table 1. Price per kilogram of milk equivalent for cows with different yields, where the differential in price per calf between a dairy \times dairy or a beef \times dairy calf varies from 0 to 200 currency units

Differential in price (currency unit)	Yield per lactation (kg)											
	5,000	5,500	6,000	6,500	7,000	7,500	8,000	8,500	9,000	9,500	10,000	
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	0.20	0.18	0.17	0.15	0.14	0.13	0.13	0.12	0.11	0.11	0.11	0.10
20	0.40	0.36	0.33	0.31	0.29	0.27	0.25	0.24	0.22	0.21	0.21	0.20
30	0.60	0.55	0.50	0.46	0.43	0.40	0.38	0.35	0.33	0.32	0.32	0.30
40	0.80	0.73	0.67	0.62	0.57	0.53	0.50	0.47	0.44	0.42	0.42	0.40
50	1.00	0.91	0.83	0.77	0.71	0.67	0.63	0.59	0.56	0.53	0.53	0.50
60	1.20	1.09	1.00	0.92	0.86	0.80	0.75	0.71	0.67	0.63	0.63	0.60
70	1.40	1.27	1.17	1.08	1.00	0.93	0.88	0.82	0.78	0.74	0.74	0.70
80	1.60	1.45	1.33	1.23	1.14	1.07	1.00	0.94	0.89	0.84	0.84	0.80
90	1.80	1.64	1.50	1.38	1.29	1.20	1.13	1.06	1.00	0.95	0.95	0.90
100	2.00	1.82	1.67	1.54	1.43	1.33	1.25	1.18	1.11	1.05	1.05	1.00
110	2.20	2.00	1.83	1.69	1.57	1.47	1.38	1.29	1.22	1.16	1.16	1.10
120	2.40	2.18	2.00	1.85	1.71	1.60	1.50	1.41	1.33	1.26	1.26	1.20
130	2.60	2.36	2.17	2.00	1.86	1.73	1.63	1.53	1.44	1.37	1.37	1.30
140	2.80	2.55	2.33	2.15	2.00	1.87	1.75	1.65	1.56	1.47	1.47	1.40
150	3.00	2.73	2.50	2.31	2.14	2.00	1.88	1.76	1.67	1.58	1.58	1.50
160	3.20	2.91	2.67	2.46	2.29	2.13	2.00	1.88	1.78	1.68	1.68	1.60
170	3.40	3.09	2.83	2.62	2.43	2.27	2.13	2.00	1.89	1.79	1.79	1.70
180	3.60	3.27	3.00	2.77	2.57	2.40	2.25	2.12	2.00	1.89	1.89	1.80
190	3.80	3.45	3.17	2.92	2.71	2.53	2.38	2.24	2.11	2.00	2.00	1.90
200	4.00	3.64	3.33	3.08	2.86	2.67	2.50	2.35	2.22	2.11	2.11	2.00

improving pregnancy rates; (3) dairy-herd expansion rates being curtailed in many developed countries, also reducing the need for additional dairy heifers; (4) a growing use of dairy-sire X-bearing sexed semen, so that more dairy female candidates are available for mating to beef sires; (5) a desire to ensure resilience to increasingly volatile milk prices by generating welcome sources of cash flow through surplus calf sales, especially in scenarios of low milk price (and high beef price); (6) an acceptance of beef \times dairy crosses in a wider range of markets relative to dairy \times dairy animals; (7) a growing availability of easy-calving, short-gestation-length beef bulls; and (8) mounting consumer concerns about the processing of young (predominantly dairy male) calves relatively soon after birth, necessitating a strategy to increase the value of these surplus animals.

Although meat from dairy herds exists in the form of cull cows, this review will focus predominantly on meat production from the progeny of dairy females mated to beef sires; it will also consider, in places, the progeny of dairy parents. Of particular interest will be the potential of beef-on-dairy breeding strategies to support to this emerging industry.

GLOBAL TRENDS

Figure 1 illustrates how the population of dairy cows has changed globally, as well as in the United States,

the EU 27, and Australia and New Zealand in recent decades. Although dairy cow numbers are declining in the EU 27, they are now relatively stable in the United States and increasing globally. Figure 2 depicts improvements in dairy cow genetic merit for longevity observed in the United States and Ireland in the past 2 decades, implying a reduced requirement for dairy female replacements. Although expanding herds still require a large number of dairy heifers to fuel expansion, the deceleration (or even shrinkage) in dairy herd growth in some countries, coupled with improved cow longevity, implies that fewer dairy heifers are required. Once the required dairy females are thought to be in utero, then an opportunity exists to mate the remaining females, especially those of poorer genetic merit, to beef semen. This opportunity is further improved with the growing uptake of sexed dairy semen (Tyrisevä et al., 2017; Li and Cabrera, 2019).

Traditionally, dairy cow breeding programs have selected aggressively for milk production (Miglior et al., 2005). Although milk production is genetically correlated with larger cows (Berry et al., 2004), animals selected solely to produce more milk also tend to become more angular, with reduced fat cover (Berry et al., 2004). Nevertheless, selection for improved reproductive performance over the past 2 decades, coupled with the known genetic correlation between greater BCS and improved reproductive performance (Berry et al.,

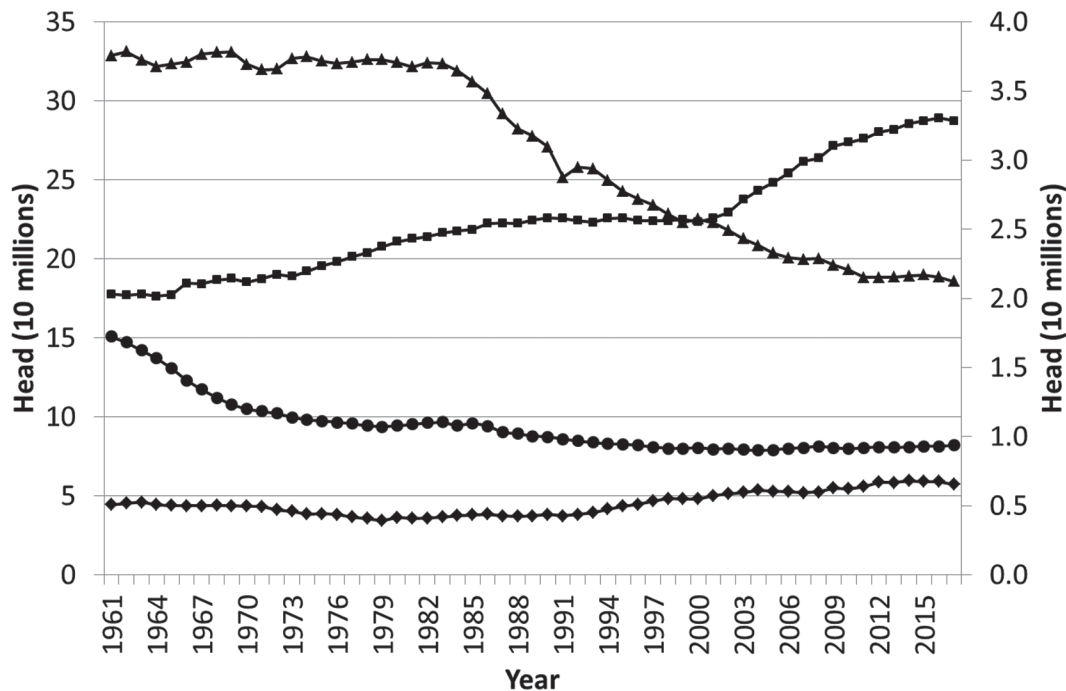


Figure 1. Number of dairy cows in the world (■; primary vertical axis), the United States (●; secondary vertical axis), Europe (▲; secondary vertical axis), and Australia and New Zealand (◆; secondary vertical axis); source: FAO (2020).

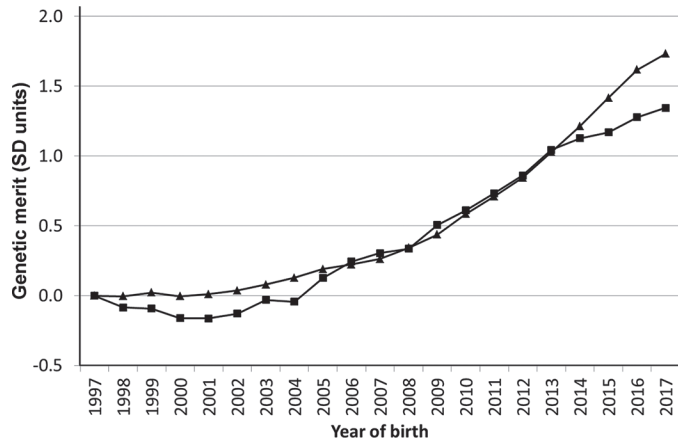


Figure 2. Genetic trends for cow longevity in genetic SD units for Irish Holstein-Friesian (■) and United States Holstein (▲) cows.

2003), is negating some of the erosion of body fat cover in some dairy cow populations. Figure 3 illustrates the change in genetic merit for stature in US Holsteins over time toward taller animals; this is not surprising given the known positive genetic correlation between milk yield and stature in dairy cows (Berry et al., 2004). Still, genetic correlation estimates between milk production and beef merit in dairy cows are lacking, although a negative relationship between milk production and both carcass fat and conformation has been suggested (McGee et al., 2005a). Using a population of 2,590 Holstein AI sires in Ireland with a reliability for milk production and carcass traits of >70%, the correlations of milk yield, protein yield, and fat yield with carcass weight ranged from -0.06 to 0.26 , whereas the correlations with carcass conformation (-0.43 to -0.22) and carcass fat (-0.29 to -0.02) were negative. Nonetheless, many dairy cow breeding programs now place a negative weight on cow size to reduce cow size or to halt or slow the expected increase in cow size associated with selection for increased milk production. Such breeding programs have implications for genetic trends in the beef characteristics of the dairy herd. Based on a population of Irish dairy cows and their progeny, Twomey et al. (2020) plotted the genetic trends by year of birth for progeny carcass weight, conformation, and fat score for dairy \times dairy animals and for beef \times dairy animals. The mean annual EBV for all 3 carcass traits decreased (i.e., lighter, less conformed carcasses with reduced fat cover) almost consistently for the dairy \times dairy animals since the year 2000, which was the first year of the study. Although the genetic trends for the beef \times dairy animals were less obvious for carcass weight (an initial reduction followed by a steady but slow increase) and carcass fat (an initial increase but relatively stagnant

thereafter), mean EBV for Irish beef \times dairy animals for carcass conformation has deteriorated considerably.

Figure 4 illustrates the proportion of dairy female matings or births to beef bulls in Ireland (Berry et al., 2020) and Canada (Van Doormaal, 2019); the proportion of matings to beef in both populations has increased steadily, especially in recent years. Davis et al. (2019) presented the annual trends in beef \times dairy calvings from Nordic countries since the year 2000, showing increasing numbers of beef \times dairy calves being born in the most recent decade, especially in Denmark. Geiger (2019) also noted a sharp increase in beef semen sales in the United States in recent years, although not all of that increase can be attributable to matings to dairy females. Similar findings have been reported elsewhere in the United States (Nehls, 2019), although there is no current path for pricing signals relative to carcass yield and quality to return to the dairy producer. Fouz et al. (2013) reported that 20.2% of first inseminations of Holsteins in northern Spain were to beef bulls. Therefore, the use of beef bulls on dairy females does appear to be increasing globally.

Available information is sparse, but traditional (British) breeds tend to predominate as the beef breeds used on dairy females (Figure 4; Halfman and Sterry, 2019; Berry and Ring, 2020c; McWhorter et al., 2020). Using insemination data from Irish dairy females, Berry and Ring (2020c) reported that 53 and 32% of beef matings to Irish Holstein-Friesian females were to Angus and Hereford sires, respectively. From a survey of 69 US dairy producers (of which 45 answered this question), 62% stated that they used Angus sires (Halfman and Sterry, 2019). Based on an edited data set for the AI beef bulls mated to US dairy cows, McWhorter et al. (2020) reported that 95.4% of the beef-on-dairy inseminations were to Angus bulls. The predominance of these

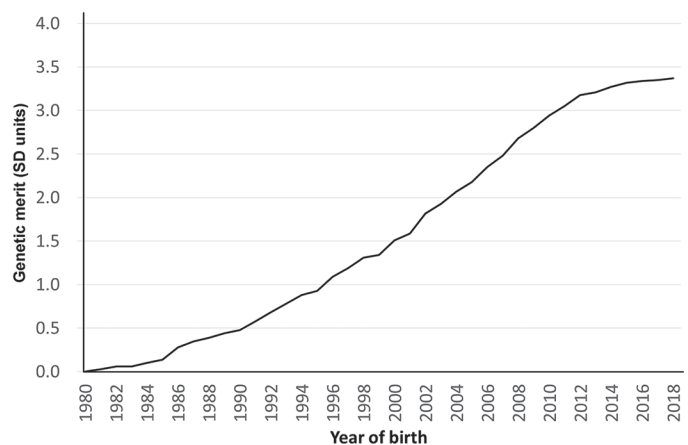


Figure 3. Genetic trends for stature in SD units in United States Holstein dairy cows by year of birth.

2 traditional breeds is likely a function of their breed average superiority for both ease of calving (Berry and Ring, 2020a) and meat quality (Bureš and Bartoň, 2018; Judge et al., 2021), despite inferior mean credentials for some carcass traits relative to continental-type sire breeds (Alberti et al., 2008; Campion et al., 2009; Berry and Ring, 2020a). Davis et al. (2019) stated that in Nordic countries in the year 2018, 41% of the beef × dairy calves had a Belgian Blue sire, and an additional 28% had a Blonde d'Aquitaine sire; in Denmark in the same year, 80% of the beef × dairy calves had a Belgian Blue sire. Still, as much variability in genetic merit exists within breeds as between breeds, demonstrated by both Berry and Ring (2020a) and Davis et al. (2019) for a range of traits in cattle; therefore, advice should be to consider the within-breed estimates of genetic merit as well as the mean breed effects. The ideal situation (discussed later) would be to have estimates of genetic merit that are directly comparable across breeds so a more informed decision can be made that considers all animals from all available breeds.

Not well publicized worldwide is dairy producers' ranking of the importance of different bull features when selecting for mating to dairy females. Berry et al. (2020) found that based on estimates of genetic merit for the direct calving difficulty of individual bulls, 1.85 more dystocia events could be expected per 100 dairy cows mated to beef versus dairy bulls, although this finding was a function of herd size. Mean genetic merit for the direct calving difficulty of dairy bulls increased from 1.39 (i.e., an expectation of 1.39 dystocia events per 100 cows calving) in heifers to 1.79 in first-parity cows and 1.82 in second-parity cows, remaining relatively constant thereafter (Berry et al., 2020); in

contrast, the mean genetic merit for calving difficulty of beef bulls chosen for dairy cows increased consistently with cow parity (Berry et al., 2020). Differences in particular for genetic merit for carcass weight and carcass conformation were also evident between the dairy and beef bulls used on dairy cows (Berry et al., 2020). From a survey of 69 US dairy producers, semen cost, conception rate, and calving ease were the top 3 criteria considered when selecting beef bulls (Halfman and Sterry, 2019). Berry et al. (2020) did not consider semen cost in their analyses, and because no published values on male fertility exist in Ireland, those were also not considered in the analysis for Irish dairy cows. Breeders and breeding companies must be cognizant of such factors in the breeding and marketing of beef bulls to dairy producers.

The demographics of dairy females that receive dairy versus beef semen have also not been widely described. The expectation is that females of inferior genetic merit for dairy performance traits would be mated to beef bulls, because they may be deemed not sufficiently elite to generate replacements for the dairy herd; empirical evidence from Irish dairy herds substantiate this hypothesis; the odds of a dairy female ranking (within herd) in the worst 10% for the Irish total genetic merit being mated to a beef bull are 2.90 times that of a dairy female in the top 10% (Berry and Ring, 2020b). Berry and Ring (2020b) also documented greater odds of an older cow being served with a beef bull; odds were also greater for cows that calved later in the year, had recently experienced dystocia or were more days calved when served. A lower frequency of mating of beef bulls to younger cows is consistent with the results from a survey of 69 US dairy herds; 20% of the surveyed pro-

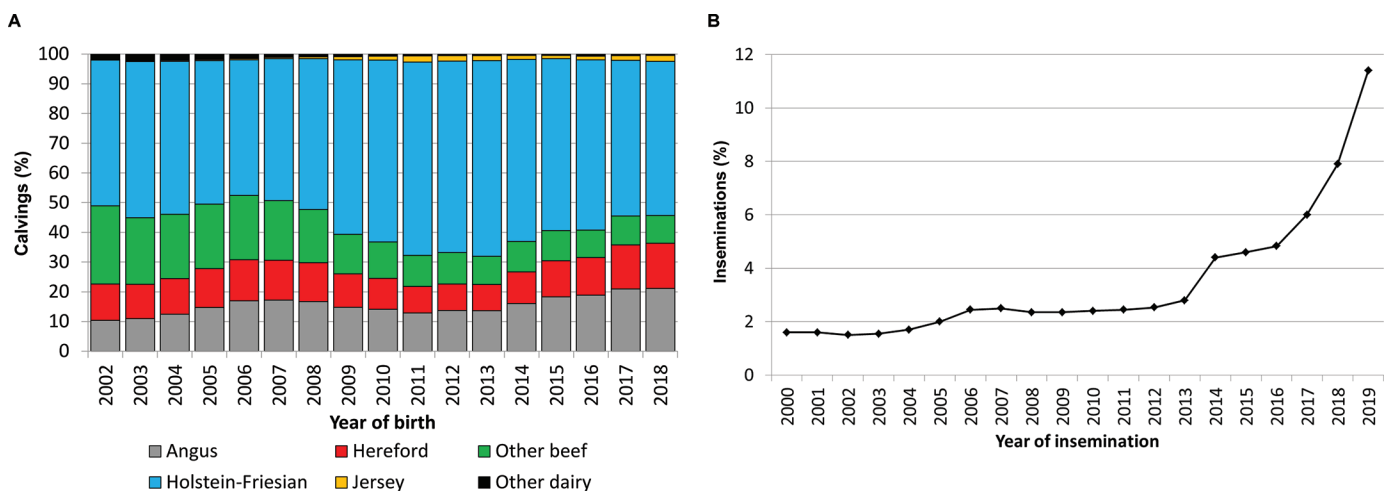


Figure 4. (A) Percentage of sire breeds by year of birth to Irish Holstein-Friesian dams (Berry and Ring, 2020c); (B) percentage of beef service sire matings to Canadian Holsteins by year of insemination (Van Doormaal, 2019).

ducers stated that cow parity was a consideration when deciding which dairy females were mated to beef bulls (Halfman and Sterry, 2019). Cows with low SCC in the previous lactation relative to their herdmates were also less likely to be mated to a beef bull, as were cows that yielded relatively higher milk solids in their previous lactation (Berry and Ring, 2020b).

DAIRY-ON-BEEF PRODUCTION SYSTEMS

Many potential markets exist for surplus (beef ×) dairy cattle; most of these opportunities are almost identical to those for cattle from beef herds except for the market for young calves born in dairy herds. Calves harvested at a very young age are termed “bobby calves” in several parts of the world, referring to calves born in dairy herds that are processed at <30 d of age; in reality, this is usually <10 d of age. The name “bobby calf” originated from the fact that producers originally received a bob (slang for a shilling or 12 pence) per calf. These bobby calves generally include almost all (dairy-bred) bull calves and some heifer calves not deemed suitable for graduation into the mature dairy herd (e.g., freemartins). Products generated from bobby calves include veal meat, ground beef, hides for leather, calf rennet for cheesemaking (from the abomasum of the calf, also called a vell), calf serum, and rendering into meat and bone meal. Calf serum is used as a growth medium for tissue and cell cultures, as well as in vaccines, dietary supplements, and cosmetics. Bobby calves are a large industry in New Zealand; in 2014, 1.7 million calves were harvested as bobby calves out of a total of 4.2 million recorded births in dairy herds (Cook, 2014). Of the 1,424,503 cattle (<36 mo of age) processed in Irish abattoirs in 2018, a total of 28,823 (i.e., 2%) were harvested at less than 6 wk of age (www.agriculture.gov.ie/animalhealthwelfare/animalidentificationmovement/cattle/bovinebirthandmovementsmonthlyreports/).

Both interest and concern are growing among consumers about how ethically their food is produced (Coleman and Toukhsati, 2006) and how it conforms to public values (Weary and von Keyserlingk, 2017). Self-regulatory conformity, as is often the norm in dairying, is often referred to as a social license. Social license has been defined as the privilege of operating within minimal formalized restrictions with respect to regulation, legislation, or market-based mandates that come from maintaining public trust by doing what is right (Fleck, 2015). Some countries enforce a minimum age limit on when calves can be moved off farm—currently 5 d in Australia and 10 d in Ireland. Irrespective of age at slaughter, however, it is imperative that all animals experience a very high quality of life, and that every effort is made to avoid compromises in animal welfare.

If, however, the perceived value of an animal product is low, then the incentive to maintain acceptable welfare standards could be compromised; this should be avoided, and one strategy for achieving this is to increase the value of the calf (i.e., beef-on-dairy).

Calves from the dairy herd are also used for veal production, which can be classified as white, red, or rosé veal. White veal, which predominates in most countries, consists of calves fed exclusively or predominantly milk or milk-based products, harvested usually younger than 8 mo of age. Iron intake in these animals is often restricted. For red veal, calves are fed almost exclusively on cereals post-weaning and are harvested at older than 10 mo of age. In 2009, veal calves accounted for 20% of bovines processed in the EU, representing about one-third of the calves from the dairy herd (Sans and de Fontguyon, 2009); 40% of the male calves from EU dairy herds were converted to veal, and approximately three-quarters of veal calves were male.

The majority of beef × dairy-cross animals worldwide are harvested as beef at greater than 12 mo of age. The systems for rearing dairy(-cross) animals for beef production are similar to those designed for beef animals originating from beef herds, although differences in key performance indicators (e.g., target weights) do exist. Cattle may be harvested as entire bulls, heifers, or steers, the latter 2 often taking particular advantage of extensive (lower-cost) production systems. Nonetheless, such extensive production systems are more at the mercy of the weather and associated seasonal fluctuations. Although in situ grazed pasture is a low-cost feed relative to ensiled forage or concentrates (Finneran et al., 2010), pasture availability does not always match demand year-round, necessitating some element of supplementation with an associated cost. In such systems, a younger age at slaughter, also maximizing the exploitation of grazed pasture in the diet, is crucially important for a successful and profitable beef × dairy extensive enterprise (Ashfield et al., 2014).

Few dairy × dairy females enter beef production systems for harvesting, so proposed production systems for dairy × dairy animals are for intact bulls or steers, the latter being more common in extensive grazing production systems. In Ireland, 2 main production systems are proposed for dairy × dairy steers, which involve slaughtering at either 21 or 23 mo of age (Supplemental Table S1; https://figshare.com/articles/figure/Supplementary_Table_1_docx/13697386). Harvesting heifers from early-maturing beef bulls at 19 mo is the recommendation in Ireland at a carcass weight of 235 kg which, when coupled with a recommended stocking rate of 3.9 animals per hectare, provides a carcass output per hectare of 914 kg (Supplemental Table S1). This is higher than the carcass output per hectare of

the 21 mo (801 kg/ha) or 23 mo (797 kg/ha) steer production system for dairy \times early-maturing beef animals (Supplemental Table S1). In Ireland, it is recommended that steers from later-maturing beef bulls \times dairy cows be harvested at 24 mo of age with a carcass weight of 340 kg, based on a stocking rate of 2.4 animals per hectare and receiving 0.50 t of concentrates during the 120-d finishing period (Supplemental Table S1). A 15-mo bull system is recommended in Ireland with a target carcass weight of 275 kg.

In the United States, beef from dairy production systems for prime beef usually involve moving the calves to rearing operations where they are weaned at approximately 10 wk of age and fed for another 10 wk until they enter a feedlot. Once in a feedlot, beef \times dairy animals are managed similarly to beef animals, where they reside in the feedlot for approximately 1 yr, with the aim of harvesting somewhere between 16 and 18 mo of age.

In New Zealand, the standard beef-on-dairy system involves artificial rearing on milk replacer and concentrates until approximately 3 mo of age, after which calves graze on pasture. Calves are usually out-wintered on pasture (albeit with very low pasture growth and thus very slow ADG). Animals are then ideally finished at pasture the following year, with animal growth rates of between 1 and 1.5 kg/d during the spring and summer and 0.8 to 1.0 kg/d in the summer and autumn. The target is to harvest before the second winter at approximately 20 to 22 mo of age.

RELATIVE PERFORMANCE CHARACTERISTICS

A great deal of research has been undertaken to evaluate dairy \times dairy, beef \times dairy, and beef \times beef cattle using controlled experiments (Campion et al., 2009; Clarke et al., 2009b; McGee et al., 2020) or cross-sectional analyses of large databases (Huuskonen et al., 2013a,b; Connolly et al., 2016; Berry et al., 2018; Kenny et al., 2020). However, many of the studies comparing the performance of different breed types often compare different beef breeds mated to dairy females without necessarily comparing with dairy breeds (Homer et al., 1997; McQuirk et al., 1998), or they compare beef \times dairy animals against dairy \times dairy animals, but not against beef \times beef animals (Huuskonen et al., 2013a,b; Berry et al., 2018). Studies that compare dairy (\times beef) animals with beef animals (Clarke et al., 2009b) are usually not a direct comparison of genetic merit differences, because both genotypes are completely confounded with early-life experiences (Twomey et al., 2020). Using solutions from a statistical model fitted to cross-sectional data for cattle from all types of breeds and crossbreds, Twomey et al. (2020) attempted to

disentangle the effect of genetic merit (of both parents separately) and early-life experiences (i.e., bucket- vs. suckle-reared, which represents systems in dairy versus beef herds, respectively) to quantify the effect of each contributing factor to eventual carcass merit. On average, animals originating from beef herds had heavier and more conformed carcasses than those from dairy herds (Twomey et al., 2020). When the genetic merit of the beef and dairy dams was equalized, beef \times beef animals still had heavier and more conformed carcasses than beef \times dairy animals (Twomey et al., 2020), and when the genetic merit of both parents of all animals were equalized, the carcasses of beef \times beef animals were still 15 kg heavier on average, with a conformation score 0.69 units higher (1 = poor to 15 = excellent) than dairy \times dairy animals (Twomey et al., 2020); the authors concluded that differences in early-life experiences between animals born in dairy and beef herds have a lasting effect, and these are additive to the difference in beef genetic merit of the parents.

When comparing breed types, of particular interest is the year the study was undertaken and the relevance of that population to the modern-day population. This is particularly pertinent for comparisons involving dairy animals where the rate of genetic gain is rapid (García-Ruiz et al., 2016), coupled with the fact that genetic merit for some carcass traits are deteriorating (Twomey et al., 2020). Extrapolation of results across country borders should also be undertaken with caution, given the differences in animal strains, especially dairy cattle, in different countries. One such clear distinction is between Holstein-Friesians bred for suitability to grazing versus confinement production systems; McCarthy et al. (2007) reported that Holstein-Friesian dairy cows of New Zealand origin (i.e., bred for grazing) were an average of 25 to 29 kg lighter than Holstein-Friesians of North American ancestry, even though they were of superior BCS. Roche et al. (2006) reached a similar conclusion for New Zealand and US strains of Holstein-Friesians, although the difference in live weight in their study was an average of 67 kg. Genomic differences between Holstein-Friesians in different populations are also known to exist (de Haas et al., 2015). Thus, any reference to Holstein-Friesians should be carried out in the context of the year the study was undertaken, and also the breeding program that generated the particular strain of Holstein, Friesian, or Holstein-Friesian. Also important when comparing dairy \times dairy animals to beef \times dairy animals is consideration of the breed of beef sire used, because large differences in performance characteristics exist between breeds, especially when comparing continental with traditional breeds; therefore, narratives comparing beef \times dairy relative to dairy \times dairy animals should also be undertaken in

the context of the beef breed. Finally, although comparing systems for mean differences in performance is the norm, the heterogeneity of the animals in a given system can also be important. Variability exists within breeds for performance, but it also exists across breeds; still, a group of animals from 1 breed (e.g., Holsteins) can be expected to be less variable than a group of animals from multiple breeds, and this has implications both inside and outside the farm gate.

Heterosis refers to the superiority of an individual over the mean performance of its parents. In the absence of heterosis (with the exception of major genes such as growth differentiation factor 8, also known as the myostatin gene or the double-muscling gene), the performance of beef \times dairy animals is expected to be somewhere between that of the breed effects of the dairy dam and the beef sire, being cognizant of the selection that is likely to occur within the beef sire breed(s) for suitability for dairy females (Berry et al., 2020). However, heterosis is known to exist for performance traits relevant to beef-on-dairy production, although heterosis estimates are lacking for performance traits in younger animals specific to beef-on-dairy matings (Berry et al., 2018). Berry et al. (2018) documented a 100% heterosis estimate for beef \times dairy cattle of 1.21 kg heavier carcass weight and 4.56 earlier days to harvest, both of which were less than 1% of the respective performance mean. Although many studies fit a general heterosis effect across all breed combinations in their statistical models (Judge et al., 2019a), heterosis is a function of genetic distance and is expected to be greater between dairy and beef breeds than among beef breeds (or among dairy breeds), because the former are more distantly related (Kelleher et al., 2017). Heterosis estimates are expected to be relatively small for performance traits such as carcass merit, but they are expected to be large for traits associated with vitality, such as perinatal mortality; therefore, the multiplicative effect on carcass value per herd is likely to be moderate, because the calf must first live to produce a valuable carcass. The influence of maternal heterosis in beef \times dairy cattle is likely to be relatively small when the calf is separated at birth, especially if it receives pooled colostrum, although in utero benefits may still exist in such situations.

Complementarity in crossbreeding implies combining breeds with different (i.e., complementary) strengths, one breed possibly compensating for the weaknesses of the other. An example of this for beef sires could be complementing the ease of calving and short gestation length associated with traditional British breeds with the superior carcass credentials of continental beef breeds. Complementarity is particularly useful for characteristics that are antagonistically correlated within

breed [e.g., milk production and fertility in dairy cows (Berry et al., 2014a) or calving difficulty and carcass weight in cattle (Berry et al., 2019a)]. Composite breeds tend to exploit complementarity more than rotational crossbreeding systems; the opposite is true for heterosis.

Calving Performance Traits

Mean differences among beef breeds in calving difficulty, perinatal mortality, and gestation length when mated to dairy cows have been clearly documented (Fouz et al., 2013; McGuirk et al., 1998; Berry and Ring 2020a; Eriksson et al., 2004). Although one should be careful about making inferences from these studies to mean breed effects because of the likely selection of sires within those breeds specific for use on dairy females, the mean calving difficulty of traditional British beef breeds tends to be less than that of continental beef breeds (McGuirk et al., 1998; Berry and Ring, 2020a). Nonetheless, using UK dairy cow data, McGuirk et al. (1998) reported a low incidence of calving difficulty in calves from dairy dams sired by Belgian Blue bulls. In an analysis of almost 1.6 million calving records from Swedish dairy herds, Eriksson et al. (2004) reported a greater incidence of calving difficulty in calves sired by late-maturing beef breeds (i.e., Charolais and Simmental sires in their study) relative to those sired by dairy sires or early-maturing beef breeds (i.e., Angus and Hereford sires in their study); the incidence of calving difficulty from Limousin-sired calves was intermediate. Digging deeper, Eriksson et al. (2004) concluded that the inter-breed differences among sires was more pronounced in primiparous dams. A greater incidence of calving difficulty from beef-on-dairy matings relative to dairy-on-dairy matings has also been reported elsewhere (Fouz et al., 2013), although Berry and Ring (2020a) demonstrated that this was not necessarily true if the beef sires were chosen based on genetic merit for calving difficulty (and gestation length).

The low expected mean calving difficulty of the traditional beef breeds, coupled with anxiety among many dairy producers about the known effect of calving difficulty on subsequent cow performance (Dematawewa and Berger, 1997; Berry et al., 2007a) is one of the main reasons why traditional beef breeds tend to be the most frequently used in temperate regions (Eriksson et al., 2004; Halfman and Sterry, 2019; Berry and Ring, 2020c; McWhorter et al., 2020). In fact, the genetic merit for the direct calving difficulty of Angus and Hereford bulls used on dairy females is not very different from that of Holstein-Friesian sires (Berry and Ring, 2020a). As well, assortative mating is likely to occur between dairy dams and choice of beef breed (McGuirk et al., 1998; Berry et al., 2020) or sire within breed (Berry et al.,

2020). McGuirk et al. (1998) reported that beef \times dairy calves born from Charolais and Belgian Blue sires were from larger dairy cows (as scored by producers on a scale of 1 to 3) on average, compared to those born from the other 6 beef sire breeds evaluated (Angus, Hereford, Limousin, Blonde d'Aquitaine, Piedmontese, and Simmental). Berry et al. (2020) reported that the use of Angus in heifers, parity 1, and parity 2 dairy cows was 11, 7, and 6%, respectively. Genetic merit for direct calving difficulty of the beef bulls used also increased consistently as parity number increased, with a notable increase especially from heifer matings to cow matings, despite the fact that the genetic merit for direct calving difficulty of matings to dairy bulls remained relatively constant across parity number (Berry et al., 2020).

Inter-breed differences among beef breeds have also been reported for gestation length (McGuirk et al., 1998; Fouz et al., 2013; Fitzgerald et al., 2015; Berry and Ring, 2020a) when mated to dairy cows. In their comparison of progeny from 8 different beef breeds (Angus, Belgian Blue, Blonde d'Aquitaine, Charolais, Hereford, Limousin, Piedmontese, and Simmental) born to English and Welsh dairy cows, McGuirk et al. (1998) reported a range of 8 d difference in gestation length, from 281 d in the Angus to 289 d in the Blonde d'Aquitaine. From a population of 6,805 Irish Holstein-Friesian dairy cows, Fitzgerald et al. (2015) reported a mean gestation length in dairy cows of 2.34 to 3.16 d longer when mated to Angus, Belgian Blue, or Hereford sires relative to Holstein-Friesian sires. Relative to a mean gestation length of 280.81 d [standard error (SE) 0.07] in Holstein-Friesian calves born from Holstein-Friesian sires, gestation lengths for those born from matings to Angus, Belgian Blue, and Hereford sires were 283.42 (SE 0.32), 283.15 (SE 0.45), and 283.97 (SE 0.67) d, respectively (Fitzgerald et al., 2015). Similarly, Fouz et al. (2013) using data from 552,571 calving events from Holstein cows reported gestation lengths 2.32 and 5.94 d longer in Limousin \times Holstein and Belgian Blue \times Holstein calves relative to Holstein \times Holstein crosses. Nonetheless, in the comparison of beef (and dairy) breed sires for gestation length, Berry and Ring (2020a) concluded that considerable (exploitable) genetic variability exists within each breed.

Differences among beef-breed sires when mated to dairy cows in both actual perinatal mortality (McGuirk et al., 1998; Eriksson et al., 2004; Fouz et al., 2013) or genetic predisposition to perinatal mortality (Berry and Ring, 2020a) have been documented. In an analysis of over 88,000 calving records from English and Welsh dairy cows mated to beef bulls from 8 different breeds, McGuirk et al. (1998) reported greater calf mortality in progeny from Charolais and Blonde d'Aquitaine sires

compared to those from Angus, Hereford, Belgian Blue, and Simmental sires. With the exception of sires from late-maturing beef breeds, Eriksson et al. (2020) reported a reduced incidence of perinatal mortality in beef \times dairy calves compared with dairy \times dairy calves; some of this difference was likely to be a function of heterosis, which tends to be greater for traits associated with fitness and vitality (Falconer and Mackay, 1996), such as perinatal mortality. Fouz et al. (2013) reported similar perinatal mortality in beef \times dairy calves compared with dairy \times dairy calves, with the exception of higher perinatal mortality in Belgian Blue \times dairy calves.

Growth and Efficiency

Although growth and efficiency are often treated as separate metrics, they are intrinsically linked. All else being equal, an animal that eats less per day for the same growth rate (i.e., a form of residual feed intake; Byerly, 1941) should be more feed-efficient, but also, all else being equal, an animal that reaches its target harvest weight earlier should eat less feed. Although quantity of feed is important, the composition (e.g., energy density) of that feed and ability to fulfill the energy demands for growth and achieve an appropriate finish is also important. In extensive grazing systems, for example, germplasm that can ingest sufficient pasture to support rapid growth but also achieve sufficient carcass fat cover is crucial for maintaining a low-cost structure (Ashfield et al., 2014). Literature comparing cattle breeds for growth is abundant, but less information is available on inter-breed differences for feed intake and efficiency; nonetheless, significant intra-breed variability in both growth rate and feed intake and efficiency in cattle has been demonstrated (for a review, see Berry and Crowley, 2013).

Using a data set of 436 purebred young bulls from 15 European breeds harvested at 15 mo of age, Albertí et al. (2008) reported similar ADG for the 3 dairy breeds of Holstein, Jersey, and Danish Red; no difference in ADG existed between these breeds and 4 of the remaining 12 beef breeds. However, the ADG of the Holsteins was slower than that of the Angus, Asturiana de los Valles, Abilena, Charolais, Limousin, Pirenaica, South Devon, and Simmental (Albertí et al., 2008). Vestergaard et al. (2019) compared the performance of 14 Danish Holstein bulls with 15 Limousin \times Danish Holstein bulls in an organic setting; no difference in ADG was detected when the time periods were collapsed into the first summer, the second winter, or the second summer, although the Limousin \times dairy animals grew faster (i.e., 1.04 kg/d) than the dairy \times dairy animals (0.97 kg/d) over their lifetime.

Although not as plentiful as studies on growth rate, many studies have compared feed intake and efficiency in dairy \times dairy animals versus beef \times dairy animals (McGee et al., 2005a; Keane, 2010; Hessele et al., 2019) or dairy \times dairy animals versus beef \times beef animals (Clarke et al., 2009b). These studies also tended to include measures of growth rate. As in other studies evaluating beef \times dairy animals, the breed of beef sire (i.e., especially traditional versus continental) affected the comparison made. Hessele et al. (2019) compared the feed intake (as well as other metrics) of 32 purebred dairy versus 32 dairy \times Charolais steers and detected no genotype difference in growth rate from weaning to slaughter, or in feed intake, feed intake as a percentage of BW, or feed efficiency, the only exception being daily feed intake in early life, which was 4% greater in the dairy \times Charolais crosses. Based on a controlled study of both bulls and steers, McGee et al. (2005a) also failed to detect a difference in grass silage feed intake of Holsteins, Friesians, or Holstein-Friesian \times Charolais animals; they observed no difference in growth rate between the Holsteins and Holstein-Friesian \times Charolais males across their lifetime, although the carcass gain per day was superior for Holstein-Friesian \times Charolais animals relative to both Holsteins and the Friesians (which did not differ from each other). Comparing Holstein versus late-maturing beef \times beef bulls using a controlled experimental study, Clarke et al. (2009b) reported a greater daily feed intake during the finishing period for the beef \times beef bulls (9.3 kg/d) relative to the Holsteins (8.7 kg/d) but detected no difference in the steer system comparing the late-maturing beef \times beef bulls to Friesian steers; compared on a per-kilogram live-weight basis, the dairy-breed animals ate more than their beef \times beef contemporaries. Because of their faster growth rate, residual feed intake was superior in the beef \times beef animals (Clarke et al., 2009b). Keane (2010) failed to detect a difference in growth rate between Holstein-Friesian and Belgian Blue \times Holstein-Friesian steers during their study, except when they were calves, when the Holstein-Friesians grew faster. However, Keane (2010) did report greater feed intake in the Holstein-Friesian animals during the finishing period (i.e., both as daily feed intake but also per kilogram mean live weight), as well as a difference in feed conversion efficiency defined per kilogram carcass weight. The energy requirement of dairy-breed animals relative to their weight is, indeed, expected to be high, because they have more active internal organs and fat depots, necessary to sustain their high milk production as dairy cows. Nonetheless, daily feed intake between dairy versus beef \times dairy growing animals does not appear to be different.

Carcass Weight

Carcass weight is important because of its potential effect on the dilution effect of fixed costs on farm but also the processing costs per kilogram of carcass. Coupled with carcass conformation, lighter carcasses with poor conformation are expected to have lighter primal cuts (Judge et al., 2019b) and thus lower revenue per carcass; this is especially true if considering the opportunity cost of harvesting a heavier versus a lighter carcass on the kill line. It is generally agreed that the carcass weight of calves from dairy herds sired by beef breeds, especially the late-maturing breeds, is heavier than those sired by dairy sires (Eriksson et al., 2004; Huuskonen et al. 2013b; Berry et al., 2018; Hessele et al., 2019), although exceptions do exist (Campion et al., 2009). Based on a comprehensive characterization of the live weight and carcass credentials of purebred young bulls from 15 different European cattle breeds, Albertí et al. (2008) concluded that Jersey bulls had a lighter carcass weight (189.7 kg on average) than all other breeds compared, except for Caina and Highland cattle. Although Holstein bull carcasses, which were similar to those of Danish Reds, were lighter than the carcasses of Asturiana de los Valles, Charolais, Limousin, Pirenaica, South Devon, and Simmental cattle, they were not different from the carcasses of Angus, Avilena, Marchigiana, or Piedmontese cattle. Therefore, carcasses of Holstein(-Friesians), although lighter than most continental beef breeds, do not tend to be different from those of traditional beef breeds, and carcasses of beef \times dairy cattle are expected to be somewhere in between, especially given the relatively small effect of heterosis on carcass weight (Berry et al., 2018). Nonetheless, population differences do exist in Holstein(-Friesians) globally, the most notable of which is a difference in live weight between dairy cows bred for grazing production systems and those bred for indoor feeding systems (Roche et al., 2006; McCarthy et al., 2007).

In their analysis of 48,875 carcass records from Irish dairy cows, Berry and Ring (2020a) failed to detect a difference in carcass weight (adjusted to a common age at harvest) in progeny from dairy dams sired by either dairy sires or beef sires selected solely on genetic merit for a combination of easy calving and short gestation. In that study, once the beef bulls were selected on a total merit index (Berry et al., 2019a), the mean carcass weight (adjusted to a common age at harvest) of the beef \times dairy calves was 8.9 kg (i.e., 3% of mean carcass weight) heavier than their dairy counterparts. Based on a series of controlled experimental studies comparing Holstein-Friesians with either Angus- or

Belgian Blue-sired calves from Holstein-Friesian dams, it is generally agreed that the Holstein-Friesians have a lighter carcass weight than the Belgian Blue crosses (although no difference may exist in live weight at harvest; Keane and Drennan, 2008; Keane 2010), and yet the carcass weight between Holstein-Friesians and Angus × Holstein-Friesian crosses is often no different. The carcass weight of Friesians was reported to be heavier than that of Holsteins based on an experimental study undertaken in Ireland, despite the fact that the Holsteins were genetically predisposed to a heavier carcass (Campion et al., 2009). McGee et al. (2020) reported lighter carcasses for Holsteins and Friesians (no difference detected between both genotypes in this study) relative to Charolais × Holstein-Friesian steers, an observation consistent with the findings of Hessele et al. (2019), who compared Swedish Red and Swedish Holsteins to Charolais × Swedish Red or Swedish Holsteins, as well as Huuskonen et al. (2013b) based on Finnish cattle. From a cross-sectional analysis of data from dairy herds, Berry et al. (2018) reported an expected difference of 46.31 kg in the carcass of pure Holstein-Friesian versus pure Jersey prime beef; this decreased to 26.49 kg when comparing an Angus × Holstein-Friesian and an Angus × Jersey beef animal. Moreover, in the same study (Berry et al., 2018), a difference of only 4.05 kg in carcass weight was evident between Holstein-Friesian and Angus × Holstein-Friesian steers.

More of an apparent concern among some processors is the length of carcasses for the rail height used on the kill line and its subsequent effect on carcass bruising. Of the 15 European cattle breeds investigated, Albertí et al. (2008) reported that Holsteins had the longest carcasses (135.1 cm)—6% longer than the average of the purebred beef bulls investigated (average of 127.6 cm). Although Holstein-Friesian primiparous cows are routinely linear-scored for conformation (Berry et al., 2004), no measure of body length is undertaken; this may merit reconsideration.

Carcass Conformation, Primal Cut Yield, and Saleable Meat Yield

In their analysis of purebred young bull carcasses from 15 different commonly used cattle breeds in Europe, Albertí et al. (2008) demonstrated that although the carcass conformation score of the 3 dairy breeds investigated (i.e., Holstein, Jersey, and Danish Red) did not differ [mean scores of 4.4 to 5.1 on a scale of 1 (poor) to 15 (excellent)], all 3 were worse than the purebred beef bulls investigated, who boasted an average score of 10.13 units. Information from beef × dairy crosses also

demonstrates how the carcass conformation in modern beef × dairy young animals is almost always superior to that of dairy animals (Eriksson et al., 2004; Hessele et al., 2019; Berry and Ring, 2020a). The differential in carcass conformation between the dairy and beef breeds is likely to widen over time with holsteinization and selection for increased milk production. Using a controlled study, McGee et al. (2005a) illustrated how the carcass conformation score of Holstein males genetically elite for milk production was inferior to that of the standard Friesian male, which, in turn, was inferior to that of the Charolais × Holstein-Friesians male. Estimates of genetic correlations between carcass conformation and traits included in modern dairy cow breeding goals are lacking, however. Regardless, the inferior carcass conformation score of the dairy breeds should translate into poor primal cut yields as a proportion of carcass weight (Judge et al., 2021); when coupled with the lighter carcass weight of Holsteins relative to most late-maturing beef breeds, this translates into lighter primal cuts. In their analysis of primal cut data for 14 different primal cuts from 54,250 crossbred cattle, Judge et al. (2020) reported lighter primal cuts for Holstein and Jersey cattle relative to the continental beef breeds, although differences were either small or nonexistent comparing the Holstein-Friesian to the Angus or Hereford; this conclusion was true irrespective of whether or not carcass weight was included as a covariate in the statistical model. Similarly, Muir et al. (2000) failed to detect any difference in the weight of individual high-value meat cuts between (New Zealand) Friesian, Hereford × Friesian and Hereford steers relative to carcass weight. In an analysis of Finnish purebred Holstein or Holstein × beef crosses, Huuskonen et al. (2013b) also failed to detect a difference in primal cut yield as a percentage of carcass weight in Angus × Holstein versus pure Holstein bulls, although EUROP carcass conformation score was higher ($P < 0.001$) in the Angus × Holstein bulls. Huuskonen et al. (2014) reached a similar conclusion when the Holstein in the analysis was replaced by the Nordic Red. However, although the weight of a given cut is important, the same weight can be achieved from a cut with different dimensions. Ribeye-muscle area, as opposed to weight, is of particular interest to meat processors. Holstein-Friesians tend to be longer than most beef cattle breeds (Albertí et al., 2008), implying a longer loin; hence, for the same loin weight, the ribeye area is expected to be less for Holsteins. This is substantiated by the fact that the loin muscle weight as a percentage of total muscle does not differ much by breed (Berg and Butterfield, 1976); therefore, a smaller ribeye area in Holsteins suggests a longer muscle. Nonetheless, the difference in ribeye-

muscle area between Holstein-Friesian animals and early-maturing breeds tend to be small (Wheeler et al., 2004; Keane, 2011).

All in all, when considering the fact that the predominant beef breed mated to dairy females is Angus (Halfman and Sterry, 2019; Berry and Ring, 2020c; McWhorter et al., 2020), the lack of difference in carcass weight between Angus (\times dairy crosses) and Holstein(-Friesians), coupled with the presence of only a small difference between purebred Angus and Holstein(-Friesians) for primal cut yield, implies potentially little actual carcass difference between dairy \times dairy versus beef (i.e., Angus) \times dairy crosses.

Carcass Fat

Beef \times dairy progeny tend to be fatter than their dairy counterparts at a given age (Eriksson et al., 2004; Berry and Ring, 2020a); this is especially true because many of these crosses tend to be from early-maturing beef breeds. Later-maturing animals, by their very name, lay down fat at heavier weights (Keane and Drennan, 2008), so if they are processed at the same weight, the dairy-born progeny from late-maturing sires may be leaner than their dairy counterparts (Keane, 2010). From a cross-sectional analysis of the EUROP 15-point fat score of over 4.5 million crossbred cattle, Kenny et al. (2020) reported reduced carcass fat cover in Jersey and Holstein-Friesian cattle compared with Angus, Hereford, Limousin, Shorthorn, and Simmental when adjusted to a common age at harvest; the Holstein-Friesian had more fat than the Aubrac, Belgian Blue, Blonde d'Aquitaine, and Charolais (Kenny et al., 2020). In an analysis of Holstein-Friesian versus Belgian Blue \times Holstein-Friesian steers harvested at the same live weight, Keane (2010) reported more fat cover in the Holstein-Friesians; the Holstein-Friesians also had more perirenal and retroperitoneal fat as weight, and as a proportion of carcass weight (Keane, 2010). This finding was similar to that presented by Campion et al. (2009) who reported more fat in Holstein and Friesian steers relative to Belgian Blue \times Holstein-Friesian steers. Interestingly, the Holsteins in that study had less fat cover than the Friesian and Angus \times Holstein-Friesian steers (Campion et al., 2009). The lesser fat cover in Holsteins relative to Friesians is not unexpected given aggressive selection in the former for greater yields with its known antagonistic genetic correlation with lower BCS (i.e., subcutaneous fat cover; Berry et al., 2003). More recent evidence of differences in marbling between dairy and beef breeds (and crossbreds) is sparse; nonetheless, Muir et al. (2000) detected a genotype difference in subcutaneous carcass fat for Friesian, Hereford \times Friesian, and Hereford steers harvested at

the same age, but failed to detect a genotype difference in chemical fat percentage (i.e., marbling). Coleman et al. (2016) also failed to detect a difference in intramuscular fat of the striploin in steers from Angus, Angus \times Holstein-Friesian, Angus \times (Holstein-Friesian \times Jersey), or Angus \times Jersey cows.

Dressing Percentage

It is generally agreed that for the same live weight, the dressing percentage of dairy animals is inferior to that of beef animals (Albertí et al., 2008; Coyne et al., 2019). In an analysis of 15 different European cattle breeds, Albertí et al. (2008) reported lower dressing percentage in the dairy breeds (i.e., Holstein, Danish Red, and particularly the Jersey) relative to most other beef breeds. This was largely due to greater weight of the gastrointestinal tract in dairy animals, as well as greater weight of the visceral organs and non-carcass fat such as mesenteric fat and omental fat (Keane, 2010). In fact, differences even exist between Holsteins and Friesians in omental and mesenteric fat; McGee et al. (2008) reported an empty gastrointestinal tract weight 15.3 kg higher (72.6 vs. 57.3 kg) in Holstein relative to Friesian steers. It stands to reason that the dressing percentage of beef \times dairy animals should be somewhere between that of dairy animals and beef animals. Coyne et al. (2019) reported a within-breed heritability estimate of dressing percentage and dressing difference (i.e., live weight minus carcass weight) of 0.48 and 0.35, respectively, from a database of 18,479 young cattle; the respective values were 0.08 and 0.28 based on a data set of 2,887 dairy and beef cull cows. Nonetheless, although many advocate for improvements in dressing percentage in cattle (including dairy cattle), caution is advised. Although not all the difference between live weight and carcass weight is due to gastrointestinal tract and visceral organs, selection for improved dressing percentage should not be to the detriment of the weight of the gastrointestinal tract and visceral organs, especially in extensive production systems where a large rumen capacity is necessary to ingest sufficient forage to meet nutritional requirements and a large gastrointestinal tract could be important in improving the availability of the nutrients. Furthermore, large livers may be required by high-producing dairy cows, especially for the production of glucose from body-fat mobilization in early lactation. From an extensive study of a range of carcass phenotypes of purebred young bulls from 15 different breeds, Albertí et al. (2008) concluded that relative to total rib weight, the percentage of "bone and others" from dissection at the sixth rib ("others" was everything but fat, bone, and muscle) was greatest for Holsteins and Jerseys rela-

tive to all other breeds, except for a lack of difference compared to Marchigiana or Simmental cattle.

Meat Quality

Meat quality could imply a whole spectrum of different metrics, but from the perspective of human consumption, most of the narrative on meat quality reflects the organoleptic properties such as tenderness, flavor, juiciness, and aroma. Meat quality, however, may also reflect other sensory characteristics such as visual cues, including intramuscular fat content and fat color. The latter is particularly important for animals with Jersey bloodlines; all else being equal, the fat color of Jersey animals is more yellow than that of other breeds, such as the Angus, Belgian Blue, Hereford, Limousin, South Devon, and Wagyu (Pitchford et al., 2002). This could be particularly important for the retail sector (Walker et al., 1990) but less so for the service sector. However, yellow fat is also a reflection of diet during the finishing period. β -Carotene exists in the pasture, which can be metabolized to vitamin A. Excess β -carotene is stored in fat, giving rise to a yellow-colored fat. Feeding diets high in grain can be one strategy for reducing the yellow color of fat.

Recent data comparing the meat quality characteristics of dairy, beef \times dairy, and beef cattle are sparse. One of the difficulties with objectively comparing different breeds is the decision about whether to harvest the animal at a common weight, age, fat score, or stage of maturity. Older studies (e.g., Beanaman et al., 1962) failed to detect any significant difference in a range of different meat-quality metrics between beef- or dairy-type cattle. In their analysis of the eating quality of beef from 6 different beef-breed progeny of dairy cows, Homer et al. (1997) detected a difference in tenderness for the topside primal cut but no difference in tenderness for the striploin. More recently, Muir et al. (2000) in their comparison of ribeye steaks from Hereford, Friesian, and Hereford \times Friesian steers in New Zealand harvested at the same weight or level of maturity failed to detect any breed difference in meat color, although the fat of the Friesian cattle was more yellow than that of the other 2 genotypes. Muir et al. (2000) also failed to detect any difference in meat shear force between genotypes when harvested at the same age, although the meat of the Friesians was less tender than the other 2 genotypes when all were processed at the same level of maturity; the Friesians were harvested 6 to 8 mo older than the other 2 genotypes. No difference in meat tenderness of the striploin was detected by Pfuhl et al. (2007) between purebred Charolais and Holstein bulls, all processed at 18 mo of age, based on samples taken either at 24 h or 14 d postmortem. However, the

extent of marbling and intramuscular fat content was greater in the Holsteins (Pfuhl et al., 2007). Schreurs et al. (2014) described the carcass and meat quality of 78 Hereford-sired steers from either pure Angus cows or Angus \times dairy-type animals, where dairy-type implied Friesian, Jersey, and Friesian–Jersey crosses; the authors concluded that the meat quality was no different [i.e., ultimate pH, shear force, meat and fat color, intramuscular fat and fatty acid concentration (except n-6 to n-3 ratio)] between genotypes. Bureš and Bartoň (2018) reported that meat from Angus animals was more tender, juicy, and flavorsome than that of Holsteins corroborating the breed effects reported by Judge et al. (2021) from 4,791 prime crossbred cattle. Regardless, advances in knowledge and perimortem protocols (such as animal handling, carcass stimulations, and carcass hanging methods) may mitigate breed differences in meat quality to a level that may not be recognizable by the average consumer, especially as processed meat.

Maternal Characteristics

Although the majority of beef-on-dairy animals are processed as prime beef, some of the females may graduate to become cows in a beef herd. This crossbred cow benefits not only from complementarity of breeds (i.e., the milk production of the dairy cow with the terminal characteristics of the beef bull) but also from both maternal and individual heterosis (even if the mated sire is of the same breed as the sire of the crossbred female). Heterosis for traits associated with viability tend to be greater than those associated with performance (Falconer and Mackay, 1996). Moreover, the benefit of heterosis can be cumulative; for example, the benefit of heterosis for more calves per cow mated, multiplied by the maternal plus individual heterosis benefit in growth rate, is multiplicative. Hence, the appropriate selection of beef bulls to correct the shortcomings of individual dairy females in the anticipation of selling the resulting crossbred females as beef dams could be a sensible option. This assortative mating strategy is aided by the high use of AI in dairy production systems, facilitating the use of a greater diversity of beef bulls; when coupled with X-sorted semen, the proposition becomes even more possible.

Based on a controlled experimental study comparing beef versus beef \times dairy cow genotypes in Ireland, McCabe et al. (2019) reported greater survival but poorer fertility in the beef cows. The progeny of beef \times dairy cows were weaned 18.5 kg heavier than their contemporaries from the beef cows, manifesting as a 7.99 kg heavier carcass (after adjusting to a common age at harvest) processed 12.8 d younger; still, the

progeny of the beef cows had more conformed carcasses and received a greater price per kilogram (McCabe et al., 2019). Corroborating the results of McCabe et al. (2019), Goonewardene et al. (2003) also documented heavier weanling progeny from a beef \times dairy synthetic dam line compared with progeny from 2 beef synthetic lines. The heavier weaning weight of progeny from dairy-cross dams is likely a function of the greater milk yield of these dams, owing to their dairy bloodline (McGee et al., 2005b). This conclusion was corroborated by Roca Fraga et al. (2018), who used a calf weigh-suckle-weigh system to evaluate the milk yield of different beef cow genotypes; the total energy intake from milk in that study was greater for steers raised by Angus \times Holstein-Friesian, Angus \times Jersey, and Angus \times Kiwicross dams than for those reared by Angus dams.

RELATIVE ECONOMIC AND ENVIRONMENTAL ASSESSMENT OF BEEF-ON-DAIRY PRODUCTION SYSTEMS

Using a bioeconomic model developed to represent Irish dairy calf-to-beef production systems, Ashfield et al. (2014) simulated the economic merit of male and female calves born to Holstein-Friesian dairy cows bred to either early-maturing beef bulls, late-maturing beef bulls, or Holstein-Friesian bulls (no heifers from Holstein-Friesian sires were modeled because these would almost all be retained in the dairy herd as replacements). The simulated age at harvest (and thus the underpinning production system) differed by sex and genotype, although a scenario of steers being processed at 28 mo of age was common to all 3 genotypes. Given these parameters, the most profitable production system for Ireland was deemed to be the 28-mo steer production system (irrespective of genotype), and the young bull production system was the least profitable (Ashfield et al., 2014). However, this conclusion was a function of ruminant production systems in Ireland, which can take advantage of the temperate climate in growing and using in situ grazed grass. In fact, Ashfield et al. (2014) noted that maximizing the proportion of grazed pasture in the diet and achieving high growth rate from grazed pasture was instrumental in generating more profit; in the 28 mo steer production system, 70% of the diet was from grazed pasture, and 81% of the live weight gain was from grazed grass, the latter taking advantage of compensatory growth. Moreover, the steer production system in the modeling exercise of Ashfield et al. (2014) was less sensitive to concentrate price than the bull production system, which relied more heavily on concentrates. Hence, the success of the steer production system was conditional on keeping the costs of production low and exploiting compensatory growth

following growth restriction when using expensive feed early in life. Karhula and Kassi (2010) reported that beef from dairy calves fattened in specialized units was generally more profitable than beef born in beef herds.

In a meta-analysis of 14 studies that undertook complete lifecycle analyses of beef production systems, de Vries et al. (2015) summarized the differences in environmental effect of beef production systems as a function of the provenance of the calves. de Vries et al. (2015) concluded that per unit of product produced, beef from dairy herds had 41% lower global warming potential relative to beef produced from calves born in beef herds, as well as 41% lower acidification potential, 49% lower eutrophication potential, and 23% lower energy usage. de Vries et al. (2015) reported that beef produced from dairy herds had a 49% lower land use per unit product on average than beef originating from beef herds, but Mogensen et al. (2015) reported the opposite, attributable to the use of semi-natural pastures for the production of the steers born in dairy herds. The lower environmental footprint of beef from the dairy herd is because 83 to 97% of the environmental effect of dairy herds is attributed to the milk produced rather than to beef output (de Vries et al., 2015). Gerber et al. (2015) stated that the difference in emissions for beef cattle born in dairy versus beef herds was due exclusively to the overhead associated with the mature herd and, in fact, when only growing animals were considered, those born in beef versus dairy herds had similar emission intensities per kilogram of carcass weight.

Economic and environmental modeling of different production systems or provenance of cattle is a function of not only the mechanistics and complexity of the model itself, but also of the values used to parameterize the model. Although broad general conclusions can be made, the true economic and environmental differences will be a function of the production systems of interest, so extrapolation of conclusions to all systems should be undertaken with caution.

GENETIC AND GENOMIC EVALUATIONS

In many populations, genetic and genomic evaluations are undertaken within breeds—both within individual dairy breeds (VanRaden, 2008) and within individual beef breeds (Saatchi et al., 2011). Some populations (e.g., the United Kingdom and the United States) undertake across-breed genetic evaluations but express each breed relative to its own breed-specific base. Other countries, mostly notably Ireland, undertake across-breed (i.e., all dairy and all beef breeds) genetic evaluations for several common traits (i.e., calving performance, carcass traits, health), and all

measures of genetic merit are expressed on the same scale relative to the same base; this is possible because of the large transfer of germplasm between Irish dairy and beef herds (Berry et al., 2006). International Genetics Solutions Inc. in the United States also undertakes across-breed evaluations for several beef breeds, expressing the generated estimates of genetic merit on the same scale relative to the same base.

Without comparable genetic evaluations across breeds, is it difficult to evaluate the merits and demerits of individual bulls from different beef breeds, despite the known inter- and intra-breed genetic variability for a range of animal characteristics relevant to dairy-beef production (Davis et al., 2019; Berry and Ring, 2020a). Many dairy producers are well aware of the expected phenotypic expression of individual PTA traits such as calving difficulty for their herd, and based on experience, have an acceptable PTA level for calving difficulty that is known to vary by cow parity (Berry et al., 2020). Therefore, being able to directly and easily compare the genetic merit estimates of candidate bulls from all breeds for traits such as calving difficulty and carcass merit (e.g., weight, conformation, and ribeye area) can make the selection of beef sires easier and less risky. Although ready-reckoners for converting genetic evaluations of 2 breeds to the same scale and base are useful (Van Vleck and Cundiff, 2006), they add more complication, which is arguably unnecessary.

However, being able to generate accurate across-breed genetic evaluations on the same base relevant to dairy producers is conditional on highly connected data across contemporary groups where beef bulls are mated to dairy females; the sire (and dam) of the resulting calf must also be known, either by recording this information, by deducing it from recorded insemination data, or through parentage discovery via the genotype of the calf and its candidate parents (Moore et al., 2019). The level of sire recording of beef \times dairy calves is often inferior to those sired by dairy bulls for 2 reasons: first, dairy producers deem it to be of lower importance because they will generally sell the animal, which will be harvested and not used for breeding, so inbreeding in future generations will not be an issue; and second, although AI is often used in dairy-on-dairy matings, natural mating, often with a mob of bulls, tends to be more the norm for beef-on-dairy mating, implying that even if a dairy producer wanted to record the sire, it could prove difficult unless the bulls were from different breeds with distinctly different characteristics (e.g., a white head for a Hereford or well-developed hindquarters in double-muscled breeds). What remains therefore is a poor level of recording of beef sires from dairy herds, rendering any performance data null and void for use in genetic evaluations. From an analysis of

7,866,410 calving events in Irish dairy herds from the years 2015 to 2020 (data from the Irish Cattle Breeding Federation database), 75% of the calves (80% of the females) with a dairy-breed sire had their sire recorded, but only 52% of calves with a beef-breed sire had their sire recorded; it is a legal requirement to record the sire breed of the calf in Ireland. Although these findings are based on Irish data, similar situations are likely to persist elsewhere. Dairy herds (especially large herds) in countries such as New Zealand do not even attempt to record the sire of the calf at birth but instead resolve it through DNA testing. However, this is almost exclusively reserved for dairy-bred heifers. Improved parentage recording and ideally verification of beef \times dairy animals will be crucial for enabling the development of across-breed genetic/genomic evaluations.

Most traits of relevance for beef \times dairy production are highly heritable, so unlike low-heritability traits, which predominate in dairy cow breeding goals (Berry et al., 2014a; Cole and VanRaden, 2018), a large quantity of progeny information per sire, or a large reference population size for genomic evaluations, is not required to achieve accurate genetic evaluations for most traits of importance. As well as pedigree information, a record is also required for the phenotype itself alongside information on any nuisance variables that contribute to variability in the performance traits; one of the largest contributing factors would be contemporary group(s), as well as age in relation to weight and progeny traits. Therefore, details on the herd(s) the animal resided in, along with information about contemporaries, is a requirement. Such information is not always available, but it is legally required in some countries (e.g., EU countries) to record all inter-location movements of animals, including date of birth, date of harvest, and animal sex. Therefore, sufficient data should be available to generate the contemporary group(s) and age of the animal at each event. However, the performance of individuals once they enter another jurisdiction (i.e., live exports) is not always available in some countries. In many cases, these cattle are specifically chosen for a purpose and may be deemed a selected population which, if not properly considered, could introduce some bias in genetic evaluations. In 2019, for example, Ireland exported 173,682 calves, which were predominantly dairy male calves. The number of dairy-herd calvings in Ireland in 2019 was 1,448,929, of which 402,892 males were recorded to have been sired by a dairy bull. Therefore, performance data on a considerable proportion of the live calves born in dairy herds are not available, although information on calving dystocia, gestation length, and perinatal mortality is available, where recorded. Although no carcass data are available on these animals (and potentially other animals), it

could be possible to use producer-scored data to predict eventual performance. Pabiou et al. (2012) reported a heritability of 0.32 for cattle weanling quality score as subjectively assessed by producers on a scale of 1 to 5, with a genetic correlation of 0.39 with eventual total meat yield and 0.49 with the proportion of the carcass that was of very-high-value primal cuts. Therefore, producer-scored information could have uses in genetic evaluations as a predictor of eventual outcome traits, increasing the accuracy of the genetic evaluations but also correcting for bias. Moreover, given the relatively high heritability of most of the output traits, it may be sensible to consider specific performance test herds with good connectedness and genetic diversity as a means of collecting data, similar to the central performance test operated in some sheep populations.

Many questions still exist about the most appropriate methodology for genetic evaluations of beef bulls for use in dairy herds. Large differences in early-life production systems exist between dairy and beef herds. Moreover, all beef \times dairy animals are crossbreeds, as opposed to the (almost) purebred animals that may exist in beef herds. Furthermore, in multi-trait, multi-breed genetic evaluations, the genetic covariances among the same traits would be assumed to be the same for all breeds, which may not necessarily be true (Doyle et al., 2018). Marketing beef bulls for use in dairy herds based on estimates of genetic merit derived from purebred data from beef herds may not be optimal, but no such test of this hypothesis in cattle has been undertaken to date. Eriksson et al. (2004) stated that because the ratio of calf to dam size affects calving difficulty, purebred evaluations of beef animals should not be used to infer predisposition levels to calving difficulty when mating to dairy cows.

Being able to predict the performance of beef \times dairy animals from genomic information is also likely to be difficult given the lack of identified quantitative trait loci that are common across breeds, even among beef breeds, let alone between dairy and beef breeds. Using imputed whole genome sequence data, Purfield et al. (2019a) identified 57 genomic windows (10 kb in length) associated with carcass weight that were common to the Holstein-Friesian breed and at least 1 of the 5 beef breeds they investigated (Angus, Charolais, Hereford, Limousin, and Simmental); this was out of a total of 1,490 windows detected to be associated with carcass weight in Holstein-Friesians. The corresponding values for carcass fat were 11 regions in common with 1 of the other 5 beef breeds from a total of 760 regions within the Holstein-Friesian breed, and 8 regions in common from a total of 1,247 regions for carcass conformation (Purfield et al., 2019a). A similar conclusion was evident for genomic regions common between

Holstein-Friesian and beef breeds for other traits such as dystocia (Purfield et al., 2020) and gestation length (Purfield et al., 2019b). Zhao et al. (2015) detected only a few common genomic regions displaying selection signatures between 6 beef breeds and the Holstein-Friesian dairy breed.

In the pursuit of multi-breed genomic predictions, Raymond et al. (2018) proposed the use of a multi-trait model (1 “trait” per breed) exploiting an underlying genetic covariance structure and 2 genomic relationship matrices, with one matrix including genotype data from preselected markers informative for the trait in question, and the other containing the remaining markers to capture the polygenic effect. If the informative SNP differ by breed, then the subset of informative SNP may become large when combined across breeds, making it potentially counterproductive, especially if the informative SNP from one breed are not informative for the others, thus capturing (some of) the polygenic effect of those breeds. In summary, while across-breed genetic evaluations with the animals of different (cross) breeds being comparable (also against dairy) is important for better-informed mating decisions, achieving this goal at a technical level is not trivial; given the growing demand for beef-on-dairy, however, the impact of success is large.

BREEDING GOALS

In animal breeding, a breeding goal (also referred to as a breeding objective) consists of a list of traits, each weighted by their perceived relative importance and summed to form a single figure per animal. This figure can then be used by producers and breeders to identify candidate parents of the next generation or generate progeny for harvesting who are expected to excel genetically for the breeding goal.

The relative weights for traits in many breeding goals are often derived using bioeconomic models or profit functions (Veerkamp et al., 2002; Wolfavá et al., 2007; Berry et al., 2019a) and reflect the expected change in profit per incremental change in a given trait. The construction of breeding goals, and a summary of the constituent traits in different dairy cow breeding goals worldwide, was presented by Cole and VanRaden (2018). Of the 21 dairy cow breeding objectives they reviewed, 13 included some emphasis on body size or weight, although this emphasis could be negative; few (e.g., Denmark, Sweden, Finland, Ireland; Berry et al., 2007b; Kargo et al., 2014) included a direct emphasis on progeny beef (or veal) merit. Given the contribution of beef output (i.e., surplus calves and cull cows) to dairy-herd profitability, consideration should be given to overall beef merit in dairy cow breeding goals. An

alternative approach traditionally used in some populations is to have candidate AI dairy bulls also undergo a performance test for growth and efficiency. Given the moderate heritability for growth and efficiency traits (Berry and Crowley, 2013), mass selection can be an effective component of a 2-stage process of selection; the estimated breeding value of an animal based on its own data is simply the heritability of the trait times the phenotypic performance of the animal as a deviation from its contemporaries. Genomic evaluations can also contribute to decisions about which bulls should graduate to become AI bulls, although accurate genomic evaluations are predicated on a large reference population of genotyped and phenotyped animals for the traits of interest (Daetwyler et al., 2008).

Although dual-purpose dairy cows in temperate regions were relatively common in the past, especially in scenarios where a milk quota was imposed, they have since been largely replaced by specialist dairy breeds. Evans et al. (2004) undertook an economic appraisal of 5 years of experimental data comparing dual-purpose Montbéliarde and Normande cows with Dutch Holstein-Friesian cows; they investigated scenarios with or without milk quotas, as well as some sensitivity of beef pricing. The scenarios they investigated affected the ranking of breeds, but risk analysis revealed that the Montbéliarde was stochastically most dominant in all scenarios (Evans et al., 2004). Nonetheless, the poorer economic performance of the Dutch Holstein-Friesian in that study was largely attributable to its poor reproductive performance (Evans et al., 2004); the overall pregnancy rate for the Dutch Holstein-Friesians was 73.7%, while overall pregnancy rates of 92.7% are now being reported for elite Holstein-Friesian cows in Ireland (O'Sullivan et al., 2020). Therefore, it is unclear whether the conclusions would hold given the improved reproductive performance of Holstein-Friesians in the period since the study. It also makes relevant comparison of specialist versus dual-purpose breeds difficult, given the relative lack of recent comparison studies and the documented genetic gain, especially in recent years. There is therefore a gap in knowledge of the benefit of modern dual-purpose dairy cows.

Beef Merit in Dairy Breeding Goals

Although most countries have a single dairy cow breeding goal per breed, multiple breeding goals are published in some countries, depending on the end use (Cole and VanRaden, 2018). Customized selection indexes are also possible, in which the weighting factors for the component traits of a breeding objective can be altered for an individual farm (Barwick and Henzell, 2005). To aid in such tailoring, some breed-

ing objectives are decomposed into a set of subindexes which, when summed together, reconstitute the overall breeding objective value of an animal (Berry et al., 2007b). This approach enables producers and breeders to easily alter the weights for groups of similar traits rather than a larger number of individual traits. One of the subindexes of the Irish national dairy cow breeding index—the economic breeding index (**EBI**; Berry et al., 2007b)—relates to beef performance. Such a strategy enables producers who are not interested in beef merit (e.g., may harvest calves at birth) to remove the subindex from the overall EBI and re-rank the animals; still, it should be noted that this strategy is suboptimal. Four traits make up the beef subindex of the Irish EBI: the carcass weight of the cull cows, and the carcass weight, conformation, and fat cover of the progeny. No consideration of veal is included in the Irish dairy breeding goal, because veal is not a large industry in Ireland, but its consideration is certainly not precluded in other populations where veal production may be more popular. The calculation of economic values of the progeny traits are described in detail by Berry et al. (2019a). Kargo et al. (2014) described in detail the calculation of the economic values for beef traits in the Danish, Sweden and Finnish dairy cow breeding goals, all of which include only growth rate and EUROP conformation score.

Using selection index theory based on the current composition of the Irish dairy cow total merit index (the EBI) the expected rate of genetic gain in carcass weight, conformation, and fat score would be -0.26 , 0.02 , and -0.08 standard deviation units per generation, and for cull cow carcass weight would be -0.09 standard deviation units, equating to an expected decrease of 1.64 kg in carcass weight per generation. Removing all elements of animal size or beef merit from the EBI would result in 2 and 4% faster genetic gain in fat and protein yield, respectively. Removing just the beef subindex from the EBI (i.e., retaining a negative emphasis on cow size) would result in 1 to 2% slower genetic gains for fat and protein yield, the latter attributable to an accelerated reduction in cow size (and its effect on milk production) without any emphasis on carcass value (which includes carcass weight or size). Still, not including the beef subindex in the EBI resulted in only a marginal reduction in profit based on the economic values currently used.

Based on a simulation study of a dairy cow breeding scheme in Finland, Hietala and Juga (2017) evaluated the effect on profit of including efficiency (cow, heifer, and growing animal), growth, and carcass-related traits in their dairy cow breeding objective. Hietala and Juga (2017) documented an improvement in gain in profit when considering the growth of the progeny as well as

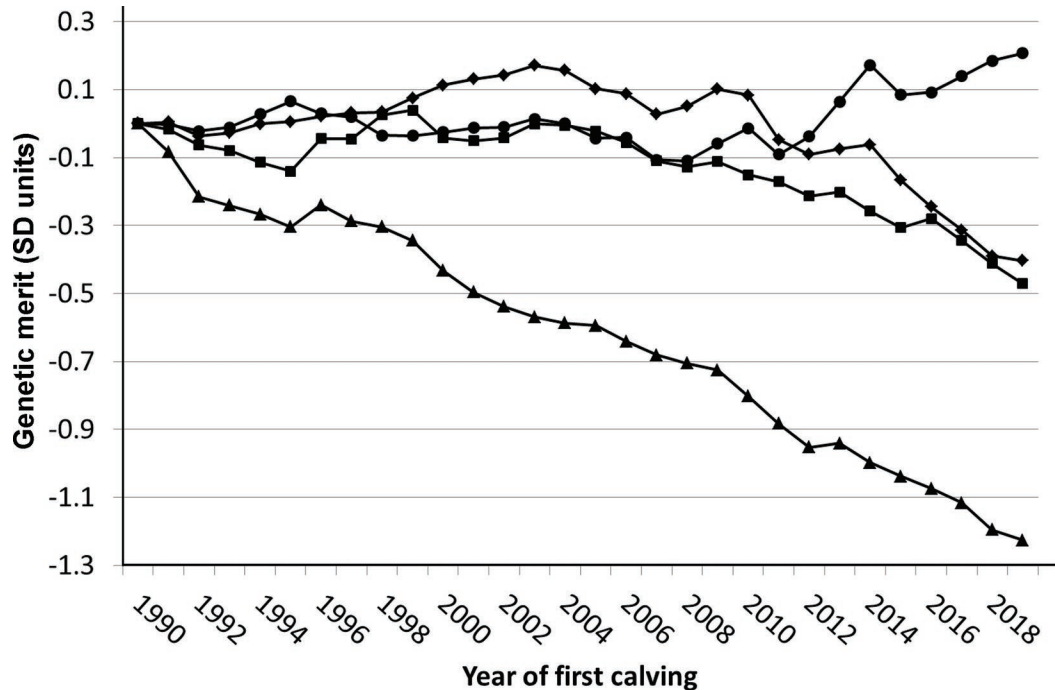


Figure 5. Mean genetic merit in genetic SD units by year of first calving of Irish dairy cows for cull cow carcass weight (●) and progeny carcass weight (◆), conformation (▲), and fat (■).

the live weight of the cow simultaneously in the breeding objective; they noted that this benefit was a function of the relatively high economic value of both factors. As is the case in Ireland, including carcass traits (i.e., fleshiness and fat cover) had minimal effect on genetic gain for profit, given their relatively low economic value in the bioeconomic model (Hietala and Juga, 2017).

The genetic trend in Irish Holstein-Friesian females by year of first calving is shown in Figure 5 for carcass weight, conformation, and fat score. Genetic merit for carcass EUROP conformation has eroded steadily by a total of 1.2 standard deviation units in the 30 years from 1990 to 2019, consistent with expectations based on selection index theory (although more rapid). That said, the economic values used in the selection theory exercise were those used currently, and beef has been included in the EBI only since 2005; in fact, based on fitting a simple linear regression through the mean EBV, the rate of decline in genetic merit for carcass conformation was faster after 2005 than before 2005. Although the genetic trends for carcass weight and carcass fat are not as dramatic, carcass weight was increasing before 2005 (coinciding with holsteinization) but is now decreasing; a similar trend has been observed for carcass fat. Phenotypic and genetic correlations between the EUROP carcass conformation scores in Ireland and primal cut yields have been documented (Judge et al., 2019a,b), suggesting that current genetic

trends for carcass conformation will manifest as less saleable meat yield; the correlations tend to be stronger with the higher-value primal cuts in the hindquarter. Although genetic merit for cull cow carcass weight is increasing slightly over time, the phenotypic effect of breeding is expected to be greater because cow longevity is also improving (Figure 2); cow weight increases with age up to a point (Berry et al., 2005). Information on the change in genetic merit of beef characteristics is not publicly available in other populations, but it should be examined; several years of a cumulative slow erosion in reproductive performance went unnoticed in Holstein(-Friesian) dairy cows globally until it was eventually detected and reversed (Berry et al., 2014a). Although one could argue whether or not an observed genetic change in beef merit is favorable, at the very least, the rate of genetic change should be quantified, projected to a long time horizon, and then debated.

Beef-on-Dairy Breeding Goals

Beef-on-dairy breeding goals can be useful for ranking beef bulls for their suitability of use on dairy females, or similarly to rank seek-stock beef cows as suitable candidate dams of beef bulls for use in dairy herds. The dual objective of dairy-beef breeding goals is to marry the desires of the dairy producer to maximize subsequent profit from the lactating female with the

requirements of the beef sector for high-quality, efficient, and profitable cattle. Although terminal indexes for the selection of beef bulls for use on beef cows do exist (e.g., Connolly et al., 2016) these indexes would not be appropriate for use in dairy cows, because the genetic parameters are likely to differ by breed (Doyle et al., 2018), and more importantly because the relative economic values of the component traits (e.g., calving difficulty, ribeye area) are likely to differ depending on whether they are used in dairy or beef herds, owing to nonlinearity in profit functions (Amer et al., 2001; Wolfová et al., 2007).

Berry et al. (2019a) described a dairy-beef breeding goal populated with costs and prices representative of Irish production systems, as well as the traits with estimates of breeding values available. This proposed dairy-beef index consisted of 11 traits, with calving difficulty separated into heifer and cow traits. Indexes to rank beef bulls for use on dairy females for the generation of terminal animals have also been developed using BreedPlan BreedObject software (Ponzoni et al., 1998) for several individual breeds (e.g., https://herefords.co.nz/cms_files/breedplan/Interpreting%20New%20Zealand%20Hereford%20Selection%20Indexes.pdf). The dairy-beef breeding objective developed for New Zealand Herefords includes animal live weight, dressing percentage, saleable meat yield, fat depth, marbling score, and calving ease. Fogh (2016) also described the construction of a dairy-beef index for Denmark, which they termed the “X-index.” The X-index consists of 4 subcomponents: calving ease, calf vitality score, ADG, and carcass conformation score. Although dairy producers use all 4 components in the X-index, beef producers use only the latter 2. In fact, the approach taken is similar to that used in Ireland, where dairy producers use the dairy-beef index (Berry et al., 2019a) to select beef bulls for use on their dairy females, but beef producers who purchase the resulting calves for processing use the transaction index (Dunne et al., 2020a), which does not include calving-related traits and incorporates non-additive genetic effects and non-genetic effects associated with carcass performance and other performance traits.

Although the objective of the aforementioned indexes is to produce superior and more profitable prime beef, it is also possible to have a selection index for veal calves. For example, van der Werf et al. (1998) described the construction of a relatively simple set of breeding indexes for veal calf production, beef production, and cull cow production. All indexes included fleshiness, fat cover, and carcass weight, with the veal index also including a breeding value for meat color. Although no standard errors were provided, of particular note were the moderate genetic correlations between the same

trait expressed in dairy veal calves (i.e., male calves harvested at less than 250 d of age) and dairy animals used for beef production (i.e., bulls from a dairy sire harvested between 350 and 850 d of age). Genetic correlations for fleshiness, fat, and carcass weight in veal calves with the corresponding trait in beef animals varied from 0.41 to 0.51 (van der Werf et al., 1998). This finding suggests that one set of traits can be used as predictors of the other. Santos et al. (2015) proposed that the genetic correlation between 2 breeding indexes, x (e.g., veal index) and y (e.g., beef index), could be calculated as follows:

$$r_{x,y} = \frac{\mathbf{a}'_x \mathbf{G}_{xy} \mathbf{a}_y}{\sqrt{\mathbf{a}'_x \mathbf{G}_x \mathbf{a}_x \times \mathbf{a}'_y \mathbf{G}_y \mathbf{a}_y}},$$

where $r_{x,y}$ is the genetic correlation between the 2 indexes; \mathbf{G}_{xy} is the genetic variance–covariance matrix between breeding objective traits in indexes x and y ; \mathbf{G}_x and \mathbf{G}_y are the genetic variance–covariance matrices within indexes x and y , respectively; and \mathbf{a}_x and \mathbf{a}_y are vectors of economic weights used in the indexes x and y , respectively. When this equation was populated with the (co)variance components and economic values for the veal and beef indexes proposed by van der Werf et al. (1998), the genetic correlation between the veal and beef indexes was only 0.32, implying a potential benefit from 2 separate breeding programs (pending a thorough analysis of the associated costs). Interestingly, neither of the indexes proposed by van der Werf et al. (1998) included any trait reflecting calving performance; the inclusion of such traits would likely strengthen the correlation between both indexes, because the genetic correlation between traits would be 1, and the respective economic value for both systems would be expected to be the same.

However, not included in any dairy-beef index so far is the effect of the sire of the calf on the subsequent performance of the cow, independent of the effect of calving difficulty. Using a data set of 346,765 calving events from 230,255 Irish Holstein-Friesian cows that had not recorded any assistance during their more recent calving, Berry and Ring (2020c) reported a reduction of 36.7 to 101.1 kg in 305-d milk yield in cows that had just given birth to a calf sired by a beef bull relative to a calf sired by a dairy bull. Although Berry and Ring (2020c) reported a statistically significant effect of the calf breed on the subsequent reproductive performance of the dam, they concluded that the effect was biologically small. Therefore, even independent of the performance cost of greater expected calving difficulty from using beef bulls relative to dairy bulls (Eriksson

et al., 2004; Fouz et al., 2013), an effect on subsequent cow milk performance still exists from using beef bulls; Berry and Ring (2020c) warned that although the mean 305-d milk yield of the cows in their study was 6,691 kg, the effect of a beef mating could be greater in higher-yielding cows if it was proportional to yield. Research is lacking on this potential effect.

Proper and transparent validation of any new tool is crucial to its acceptance by industry. Breeding goals can be validated using a controlled experimental study (Clarke et al., 2009a; Coleman et al., 2009) or a cross-sectional analysis of a large data set; the latter can be undertaken at the level of the animal (Connolly et al., 2016; Berry et al., 2019c; Twomey et al., 2020) or the herd (Ramsbottom et al., 2012). Berry and Ring (2020a) used a data set of 123,785 calving records and carcass information from 48,875 animals to validate the dairy-beef index proposed by Berry et al. (2019a); of particular interest in their validation study was a comparison with the status quo of selecting beef bulls for use on Irish dairy females based on a combination of genetic merit for easy calving and short gestation. The percentage of primiparous dairy cows that required assistance at calving was 2 to 3 percentage units greater when the sire excelled on the dairy-beef index relative to both dairy sires or beef sires that ranked highly on a combination of genetic merit for easy calving and short gestation length; no difference existed in multiparae. Furthermore, no difference in progeny gestation length was evident between beef sires that ranked highly on the dairy-beef index or those that ranked highly on a combination of genetic merit for calving difficulty plus gestation length; however, both groups of beef sires had a gestation more than 2 d longer than the dairy sires used (Berry and Ring, 2020a). Beef sires that excelled on the dairy-beef index produced progeny with heavier, more conformed carcasses relative to the progeny from dairy sires or beef sires that were ranked highly for a combination of calving difficulty and gestation length (Berry and Ring, 2020a). Berry and Ring (2020a) concluded that (assuming no market failure) using beef bulls that were genetically elite for the dairy-beef index could increase dairy-herd profit by 3 to 5% above the status quo approach based on the selection of beef bulls for a combination of genetic merit for calving difficulty and gestation length. However, further monetary evidence substantiating or refuting such strategies of bull selection (i.e., beef versus dairy or within beef-breed selection) are necessary from other populations. Moreover, these results are from a single point in time when an optimized breeding scheme for beef-on-dairy was not in place; an optimized breeding scheme could achieve genetic gain in both suites of traits, even where antagonistic genetic relationships exist among the traits.

BREEDING SCHEMES

Most breeding schemes in dairy cattle can be considered one stage in that candidate sires of the next-generation progeny are selected, usually from a combination of parental average breeding values and expected coancestry with the future population of breeding females; consideration is also given to other characteristics, such as the health status of the herd of origin, as well as the phenotypic performance (including conformation score) of the dam. More recently, selection of sires of the next generation has been based on a genomic evaluation; bull calves chosen for genotyping are initially screened using parental average estimates of genetic merit and coancestry with the future population of breeding females. Several populations (e.g., Norway, France) historically subjected candidate AI dairy bulls to a performance test, but that practice has largely been abolished. The practice made sense because most of the traits of interest, such as ADG and feed intake, were heritable (Crowley et al., 2010) and not all traits of interest required the animal to be slaughtered, or if they did (e.g., carcass credentials), genetic merit could be predicted from heritable predictor traits (Berry et al., 2019b). Moreover, all candidate bulls were co-located in several locations, usually of sufficient numbers to form a contemporary group. One of the downsides of such an approach was the capital cost of measuring traits such as feed intake, the associated biosecurity risks, and any potential effect on genetic gain (via selection intensity) for dairy traits in the breeding goal.

If feed intake in growing bulls correlates genetically with feed intake in dairy cows, then such a performance test strategy may again gain favor. Very few studies have estimated the genetic correlation between feed intake in growing dairy animals (i.e., bulls or heifers) and feed intake in cows, and those that have (Nieuwhof et al., 1992; Berry et al., 2014b) reported positive genetic correlations (0.67 and 0.80), although standard errors were not presented or were large. Assuming a heritability and genetic standard deviation of feed intake in growing bulls of 0.49 and 0.79 kg/d, respectively (Crowley et al., 2010), and in lactating cows of 0.34 and 1.13 kg of DM/d, respectively (Berry et al., 2014b), as well as a conservative genetic correlation estimate between the 2 traits of 0.70 (Nieuwhof et al., 1992; Berry et al., 2014b), the response to selection in dairy cows (based on single trait selection, which would not be advised) per generation based on the feed intake phenotype of the bull himself would be -0.55 kg of DM/d; the accuracy of selection would be 0.49. Of more potential interest in recent times is whether methane emissions in growing bulls (on the diet they are fed) are genetically correlated with methane emissions in

lactating cows (on the diet they are fed). Given the relatively high heritability of both feed intake (Crowley et al., 2010) and daily predicted methane emissions in cattle (Donoghue et al., 2016; Lassen and Løvendahl, 2016), using just traditional genetic evaluations and ignoring the contribution of parental information to the genetic evaluation of an animal, the reliability of a genetic evaluation for a bull with its own phenotype estimated in a univariate analysis is equal to the heritability. The relatively high heritability for both traits also implies that a large reference population for generating genomic evaluations would not be required as it would for a lower-heritability trait (Daetwyler et al., 2008). Still, irrespective of the genetic correlation between growing bulls and dairy cows, the direct male progeny themselves or grand-progeny (even if from a beef sire) will express the inherited genetic merit of that dairy sire for beef characteristics relevant to a growing animal. Therefore, given the growing contribution of beef from the dairy herd to the total beef output in most countries, as well as the growing number of traits of interest that can be measured in growing animals (e.g., methane emissions and nitrogen use efficiency), performance-testing bulls during their rearing phase may warrant reconsideration. At the very least, genetic evaluations based on these data should reflect some measures in the growth of the (male)(grand)progeny of dairy sires. However, attention needs to be paid to the potential genotype \times environment interaction between the diet and environment of the performance test station (and sex) compared to that experienced by commercial beef \times dairy cattle.

Even in the absence of a breeding program that includes a performance test on the candidate bull himself, achieving high accuracy of selection (and by extension rapid genetic gain) should be possible for dairy-beef breeding goals. This is because, unlike dairy cow breeding goals, many of the traits that contribute to the dairy-beef indexes are measured very early (e.g., calving performance) or early (growth rate) in life, many before sexual maturity; furthermore, they are not sex-linked and are highly heritable. Therefore, measurement of such performance traits on siblings of the candidate bulls is informative. It is well accepted that the relationship between the reference and validation populations in genomic evaluations affects the accuracy of the evaluation of the test population. Although Mendelian sampling during gametogenesis imposes an upper threshold on the accuracy of selection for a candidate bull based on traditional genetic evaluations that exploit sibling information, genomic evaluations based on genotype information from phenotyped siblings can be very informative. The upper limit on the accuracy of selection using traditional pedigree-based approaches

is 0.50 based on half-sib information only, and 0.707 based on full-sib information only. In theory, it should be relatively easy to introduce favorable characteristics into a family line (e.g., introducing improved carcass merit in easy-calving Angus lines).

The breeding of beef bulls destined for use on dairy females could benefit from a 2-stage selection process, but its financial feasibility would need to be assessed on a case-by-case basis, especially in light of advancements in the past decade in both genomic evaluations and agritech. A separate regimen for beef bulls destined for dairy or beef females may not be needed, because the animal characteristics of interest are largely the same; only the relative importance of each is likely to differ. Of utmost importance in identifying beef bulls for suitability on dairy females is confidence in the genetic evaluation, especially for ease of calving. Fortunately, this trait is one of the first to be assessed in cattle and has moderate heritability (Crowley et al., 2011); therefore, information on the candidate itself can be a useful addition to achieving decent accuracy of selection, but also data on a large number of progeny are not required to achieve the desired high accuracy. For example, assuming a heritability of 0.24 (Crowley et al., 2011), an accuracy of selection from traditional evaluations of 0.70 can be achieved with only 15 progeny, or even 10 progeny if information on the candidate animal itself is available. Heritable correlated traits such as birth weight can further augment this accuracy. Assuming a heritability of birth weight of 0.46 and a genetic correlation with calving difficulty of -0.93 (Mujibi and Crews, 2009), the accuracy of selection for calving difficulty based on phenotypic data for calving difficulty and birth weight of the 10 progeny plus the animal itself increases from 0.70 to 0.89.

Although beef breeding in many populations has traditionally relied on purebred seedstock populations, the role of crossbred or composite breeds that exploit complementarity should not be discounted. In their presentation of an index framework to select (and breed) beef bulls for suitability to dairy females, Berry et al. (2019a) proposed exploring the use of crossbred bulls. The proposed dairy-beef indexes (Fogh, 2016; Berry et al., 2019a) attempt to marry the bull features of interest to the dairy producer (e.g., easy calving and short gestation) with those being sought by the beef producer (e.g., growth and carcass value). Although within-breed variability exists, some breeds such as the Angus excel in easy calving and short gestation but struggle with carcass value; other breeds such as the Limousin are not the easiest for calving (but also not the worst), but they boast decent carcass value. Such a cross (breeds chosen purely for illustrative purposes) could benefit greatly from complementarity. The notion of cross-

bred parents is not novel to dairy producers, many of whom actively use crossbred parents (Winkelman et al., 2015), so acceptance of crossbred or composite beef bulls should not be a massive leap of faith.

The main objective of optimized breeding schemes is to achieve long-term genetic gain, which is predicated on maintaining genetic diversity, and inbreeding can erode this genetic diversity. Although coancestry, and by extension, inbreeding, is certainly important in the beef seedstock sector for producing candidate beef bulls, beef-on-dairy breeding programs do not necessarily have to pay the same attention to this factor; this is because coancestry between the beef and dairy population will be low to nonexistent. Therefore, once the rate of accumulation of inbreeding is managed in the seedstock industry, inbreeding should not be a concern for beef-on-dairy matings.

Although AI is the predominant mating type for dairy bulls with dairy females, natural mating of beef bulls with dairy females is common. Although the genetic merit of natural mating bulls should be lower than the top AI bulls on average (because of selection intensity), one of the main reasons producers were dissuaded from using natural mating bulls (other than health and safety and potential temporal subfertility or infertility) was the low reliability of genetic evaluations. Although the disadvantages of subfertility and the health and safety of intact bulls still persist, the availability of genomic evaluations for natural mating bulls contributes to a higher accuracy of selection. Natural mating bulls can be particularly useful toward the end of breeding seasons, when the number of females in estrus is lower and therefore more difficult to detect. Regardless, consideration should be given to some element of male fertility, including libido, in beef breeding programs.

DECISION SUPPORT

Decision-making is a routine part of day-to-day herd management. Breeding decisions and the assessment of what to do with the resulting progeny is just one module of a complex decision-making process (Figure 6). Before breeding, a dairy producer must decide which females to cull and which to retain (i.e., to mate). Kelleher et al. (2015) described a relatively simple framework for deducing the expected profit potential remaining for a given dairy female; they suggested that the cows with the lowest expected profit potential would be candidates for culling. Of the females to be bred, a further decision must be made about which to breed with a dairy bull (in the hope of producing a heifer that will eventually graduate into the mature herd) and which to breed with a beef bull (Figure 6); Berry and Ring (2020b) outlined some of the animal-level criteria that affect such deci-

sions in dairy herds. Choices can then be made about whether to use sexed or conventional semen, depending on the likely pregnancy success based on the particular features of the cow herself, such as parity, days since calving, and history of calving difficulty. Hempstalk et al. (2015) used a series of machine-learning approaches in an attempt to estimate the likelihood of conception in 1,789 dairy cows. Although the average prediction of conception was relatively poor, this approach achieved a reasonable accuracy of predicting conception when limited to model solutions that suggested a high predicted likelihood of conception. Once the calf is born, a decision needs to be made about its fate: retain as a replacement or sell and, if selling, its expected value. Dunne et al. (2020a) and Fogh (2016) described indexes to aid in this decision process. Genotyping all animals at this stage can provide useful information such as parentage (particularly for dairy females, but also beef \times dairy females destined to become replacements in beef herds), breed prediction, and a more accurate estimate of genetic merit.

Given the often-cited cumulative and permanent benefit (or demise) of breeding to performance, decision-support mechanisms related to dairy cow breeding are an integral component of successful dairy operations. Although the use of breeding indexes to identify dairy-breed parents for the next generation of the milking herd is ubiquitous (Cole and VanRaden, 2018), less common are indexes for the identification of beef bulls to mate with dairy females. Similarly, although algorithms exist to support decisions about which bull to mate to a given female for dairy-breed parents (Carthy et al., 2019), no scientific publication exists outlining a strategy for appropriately selecting beef bulls for mating to dairy females. Such a tool should consider the size of the female, as well as her history of calving difficulty (after accounting for the genetic merit for calving difficulty of the historical bulls used) when selecting a bull based on genetic merit for calving difficulty, as well as the associated reliability of that genetic evaluation. Large within- and across-breed genetic variation exists in direct calving difficulty among beef bulls, many of which have less of a genetic predisposition to a difficult calving than Holsteins (Berry and Ring, 2020a). In seasonal breeding herds, if the end of the breeding season is near, then consideration should also be given to genetic merit for direct gestation length, as well as the male fertilization capacity of the bull. Identifying easy-calving bulls (Martin-Collado et al., 2017) and ensuring that the cow establishes pregnancy and re-calves within the calving season the following year are of utmost importance for dairy producers; the beef merit of the resulting calf is generally of secondary concern. Matching the genetic merit of the sire for beef creden-

tials (e.g., carcass weight, ribeye area, or conformation) to complement that of the dairy female and maximize the chances of achieving the minimum specification for given carcass grades (Prime versus Choice versus Select in the United States or suitable EUROP conformation and fat score in the EU) with minimal compromise in other traits is then key. Consideration of the reliability of the parents will also affect the likelihood of achieving certain specifications (Berry et al., 2019a).

Although it is impossible to know a priori which allele at a given heterozygous locus will be transmitted from parent to offspring, the allele transmitted from a homozygous locus is known. Hence, the likely genotype of the resulting progeny can be predicted at some loci (Carthy et al., 2019). This can be useful not only for estimating the expected additive genetic merit (simply the mean of the 2 parents) but also the expected non-additive genetic merit if intra- and inter-locus interactions are known. Moreover, such an approach of simulating the possible genotypes of phantom progeny (Santos et al., 2019) can be used to identify matings across the entire herd that are likely to result in more homogeneous progeny that might be more acceptable to the purchaser. In such situations, producers may opt for bulls that are slightly poorer genetically for calving difficulty but that are likely to produce more homoge-

neous birth weights (i.e., no extremely large calves with associated calving difficulty) instead of bulls that are likely to produce more heterogeneous progeny. Therefore, decision-making may shift from mean risk to the likely variability in risk. Once the calf is born, it should be possible to estimate the non-additive genetic effects for the different traits, and these can then be used for precision genomic management. For example, animals can be penned based on total merit (i.e., additive genetic, non-additive genetic, and other non-genetic effects).

Once the calf is born, decisions about its potential market (i.e., replacement female within the beef herd or finishing for harvest) and value have to be made. Dunne et al. (2020a,b) developed 2 separate tools, which combined can help in making decisions about the value of the calf for each market. These tools (Dunne et al., 2020a,b) have been built using a selection index framework populated with “production values” of each animal for a whole series of traits affecting its eventual profit; production values include additive genetic effects, nonadditive genetic effects, and nongenetic effects. Although the indexes proposed by Dunne et al. (2020a,b) consist of a list of traits with data available, each weighted based on the expected profit derived from a bioeconomic model, the index can be tailored

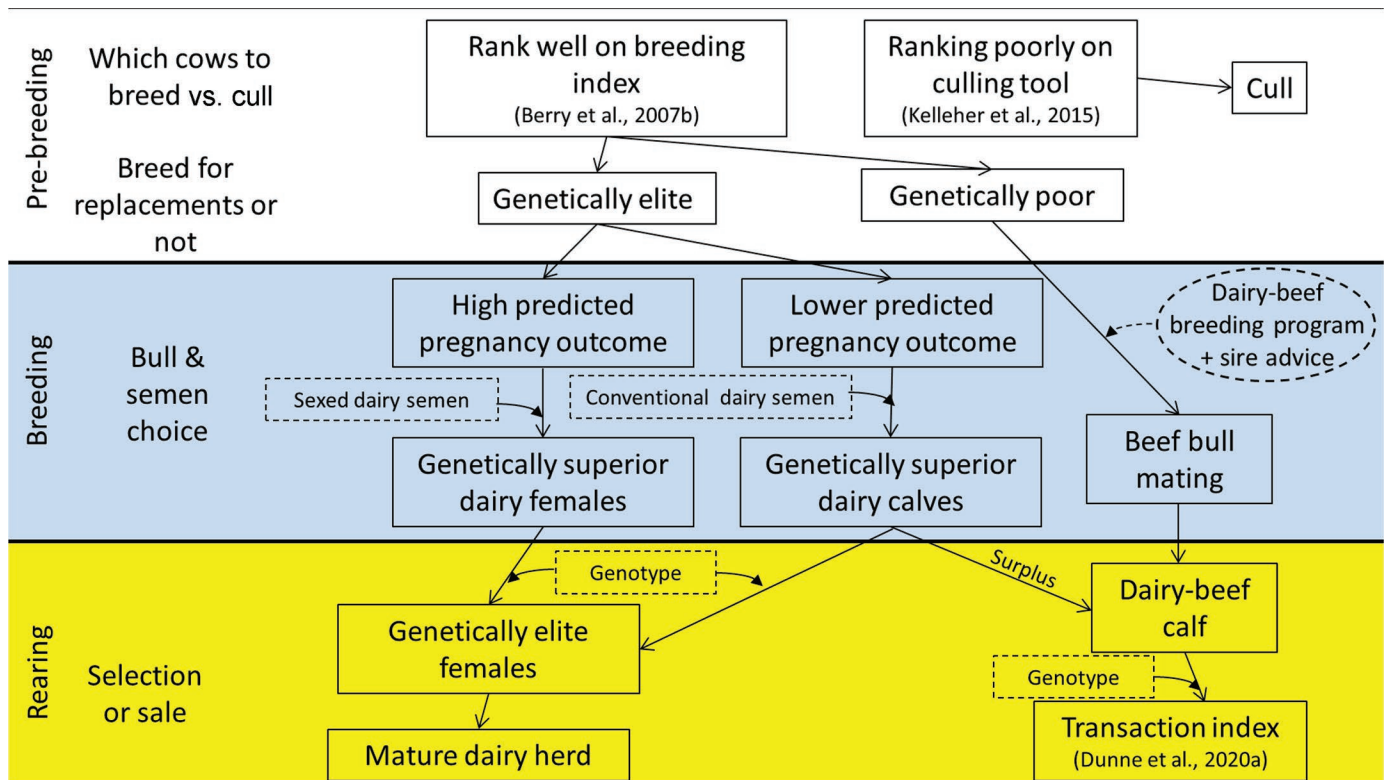


Figure 6. Critical control decision points during the annual productive cycle of the dairy cow.

relatively simply, in the traits used and in their relative emphasis making it bespoke for the individual purchaser. Similarly, using the best linear unbiased estimations (BLUEs) of the purchasing herd derived from national genetic evaluations, it is possible to inflate or deflate the expected responses per trait for a given production value (Dunne et al., 2019). These modifications can be relatively easily incorporated into the back-end web service or application of a service provider who has access to all the necessary details. This facility could be available to the seller and purchaser through a brokerage system that could be underpinned by a distributed ledger to ensure confidence in the product (i.e., recorded sire of the calf matings, sire used to inseminate the dam, quantity of colostrum fed, any medical treatments received) and enable the financial transaction to be securely completed as soon as the animals are exchanged. Such a system could be particularly useful when livestock auctions are not possible, such as during pandemics.

Decision-support tools and systems also have uses outside the farm gate. For example, they can be used by breeding companies or breeders to identify suitable bulls (AI or natural) for particular dairy herds; this could be underpinned by self-declared information from the dairy producer about acceptable levels of calving performance and the likely market of the resulting calves. Techniques such as multi-attribute value models using pairwise rankings of alternatives (Hansen and Ombler, 2009) could be used to decide on trade-offs for different components of the dairy-beef pipeline, the outcome being a tool (analogous to a breeding objective) to rank candidate bulls for their suitability for a given herd.

Decision-support tools predicting the likely carcass merit of individual carcasses could be useful for those purchasing live cattle, such as traders or procurement officers for meat processors. Because the narrow-sense heritability of many carcass traits is moderate (Pabiou et al., 2012), the additive genetic merit of the individuals could be a relatively good reflection of subsequent phenotypic performance, especially when complemented by nonadditive genetic and nongenetic effects (Dunne et al., 2020a,b). Although some of these carcass credentials are available at slaughter, other metrics such as sensory quality are not readily available. The median heritability estimates for meat sensory characteristics in cattle are between 0.15 and 0.45 (Berry et al., 2017), implying that the additive genetic merit of individual animals may not be a very accurate prediction of meat sensory value, although Berry et al. (2017) demonstrated how one could compile the information on genetic merit of a group of individuals to form a more reliable estimate of the mean of the group. None-

theless, these estimates of genetic merit could be used as prior knowledge in Bayesian-type analyses supplemented with additional data such as animal sex (Judge et al., 2021), herd BLUEs (Dunne et al., 2019), and data from available inline technologies such as infrared spectroscopy (Berri et al., 2019) to form a more accurate estimate of the expected sensory value of a given sample. Such predictions can also be displayed for the consumer alongside other metrics, such as environment, feed and water sustainability, as well as the actual sustainability credentials of the producer(s) who produced the goods. The price of the meat product can be scaled accordingly, and the choice given to the consumer. This approach is not dissimilar to current approaches for organic or fair-trade products.

In summary, the opportunities to use decision-support tools from pasture to plate are immense. The accuracy of such tools can only improve as the quality and quantity of data improve with the growing datafication of the agrifood chain, coupled with advances in the data sciences.

ANALYSIS OF STRENGTHS, WEAKNESSES, OPPORTUNITIES, AND THREATS OF BEEF-ON-DAIRY

An inexhaustive analysis of the strengths, weaknesses, opportunities, and threats (SWOT) for beef-on-dairy from the perspective of dairy and beef producers is summarized in Figure 7.

Strengths

Dairy producers typically use more AI than beef producers, enabling the application of greater selection pressure on the choice of bulls but also enabling them to assortative-mate individual bulls with dairy females. These parents can be selected using available estimates of genetic merit for both the cow and bull, although the mating decision itself is aided by not having to consider the coancestry between the dairy female and the beef bull. Given the higher value of beef \times dairy calves (Dal Zotto et al., 2009; Mc Hugh et al., 2010), the extra revenue generated can provide a welcome source of income for dairy producers, especially in times of low milk prices. From the perspective of the beef producer, the initial capital cost of the beef \times dairy calf should be low relative to that of a beef \times beef calf, so less capital is tied up until harvest. Related to this, the cost of maintaining mature beef cows can be substantial (Montaño-Bermudez et al., 1990), so the value of the beef offspring to the seller must be enough to recoup the costs of the mature herd (including cows that never produced a calf for sale). The price

of the beef × dairy calf, like most commodities, is a function of supply and demand and, in most countries, beef × dairy calves are readily available. The need for infrastructure for beef × dairy animals can also be relatively low in some production systems if the calf is already weaned.

Weaknesses

The generally poorer performance of beef × dairy animals (especially with Jersey bloodlines) for some performance statistics relative to some beef × beef animals is one of the weaknesses of beef × dairy animals. For many traits, beef × dairy animals do outperform dairy × dairy animals, especially from late-maturing beef breeds, although differences between dairy bloodlines and some early-maturing beef bloodlines when crossed with dairy females are often small or nonexistent. However, the lack of large differences may be a function not of the beef breed themselves, but of the sires of those breeds chosen by dairy producers. Regardless, it is unlikely that the breeding policies of dairy producers will change much, because beef output in most dairy herds contributes little (and probably less and less) to

overall profitability; producing a calf is often viewed as simply a means to initiate a (profitable) lactation in the cow rather than generating an additional source of income from the sale of the calf. It may be difficult to encourage change.

Many dairy producers seek to move their surplus calves off the dairy enterprise as soon as possible after birth; preweaning calves can require specialized infrastructure, are usually labor-intensive to keep, and suffer from higher mortality relative to calves of older ages (Ring et al., 2018). Morbidity can ensue when groups of young calves from different herds are mixed, leading to the need for an ever-more vigilant and skilled labor force. The beef sector in most countries tends to be a low-profitability sector on average, and although beef × dairy systems have been demonstrated to be more profitable than beef × beef systems (Karhula and Kassi, 2010), they still have low margins, which is a major weakness of the system. This can be compounded by volatility in input and output prices, which can be especially important if the beef × dairy animals are purchased at a younger age relative to weaned beef × beef animals, extending the duration until realization of the return on investment.

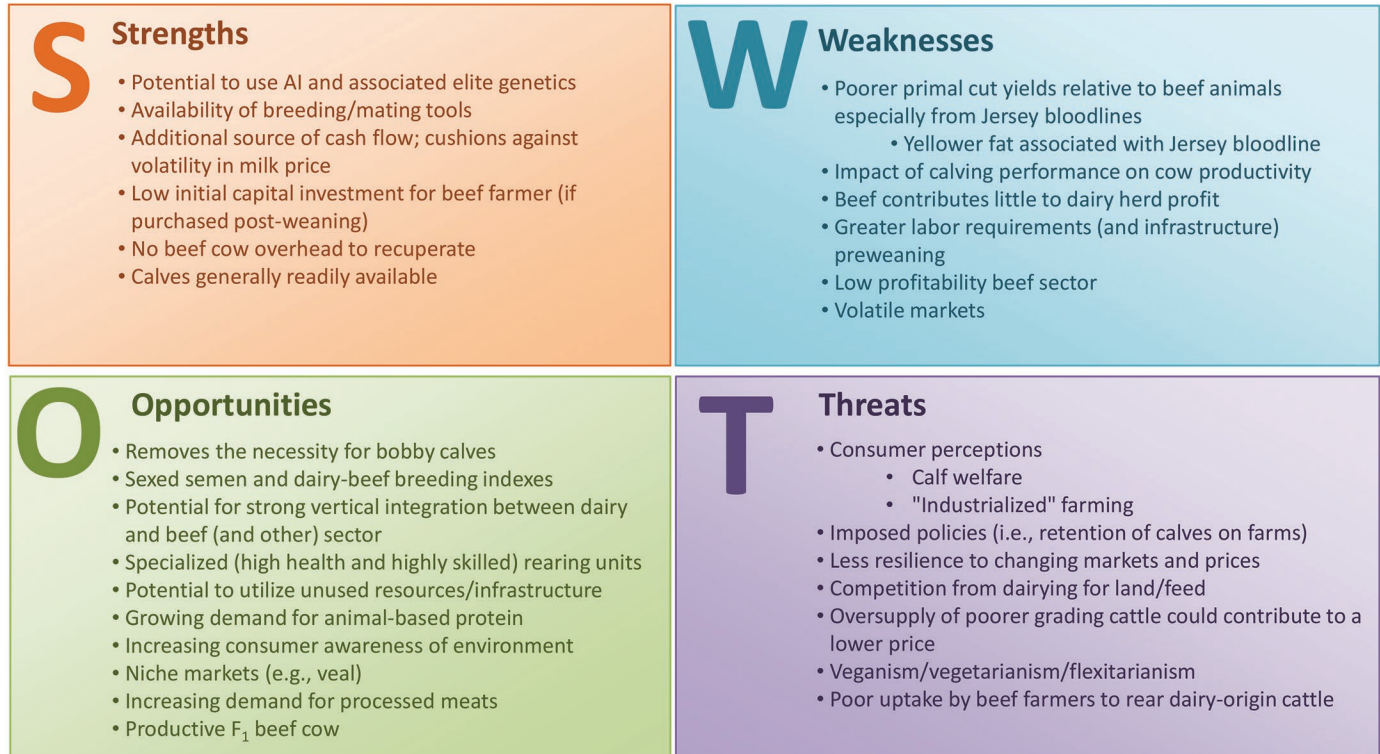


Figure 7. Strengths, weaknesses, opportunities, and threats (SWOT analysis) for beef-on-dairy production systems from the perspective of dairy and beef producers.

Opportunities

The growing influence of the consumer on how food is produced will likely focus the spotlight more on the production of bobby calves, which is unacceptable to many in society. By creating a more valuable calf product, a market for all calves may exist, removing the necessity for a bobby calf industry. However, it should be noted that disbandment of a system to remove calves at a very young age will increase the total environmental load unless they displace less environmentally efficient systems such as beef cow herds. The availability of sexed semen, coupled with indexes to select beef bulls for use on dairy females, can facilitate the production of more high-quality calves and fewer low-value calves. Nonetheless, supply and demand dictate price, and like most quantitative traits, price follows a normal distribution, with a group of animals on both sides of the distribution. If the mean of the distribution changes, the presence of both good- and poor-quality calves does not, so the relative price differential may not change; in fact, variance will likely increase as the mean increases. Nevertheless, the price of the (poorer) calf relative to the milk price may change.

Vertical integration of the dairy and beef production systems, with market signals from the beef processor via the beef producer being relayed to the dairy producer when selecting bulls has huge potential; having a guaranteed market and forward price contract models at each stage of the production cycle could influence decision-making. In seasonal-calving dairy production systems, many calves are born over a relatively short period of time, usually requiring decent infrastructure for rearing until weaning. Some underused buildings and resources may be available in other enterprises during this period, such as on tillage or horticultural farms; such farmers may opt to become specialized calf-rearers for a specific period of time before selling to beef producers; however, this period of the animal's life does require skilled labor.

Although the growing global demand for animal-derived protein and energy sources is a massive opportunity for beef in general, the lower environmental footprint of beef \times dairy animals (assuming the environmental footprint of the cow is attributed to her milk production) could help allay consumer concerns about the environmental cost of ruminant production. Such beef \times dairy products could be marketed as such, with particular points of differentiation or unique selling points. Therefore, although the quality of the primal cuts may be deemed inferior by some, they may excel in other characteristics, including meat quality. Moreover, the growing demand in many developed countries for smaller meat servings but also convenient (processed)

meats may negate the benefit of larger primal cuts, which are more associated with late-maturing beef \times beef animals. Although much of the discussion about beef \times dairy calves revolves around their value as a carcass, their maternal characteristics as beef cows have also been publicized (Roca Fraga et al., 2018; McCabe et al., 2019).

Threats

Impressions of the end user or customer (whether factual or not) about the ethical nature by which any good (e.g., clothing, food) is produced affects whether they will purchase the product. Social media is affecting consumer impressions of modern-day dairy production systems, especially in relation to calf welfare or the industrialization of dairy farming. To address the desire on the part of some dairy producers to move surplus calves off the dairy farm as soon as possible, policies have been enacted (rapidly) in some jurisdictions enforcing a lower age limit at when calves can leave the farm. It is the prerogative of government, or even milk processors, to unilaterally impose these and other policies as they see fit. Breeding programs are faced with a particular predicament in that they are breeding for animals of the future and must therefore predict the environment that is likely to prevail when the progeny and their descendants are born. This carries huge risk.

Most dairy producers are specialists in the production of milk, and many have only the minimum required calf-care facilities; this has implications if downturns in the markets for dairy calves materialize (including disease outbreaks such as foot and mouth disease, which prohibits animal movements) resulting in no meaningful trade and an accumulation of calves on the farm. This can be compounded by the competition from dairying to expand into farms that traditionally reared beef, but also the growing interest in alternative human eating habits that minimize meat intake. Anecdotal evidence is also appearing of a growing reluctance among some beef producers to rear beef animals from dairy herds, again affecting the price and ability of offload surplus dairy calves.

CONCLUSIONS

Beef-on-dairy is increasing in popularity among dairy producers as a means of generating more revenue while avoiding the temptation to cull very young calves because of a lack of a market. Many of the studies that have compared the performance characteristics of dairy \times dairy versus beef \times dairy animals are now dated, and a description of the dairy and beef germplasm relative to the breed as a whole is not well defined; this

gap in knowledge should be rectified. Breeding objectives and underpinning breeding schemes to generate suitable beef bulls for use on dairy females is lagging behind those for dairy bulls. Nonetheless, both breeding and decision-support tools are being developed to guide decision-making along the various critical control points of the annual dairy cow cycle.

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