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Crossbreeding as a strategy in dairy cattle herds

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Abstract

This thesis aimed to explore benefits of dairy crossbreeding at herd level and form recommendations for dairy farmers, advisors, and breeding companies. A survey study revealed that Swedish dairy farmers can be divided into two groups: those supporting crossbreeding and those not supporting it. SimHerd Crossbred and ADAM were used to simulate various crossbreeding strategies and estimate the economic effects. Both terminal and rotational crossbreeding involving Swedish Red and Swedish Holstein increases the yearly economic return in organic and conventional Swedish production systems, compared with purebreeding Swedish Holstein. Also, terminal crossbreeding combined with the genetic benefits of sexed semen and genomic testing of purebred animals is economically beneficial. Terminal crossbreeding between a low-yielding native breed and a high-yielding breed improves the economic result. Combined with marketing of niche products, terminal crossbreeding may be beneficial as a strategy for conserving native dairy cattle breeds. Genomic breeding values for crossbred animals could be predicted with a model using summary statistics from purebred reference populations with almost as high prediction accuracies as if full genotype and phenotype information was available. Future research is needed on crossbreeding schemes utilizing genomic data and the effect of crossbreeding on the environmental footprint.

Keywords: crossbreeding, heterosis, dairy cattle, sexed semen, beef semen, genomic prediction

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Crossbreeding as a strategy in dairy cattle herds

Sammanfatning

Syftet med denna avhandling var att utforska fördelarna med mjölkraskorsning på besättningsnivå och utforma rekommendationer för mjölkbönder, rådgivare och avelsföretag. En enkätundersökning visar att svenska mjölkbönder kan delas in i två grupper: de som är positiva och de som är negativa till korsning. SimHerd Crossbred och ADAM användes för att simulera olika korsningsstrategier och skatta de ekonomiska konsekvenserna. Både slutkorsning och rotationskorsning med röda kor (SRB) och holstein-kor ökar den årliga ekonomiska avkastningen i konventionella och ekologiska besättningar, jämfört med renrasiga holstein-kor. Slutkorsning i kombination med de genetiska fördelar som könssorterad sperma och genomisk analys av renrasiga djur ger är också ekonomisk fördelaktigt. Slutkorsning mellan en lantras och en högavkastande ras förbättrar det ekonomiska resultatet jämfört med en renrasig lantrasbesättning. Kombinerat med marknadsföring av nischprodukter kan slutkorsning vara en bra strategi för bevarande av lantraser. Genomiska avelsvärden för korsningsdjur kan skattas med en modell som använder sammanfattande statistik från renrasiga referenspopulationer. Det ger nästan lika höga säkerhet som om fullständig genotyp- och fenotypinformation används. Framtida forskning behövs om nyttjandet av genomisk data vid strategisk användning av mjölkraskorsning, och om klimateffekten av mjölkraskorsning.

Nyckelord: korsning, heterosis, mjölkkor, könssorterad sperma, köttrassemin, genomisk analys

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Dedication

To dairy farmers around the world. Thank you for your hard work and dedication to providing food on the table.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Clasen, J. B., Bengtsson, C., Källström, H. N., Strandberg, E., Fikse, W. F., and Rydhmer, L. (2021). Dairy cattle farmers' preferences for different breeding tools. Animal. *Accepted for publication.*

II. Clasen, J. B., Fikse, W. F., Kargo, M., Rydhmer, L., Strandberg, E. and Østergaard, S. (2020). Economic consequences of dairy crossbreeding in conventional and organic herds in Sweden. J. Dairy Sci. 103:514–528.

III. Clasen, J. B., Kargo, M., Østergaard, S., Fikse, W.F., Rydhmer, L., and Strandberg, E. (2021). Genetic consequences of terminal crossbreeding, genomic test, sexed semen, and beef semen in dairy herds. J. Dairy. Sci. 104:8062 – 8075

IV. Clasen, J. B., Kargo, M., Fikse, W.F., Strandberg, E., Wallenbeck, A., Østergaard, S., and Rydhmer, L. (2021). Conservation of a native dairy cattle breed through terminal crossbreeding with commercial dairy breeds. Acta Agric. Scand. Sect. A — Anim. Sci. 1–12.

V. Clasen, J. B., Fikse, W. F., Su, G. and Karaman, E. (2021). Multi-breed genomic prediction using summary statistics and a breed-origin-of-alleles approach. *In manuscript*

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Abbreviations

BOA	Breed origin of alleles
BS	Beef semen
CS	Conventional dairy semen
DCE	Discrete Choice Experiment
GEBV	Genomically enhanced breeding value
GT	Genomic testing
LD	Linkage disequilibrium
MOET	Multiple ovulation embryo transfer
NTM	Nordic Total Merit Index
QTL	Quantitative trait loci
SH	Swedish Holstein
SKB	Svensk Kullig Boskap/Swedish Polled Cattle
SNP	Single nucleotide polymorphism
SR	Swedish Red
SS	Sexed dairy semen
XB	Dairy crossbreeding

1. Introduction

Increasing demands on dairy products, consumer concerns about animal welfare, and climate changes (Ingenbleek & Immink 2011; Hristov et al. 2013; Gustavsen & Rickertsen 2018; Hempel et al. 2019) are what dairy farmers are facing today and in the future. Those challenges are forcing farmers to be innovative and to adapt to new strategies of dairy cattle breeding and management.

The Holstein breed is the dominating dairy breed worldwide because of its superior milk yield (Oltenacu & Broom 2010). However, inbreeding and selection emphasizing milk yield have for a longer period caused negative trends for reproduction and health traits in the breed (Bjelland et al. 2013; Buckley et al. 2014; Miglior et al. 2017). Small populations of locally adapted breeds can compete with Holstein, mainly because of their excellent reproduction and health traits (Ahlman 2010; Ferris et al. 2014; Sørensen et al. 2018). Crossbreeding locally adapted breeds with Holstein has proven a valuable shortcut to make robust dairy cows that are healthy and fertile animals with a rather high milk yield (Freyer et al. 2008; Sørensen et al. 2008; Clasen et al. 2019; Hazel et al. 2021).

In New Zealand, half of the dairy cows today are crossbreds due to an emerging need for animals well-adapted to a pasture-based production system and seasonal calving (Clark et al. 2007; Washburn & Mullen 2014; DairyNZ 2021). In comparison, less than 15% of the dairy cows within other countries, including Sweden, are crossbreds, but the interest is gradually growing (Table 1). Considering the international pressure on the dairy cattle industry, crossbreeding in dairy cattle may be part of the solution.

2. Background and theory of crossbreeding

Crossbreeding is about combining desirable traits from different breeds and utilizing the non-additive genetic effects that occur when unrelated animals are mated (Hill 1971; William & Pollak 1985; Mäki-Tanila 2008). It is the foundation of commercial poultry and pork production today and is used widely in beef cattle and sheep as well (Simm 1998). Crossbreeding in dairy cattle has been well explored in the past (Ellinger 1923; McDowell & McDaniel 1968; Pedersen & Christensen 1989; Touchberry 1992). But it never caught on as it did for other livestock species, mainly because of the relatively low reproductive rate and long generation interval in dairy cattle (Swalve 2007; Sørensen et al. 2008).

Table 1. The proportion of crossbred dairy cattle in various countries

Country	% crossbreds	Source
New Zealand	49	DairyNZ (2021)
Denmark	12	RYK (2021)
Sweden	9	Växa Sverige (2021)
France	6	Magne & Quénon (2021)
USA	5	Guinan *et al.* (2019)

2.1 Brief theory of crossbreeding

2.1.1 Heterosis

Breeding within closed populations leads to inbreeding. Inbreeding causes a loss of genetic diversity and increases the homozygosity of undesirable recessive alleles, leading to inbreeding depression. Inbreeding depression occurs when the loss of genetic heterozygosity decreases the fitness of the animals within the population (Falconer & Mackay 1996). Loss of fertility in the Holstein breed is an example of how inbreeding and intensive selection for a single trait has caused deterioration of other traits within a population (Royal et al. 2000; Lucy 2001; Sørensen et al. 2005; Oltenacu & Broom 2010). The occurrence of inbreeding depression can only be reversed when the population is outbred – or crossbred – with another, unrelated breed population. When unrelated breeds or lines are crossed, the homozygote pairs of detrimental alleles are broken, and the crossbred offspring will most often turn out as more robust or better performing than the average of the parental breeds. This is called "heterosis" or "hybrid vigor" and can be measured as the relative performance of the crossbred offspring compared to the parental average. The improved performance is due to a higher degree of heterozygosity, which changes the interaction of genes within (dominance effects) and between (epistatic effects) loci (Sørensen et al. 2008). However, crossing different pure breeds may also break favorable gene combinations that are established within the pure breed, referred to at recombination loss. Heterosis can be interpreted as the opposite of inbreeding depression, although the success of reversing the loss of fitness depends on the breeds crossed (Falconer & Mackay 1996).

The initial cross (F1) between two unrelated breeds will always yield the maximum (100%) heterosis in the offspring. The more unrelated the breeds are, the higher heterosis is expected when the breeds are crossed (Mäki-Tanila 2008). When the crossbred animal is bred back to one of its parental breeds, the maximum expected heterosis is halved for every generation it is backcrossed (Figure 1).

The heterosis effect is usually higher for traits with low heritability than for traits with high heritability (Touchberry 1992). The largest heterosis effect in F1 crosses is commonly estimated for fertility, health, and longevity traits in dairy cattle, while the lowest is estimated for production traits (Table 2). The effect of recombination loss in F1 crosses is typically unfavorable for milk production traits, but favorable or insignificant for fertility and health traits (Wall et al. 2005; Wolf et al. 2005; Konstantinov et al. 2006; Dechow et al. 2007).

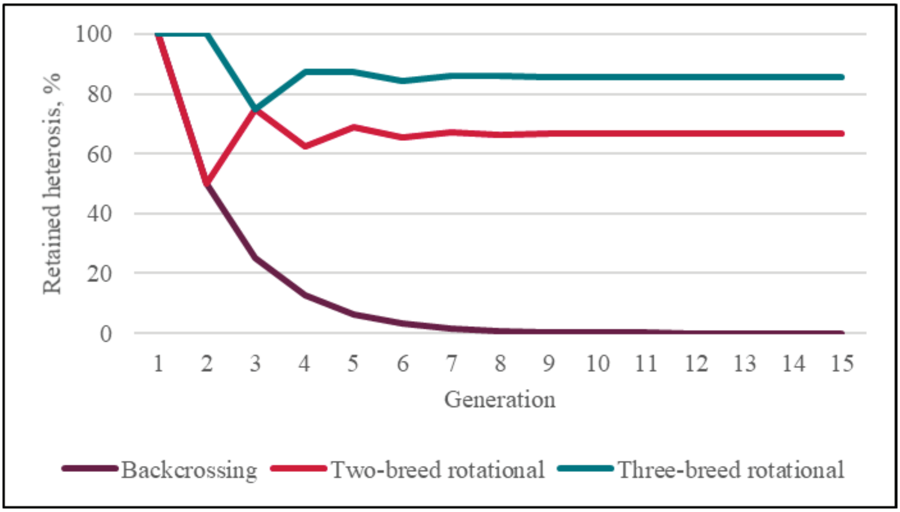

Figure 1. Maximum heterosis retained per generation of backcrossing. Generation 1 is the initial cross (F1) (from Bourdon 2000)

Table 2. Commonly estimated heterosis effects for different traits in F1 dairy crossbreds (e.g., VanRaden & Sanders 2003; Sørensen *et al.* 2008; Jönsson 2015; Clasen *et al.* 2017; Kargo *et al.* 2021)

Trait	**Heterosis (all are favorable)**
Milk, fat, and protein yield	1 – 10%
Fertility	5 – 12%
Calving performance and stillbirth	5 – 15%
Udder health	0 – 7%
Other diseases	5 – 20%
Longevity	5 – 20%

2.1.2 Systematic crossbreeding strategies in livestock production

The term “systematic” crossbreeding refers to crossbreeding strategies that continuously follow the same pattern or cycle or crossing specific breeds within a herd or population. Unsystematic crossbreeding does not follow a specific pattern and refer to sporadic or uncontrolled crossbreeding.

The most used crossbreeding strategy within pork and poultry is "terminal crossbreeding", which implies that the crossbreds are never bred back to the same pure breed, and therefore 100% of the maximum heterosis is retained by using this strategy. The crossbred offspring may either be the end of the breeding cycle (hence, terminal crosses) or bred to another breed or unrelated crossbred (Figure 2). Technically, all groups of animals (purebreds and crossbreds) can be kept within the same herd. However, at a population-wide scale of crossbreeding (as in pork and poultry), each animal group is usually delegated to specialized herds for purebreeding and crossbreeding, respectively.

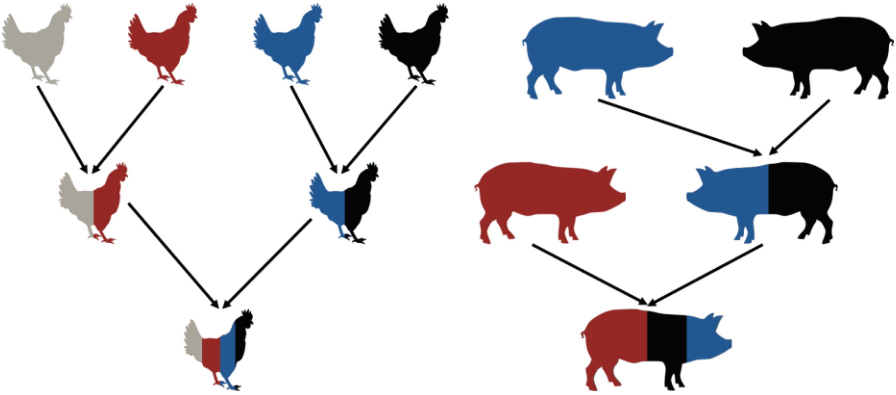

Figure 2. Examples of terminal crossbreeding strategies commonly used in poultry and pork production

Rotational crossbreeding (Figure 3) is often used in beef and sheep production. In this strategy, it is most often crossbred females that are bred to the sire (pure) breed they consist less of. In a two-breed rotational crossbreeding system, 67% of the maximum heterosis is retained, while 86% is retained in a three-breed system (Figure 1) and heterosis increases with the number of breeds included.

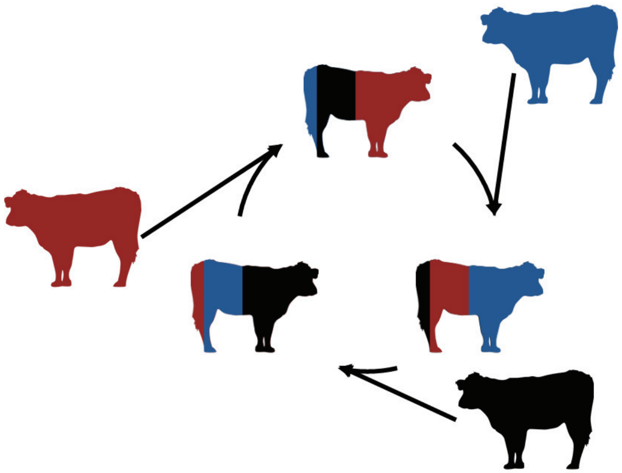

Figure 3. Example of a rotational crossbreeding strategy using three breeds

2.2 Crossbreeding in dairy cattle

As mentioned previously, crossbreeding is not commonly used in modern dairy production, except in New Zealand. As in many other countries, New Zealand imported semen from North American Holstein bulls during the 1970-90ies to increase milk production. However, along with higher milk production, the fertility of the cows deteriorated, which became a critical problem in the spring-calving production system. Furthermore, the Holstein-Friesian cows became heavier, which caused complications in the pasture-based production system. This led farmers to utilize heterosis from crossbreeding Holstein-Friesian with Jersey to overcome the loss of reproductive abilities and to create smaller cows that were more suitable on pasture (Montgomerie 2005; Clark et al. 2007; Rowarth 2013). Today, the Holstein-Friesian x Jersey crossbred is named KiwiCross[1] by the industry and is both a rotational and composite crossbreeding strategy, where also crossbred bulls are utilized for composite breeding with crossbred cows, Jersey, or Holstein-Friesian.

The reasons why crossbreeding is less utilized in modern dairy cattle production in other countries are not clear. Changes in breeding goals (in pure breeds) or changes in management practices may have avoided

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[1] https://www.lic.co.nz/products-and-services/artificial-breeding/crossbreeding-kiwicross/

potential bottlenecks (such as the New Zealand example) in dairy cattle production. It has been (and maybe still is) a common opinion that crossbreeding is the "last solution" and only beneficial under poor conditions. However, most research disproves this "myth" and shows that crossbreeding is beneficial at any level of herd management (Bryant et al. 2007; Kargo et al. 2012; Lembeye et al. 2015; Dezetter et al. 2017; Clasen et al. 2019).

As the global demands for more resilient and locally adapted dairy production increase, farmers worldwide are slowly regaining the interest in crossbreeding (Delaby et al. 2018; Ollion et al. 2018; Rodríguez-Bermúdez et al. 2019; Magne & Quénon 2021). Crossbreeding trials have been ongoing at the University of Minnesota since the early 2000s in research facilities and commercial herds. This includes a comprehensive study on rotational crossbreeding between Holstein, Montbéliarde, and Swedish Red (Shonka-Martin et al. 2019a; Hazel et al. 2021), which today is commercialized as ProCross[2] and is gaining popularity in several countries around the world.

2.2.1 Economic profitability of crossbreds

Studies of crossbred dairy cattle use different methods for estimations of profitability. Some are estimating profitability of the individual cows, i.e., at animal level, while others take herd dynamics into account. In a simulation study, Lopez-Villalobos *et al.* (2000) estimated a yearly net income per cow and hectare between 32–107 NZD higher for rotational crossbreds between Holstein-Friesian and Jersey, Holstein-Friesian and Ayrshire, Jersey and Ayrshire, and three-breed crosses compared with Holstein-Friesian in New Zealand herds. In six commercial Californian herds, Heins *et al.* (2012) estimated the lifetime profitability of Montbéliarde x Holstein and Scandinavian Red x Holstein crosses of 2,156 and 1,925 USD higher than Holstein. More recently, a similar study in eight Minnesotan herds on F1 Montbéliarde x Holstein and VikingRed x Holstein crossbreds estimated 1,638 and 498 USD higher lifetime profitabilities than Holstein (Hazel et al. 2021). In French cattle, Dezetter *et al.* (2017) simulated the profitability of rotational crossbreeding with Holstein x Montbéliarde, Holstein x Montbéliarde x Normande, and

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[2] www.procross.info

ProCross and found 20–91 € higher discounted margin over variable costs per cow-year compared with purebred Holstein. Using a herd simulation tool, Østergaard *et al.* (2018) estimated between 712 and 974 DKK higher net returns for rotational and terminal crossbreeding strategies with Holstein, Danish Red and Danish Jersey, compared with a pure Danish Holstein herd.

2.2.2 Sexed semen and beef semen

Two breeding tools that are rapidly gaining popularity in dairy herds are sexed semen (SS) and beef semen (BS) (Burnell 2019; SEGES 2021a). X-sorted SS increases the chance of a heifer calf to about 90% (Borchersen & Peacock 2009; DeJarnette et al. 2009; Healy et al. 2013), making it possible for the farmer to produce future replacements out of the best breeding females in the herd.

Crossbreeding dairy with BS is an effective tool to limit the surplus of replacement heifers in the dairy herd, and dairy x beef cross calves are more valuable slaughter animals than dairy bull calves (Ettema et al. 2017; Pahmeyer & Britz 2020). Furthermore, if more beef is produced in dairy herds, e.g., by beef x dairy crosses, rather than beef herds, the overall greenhouse gas emissions from beef production can be reduced as well (Cederberg & Mattsson 2000; Holden & Butler 2018).

A strategy of using SS on the highest-ranking breeding dams and BS on the lowest-ranking dams in the herd can improve the genetic level and economic profitability (Ettema et al. 2017; Pahmeyer & Britz 2020). Theoretically, the need for conventional dairy semen (CS) can be entirely omitted in the dairy herd by using a sufficient amount of SS to ensure enough replacement heifers while the rest of the herd is crossbred with beef.

The author knows no published studies on the use of SS and BS in a herd using dairy crossbreeding, and therefore the genetic and economic consequences of dairy crossbreeding combined with the use of SS and BS ought to be investigated.

2.2.3 Effects of crossbreeding on purebreeding

Crossbreeding high-yielding breeds with local breeds to improve production traits resulted from the desire to increase milk yields in the second half of the twentieth century (Montgomerie 2004; Lauvie et al.

2008; Bett et al. 2013; Miglior et al. 2017). However, the so-called "upgrading" of local breeds has severely eradicated the original breeds. For example, the use of North American Holstein bulls in the Swedish Lowland Cattle (today known as Swedish Holstein) means that today less than 5% of the genes in Swedish Holstein cattle stem from the original breed (Bett et al. 2013). In general, North American Holstein has been used for upgrading many local black-and-white cattle breeds worldwide. Another example is the Flemish Red cattle, where crossbreeding with Danish Red was intended to conserve the breed but got out of control, resulting in very few Flemish Red cattle without Danish Red genes (Lauvie et al. 2008). Even said Danish Red lost its originality when trying to save it from inbreeding depression and is now a mix of other Nordic red breeds (Sørensen et al. 2005; SEGES 2021b). These examples are results of uncontrolled crossbreeding.

There may be a potential to use systematic crossbreeding to conserve local dairy cattle breeds (Shrestha 2005). A global agreement on conserving local livestock breeds is currently in action (UN 1992; FAO 2007), and guidelines for conservation breeding programs, including crossbreeding, have been published (FAO 2010, 2012). However, the current success for conservation of local dairy breeds in some countries is more likely due to the production of PDO-labelled (Protected Designation of Origin; INAO (2019)) niche products, such as cheese (Verrier et al. 2005; Gandini et al. 2007; Lambert-Derkimba et al. 2019). In other countries, the market for niche products of local breeds is minimal, and local breed populations keep disappearing despite financial efforts from governments. The potential of using crossbreeding as a conservation strategy in local dairy cattle needs to be explored more.

2.2.4 Genomic prediction of crossbred animals

Genomic selection in dairy cattle was introduced commercially in 2008 and is the primary way of selecting dairy sires today (Hutchison et al. 2014; Mäntysaari et al. 2020). With genomically enhanced breeding values (GEBVs), young bulls can be selected with prediction accuracies nearly as high as daughter-proven bulls. As the cost of genomic testing (GT) has decreased in recent years, dairy farmers have become interested in genomic selection among the cows in their herds, which can improve the genetic gain at both herd level and population level (Pryce et al. 2012; Calus et al.

2015; Hjortø et al. 2015; Thomasen et al. 2020). Furthermore, GT can be used to verify the ancestry of the animals, give information on monogenic traits (such as polledness or monogenic diseases), and avoid inbreeding (Pryce et al. 2012).

The accuracy of genomic prediction relies on the level of linkage disequilibrium (LD) between single nucleotide polymorphisms (SNPs) markers and quantitative trait loci (QTL), the size of the reference population of genotyped and phenotyped animals, and the genetic relationship between the animals within the reference population and between the reference and test population (De Roos et al. 2009; Goddard 2009; Clark et al. 2012; Vandenplas et al. 2016). Genomic prediction of a breed population based on a reference population of another breed or multiple breeds is complicated when the LD structure differs between pure breeds. Nevertheless, using information from multiple breeds for genomic prediction is rapidly evolving, although it has proven mostly beneficial for breeds with small reference populations (Haile-Mariam et al. 2019; van den Berg et al. 2020; Karaman et al. 2021). Including crossbreds in a multi-breed reference population has shown to improve the genomic prediction of purebreds (Khansefid et al. 2020; Karaman et al. 2021).

Genomic prediction in crossbred animals may be more complicated than in purebreds because the LD structure differs within crossbreds and between crossbreds and the originating purebreds. The LD structure differs within crossbreds because genomic breed proportions are not necessarily the same within crosses of the same breeds (Wu et al. 2020), except for F1 crosses. For example, an F1 crossbred may pass on half of those genes originating from just one of its parental breeds. Furthermore, since the benefits of crossbreeding is based on the non-additive genetic effects, those need to be accounted for to avoid bias in genomic prediction of crossbreds (Wittenburg et al. 2011; Esfandyari et al. 2016). Models for genomic prediction in crossbreds exist but tend to 1) assume that the effects of individual breeds are the same across SNPs, 2) ignore non-additive genetic effects, 3) not exploit crossbred information in the reference population, or 4) be limited to only specific breeds.

Sharing genotype data between countries or breeding companies effectively improves genomic prediction (Lund et al. 2011; Jorjani et al. 2012) but is rarely possible due to privacy matters and differences in data handling (Tenopir et al. 2011; Liu & Goddard 2018). This problem has been solved in human genetics by joining summary statistics of estimated allele substitution effects of markers and the prediction error variances from different populations into meta-analyses (Maier et al. 2018; Lloyd-Jones et al. 2019). Such an approach can be advantageous in genomic prediction in crossbreds that rely on foreign breeds (Vandenplas et al. 2018), such as ProCross. The summary statistics approach for utilizing foreign data within the same breed populations is currently under development (Jighly et al. 2019) and could potentially be enhanced to multi-breed and crossbred predictions.

3. Objectives of the PhD project

The present thesis' main objective was to investigate the economic and genetic aspects and summarize the findings to form recommendations on using dairy crossbreeding as a strategy in dairy cattle herds.

More specifically, the objectives were:

- Investigating Swedish dairy farmers' preferences for using dairy crossbreeding and other tools in their breeding strategy
- Estimating the economic potential of two crossbreeding strategies in average conventional and organic Swedish Holstein dairy herds
- Evaluating the economic potential of using terminal crossbreeding as a conservation strategy using a native Swedish dairy breed as an example
- Estimating the economic and genetic consequences of terminal crossbreeding combined with various strategies for using sexed semen, beef semen, and genomic testing in conventional Swedish dairy herds
- Evaluating a genomic prediction model for estimating genomic breeding values in crossbred animals, using summary statistics from purebred reference populations

4. Summary of studies

Dairy cattle breeding relies much on the dairy farmers' breeding decisions in their herds, selecting the right cows and heifers to produce future breeding and production animals that fit the herd. There are several breeding tools in modern dairy production to support the farmers' breeding decisions, such as SS, BS, GT, multiple ovulation embryo transfer (MOET), and dairy crossbreeding (XB). However, their use is somewhat limited, and therefore the scope of **paper I** was to study farmers' preferences for those breeding tools through a survey.

Numerous studies in the literature show that XB can improve economically important traits in dairy cattle production (e.g., Lopez-Villalobos *et al.* 2000; Sørensen *et al.* 2008; Hazel *et al.* 2021). Hence, it suggests that XB can improve the economy in dairy herds. The economic consequences of rotational and terminal crossbreeding in Swedish organic and conventional herds were investigated in **paper II**. Improving the genetic level of the cows is a base for improving profitability in dairy herds. Breeding tools such as SS, GT, and BS are recommended to increase the genetic level in the herd (Hjortø et al. 2015; Bérodier et al. 2019). The effect of combining these breeding tools with XB on genetic progress, which was the aim of **paper III**, has not been investigated.

The economic advantage of crossbreeding may not just apply to dairy production with high-yielding breeds but can potentially be used as financial motivation in a conservation strategy, which was investigated in **paper IV**.

The study in paper III did not consider the use of GEBVs for crossbred animals, as models for that are still under development. In **paper V**, we evaluated a model using full genotype and phenotype data from a crossbred reference population combined with summary data from purebred reference populations to predict GEBVs in crossbred dairy cattle.

4.1 Farmers’ preferences for breeding tools (paper I)

4.1.1 Material and methods

This study investigated Swedish dairy farmers’ preferences for SS, BS, GT, XB, and MOET. We invited 1,521 dairy farmers across Sweden to participate in an online survey and had an additional public link to the survey available for a shorter period. In total, we received 204 completed responses. The respondents were split into two groups depending on if they had used XB (CROSS) or not used XB (NOCROSS) within the past 12 months.

The survey design was divided into three parts. The first part consisted of 16 demographic and general questions about the respondent and the farm. The second part was a discrete choice experiment (DCE) with five breeding tools (SS, BS, GT, XB, and MOET) combined into 48 sets of breeding strategies. For MOET, the options were to buy embryos, flush own animals, or not including MOET as a breeding tool, while for SS, BS, GT, and XB, the options were to include or not to include as breeding tool in the breeding strategy. The respondent was given ten tasks with two random sets of breeding tools and was asked to choose the one set he or she liked the most (or disliked the least). The third part consisted of five seven-point scale matrices with 6 – 10 statements for each breeding tool. Those statements were partly drawn from Wallin & Källström (2019) and partly from breeding advisors and the authors’ own experiences. The respondents were asked whether they agreed or disagreed with the statements.

For the statistical analysis of the DCE, we used a random utility approach and estimated utility values with a conditional logit model from the “mlogit” package in R (Croissant 2020). The model estimates utility values as regression coefficients for each option within each attribute (breeding tool). A positive utility value means that the respondents favor using the breeding tool at the given level, while a negative value means they are against it. The magnitude of the utility values can be compared to each other to indicate how much a tool, e.g., XB is favored (or disfavored) relatively between groups.

4.1.2 Results and comments

Considering all the responses in one analysis, the utility value for XB was low and insignificant (-0.008; Table 3). This was initially interpreted as respondents having a neutral preference for crossbreeding, but the analysis of responses within the CROSS and NOCROSS groups revealed that it is the outcome of an "average" of two contradictory groups. The CROSS group respondents favored XB (0.414) highly, while the NOCROSS groups wanted to avoid XB in their breeding strategy (-0.271).

Table 3. Utility values of the five breeding tools: sexed semen (SS), beef semen (BS), genomic testing (GT), dairy crossbreeding (XB), and multiple ovulation embryo transfer on own animals (MOET own) or buying embryos (MOET buy) for all respondents and groups of respondents that have used XB (CROSS) or not used XB (NOCROSS) within the past 12 months. Negative values indicate a preference not to use the breeding tool, while positive values indicate a preference in favor of the breeding tool. Asterisks (*) indicate a significance level of $p < 0.05$

	All	**CROSS**	**NOCROSS**
SS	0.520*	0.662*	0.480*
BS	0.387*	0.424*	0.378*
GT	0.244*	0.213*	0.274*
XB	-0.008	0.414*	-0.271*
MOET own	-0.239 *	-0.287*	-0.251*
MOET buy	-0.008	0.083	-0.031

We did not ask for specific reasons why the respondent favored or disfavored XB, but the responses to the statements (Figure 1) indicated their opinions about it. The majority of the respondents in the NOCROSS group agreed that XB makes the herd uneven and threatens the pure breeds, while the respondents in the CROSS group predominantly disagreed with those statements. The majority of the respondents in the CROSS group agreed that XB makes robust animals and that it is an excellent solution to avoid inbreeding. Furthermore, they certainly disagreed that the milk price is too unstable to use XB and that the full effect of XB takes too long. The NOCROSS group, however, was generally neutral to those two statements. Furthermore, the NOCROSS group tended to agree that XB is insecure without breeding values on crossbred animals, while the CROSS group disagreed.

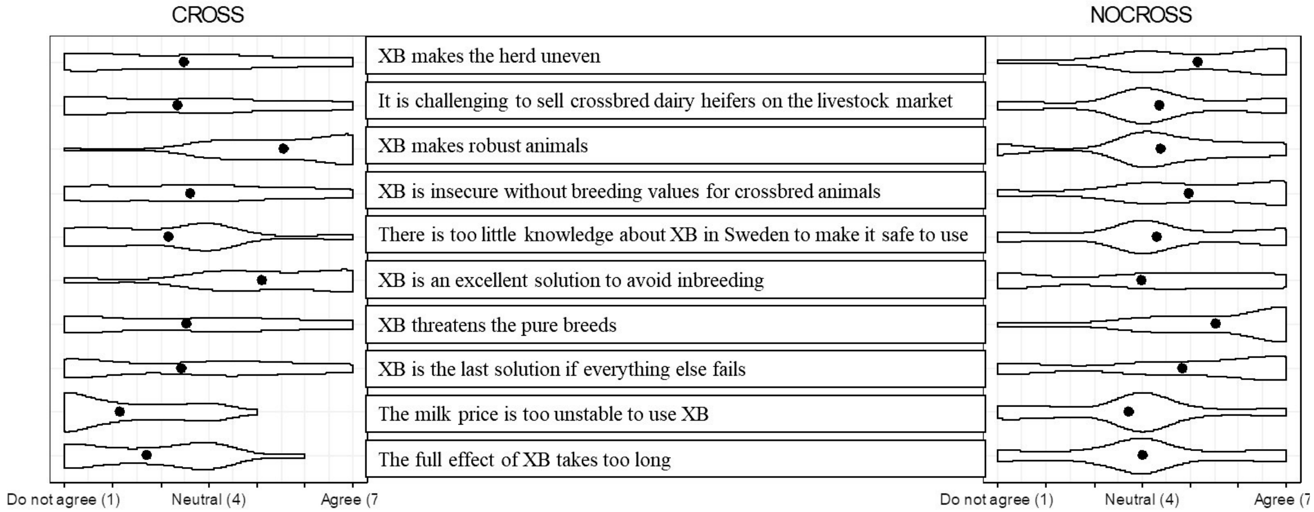

Figure 4. Responses to statements about dairy crossbreeding (XB) for all respondents and groups of respondents that have used XB (CROSS) or not used XB (NOCROSS) within the past 12 months, on a seven-point scale from 1 (do not agree) to 7 (agree). Black dots indicate the mean of responses. This figure is not included in the paper

In addition to the statements, some of the respondents wrote in the free text comments that they wish to have other crossbreeding strategies available on the market. Currently, the only crossbreeding strategy that is promoted in Sweden is ProCross.

Table 4. Overview of responses to questions about the respondents, the farms, and the use of five breeding tools: sexed semen (SS), beef semen (BS), genomic testing (GT), dairy crossbreeding (XB), and multiple ovulation embryo transfer (MOET) within the past 12 months for all respondents and groups of respondents that have used XB (CROSS) or not used XB (NOCROSS) within the past 12 months. Frequencies and mean values (with stand. dev.)

	All	**CROSS**	**NOCROSS**
N	204	80	124
Herd size, no. of cows	123 (132)	145 (180)	109 (88)
Crossbred cows (%)	5.2	11.1	1.5
Organic production (%)	24	20	26
Breeding interest, 1 (low) – 5 (high)	3.9 (0.9)	3.8 (0.8)	4.0 (0.9)
Used breeding advisor (%)	47	46	48
Used SS last 12 months (%)	77	85	73
Used BS last 12 months (%)	75	76	73
Used GT last 12 months (%)	47	51	44
Used XB last 12 months (%)	39	100	0
Used MOET last 12 months (%)	14	13	15

Having used XB in the herd within the year before the survey did not necessarily mean that they were using XB as a breeding strategy or used it in the entire herd, which the frequency of the crossbred cows in the CROSS indicated (11.1%; Table 4). Even in the NOCROSS group, with farmers who had not used XB in the past year, there were still 1.5% crossbred cows among the herds. Thus, some of the respondents in the NOCROSS group may have some experience with XB in the herd.

The herds in the CROSS group appeared to be somewhat larger than the NOCROSS group. We know no studies focusing on the interaction between herd size and crossbreeding in dairy herds, although a few studies have shown a connection between XB and expanding dairy herds (Jago & Berry 2011; Quénon et al. 2020).

The frequency of organic farms in the CROSS group was lower than in the NOCROSS group (Table 4). Additionally, the frequency of crossbred cows in the organic herds across all respondents (not shown in a table) was 4.3%, and it was 5.6% in conventional herds. That contrasts to other studies, where crossbred cows appear more frequently in organic than in conventional herds (Rozzi et al. 2007; Slagboom et al. 2016; Sorge et al. 2016).

4.2 Economic consequences of crossbreeding (paper II)

4.2.1 Material and methods

This study aimed to estimate the economic consequences of rotational and terminal crossbreeding in a dairy herd. We used SimHerd Crossbred (Østergaard et al. 2018), a modified version of the SimHerd model (Østergaard et al. 2000), for simulation of herd dynamics. The simulated herd is defined by stochastic simulation of the life cycle of individual cows in the herd based on a large set of animal and herd parameters. In addition, the SimHerd Crossbred model can distinguish between up to three different dairy breeds and crossbreeding between them by a set of breed-specific and heterosis parameters for different traits. The breeds used in this study were Swedish Red (SR) and Swedish Holstein (SH). The breed parameters were mainly based on data from the Swedish Cattle database (Kokontrollen, managed by Växa Sverige, Uppsala). The heterosis parameters were based on previous studies on crossbreeding between SR and SH (Sørensen et al. 2008; Jönsson 2015).

Two base herds were set up to illustrate average Swedish conventional and organic herds having purebred SH. We simulated three breeding strategies for each herd: purebreeding SH, two-breed terminal crossbreeding with SH in the purebred nucleus and F1 SR x SH crosses, and two-breed rotational crossbreeding in the entire herd with SR x SH (Figure 5).

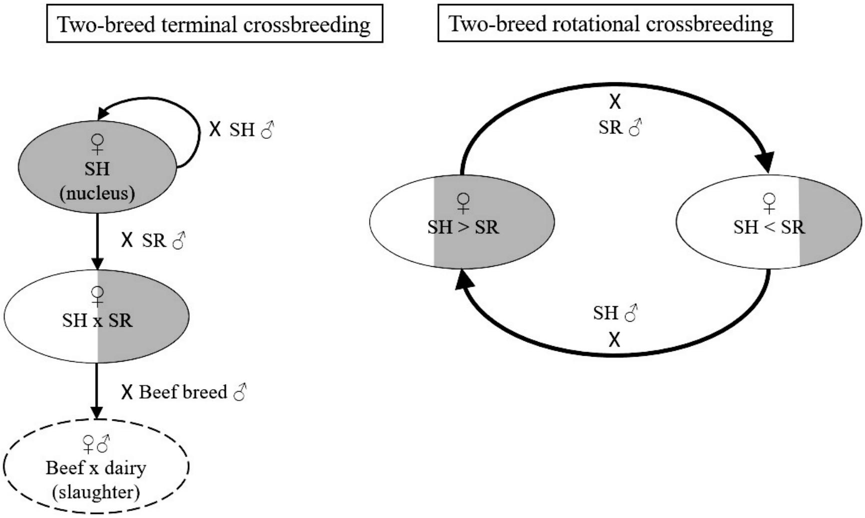

Figure 5. Illustration of two-breed rotational crossbreeding (right) and two-breed terminal crossbreeding (left). Terminal crossbreeding requires a nucleus of pure-bred Swedish Holstein (SH), where some of the females are bred to a sire of the same breed to maintain the size of the nucleus. The remainder of the SH females are bred to a Swedish Red (SR) sire to produce F1 crossbred production cows. The crossbred SR x SH females are mated to a sire of beef breed, and all of the resulting offspring are for meat production only. In rotational crossbreeding, females are rotated between the two sire breeds in each generation. Females with an SH sire are bred to an SR sire and vice versa.

Across all scenarios, we wanted to keep a surplus of heifers between 1 and 3; otherwise, the results would reflect selling or buying replacement heifers instead of other economic effects. In the purebreeding and rotational crossbreeding scenarios, the surplus was adjusted by using BS on some of the oldest cows in the herd. The beef x dairy cross offspring were sold with dairy bull calves when two weeks old.

In the terminal crossbreeding scenarios, the females in the purebred nucleus were used for breeding both purebred and crossbred replacement heifers. Therefore, the adjustment of surplus replacement heifers was based on the proportion of purebred SH cows in the nucleus bred to an SR bull, which in turn also reflected the proportion of crossbred cows in the herd. Furthermore, we wanted to reach an adequate proportion of crossbreds in the herd, and therefore, all purebred heifers were bred twice with SS, regardless of the breed of the AI bull, whereafter they were inseminated with CS if both attempts with SS failed. The crossbred cows and heifers were bred to BS.

The output from the simulations was technical figures on calvings, animal flow, milk production, feeding, disease treatments, and inseminations used to calculate economic figures for feeding, milk, live animals, slaughter, inseminations, and veterinarian expenses. We assumed that capital and labor costs were the same across the scenarios, so we did not include them in the calculations. The results are an average of 1,000 replicates over ten years of equilibrium where the breed proportions across the herd were stable between the years.

In addition to the six scenarios, we included three sensitivity analyses of changing the milk price, the feed costs, and the difference in 305-day ECM production between SR and SH.

4.2.2 Results and comments

The flow of animals in the herd, i.e., the proportion of crossbreds, distribution of first, second, and older parity cows, number of youngstock, and number of dairy bulls and beef crosses sold, were similar in both production systems within breeding strategy (Table 5). In the terminal crossbreeding scenarios, the proportion of F1 crossbreds was 31% due to the use of SS in the purebred heifers. The replacement rate was reduced when moving from purebreeding to rotational crossbreeding due to improved reproduction, health, and survival in the crossbred cows and heifers.

The total return for the terminal and rotational crossbreeding scenarios in the organic production system was 1.9% and 2.2% higher than purebreeding, respectively, while the corresponding figures for the conventional production system were 0.9% and 1.7%. (Table 6). The main positive economic effects of crossbreeding were higher income from beef x dairy calves and reduced feed cost of youngstock. A few adverse economic effects of crossbreeding were slightly reduced income from milk production (except for terminal crossbreeding in the organic production system) and reduced income from slaughter cows because fewer cows were culled every year.

Table 5. Simulated herd dynamics in conventional and organic herds with purebred Swedish Holstein, two-breed terminal crossbreeding system with Swedish Holstein purebreds and F1 Swedish Red x Swedish Holstein crossbreds, and two-breed rotational crossbreeding

	Organic			Conventional		
	Purebred	**Terminal**	**Rotation**	**Purebred**	**Terminal**	**Rotation**
Cows	103	103	103	103	103	103
Crossbred cows (%)	0	31	100	0	31	100
1st parity cows (%)	39	36	30	39	36	30
3rd parity and older cows (%)	37	41	49	37	41	49
Replacement (%)	38.2	36.4	30.3	39.3	35.8	30.1
Young stock (n)	90	88	73	93	84	72
Surplus heifers sold (n)	1	2	2	1	1	2
Dairy bull calves sold (n)	45	27	37	46	26	37
Beef x dairy crosses sold (n)	9	31	28	6	30	28
305-d ECM yield (kg)	9,148	9,178	9,033	10,007	9,969	9,823
Calving interval (days)	415	409	401	409	406	400
Conception rate (cows)	0.36	0.38	0.43	0.36	0.39	0.43
Total disease treatments/100 cows	41.9	42.0	40.4	40.3	38.4	34.9
Cow mortality (%)	6.3	5.7	4.7	6.3	5.8	4.5
Calf mortality (%)	5.8	5.3	4.7	8.6	7.7	6.3
Young stock mortality (%)	3.6	3.5	3.4	3.6	3.5	3.5

Table 6. Simulated annual economic consequences (€/cow) in conventional and organic herds with purebred Swedish Holstein, two-breed terminal crossbreeding system with Swedish Holstein purebreds and F1 Swedish Red x Swedish Holstein crossbreds, and two-breed rotational crossbreeding. The total contribution margins are not exactly sums of the sub-values, due to rounding of each sub-value. Percentages in parenthesis are the increase from the purebreeding scenario within production system

	Organic			Conventional		
	Purebred	**Terminal**	**Rotation**	**Purebred**	**Terminal**	**Rotation**
Income						
Milk sales	4,360	4,383	4,323	3,730	3,694	3,652
Slaughter cows	269	259	218	270	248	214
Live calves	109	131	150	104	127	146
Surplus heifers	12	26	26	16	16	20
Total income	4,751	4,798	4,717	4,093	4,085	4,033
Costs						
Feeding, cows	1,442	1,446	1,431	1,245	1,242	1,230
Feeding, young stock	345	336	281	250	226	192
Inseminations	50	53	46	51	52	45
Disease treatments	55	55	53	35	34	30
Other, cows	142	142	140	144	142	140
Other, young stock	54	52	43	55	50	43
Total costs	2,078	2,073	1,985	1,780	1,747	1,681
Total return	2,674	2,725 (+1.9%)	2,733 (+2.2%)	2,313	2,333 (+0.9%)	2,352 (+1.7%)

The milk yield was expected to decrease when introducing crossbreeding because SR has a lower milk yield than SH. However, the relatively small change in milk yield was due to a combination of heterosis and having more older cows in the herd. According to our simulations, the economic benefit of XB will eventually vanish if the relative ratio in milk yield between the breeds is less than 0.92.

The economic return in a dairy herd is very dependent on milk and feed prices and is thus sensitive to changes in them. If the milk prices increased, the benefit of XB decreased. On the other hand, a drop in milk price made XB even more beneficial because the other economic effects (e.g., slaughter calves, reduced costs from fewer youngstock) became relatively more important. Changing the feed prices had the opposite effect. If the feed prices dropped, a high milk yield was more important than lower feed costs to the total return. A higher price for feed caused a higher benefit of XB versus purebreeding.

4.3 Combining crossbreeding with sexed semen, beef semen, and genomic testing (paper III)

4.3.1 Material and methods

In this study, the aim was to estimate economic and genetic consequences of terminal crossbreeding combined with various strategies of using sexed semen, beef semen, and genomic testing. Two base herds were created to illustrate average Swedish conventional dairy herds having pure SR or SH cows. Forty different scenarios were simulated with purebreeding or terminal crossbreeding with the other breed, various amounts of SS, and with or without genotyping purebred heifers. Twenty-four of the scenarios will be discussed further in this summary of the study.

The scenarios were simulated by two stochastic simulation models: SimHerd Crossbred (Østergaard et al. 2018) for the simulation of herd dynamics, breed and heterosis effects, and ADAM to simulate the genetic progress in the simulated herd (Pedersen et al. 2009). The breed-specific input parameters for SimHerd Crossbred were the same as for the conventional production system in paper II. The output from SimHerd Crossbred was used to calculate the operational return and form input parameters for ADAM describing the breeding scheme and flow of animals

(Figure 6). This way, the simulated herd scenarios were the same across the two simulation models. The output from ADAM was used to calculate the genetic return as the average economic value of the genetic level of replacement heifers born in the herd. The sum of the operational return and the genetic return constituted the total return.

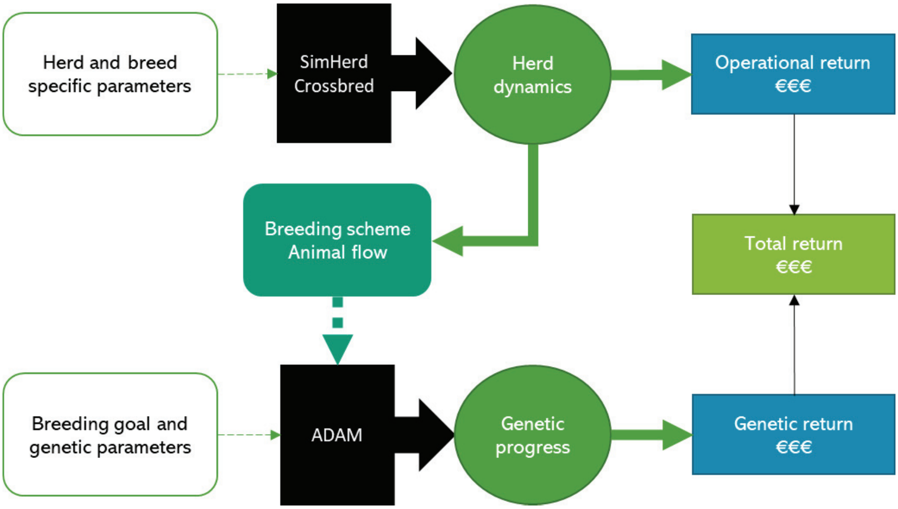

Figure 6. Illustration of the simulation flow starting with adding herd and breed-specific input parameters to simulate herd dynamics in the SimHerd Crossbred model. Output from this model was used to calculate the operational return and described the breeding scheme and animal flow within the herd used as input parameters in the ADAM model and input parameters concerning the breeding goal and genetic parameters. Output from ADAM was used to calculate the genetic return, which summed to a total return together with the operational return

The breeding schemes (Table 7 and Table 8) had predetermined use of SS and the three levels were: no SS (0:0), 90% SS in heifers (90:0), or 90% SS in heifers and 45% SS in first parity cows (90:45). The use of SS in purebred heifers and cows only implied two SS attempts, whereafter conventional dairy semen (CS) was used if additional inseminations were needed. Across the scenarios, we wanted to keep a limited and similar surplus of heifers by using BS. In the purebreeding scenarios, BS was prioritized for the oldest cows to limit the surplus of heifers (Table 7).

Table 7. Breeding schemes for **purebreeding** scenarios based on Swedish Holstein and Swedish Red showing the proportion of sexed semen (SS), beef semen (BS), and conventional semen (CS) used for heifers, first parity cows (1st), second parity cows (2nd), and third parity and older cows (3rd +)

Base breed	**Scenario**	**Type**	**Heifers**	**1st**	**2nd**	**3rd +**
Swedish Holstein	**0:0**	SS	-	-	-	-
		BS	-	-	-	60
		CS	100	100	100	40
	90:0	SS	90	-	-	-
		BS	-	-	15	100
		CS	10	100	85	-
	90:45	SS	90	45	-	-
		BS	-	-	60	100
		CS	10	55	40	-
Swedish Red	**0:0**	SS	-	-	-	-
		BS	-	-	-	60
		CS	100	100	100	40
	90:0	SS	90	-	-	-
		BS	-	-	70	100
		CS	10	100	30	-
	90:45	SS	90	45	-	-
		BS	-	-	100	100
		CS	10	55	-	-

The terminal crossbreeding scenarios used the same breeding scheme for SS and implied having a nucleus of purebred females while the rest of the herd would consist of F1 crossbreds (Table 8). The size of the nucleus was regulated by producing sufficient purebred replacement heifers bred from the youngest animals in the nucleus, and crossbred replacement heifers bred from the oldest cows in the nucleus. Hence, the proportion of crossbred animals in each herd scenario resulted from the breeding scheme and the difference in fertility and survival between the two breeds. There was no difference in the proportion of crossbreds in the SR herd between 90:0 and 90:45 because there were relatively few first parity cows to select from for SS.

Table 8. Breeding schemes for **terminal crossbreeding** scenarios based on Swedish Holstein and Swedish Red showing the proportion of sexed semen (SS) and conventional semen (CS) used for purebred heifers, first parity cows (1st), and second parity and older cows (2nd), as well as the proportion of purebred females used for dairy crossbreeding (XB) in the respective age groups. The proportion of crossbreds (F1) is a result of the breeding scheme

Base breed	**Scenario**	**Type**	**Heifers**	**1st**	**2nd +**	**F1**
Swedish Holstein	**0:0**	SS	-	-	-	
		CS	100	100	100	
		XB	-	-	10	5
	90:0	SS	90	-	-	
		CS	10	100	100	
		XB	-	10	65	27
	90:45	SS	90	45	-	
		CS	10	55	100	
		XB	-	10	85	33
Swedish Red	**0:0**	SS	-	-	-	
		CS	100	100	100	
		XB	-	-	60	34
	90:0	SS	90	-	-	
		CS	10	100	100	
		XB	-	10	100	46
	90:45	SS	90	45	-	
		CS	10	55	100	
		XB	-	15	100	46

The crossbred cows and heifers were bred to BS and did therefore not contribute with new breeding animals. In SimHerd Crossbred, first parity cows in the 90:45 breeding scheme (Table 8) could potentially be selected for both breeding with SS and XB. Thus, some crossbred heifers in this scheme might be born from SS.

The same breeding schemes were used in scenarios with GT. The purebreeding scenario with breeding scheme 0:0 and without GT within base breed was considered as the base scenarios.

The prices used in this simulation study were the same as in paper II, except we also included the labor costs for heifers in this study. This cost was set to €261.6 per replacement heifer per year (Länsstyrelsen Västra Götaland 2019).

The scenarios using GT implied that all purebred heifers were genotyped at the time they were ear-tagged. In SimHerd Crossbred, there was only a cost associated with GT set to €22.5 per genotype. In ADAM, the genotyped females were selected based on GEBVs, associated with a higher prediction accuracy than pedigree-based breeding values.

The breeding goal and economic weights simulated in ADAM mimicked the Nordic Total Merit Index[3] (NTM) (Buch et al. 2012). Furthermore, breeding value estimation of crossbred animals was not implemented in ADAM at the time of simulation, and therefore we assumed that SR and SH had identical genetic parameters.

The operational and genetic return were means of 1,000 replicates of ten years of simulations at equilibrium from the respective models. In SimHerd Crossbred, equilibrium occurred when the effect of the input parameters and breed proportions (in the terminal crossbreeding scenarios) were steady between the years. In ADAM, equilibrium occurred when the genetic progress between the years was steady.

4.3.2 Results and comments

Regardless of the breed in the base herd, the results showed positive total returns when including SS, GT, terminal crossbreeding, or combinations of the breeding tools. For the SH herd, the best scenario was with SS breeding scheme 90:45 including both terminal crossbreeding and GT where the total return was +€58 higher per cow-year than the base scenario (0:0 without terminal crossbreeding and without GT; Figure 7). For the SR herd, the best scenario was with SS breeding scheme 90:0 including both terminal crossbreeding and GT and had a total return of +€94 per cow-year (Figure 8), though followed closely by the 90:45 scheme including terminal crossbreeding and GT (+€93). Because we simulated the same genetic parameters for both breeds in ADAM, the breed differences in the genetic and operational returns were due to phenotypic differences assumed in SimHerd Crossbred.

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[3] www.nordicebv.info

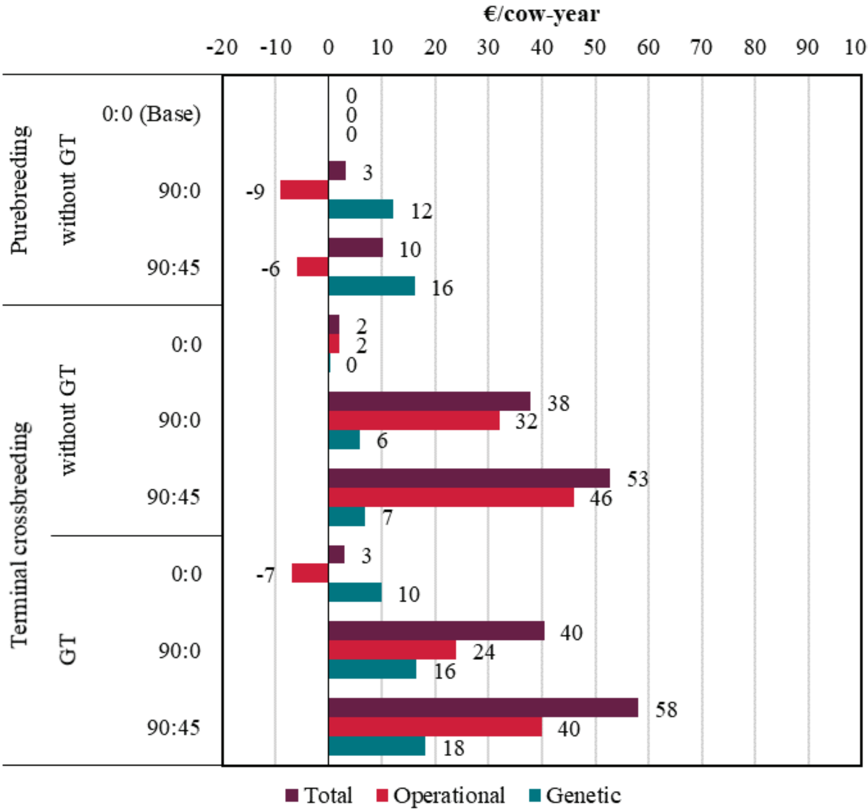

Figure 7. Operational (red), genetic (blue), and total economic returns (purple) in € per cow-year for simulated **Swedish Holstein** scenarios with purebreeding or terminal crossbreeding, using genomic selection (GT) or not using genomic selection (no GT) within sexed semen schemes where 0% (0:0), 90% of the heifers (90:0), and 90% of the heifers + 45% of the first parity cows (90:45) were bred to sexed semen

Terminal crossbreeding caused an increase in the operational return. The crossbred animals in the SH herd had better functional traits, thus better longevity, but slightly lower milk yield than the purebred SH. The crossbred animals in the SR herd had similar functional traits as the SR purebreds, and a higher milk yield. Using terminal crossbreeding in the SR herd with breeding scheme 0:0 had a much higher effect (+€69; Figure 8) than in the SH herd (+€2; Figure 7) because of much more crossbreds in the SR herd (Table 8).

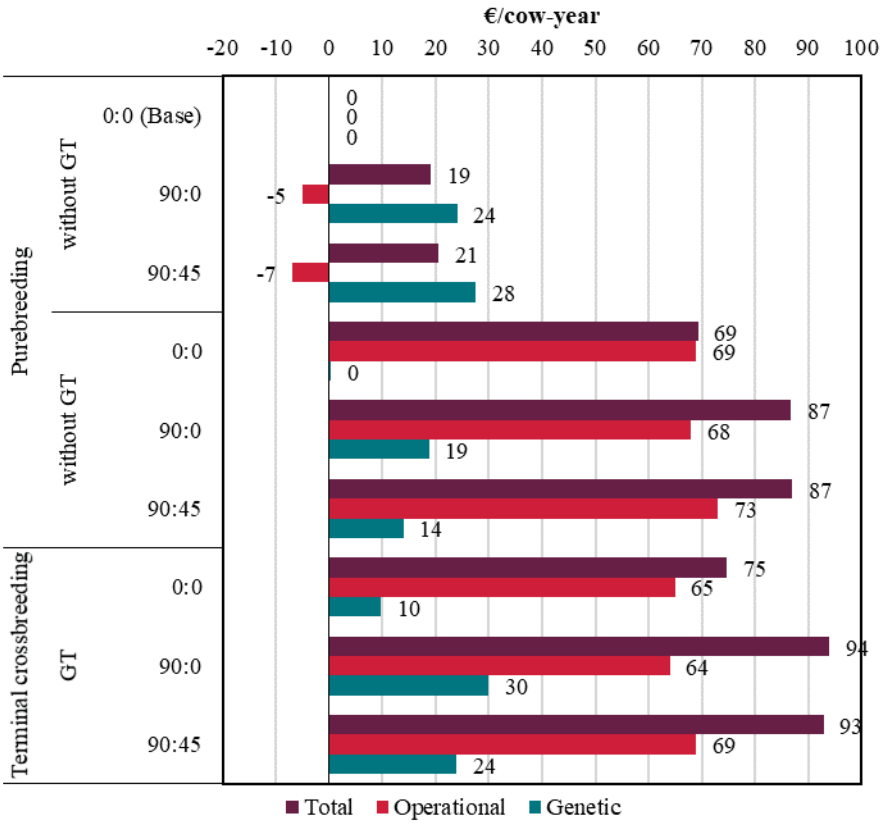

Figure 8. Operational (red), genetic (blue), and total economic returns (purple) in € per cow-year for simulated **Swedish Red** scenarios with purebreeding or terminal crossbreeding, using genomic selection (GT) or not using genomic selection (no GT) within sexed semen schemes where 0% (0:0), 90% of the heifers (90:0), and 90% of the heifers + 45% of the first parity cows (90:45) were bred to sexed semen

In the GT scenarios, the total cost of genotyping depended on the number of purebred replacement heifers, which was somewhat higher across the SH scenarios than the SR scenarios. The SR breed was better in terms of reproduction traits, and therefore, the herd scenarios for this breed did not need as many youngstock for replacement as needed in the SH herd scenarios. Terminal crossbreeding reduced the cost of genotyping as the size of the purebred nucleus decreased.

Terminal crossbreeding had a negative effect on the genetic return. The genetic level of the crossbreds was lower than the purebreds because they were bred from the oldest and (possibly) genetically inferior females in the nucleus. However, increasing the proportion of crossbred animals in the herds did not decrease the genetic return, probably because the genetic level in the purebred nucleus increased with higher selection pressure from using SS, which passed on to the crossbreds a generation later.

The genetic returns in the terminal crossbreeding scenarios did not go below the genetic returns in the base scenario. The SimHerd Crossbred model does not include genetic progress, and therefore the selection of breeding animals was fixed in age groups given in the breeding schemes. The fixed age distributions passed on to ADAM, limited it to select the genetically best females within age groups instead of across the herd. Additionally, the parameters in SimHerd Crossbred controlling selection for BS in the purebreeding scenarios were available for four age groups (heifers, first parity cows, second parity cows, and older cows), while parameters controlling selection for XB was only available for three age groups in the terminal crossbreeding scenarios (heifers, first parity cows, and older cows). Thus, an artefact of the simulation setup might have added a small advantage on the genetic return to the terminal crossbreeding scenarios, because purebred dams selected for XB could potentially be younger than those selected for BS in the purebreeding scenarios.

4.4 Crossbreeding as a conservation strategy (paper IV)

4.4.1 Material and methods

In this study we evaluated the economic potential of using terminal crossbreeding as a conservation strategy. Three herd scenarios were created in SimHerd Crossbred (Østergaard et al. 2018): a herd with purebred SKB, to illustrate a dairy herd with a native breed, a herd with purebred SR, and a herd with terminal crossbreeding having purebred SKB and F1 crosses between SR and SKB.

For the two purebreeding scenarios, we ensured a limited surplus of 1 – 3 replacement heifers by inseminating 25% of the cows in the herd with BS. In the terminal crossbreeding scenario, both purebred and crossbred heifers were produced by the purebred nucleus, while the crossbred cows in the herd only produced beef x dairy crosses. The limit of surplus replacement heifers was thus kept by using an adequate number of purebred females for crossbreeding with SR. This was achieved by applying 20% crossbreeding of the purebred nucleus.

The simulated SKB and SR herds were set up as average organic Swedish herds within their breeds, using phenotypic breed parameters based on the Swedish cattle database (Kokontrollen managed by Växa Sverige). The SKB cows were inferior to SR in most traits. However, the number of SKB contributing with data was very meager, and therefore the parameters used for SKB cows may not illustrate the actual characteristics of the breed. To our knowledge, heterosis for crosses between SKB and SR has never been documented, and therefore we used the same heterosis as in paper II (for crosses between SR and SH). We also used the same prices as in paper II and added specific SKB breed prices. Furthermore, we did not include financial subsidies for keeping SKB paid by the government in the economic calculations.

4.4.2 Results and comments

The terminal crossbreeding scenario resulted in 75% purebred SKB cows in the nucleus, and 25% F1 crosses between SR and SKB. The yearly total economic return was €181 (12%) higher per cow than having purebred SKB (€1,334). Relative to the herd with purebred SR (€2,552), the total return in the terminal crossbreeding scenario was €1,037 lower per cow. The proportion of crossbreds allowed was primarily an effect of better fertility and less youngstock mortality. Cows in the SR herd performed better cows in the SKB herds. Despite only 12.5% SR genes, the average performance of the cows in the terminal crossbreeding herd was mainly the average of the performances in the SR and SKB herds (except for milk yield, which was lower than the average).

From a societal perspective, a terminal crossbreeding strategy may not be beneficial for the conservation of native breeds. If a certain number of cows of the native breed population is to be maintained, having crossbred animals in the herds will not change the total amount of subsidies paid by the government. In case the subsidy is supposed to fully compensate the economic difference between the native and the modern breed, the terminal crossbreeding scenario in our study will need more subsidies ((2,552-1,515)/0.75 = €1,383/cow) than the purebreeding scenario with SKB (2,552-1,334 = €1,228/cow).

From a herd perspective, the economic benefit from the terminal crossbreeding strategy can as a motivation to keep the SKB cows in the herd. For the herd having SKB cows in our study, the loss of subsidies from having 75% SKB cows instead of 100% can be covered by the crossbred cows, since €181 earned per cow in the terminal crossbreeding strategy is higher than the current subsidy in Sweden (€145 per cow; Swedish Board of Agriculture 2021).

A better economic alternative to crossbreeding would be keeping purebreds of a high-yielding breed in the same herd as the native breed. If the 25% crossbreds in the terminal crossbreeding scenario were exchanged with SR, then the yearly total return is expected to be 1,334*0.75+2,552*0.25 = €1,639 per cow, which is a benefit of €124 more than crossbreeding. However, keeping purebred cows of two very different breeds may be impractical if the breeds require different management routines.

4.5 Genomic prediction using summary statistics (paper V)

4.5.1 Material and methods

The aim of this study was to evaluate a genomic prediction model for estimating genomic breeding values in crossbred animals, using summary statistics from purebred reference populations. We worked with three breed populations with genotype data at 51,477 loci: Danish Holstein (HOL), SR, and Danish Jersey (JER) as in Karaman *et al.* (2021). For computational reasons, only the 12,664 SNPs located on the first five chromosomes were considered. Using a subset of the data, we simulated a base population of 1,000 females and 50 males from both HOL and SR and 200 females and 20 males from the JER data. Then twelve generations of animals were bred in each breed population by randomly mating the same number of females (1,000 and 200) and males (50 and 20) from the previous generation. Simultaneously two populations of rotational crossbreeding systems were made using the bulls in the purebred populations. One was a three-breed rotational crossbreeding system (MIX) with HOL x JER x SR, and the other was a two-breed rotational crossbreeding system (JXH) with JER x HOL crosses. Both crossbred populations consisted of 1,000 females and

50 males, although the males were not used for breeding in subsequent generations. In the twelfth generation, both JXH and MIX animals were HOL-sired. All animals had known breed of origin of alleles traced back to the base population. That way, we calculated the genomic breed proportions in each of the crossbred animals.

The genotypes from the animals simulated in the base population were used to calculate QTL effects and breed-specific QTL substitution effects at each locus to compute genotypic values. The phenotypic values were computed by adding an environmental effect to the genotypic values of each animal. The simulated trait had a heritability of 0.40 among all breeds.

The five test populations (HOL, SR, JER, MIX, and JXH) were animals from generation 12. The reference populations were formed from generations 9, 10, and 11. Hence the reference population for the individual breed groups consisted of 3,150 (HOL, SR, MIX, or JXH) or 660 animals (JER). The combined reference population consisted of 13,260 animals.

Each test population had GEBVs predicted from each of the single breed reference populations (within-breed approach) or from the combined reference population where the model considered the SNP effects among the breeds homogeneous (joint-breed approach) or heterogeneous (breed origin to alleles approach, from now on called BOA approach). Furthermore, the two crossbred test populations had GEBVs estimated using a model including the pure breed reference populations (HOL, SR, and JER), tracing alleles back to their pure breed of origin in the base population (pure-BOA approach).

The BOA approach was used further for analyses of different information available in the reference populations. The analyses included full genotype and phenotype information from MIX and JXH reference populations and different combinations of full information and summary statistics or no information available from the pure-breed references. Summary statistics implied using means of SNP effects, estimated from the within-breed approach, and their prediction error variances, instead of using the full genotypic and phenotypic data from the purebred reference populations.

4.5.2 Results and comments

Predicting GEBVs using a within-breed approach achieved the highest accuracies when the reference population was of the same breed as the test population (Table 9). However, for MIX, the accuracies were not significantly different between predictions based on a MIX (0.559) or HOL (0.546) reference population. Using the pure-BOA approach increased the prediction accuracies for MIX, but for JXH, it was the same as a prediction based on the JXH reference population only. The highest prediction accuracies were achieved when all breed groups were combined in the reference population (joint-breed or BOA), and that also applied to the pure breed test populations – especially the breed with a small population (JER). Furthermore, the prediction accuracies for JXH using the joint or BOA approaches were as high as for HOL.

Table 9. Prediction accuracies for three-breed rotational crosses (MIX) between Danish Holstein (HOL), Danish Jersey (JER), Swedish Red (SR) and two-breed rotational crosses between JER and HOL (JXH) using individual breed groups, only pure breeds, or all breed groups in the reference population. Different characters in subscript mean significantly different values ($p<0.05$) compared within test population (column-wise)

Reference	Approach	HOL	RDC	JER	MIX	JXH
HOL	Within-breed	0.764_c	0.149_e	0.068_f	0.546_d	0.595_d
SR	Within-breed	0.120_f	0.739_c	0.075_f	0.362_f	0.117_g
JER	Within-breed	0.017_g	0.056_g	0.644_c	0.147_g	0.262_f
MIX	Within-breed	0.479_e	0.542_d	0.513_e	0.559_d	0.537_e
JXH	Within-breed	0.549_d	0.105_f	0.627_d	0.473_e	0.662_c
Pure breeds only	Pure-BOA	-	-	-	0.663_c	0.656_c
All breed groups	Joint-breed	0.791_b	0.754_b	0.734_b	0.764_a	0.792_a
All breed groups	BOA	0.798_a	0.761_a	0.743_a	0.753_b	0.789_b

In contrast to our expectations, the BOA approach was not superior to the joint-breed approach in this study. An explanation for this is probably a high genetic correlation between the breeds (0.62 – 0.87, computed from genetic variances and covariances). Assuming homogeneous SNP effects in the joint-breed approach tends to neutralize SNP effects unique for individual breeds. If the genetic relationship is high, the number of unique SNP effects will be minimal, and the prediction accuracies will eventually be high for all test populations (Karaman et al. 2021). A distant genetic relationship between the breeds will create an advantage for the BOA approach because tracing back to the alleles of origin will capture the unique SNP effects that would have been underwhelmed by the joint-breed approach (Sevillano et al. 2017; Karaman et al. 2021).

When full genotype and phenotype data are unavailable from the pure breeds, a promising alternative is to use summary statistics (Table 10). The difference between accuracies of predictions based on full data from all breeds and only summary statistics from pure breeds was smaller than the difference between using summary statistics and having no information available from pure breeds.

Table 10. Prediction accuracies for three-breed rotational crosses (MIX) between Danish Holstein (HOL), Danish Jersey (JER), Swedish Red (SR), and two-breed rotational crosses between JER and HOL (JXH) in different scenarios, including full phenotype and genotype data (F), summary statistics (S), or no information (-). Different characters in subscript mean significantly different values ($p<0.05$) compared within the test population (column-wise)

Data from reference population					Test population	
HOL	SR	JER	MIX	JXH	MIX	JXH
F	F	F	F	F	0.753_{b}	0.789_{b}
S	S	S	F	F	0.720_{c}	0.768_{c}
F	S	S	F	F	0.718_{c}	0.782_{e}
F	S	F	F	F	0.718_{c}	0.785_{d}
F	F	S	F	F	0.755_{a}	0.791_{a}
-	-	-	F	F	0.590_{f}	0.676_{gh}
F	-	-	F	F	0.647_{e}	0.669_{h}
F	-	F	F	F	0.655_{d}	0.693_{f}
F	F	-	F	F	0.706_{c}	0.679_{g}

5. General discussion

5.1 Crossbreeding in different production systems

Crossbreeding is often associated with organic and pasture-based production systems with low concentrate feeding inputs because such systems rely more on functional traits and grazing abilities than milk yield compared with conventional production systems (Vance et al. 2012; Washburn & Mullen 2014; Quénon et al. 2020). The study in paper II confirms that organic production may benefit the most from crossbreeding, but the conventional production system can also benefit. During my visits to organic farms with crossbreeding in Sweden and Denmark, the farmers indicated that the crossbred cows were much better at finding the grass on the pasture than the Holstein cows they had on the farm. Studies support that crossbreds perform better on pasture or grass-based diets than their purebred herd mates (Xue et al. 2011; Coffey et al. 2018).

There is no doubt that milk yield is of high importance for the total economic profit in a dairy herd and that Holstein is the superior breed when it comes to milk production. However, many other breeds have better performance in functional traits, which farmers may prioritize over profit (Bock et al. 2007). Improving welfare-related traits such as udder health, claw and leg health, and longevity is often weighted higher than improving milk yield (Ahlman et al. 2014; Martin-Collado et al. 2015; Slagboom et al. 2016; Skjerve et al. 2018; Paakala et al. 2020). Combining high milk yield from Holstein and good reproduction and health from another breed, such as the SR breed, in a crossbreeding strategy can improve profitability (papers II and IV) and animal welfare in a dairy herd.

This thesis did not aim to find the optimal crossbreeding strategy, as the optimal strategy may vary between individual herds, depending on the herd conditions, production system, capacity, and expectations. Nevertheless, the findings of the studies in papers I-V can be the basis for recommendations for implementing systematic dairy crossbreeding.

5.2 Effect of reducing young stock

The simulations in papers II and III revealed that better reproductive performance in crossbred cows is a key to improved profitability in crossbred herds because the number of young stock for dairy replacement can be reduced when fertility improves. In paper II, we ignored the effects of reducing labor costs of young stock in the herd. If we had included the same labor costs as in paper III for the conventional production system (€261.6 yearly per replacement heifer), the total return would have been €43 (+2.1%) and €92 (+4.4%) per cow-year higher than the purebreeding scenario for the terminal and rotational crossbreeding scenarios, respectively. That is more than twice the increase in total returns of crossbreeding without labor costs included. It is also worth emphasizing that the results achieved for terminal crossbreeding is an effect of just 31% crossbreds in the herd. In another study, terminal crossbreeding having a purebred SR nucleus and 41% F1 crosses between SH and SR achieved 3.8% (conventional) and 5.0% (organic) higher total returns compared with purebreeding with SR, including labor costs on young stock (Clasen et al. 2020). The profitability of terminal crossbreeding in the study by Clasen *et al.* (2020) was due to a higher milk yield in the terminal crossbreeding scenario while maintaining the same level of health and reproductive performance and number of young stock as in purebreeding with SR.

The future climate changes call for dairy cows that emit less methane (Hristov et al. 2013). Genetically improving the dairy breeds to become more climate-friendly may take several generations to show noticeable effects. Measuring phenotypes of climate-related traits on a large scale in commercial dairy herds is currently difficult, time-consuming, or expensive (Hellwing et al. 2012; Negussie et al. 2017; Sorg et al. 2018), which makes data for predicting breeding values limited. The enteric methane output from a dairy herd can be reduced by reducing the number of replacement heifers and improving heifer fertility (Knapp et al. 2014; Davis et al.

2020a). Studies on enteric methane emissions from crossbred animals are scarce and show no significant difference between crossbred and purebred cows (Ferris et al. 2014; Hynes et al. 2016).

Selection of dairy cows based on production efficiency, i.e., higher milk production per unit of feed used, is more manageable and may reduce methane emissions per kg of milk produced (Bell et al. 2010; Richardson et al. 2021). Studies on feed efficiency in crossbred cattle show that crossbreds are either equally efficient or more efficient than their purebred Holstein herd mates (Anderson et al. 2007; Heins et al. 2008; Olson et al. 2012; Shonka-Martin et al. 2019b). Hence, if crossbreeding results in more feed efficient cows and can reduce the number of young stock in the herd, it may be an efficient and relatively fast strategy towards less methane emissions from the dairy herd. Furthermore, improving feed efficiency and reducing the number of young stock can reduce land use for feed production (Bell et al. 2011).

5.3 Terminal and rotational crossbreeding

This PhD project showed the benefits of terminal and rotational crossbreeding strategies on herd dynamics and profitability. However, the different crossbreeding strategies also come with other benefits as well as challenges. The crossbred animals in a terminal crossbreeding strategy will achieve maximum heterosis of 100%, while crossbred animals in a rotational crossbreeding system will achieve less depending on the number of breeds involved. However, across the whole herd, the terminal crossbreeding strategy is likely to benefit less from heterosis. For example, at least 67% of the animals in the herd need to be crossbreds in a terminal crossbreeding strategy to achieve as much total heterosis as a two-breed rotational crossbreeding strategy.

Regardless of crossbreeding strategy, there is still a need to maintain purebred lines to produce AI bulls and to improve genetic gain in purebreds to improve the crossbred animals. In the terminal crossbreeding strategy, purebreeding can occur within the same herd, because it requires a purebred nucleus responsible for breeding all of the future replacement heifers. The intention of rotational crossbreeding in a herd is to have only crossbred animals, and thus it relies more on other herds to maintain the purebred populations. Practicing a mix of purebreeding and rotational crossbreeding within a herd is also possible, but such a strategy will require additional attention to avoid one group replacing the other.

The optimal nucleus size in the terminal crossbreeding herd will mainly depend on the reproductive performance of the purebreds, the use of SS, and the replacement rate. If the reproductive performance is low, the replacement rate is high, or the use of SS is limited, the nucleus size needs to be large; hence the proportion of crossbreds becomes small, and the benefits of crossbreeding at herd level may be marginal. We showed in paper III that having only 5% crossbreds increased the total return by €2 per cow-year, while with 27% crossbreds, the total return increased by €38 per cow-year (Figure 7).

Selection of purebred females for purebreeding and crossbreeding in the nucleus in terminal crossbreeding can be challenging. The study in paper III illustrated the strategy of selecting the oldest females in the nucleus for crossbreeding, which led to an average larger genetic lag (difference) across the herd compared with the purebreeding scenarios. Selecting the youngest, and possibly the genetically best females in the nucleus for crossbreeding, would probably lead to an increasing genetic lag between the herd and the AI bulls, because the next generation of purebred breeding females would fall behind genetically. The optimal selection strategy probably lies somewhere in between those two strategies. Additionally, if breeding values for crossbred performance becomes available in the future (paper V), the purebred females could be selected according to their predicted crossbreeding and purebreeding performance.

Breeding values are a measure of reproduction worth of an animal, i.e., expected performance of its future offspring. In a terminal crossbreeding strategy, the reproduction worth of the terminal crossbred cows does not matter, because they are not used for breeding future replacement heifers. However, knowing their production worth, i.e., their expected performance as a dairy cow, may be valuable for the farmers.

A current challenge in a rotational crossbreeding strategy is to select future breeding cows without breeding values for crossbred animals. As discussed in paper V, it is expected to have breeding values available in the future. Furthermore, if the purebred AI bulls will get breeding values on crossbred performance, the selection of sires becomes easier. Until crossbred breeding values becomes available, the best strategy is probably to select the crossbred cows based on their purebred sires' and maternal grandsires' breeding values for purebreds, and the AI sires based on their breeding values for purebreds.

5.4 Genomic prediction of crossbred animals

The sizes of the prediction accuracies estimated on the simulated data in paper V may be a bit optimistic. We simulated crossbred reference populations at the exact size of HOL and SR. However, in reality, crossbred reference populations may be much smaller than purebred reference populations because of a paradox of lack of prediction models causing genotyping of crossbred animals less attractive (Wallin & Källström 2019), while the development of prediction models requires an adequate number of genotyped animals. Crossbred reference populations may also contain different crosses than strictly rotational crosses, for example, F1 crosses. Furthermore, the simulations of phenotypic and genetic values in paper V ignored heterosis and non-additive effects, which will likely be present in real data. Therefore, the prediction accuracies for the crossbred animals in paper V can be considered an upper limit of what would be expected.

When non-additive effects are ignored, the unbiasedness of genomic prediction increases (Su et al. 2012; Esfandyari et al. 2016), and therefore these need to be included before applying the model from paper V for predicting GEBVs on real animals. Accurate estimations of non-additive effects require large reference populations (Su et al. 2012; Lund et al. 2014), which may be a limitation for including non-additive effects in genomic prediction models for some breed (and crossbred) populations.

Including dominance effects in models for genomic prediction of the crossbred performance of purebred animals have shown higher prediction accuracies and less prediction bias than models only considering additive genetic effects (Su et al. 2012; Wellmann & Bennewitz 2012; Esfandyari et al. 2016). The inclusion of epistatic effects in a model may improve prediction accuracies, but the effect is relatively small compared with the effect of including dominance (Wittenburg et al. 2011; Su et al. 2012). Furthermore, the effect of including epistatic effects on genomic prediction accuracies may disappear if the number QTLs that are responsible for the genetic variation is large (Wittenburg et al. 2011; Mäki-Tanila & Hill 2014) and if a high LD is present (Vitezica et al. 2017). On the other hand, variance explained by dominance effects is not affected by LD (Hill & Mäki-Tanila 2015).

There is a potential of using summary statistics for genomic prediction in crossbred animals. A base for sharing summary statistics from foreign dairy cattle breed populations is developed in the Interbull SNPMace project (Jighly et al. 2019). The SNPMace model includes prediction error co-variances between SNPs (Jighly et al., 2019), whereas our model in paper V only considers prediction error variances of estimated SNP effects. Thus, the SNPMace model may be more accurate than our model for summary statistics. However, SNPMace only accommodates combining data of the same breeds but could potentially be used for multi-breed and crossbred predictions.

5.5 Selecting crossbreds and purebreds for crossbreeding

The survey in paper I, an interview study by Wallin & Källström (2019), and personal communications with farmers suggest that some farmers hesitate to implement crossbreeding because they are missing the ability to select their future replacement heifers according to breeding values. Hopefully, the publication of breeding values for crossbred animals in the nearest future will make more farmers consider crossbreeding. However, questions remain on how crossbred breeding values should be compared, which breeding goal it should reflect, and how to select purebred sires for crossbreeding.

Selecting purebred animals based on breeding values for crossbred performance has improved terminal crossbreds in pigs (Esfandyari et al. 2018). Stock *et al.* (2021) simulated genetic gain in a rotational breeding scheme between Angler and German Holstein. They did not find a difference in gain for true genomic values for the crossbreds regardless of if the purebred Angler sires were selected based on purebred breeding values, crossbred breeding values, or a weighted combination. Strategies for selecting animals in different crossbreeding scenarios needs to be investigated further.

Predicting the crossbred breeding values on a purebred scale may be unfair because the crossbred animals will risk being underestimated (or overestimated) compared to the purebred – especially those sired by another breed than the breed compared to. It would essentially be the same as comparing two breeds on the same scale. Maybe a better alternative is to compare crossbred breeding values based on the sire the cow is expected to be bred to according to the crossbreeding strategy. Thus, comparing cows that are expected to be bred to the same sire breed.

Phenotypic selection of crossbred animals can lead to genomic breed proportions favoring a specific breed (Wu et al. 2020) and potentially decrease heterosis in further generations (Akanno et al. 2017). Knowing the genomic breed proportion of a crossbred animal creates an opportunity to optimize heterosis in the future generation. The genomic breed proportion of a crossbred animal (through more than one generation) is not necessarily as expected from the pedigree. For example, in the simulated three-breed rotational crossbreeding strategy in paper V, the genomic breed proportions for animals in the latest generation were on average 52% HOL, 28% SR, and 15% JER as expected, but ranged between 50 – 81% HOL, 2 – 50% SR, and 0 – 37% JER. According to the breeding scheme, all these animals were supposed to be bred to a JER sire next. However, it may be more beneficial to breed the animals where the genomic breed proportion of JER was higher than that of SR to an SR sire, and thus base the mating on the highest expected heterozygosity in the offspring.

5.6 Crossbreeding combined with other breeding tools

The simulated scenarios in papers II and IV were not optimized in terms of economic output, and therefore these results should not be considered the best breeding strategies for the given herd. For example, using SS and more BS in the rotational crossbreeding scenarios (paper II) might have returned a higher income from beef x dairy crosses. Additionally, SimHerd Crossbred is not programmed for modeling breeding values and genetic progress, and therefore any genetic (dis)advantages of the simulated breeding strategies were ignored in paper II. The study in paper III included the genetic consequences of the terminal breeding strategy, but the selection of dams for purebreeding and crossbreeding was not optimized for the highest genetic profit.

Sexed semen has 5 – 30% lower conception rates (Borchersen & Peacock 2009; Butler et al. 2014; Maicas et al. 2020) and is more expensive than CS. These features may make farmers hesitant to use SS (Wallin &

Källström 2019). Insemination with BS has shown improved conception rates in dairy cattle (Bittante et al. 2020a). If higher conception rates are associated with semen from another breed, SS may be more efficient in a crossbreeding strategy than in a purebreeding strategy.

The studies in this thesis did not consider the optimal beef x dairy crossbreeding strategy regarding the combination beef sire breeds and dairy dam breeds. Researchers have investigated the beef sire breed effects of beef x dairy crossbreeding regarding the performance of slaughter calves and the calving performance of their dairy dams (Fouz et al. 2013; Bittante et al. 2020b; Davis et al. 2020b; Eriksson et al. 2020; Bittante et al. 2021). Studies suggest equal or better meat quality of dairy breeds than beef breeds, although lower carcass yields (Pfuhl et al. 2007; Christensen et al. 2011). Thus, a dairy crossbreeding strategy can be optimized for beef production by using dairy and beef breeds with high meat quality and carcass yields.

The use of embryo technologies (such as MOET) decreases the generation interval and potentially increases genetic gain in dairy cattle populations (Meuwissen 1998; Pedersen et al. 2012; Bouquet et al. 2015; Thomasen et al. 2016). The use of MOET in a crossbreeding strategy has not been investigated but may create some opportunities to improve the genetic level in the herd and speed up the transition from purebreeding to crossbreeding in the herd. It is also possible to utilize crossbred females as recipients for purebred embryos. The responding farmers in the survey study (paper I) were against flushing their own animals for embryos, but neutral to buying embryos.

5.7 Importance of purebreeding and conservation of native breeds

It is essential to maintain purebred lines for the benefit of genetic gain and heterosis in crossbreeding. The parental breeds need to be economically equivalent if crossbreeding is expected economically superior (Freyer et al. 2008; Sørensen et al. 2008), and therefore they need to improve simultaneously. The numerically largest dairy breeds in the Nordic countries, are economically equivalent (Stålhammar 2014; Kargo et al. 2020) – at least for now. Statistics in Swedish dairy cattle show that the SH is currently improving in milk yield, reproduction, and health traits – and improving faster than SR (Växa Sverige 2019, 2021) – meaning that if this trend continues, the SR and crossbreds between SH and SR will no longer be economically competitive to SH in the future. The study in paper II showed that crossbreeding was no longer economically beneficial if the relative ratio in milk yield between the two breeds went below 0.92. Nevertheless, crossing Holstein with SR may be a way to keep SR attractive on the international market, if not the Swedish.

Using crossbreeding as a strategy for the conservation of breeds needs to be carefully managed but can potentially turn out successfully (Verrier et al. 2005; Lambert-Derkimba et al. 2019). It has already been decided globally (UN 1992; FAO 2007) and nationally (Swedish Board of Agriculture 2009) and nationally that native livestock breeds should be conserved for sustainable and cultural reasons. Governments are paying farmers to keep the native breeds and breed them according to breeding plans (Swedish Board of Agriculture 2021). Nevertheless, the native breed populations are still decreasing in size, at least the Swedish native cattle breeds, and therefore calls for other conservation strategies.

In the future, more economic emphasis may be put on the milk composition instead of the quantity of fat and protein, which is the current situation in the Nordic countries. Some native dairy breeds carry high frequencies of favorable alleles for cheese production, such as the kappa-casein A2-allele and beta-casein B-allele (Petrovska et al. 2017; Poulsen et al. 2017). There is also evidence that the fatty acid and mineral composition in milk from some native dairy breeds is more healthy for human consumption, compared with e.g., Holstein (Gottardo et al. 2017; Poulsen et al. 2020). These properties of native cattle breeds are worth considering in creating a niche market of locally produced dairy products. Those favorable milk alleles also exist in modern dairy breeds (Gustavsson et al. 2014; Poulsen et al. 2016; Chessa et al. 2020), and therefore crossbreeding native breeds with modern breeds may improve the yield of niche products (Saha et al. 2017) if modern AI bulls used also carry the desired alleles. There is also a great potential for utilizing GT and select cows and bulls based on desired alleles.

Genomic selection can be a valuable tool for improving also small cattle populations (Hozé et al. 2014; Thomasen et al. 2014; Schöpke & Swalve 2016; Karaman et al. 2021), and exploiting information on crossbred animals may even be a key to conserve the local breeds (Stock et al. 2021).

5.8 Farmers' perception of crossbreeding

The study in paper I revealed that dairy farmers could (roughly) be divided into two groups: those supporting crossbreeding and those not supporting it. Believing that crossbreeding threatens the pure breeds is valid, especially for breeds from a small or decreasing breed population, such as SR. Unlike poultry, beef, or sheep breeders, dairy farmers tend to be more personally attached to their animals (Bock et al. 2007), which probably makes them more attached to animals with specific characteristics (breeds). Thus, introducing a new breed or crossbreeding may be considered a significant change for dairy farmers.

In France, farmers who changed to crossbreeding had to 'stand on their own feet,' giving up on breeding advisors and genetic merit indices, and basically, they had to 'figure it out' by themselves (Ollion et al. 2018; Quénon et al. 2020; Magne & Quénon 2021). Some farmers even indicated that the feeling of being 'locked into a system' and following 'mainstream' purebreeding and following specific breeding goals led them to consider crossbreeding. Furthermore, breeding associations, advisors, and public research institutions showed limited support for crossbreeding (Magne & Quénon 2021). Farmers did not seem to be giving up on breeding advisors in our study in paper I, but since none of them had herds of entirely crossbreds, it is unknown if they only used the breeding advisors for purebreeding. Several negative comments from the respondents about the breeding goal and selection of bulls in the Nordic countries could reflect a 'locked in' feeling. Thus, more support from breeding advisors and breeding companies may motivate more farmers to consider crossbreeding.

In paper I, more of the responding farmers in the CROSS group had used or tried SS, BS, and GT than the average of all respondents (Table 4), suggesting that farmers using crossbreeding may be more open-minded to try various breeding tools. It supports the findings from the French studies that farmers using crossbreeding dared to change breeding strategy without the support from breeding advisors (Ollion et al. 2018; Quénon et al. 2020; Magne & Quénon 2021).

6. Final conclusions

- Swedish dairy farmers can be divided into two groups: those supporting dairy crossbreeding and those against it.
- Swedish dairy farmers who have tested dairy crossbreeding seem to be more interested in using sexed semen, beef semen, and genomic testing
- Terminal and rotational crossbreeding strategies between Swedish Holstein and Swedish Red are economically beneficial in average Swedish conventional and organic dairy herds
- Terminal and rotational crossbreeding strategies between Swedish Holstein and Swedish Red reduces the number of replacement heifers, compared to a herd having purebred Swedish Holstein. This gives opportunities for reduced costs of keeping young stock in the herd and potentially a reduced environmental footprint from the dairy herd
- The economic benefits of terminal crossbreeding can be improved by combining the strategy with the use of sexed semen, beef semen, and genomic testing
- There is an economic potential for dairy farmers of using terminal crossbreeding as a conservation strategy, although it may not be economically beneficial for the government. Crossbreeding alone cannot compensate for the economic gap between native and modern breeds
- In the situation where sharing of genotype and phenotype data from different breeds is impossible, the use of summary statistics can yield accuracies on genomic prediction for crossbred animals almost as high as having full data available

7. Practical recommendations

Before converting to a crossbreeding strategy, some considerations need to be made by the farmer. The most beneficial strategy depends on the herd conditions, production system, and the purpose of changing the herd by crossbreeding. The potential benefits differ between herds, and therefore the crossbreeding strategy should also be planned for the individual herds. In Table 11, general recommendations for terminal and rotational crossbreeding are given.

The number of breeds chosen depends on the traits that are of interest to combine. The more breeds involved, the more difficult the breeding strategy may become to manage, although digital mating tools can be helpful in this. For the terminal crossbreeding strategy, adding a third dairy breed to be mated with the F1 crosses can be considered, while more than three breeds (excluding the terminal beef breed) may be difficult to fit within the same herd. Having several dairy breeds in the terminal crossbreeding strategy will reduce the number terminal dairy crosses and the benefit of the terminal cross will become marginal. For rotational crossbreeding, more than three breeds can be used to maximize the benefits of heterosis.

The dairy breeds chosen for the crossbreeding strategy should be based on their complementarity and desire traits. Proven breed combinations that are promoted already on the market, such as KiwiCross and ProCross, are recommended, but other breed combinations may work just as well or even better depending on the herd conditions. Choosing sire breeds that are easily accessible is recommended.

A rotational crossbreeding strategy is easy to manage because it is simply about rotating between sire breeds for each generation. A terminal crossbreeding strategy requires more management to ensure that an adequate nucleus size is kept for producing both purebred and crossbred replacement heifers. Based on our findings in paper III, at least 25% of crossbred cows in the herd are recommended for economic benefit.

SimHerd Crossbred is a useful tool for estimating the economic benefits of crossbreeding in an individual herd (Østergaard et al. 2018). The benefits from heterosis across the herd are expected to be higher in the rotational crossbreeding strategy.

For herds having native breeds, if crossbreeding is to be used, terminal crossbreeding is recommended to conserve the pure breed.

Table 11. Recommendations for terminal and rotational crossbreeding strategies based on findings in this study

	Terminal	**Rotational**
Number of dairy breeds involved	2-3	≥ 2
Proportion of crossbred animals	Min. 25%	100%
Possibility to conserve pure breeds	Directly	Indirectly
Sexed semen	Highly recommended	Recommended
Beef semen	Required	Recommended
Genomic testing of crossbreds	Recommended if >2 breeds	Recommended
Difficulty of breeding management	Intermediate	Easy

It is highly recommended to utilize other breeding tools combined with crossbreeding to improve economic and genetic benefits. Sexed semen and BS should be used to ensure replacement heifers are bred from the best cow dams. In the case of using BS, the choice of beef sire breeds should be considered to produce slaughter calves of high quality and easy to calve for the dairy cow. Beef semen is required in the terminal crossbreeding strategy, and SS is highly recommended to ensure an optimal proportion of crossbreds in the herd.

Genomic EBVs for crossbred animals are expected soon, and therefore it is recommended to genotype crossbred heifers to contribute to a crossbred reference population for higher prediction accuracy. Furthermore, GT can be used to detect monogenic traits, such as polledness, monogenetic diseases, and alleles favorable for milk and cheese production. If GT reveals the genomic breed proportions, those can also be used as additional information in a rotational crossbreeding strategy to select animals. Thus, GT of crossbred animals will become as valuable as for purebred animals in the future and may even support purebreeding.

The economically best strategy for transitioning a purebreeding herd to a crossbreeding herd was not studied. For a fast transition, an immediate recommendation is to use SS for crossbreeding or crossbred embryos to avoid spreading diseases by moving animals between herds.

8. Future research

For future crossbreeding strategies, continued research on the heterosis and performance of crossbreds of various breeds is needed. There is a lack of studies on crossbreeding at herd level, such as transition periods, combination with other breeding tools, and selection strategies. Furthermore, the effects of having more herds with crossbreds on a national and international level need to be studied regarding the environmental footprint and population genetics of pure breeds. Additionally, the methane output per kg protein in meat and milk from herds having purebreds and herds using crossbreeding needs to be compared.

Pure breeds need to be conserved, monitored, and continuously improved to be attractive candidates for crossbreeding. The responsibility of maintaining (and improving) pure breeds needs to be considered if crossbreeding increases in popularity. Genomic prediction using information from other breeds and crossbreds is expected to be a new tool for improving and conserving small breed populations in the future (Thomasen et al. 2014; Schöpke & Swalve 2016; Britt et al. 2018; Stock et al. 2021), but this needs further studies.

The use of crossbreeding in dairy herds seems to be slowly increasing. Still, many farmers are skeptical of crossbreeding which may be partly due to a lack of support from breeding organizations, breeding companies, and breeding advisors (Magne & Quénon 2021). There is a need for the stakeholders – and maybe even national and international authorities – to support dairy crossbreeding. Participatory research, including farmers and stakeholders, on how to develop crossbreeding strategies is needed.

Genomic prediction of crossbred dairy cattle is already implemented in the US and New Zealand (Winkelman et al. 2015; VanRaden et al. 2020) and will most likely be implemented in other countries within the next few years. Continued research of models for genomic prediction in crossbred cattle that includes non-additive effects is needed. Furthermore, selection and mating schemes for different crossbreeding strategies using genomic information at herd and population level needs to be investigated.

In a vision for future dairy production, Britt *et al.* (2018) predicts that genomic selection based on mixed reference populations will lead to specialized lines of breeds for different production systems and consequently decrease the need for crossbreeding. However, the question is if purebreeding can improve dairy cows fast enough for coping with future climate challenges when the climate is changing faster than previously reckoned (IPCC, 2021). In light of increasing demands for a more sustainable dairy production, dairy farmers have an incentive to consider crossbreeding. Crossbreeding may change the cows faster than purebreeding and having more crossbred cows could make a difference in the future mitigation of greenhouse gases from dairy production on a global scale. However, there is a need for research on that hypothesis.

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Popular science summary

Future milk production requires new strategies for breeding and management. Increased demand for dairy products, greater awareness of animal welfare among consumers, and climate changes are all contributing to development and changes in dairy production. In this context, the breeding material and the breeding opportunities are often overlooked elements at herd level. This should be changed as breed choices and combination of breeds using systematic crossbreeding programs are very important elements of a herd management strategy.

Mating unrelated breeds or lines will break unfavorable genetic combinations that occur during inbreeding. Crossbreeding is the most widespread breeding strategy in pig and poultry production but less in dairy cattle, despite scientific evidence that crossbreds often perform equally or better than the purebred parental breeds. New Zealand has many crossbred cows (50%), while in 2021, Sweden and Denmark have 9 and 12% crossbred cows, respectively. In other countries, the proportion of crossbred cows in 2021 is below 10%.

The most popular dairy breed in the world is the black and white Holstein cow. However, a historical focus on high milk yield, and inbreeding, has created fertility problems, which affects the economy of dairy herds. Other breeds have lower milk yield but often better functional traits, such as fertility and longevity, making them economically equivalent to Holstein. Crossbreeding between Holstein and other breeds can create cows with high milk yield without compromising on functional traits. However, it is essential to emphasize that the genetic improvement and preservation of pure breeds is the basis for successful crossbreeding.

This doctoral thesis aimed to investigate the economic and genetic aspects of crossbreeding in dairy herds and summarize the results in a recommendation to farmers, advisors, and breeding organizations.

I the first study, we examined Swedish dairy farmers' preferences for crossbreeding and four other breeding tools: sexed semen, beef semen, genomic testing, and embryo transfer. The survey was designed as a questionnaire where the respondent had to choose between two alternatives in ten questions. The options included breeding strategies where each of the five breeding tools was included or not. We received 204 responses, showing that the preference for crossbreeding was twofold: one group supported crossing, while another group did not support it.

In the second study, we used the simulation tool SimHerd Crossbred to estimate the economic effect of using crossbreeding in an average conventional or organic Swedish Holstein herd. We simulated a terminal crossbreeding strategy, which means that the herd consists partly of purebred Holstein and partly of crosses between Holstein and Swedish Red (SRB). We also simulated a rotational crossbreeding strategy, which means that all cows are crosses between Holstein and SRB. Regardless of the production system, the herd can increase the economic return by introducing a crossbreeding strategy. The improved economic result was mainly because crossbreeding cows had a milk yield similar to Holstein, while their fertility and health were similar to SRB, which led to fewer young stock and thus lower feed costs for those. Including the saved labor costs for fewer young animals, the profit is expected to be even greater.

In the third study, we estimated the economic impact of different scenarios with combinations of the terminal crossbreeding strategy along with the use of sexed semen and genomic testing of purebred animals. Using sexed semen and genomic testing, the genetic level of purebred animals in the herd can be increased, which is transmitted to the crossbred animals. The results thus showed an increased economic gain by combining an increased genetic level for purebred animals and the benefits of improved traits with crossbreeding.

In the fourth study, we examined the economic benefits of using a terminal crossbreeding strategy to conserve endangered cattle breeds. Such breeds often have a low milk yield, and, despite other good characteristics, they cannot compete with modern dairy cattle, such as Holstein and SRB. Once again, the SimHerd Crossbred tool was used, and we compared a herd of purebred Swedish Polled Cattle (SKB) with an SRB herd, and a herd consisting of 75% SKB and 25% crosses between SRB and SKB. Introducing crossbreeding into an SKB herd resulted in a significant economic improvement, even though it could not reach the same economic level as an SRB herd. Having only 25% crossbred cows in the herd was enough to compensate for a possible loss of financial support from the government for endangered breeds, but not enough to cover the economic gap between the purebred SRB and SKB herds. Combining a terminal crossbreeding strategy with the marketing of niche products from endangered breeds can potentially create a financial motivation for conserving these breeds in milk production.

The fifth study evaluated a model for genomic breeding value prediction of crossbred cows using summary statistics on genetic effects from purebred reference populations instead of complete data on genotypes and phenotypes. Crossbreeding strategies can consist of breeds where the reference populations are found in different countries but sharing large amounts of data between countries is often difficult when breeding organizations compete on the same market. Based on real genotypes from Danish Holstein, Jersey and SRB, we simulated three purebred populations and two populations of two-breed (Holstein x Jersey) and three-breed crosses. The accuracy of predicted breeding values for the crossbreds was highest if we included complete genotypic and phenotypic data from both crosses and purebred animals in the reference population. If we only had complete data from crossbred animals and summary statistics from purebred animals, the accuracy of the prediction was almost as high - and somewhat higher than the case where there was no data on purebred animals. This means that summary statistics can replace the lack of available data from pure breeds with almost as much certainty as complete data.

Future research should concern crossbreeding strategies where genomic information is included in the breeding plan. In addition, there is also a great need to clarify the effect on the environmental footprint of introducing crossbred cows in large parts of global milk production. If the proportion of crossbred cows is to be increased nationally and globally, crossbreeding strategies must also be organized at population level so that pure breeds are maintained and kept attractive for crossbreeding.

Populärvetenskaplig sammanfattning

Framtidens mjölkproduktion kräver nya strategier för avel och skötsel. Ökad efterfrågan på mejeriprodukter, större medvetenhet om djurvälfärdens betydelse bland konsumenter och klimatförändringar bidrar alla till att branschen utvecklar och förändrar mjölkproduktionen. I detta sammanhang är avelsmaterialet och avelsmöjligheterna ofta förbisett på besättningsnivå. Detta bör ändras eftersom val av ras och kombination av raser med systematiska korsningsprogram är mycket viktiga element i en besättnings managementstrategi.

Om man korsar djur från olika raser eller linjer som inte är släkt, bryts alla ogynnsamma genetiska kombinationer som uppstår vid inavel. Korsning är en mycket vanlig avelsstrategi inom gris- och fjäderfäproduktion. För mjölkkor är korsning ovanligt, trots vetenskapliga bevis för att korsningsdjur presterar minst lika bra och ofta bättre än de renrasiga föräldradjuren. I Nya Zeeland är hälften av mjölkkorna korsningskor, medan Sverige har 9% och Danmark 12% korsningskor i mjölkkontrollen. I de flesta andra länder är andelen korsningskor under 10%.

Den mest populära mjölkrasen i världen är den svartvita holstein-kon. Ett historiskt fokus på hög mjölkavkastning i avelsmålet har tillsammans med inavel dock lett fruktsamhetsproblem som påverkar besättningens ekonomi. Andra raser, t ex röda kor (SRB), har lägre mjölkavkastning, men ofta högre fruktsamhet och bättre funktionella egenskaper, såsom hälsa och hållbarhet. Det gör dessa raser ekonomiskt likvärdiga med holstein. Korsning mellan holstein och andra raser ger kor med hög mjölkavkastning, god hälsa och hög fruktsamhet. Det är dock viktigt att betona att genetisk förbättring och bevarande av rena raser är grunden för en framgångsrik korsningsavel. Syftet med denna doktorsavhandling var att undersöka de ekonomiska och genetiska aspekterna av korsning i mjölkbesättningar och sammanfatta resultaten i rekommendationer till lantbrukare, rådgivare och avelsorganisationer.

I den första artikeln undersökte vi svenska mjölkbönders inställning till korsning och fyra andra avelsverktyg: könssorterad sperma, köttrassperma, genomisk analys och embryotransplantation. Vi gjorde en enkät där mjölkbonden fick välja mellan två alternativ i tio frågor. Alternativen handlade om avelsstrategier där de olika avelsverktygen ingick eller inte. Vi fick 204 svar, och de visade att mjölkbönderna kan delas in i två grupper: en grupp som gillar korsning, och en grupp som ogillar korsning.

I den andra artikeln använde vi ett simuleringsprogram som kallas SimHerd Crossbred för att uppskatta den ekonomiska effekten av att använda korsning i en genomsnittlig konventionell eller ekologisk svensk holsteinbesättning. Vi simulerade två olika korsningsstrategier: slutkorsning och rotationskorsning. Slutkorsning innebär att besättningen består av en renrasig holsteinkärna och holstein-SRB-korsningar. Rotationskorsning innebär att alla kor är korsningar mellan holstein och SRB enligt ett rullande schema. Oavsett om produktionen är konventionell eller ekologisk ökar den ekonomiska avkastningen med korsning. Det positiva ekonomiska resultatet beror främst på att korsningskorna har lika hög mjölkavkastning som holstein och lika god hälsa och fruktsamhet som SRB. Det leder till att färre kvigor behövs och därmed sjunker kostnaderna för foder. Färre kvigor innebär även lägre arbetskostnader vilket ökar vinsten ytterligare.

I den tredje artikeln skattade vi hur flera olika avelsverktyg tillsammans påverkar det ekonomiska resultatet. Slutkorsning kombinerades med användning av könssorterad sperma och genomisk testning av renrasiga djur. Med hjälp av könssorterad sperma och genomisk testning kan den genetiska nivån för renrasiga djur i besättningen höjas. Den genetiska förbättringen förs över till korsningsdjuren och tillsammans med korsningseffekten ger det en ökad vinst.

I den fjärde artikeln undersökte vi de ekonomiska fördelarna med att använda slutkorsning för att bevara hotade lantraser. Lantraser har ofta så låg mjölkavkastning att de, trots andra goda egenskaper, inte kan konkurrera med raser som holstein och SRB. Vi använde SimHerd Crossbred-programmet för att jämföra tre slags besättningar: en besättning med 100% renrasig svenska kullig boskap (SKB), en besättning med 100% renrasig SRB och en besättning med 75% SKB och 25% SRB-SKB-korsningar. Att införa korsning i en SKB-besättning ger en stor ekonomisk förbättring, men resultatet blir inte lika bra som i en SRB-besättning. Det räcker 25% korsningar i besättningen för att ersätta en förlust av statligt ekonomiskt stöd för hotade raser, men det är inte tillräckligt för att täcka den ekonomiska skillnaden mellan renrasig SRB och SKB. Att kombinera slutkorsning med marknadsföring av nischprodukter från hotade raser kan göra det ekonomiskt möjligt att bevara lantraser i mjölkproduktionen.

I den femte artikeln undersökte vi en modell för genomisk avelsvärdering av korsningskor med hjälp av sammanfattande statistik över genetiska effekter från renrasiga referenspopulationer. Sammanfattande statistik är ett alternativ till fullständiga data om djurens genotyp och fenotyp. Korsningsprogram kan använda raser från olika avelsorganisationer och helst skulle de inblandade avelsorganisationerna dela på data från sina genotypade djur. Det kan dock vara svårt för konkurrerande avelsorganisationer från olika länder att dela på data. Baserat på verkliga genotyper från danska holstein-, jersey- och SRB-kor simulerade vi tre renrasiga populationer och två korsningspopulationer varav en bestod av holstein-jersey-korsningar och en av tre-raskorsningar. Genomiska avelsvärden för korsningsdjuren skattades. Säkerheten för dessa avelsvärden blir högst när vi använder all genotypisk och fenotypisk information från både renrasiga och korsningsdjur i referenspopulationen. Om vi använder all genotypisk och fenotypisk information från korsningsdjur men bara sammanfattande statistik från renrasiga djur blir säkerheten för avelsvärdena nästan lika hög. Detta innebär att om avelsorganisationerna inte kan dela med sig av fullständiga data från renrasiga djur kan sammanfattande statistik ändå ge avelsvärden som har en hög säkerhet.

Framtida forskning bör innefatta korsningsprogram där genomisk information från korsningsdjur ingår i avelsarbetet. Dessutom behövs studier som visar vad omfattande korsning skulle få för konsekvenser för mjölkproduktionens klimatpåverkan ur ett globalt perspektiv. Om andelen korsningskor ska öka i Norden och globalt måste avelsarbetet organiseras så att de rena raserna fortsätter att förbättras genetiskt och bevaras långsiktigt.

Populærvidenskabeligt resumé

Fremtidens mælkeproduktion kræver nye strategier for avl og management. En øget efterspørgsel på mælkeprodukter, større opmærksomhed på dyrevelfærd blandt forbrugerne og klimaforandringer bidrager alle til at landbruget udvikles og forandrer mælkeproduktionen. I den sammenhæng er avlsmaterialet og de avlsmæssige muligheder ofte oversete elementer på besætningsniveau. Det bør ændres, da valg af race og kombination af racer ved brug af systematiske krydsningsprogrammer er meget vigtige elementer i en besætnings management strategi.

Krydser man ubeslægtede racer eller linjer, bryder man eventuelle ugunstige genetiske kombinationer, som opstår ved indavl. Det er den mest udbredte avlsstrategi i svine- og fjerkræsproduktion, men er knap så udbredt i malkekvæg, trods videnskabelige beviser på at krydsningskøer ofte præsterer på lige fod eller bedre end de rene forældreracer, samtidig med at de er mere robuste. På New Zealand har man exceptionelt mange krydsningskøer (50%) mens Sverige og Danmark i 2021 havde hhv. 9 og 12% krydsningskøer. I andre lande med en højtudviklet mælkeproduktion var andelen af krydsningskøer i 2021 under 10%.

Den mest populære malkerace i verden er den sort-hvide Holstein-ko. Et historisk fokus på høj mælkeydelse og indavl har dog skabt problemer med især frugtbarheden hos Holstein-racen, hvilket påvirker økonomien i besætningen. Andre racer har knap så høj en mælkeydelse, men ofte bedre funktionelle egenskaber, såsom frugtbarhed og holdbarhed, hvilket gør dem økonomisk ligeværdige med Holstein. Krydsning mellem Holstein og andre racer kan skabe køer, som har en høj mælkeydelse uden at gå på kompromis på funktionelle egenskaber. Det er dog vigtigt at understrege, at forbedring og bevaring af rene racer er grundlaget for succesfuld krydsningsavl.

Formålet med denne Ph.d.-afhandling var at undersøge de økonomiske og genetiske aspekter af krydsningsavl i malkekvægsbesætninger og opsummere resultaterne i en anbefaling til landmænd, rådgivere og avlsorganisationer.

I den første artikel undersøgte vi svenske landmænds præference for krydsning samt fire andre avlsværktøjer: kønssorteret sæd, kødkvægssæd, genomisk test og ægtransplantation. Undersøgelsen blev udformet som et spørgeskema, hvori kvægbrugeren (respondenten) skulle vælge mellem to alternativer ad ti omgange. Alternativerne indeholdt avlsstrategier, hvori hver af de fem avlsværktøjer indgik eller ej. Vi fik 204 svar, og i disse kunne vi bl.a. se at præferencen for krydsning var todelt: en gruppe støttede op om krydsning, mens en anden gruppe ikke støttede op om det.

I den anden artikel brugte vi simuleringsværktøjet SimHerd Crossbred til at beregne den økonomiske effekt af at anvende krydsning i en gennemsnitlig konventionel eller økologisk svensk Holstein-besætning. Vi simulerede en terminal krydsningsstrategi, som indebærer at besætningen består af en andel renracede Holstein samt en andel førstegangskrydsninger mellem Holstein og svensk rødt og hvidt kvæg (SRB – den svenske del af den nordiske røde malkerace), samt en rotationskrydsningsstrategi, som indebærer, at alle køer er krydsninger mellem Holstein og SRB. Uanset produktionssystem, kunne besætningen øge det økonomiske afkast ved at indføre en krydsningsstrategi. Den forbedrende økonomiske effekt skyldtes primært, at krydsningskøerne havde en mælkeydelse på niveau med Holstein, mens deres frugtbarhed og sundhed var på niveau med SRB, hvilket ledte til færre ungdyr og hermed lavere foderomkostninger for disse. Indregner man den sparede arbejdstid ved færre ungdyr, forventes gevinsten at være endnu større.

I den tredje artikel estimerede vi den økonomiske effekt med SimHerd Crossbred på forskellige kombinationer af den terminale krydsningsstrategi brugt sammen med kønssorteret sæd og genomisk test af renracede dyr. Ved brug af kønssorteret sæd og genomisk test kan det genetiske niveau af renracede dyr i besætningen øges, hvilket overføres til krydsningsdyrene. Dermed viste resultaterne, at der er en øget økonomisk gevinst ved at kombinere et øget avlsniveau af renracede dyr samt fordelene ved forbedrede egenskaber med krydsning.

I den fjerde artikel undersøgte vi de økonomiske fordele ved at anvende en terminal krydsningsstrategi til bevaring af udrydningstruede kvægracer.

Sådanne racer har ofte en så lav mælkeydelse, at de trods andre gode egenskaber, ikke kan konkurrere økonomisk med moderne malkekvægsracer, som f.eks. Holstein og SRB. Endnu engang blev SimHerd Crossbred-værktøjet anvendt og vi sammenlignede en besætning med renracede Svensk Kullig Boskap (SKB) med en SRB-besætning og en besætning bestående af 75% SKB og 25% førstegangskrydsninger mellem SRB og SKB. At indføre krydsning i en SKB-besætning gav en stor økonomisk forbedring, trods at den ikke kunne nå på samme økonomiske niveau som en SRB-besætning. At have blot 25% krydsninger var nok til at erstatte et eventuelt tab af finansiel støtte fra staten til udrydningstruede racer. Kombinerer man en terminal krydsningsstrategi med markedsføring af nicheprodukter fra udrydningstruede racer, kan dette potentielt skabe den økonomiske motivation til bevaring af disse racer i mælkeproduktionen som vi som nation er forpligtiget til i forhold til de internationale aftaler staten har indgået.

Den femte og sidste artikel undersøgte en model til genomisk avlsværdivurdering af krydsningskøer ved brug af opsummerende statistik af genetiske effekter fra renracede referencepopulationer, i stedet for komplette data om genotyper og fænotyper. Krydsningskøer kan bestå af racer, hvor referencepopulationerne findes i forskellige lande, men at dele store datasæt mellem lande er ofte besværligt fordi avlsorganisationer konkurrerer på samme marked. Baseret på rigtige genotyper fra danske Holstein, Jersey og SRB, simulerede vi tre renracede populationer, samt to populationer af to-race (Holstein x Jersey) og tre-racekrydsninger. Sikkerheden på avlsværditallene for krydsningsdyrene var højest i det tilfælde at vi inddrog komplet genotypisk og fænotypisk data fra både krydsningsdyr og renracede dyr i referencepopulationen. Hvis vi blot inddrog komplet data fra krydsningsdyr samt sammenfattende statistik fra renracede dyr, blev sikkerheden på avlsværditallene dog næsten lige så høje. Det betyder, at eventuel mangel på data fra rene racer kan erstattes af opsummerende statistik med næsten lige så stor en sikkerhed som har man komplet data til rådighed.

Fremtidens forskning bør omfatte krydsningsstrategier, hvor genomiske informationer er inddraget i avlsplanen. Desuden er der også et stort behov for at klarlægge de potentielle klimamæssige fordele ved at indføre systematiske krydsningsprogrammer i store dele af den globale mælkeproduktion. Hvis andelen af krydsningskøer skal øges nationalt og globalt, skal krydsningsstrategier også tilrettelægges på populationsniveau, således at rene racer bevares og holdes attraktive for krydsningsavl.

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II

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Economic consequences of dairy crossbreeding in conventional and organic herds in Sweden

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ABSTRACT

This study simulated the consequences of crossbreeding between Swedish Holstein and Swedish Red on herd dynamics and herd profitability under Swedish conditions. Two base herds were simulated using a stochastic herd simulation model, SimHerd Crossbred. The herds reflected average Swedish conventional and organic herds having purebred Swedish Holstein. For each base herd, 3 breeding strategies were simulated: pure-breeding, 2-breed terminal crossbreeding, and 2-breed rotational crossbreeding. The terminal crossbreeding strategy implied having a nucleus of Swedish Holstein and a proportion of F_1 Swedish Red × Swedish Holstein crossbred cows within the same herd. The crossbreds in this herd did not produce replacement heifers but exclusively beef × dairy cross calves. Beef semen was also used in the pure-breeding (10–20% in cows) and the rotational crossbreeding (40% in cows) strategies to retain a limited surplus of replacement heifers. To ensure an adequate number of crossbreds in the terminal crossbreeding strategy, X-sorted sexed semen was used for insemination in all the purebred heifers. The outcome was 67% purebred and 31% F_1 crossbreds in the herd. In addition, 31% heterosis was expressed compared with 67% heterosis expressed using a 2-breed rotational crossbreeding strategy. Compared with the pure-breeding strategy, crossbreeding increased the annual contribution margin per cow by €20 to €59, with the rotational crossbreeding strategy creating the largest profitability. The increased profitability was mainly due to improved functional traits, especially fertility. For the conventional production system, the replacement rate was 39.3% in the pure-breeding strategy and decreased to 35.8 and 30.1% in the terminal and rotational crossbreeding strategy, respectively. Similar changes happened in the organic production system. Additionally, the crossbreeding strategies earned €22 to €42 more annually per cow from selling live calves for slaughter due to the extended use of beef semen. Milk production was similar between pure-breeding and terminal crossbreeding, and only decreased 1 to 2% in rotational crossbreeding. These results show that crossbreeding between Swedish Holstein and Swedish Red can be profitable in both conventional and organic Swedish herds using the strategies we have simulated. However, some aspects remain to be investigated, such as the economically optimal breeding strategy, genetic improvement, and transition strategies.

Key words: crossbreeding, herd management, herd profitability

INTRODUCTION

In some species of production animal, such as pigs, broilers, and beef cattle, crossbreeding at the herd level is the main breeding strategy. The crossing of parents of unrelated strains, or breeds, often results in offspring that are more robust, with better health, growth, fertility, and production. In dairy cattle, crossbreeding has also been shown to improve functional traits such as fertility, health, calving ability, and survival (e.g., Sørensen et al., 2008; Clasen et al., 2017; Hazel et al., 2017). Thus, the evidence from previous studies indicates that crossbreeding can deliver economic advantages for the farmer and society.

The economic benefits of crossbreeding have been previously studied. Lopez-Villalobos et al. (2000) simulated the profitability of different crossbreeding systems in New Zealand. The annual net income per cow in herds with 2- or 3-breed rotational crossbreeding Holstein with Jersey, Ayrshire, or both was NZ$6 to $28 larger than that in herds with only Holstein. In another study, Heins et al. (2012) compared Holstein cattle with Holstein × Scandinavian Red, Holstein × Montbéliarde, and Holstein × Normande in 6 US com-

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mercial herds and estimated larger projected profits of US$0.15 to $0.22 per day per animal for the crossbred cows.

Despite the compelling evidence of the benefits of crossbreeding, the majority of dairy farmers in Sweden still prefer traditional pure breeding, mainly of Swedish Red (**SR**) and Swedish Holstein (**SH**). In Sweden, crossbreeding in dairy cattle is far from common, although the proportion of crossbred dairy cows has increased slightly, with a visible upward trend since the beginning of the millennium, and is currently around 7% (Växa Sverige, 2018).

In Sweden, only a few studies to date have investigated the effects of crossbreeding between SR and SH at the animal level, and no studies have examined the impact of crossbreeding on herd profitability. Ericson et al. (1988) found almost 2% heterosis for production traits, while Jönsson (2015) found 2 to 5% heterosis for those traits. The latter study also estimated heterosis for functional traits and found 1 to 12% for fertility traits, 6 to 15% for calving traits, 5 to 13% for cow survival, and up to 35% for health traits.

The breeds considered for crossbreeding must be economically similar to make the crossbreeding system economically beneficial relative to pure-breeding (Sørensen et al., 2008). Swedish Holstein and SR were previously estimated to be at the same economic level (Stålhammer, 2014), although the former provide higher income from milk yield and the latter incur lower costs related to health and other functional traits. In other words, the 2 breeds complement the strengths and weaknesses of each other and are therefore potentially suited for use in a crossbreeding system.

The reluctance of Swedish farmers to use crossbreeding as a strategy in their herds may be due to their lack of knowledge of the economic gains. The aims of this study were to simulate the outcomes for herd dynamics and profitability when terminal or rotational crossbreeding strategies with SH × SR are implemented and to compare these outcomes with those for pure-breeding with SH. We hypothesized that crossbreeding between the 2 breeds would generate economic gain in both organic and conventional Swedish herds.

MATERIALS AND METHODS

In this simulation study, we used the SimHerd model, which has been applied in several studies of dairy herd management (e.g., Sørensen and Østergaard, 2003; Nielsen et al., 2006; Ettema et al., 2017). To simulate crossbreeding, we used a modification (SimHerd Crossbred) to account for breed proportion and heterozygosity in each individual animal and to simulate phenotypic breed effects and heterosis effects. This approach allows for the simulation of different crossbreeding systems at the herd level (Østergaard et al., 2018).

In SimHerd, the state of an animal is defined by its age, lactation stage, milk yield (actual and potential), body weight, stage in estrus cycle, pregnancy stage, somatic cell count, disease status, and culling status. The SimHerd model predicts consequences of given changes in biology and management in a dairy herd by stochastic simulation of state changes at the animal and herd levels. From one week to the next, an animal's state may change. Relevant probabilities trigger discrete events (e.g., disease, heat detection, abortion, conception, death, and culling). The state of all the animals in the herd defines the state of the herd including the herd demography (Østergaard et al., 2010). Several input parameters act as decision variables that control herd dynamics, baseline risks of diseases, heat observation rate, culling strategy production level, fertility, and health. Outputs of the SimHerd model in terms of technical herd figures can be used to make economic calculations.

Scenarios

Two base herds were specified to reflect average Swedish organic and conventional herds with purebred SH. For each base herd, we simulated 3 breeding strategies—pure-breeding, 2-breed terminal crossbreeding, and 2-breed rotational crossbreeding (Figure 1, and described later)—in a total of 6 scenarios. The simulated herd size was approximately 100 cows. Average herd size in Sweden is currently around 90 cows, but it is increasing (Växa Sverige, 2018). We simulated the scenarios for 50 yr to ensure that an equilibrium was reached; for most scenarios, the equilibrium was reached at approximately yr 20 of the simulation. The results shown in this study are averages of 1,000 replicates over the last 10 yr at equilibrium.

Breed Differences and Heterosis Estimates

Phenotypic breed differences (Table 1) were specified as input parameters in the SimHerd Crossbred model for production, risk of diseases, fertility, and mortality. We based the input parameters on raw means drawn from data collected from the Swedish cattle database (organized by Växa Sverige, Uppsala, Sweden) on cows that had a calving event between 2011 and 2016. The data set consisted of milk recording data from 41,275 organic and 687,828 conventional SH cows and 35,860 organic and 440,924 conventional SR cows.

The heterosis effects for F_1 crossbreds used in the model are all favorable (see Table 2). They are based on findings from Jönsson (2015) and a review by Sørensen

Table 1. Phenotypic breed differences of Swedish Red relative to Swedish Holstein as input parameters in the model for production, risk of diseases, fertility, and mortality[1]

Item	Unit	Conventional	Organic
305-d kg of ECM, first parity	Relative ratio	0.95	0.95
305-d kg of ECM, second parity	Relative ratio	0.91	0.91
305-d kg of ECM, third parity	Relative ratio	0.90	0.89
Feed conversion efficiency	Additive change	0.00	0.00
Mastitis	Odds ratio	0.74	0.86
Milk fever	Odds ratio	1.00	0.80
Retained placenta	Odds ratio	1.00	0.81
Metritis	Odds ratio	0.60	0.60
Displaced abomasum	Odds ratio	0.60	0.44
Ketosis	Odds ratio	1.00	1.58
Digital dermatitis	Odds ratio	0.80	0.97
Interdigital hyperplasia	Odds ratio	0.84	0.96
Hoof horn diseases	Odds ratio	0.62	0.75
Dystocia	Odds ratio	0.81	0.88
Cow mortality	Odds ratio	0.55	0.55
Calf mortality within 24 h	Odds ratio	0.59	0.74
Calf mortality after 24 h	Odds ratio	1.08	1.11
Insemination rate, heifers	Odds ratio	1.00	1.00
Insemination rate, cows	Odds ratio	1.23	1.23
Conception rate, heifers	Odds ratio	1.00	1.00
Conception rate, cows	Odds ratio	1.52	1.52
Calving—first AI, cows	Additional, days	−3	−9

[1] Values are calculated from data obtained from the Swedish cattle database (organized by Växa Sverige, Uppsala, Sweden).

et al. (2008). In a departure from the original SimHerd model, the effect of diseases on reproduction and milk yield was turned off in SimHerd Crossbred to prevent double counting from the combined effect of heterosis on milk yield and diseases. In other words, the heterosis effects on milk yield and reproduction parameters already include effects of diseases; therefore, the direct effect of a disease on those parameters was reset. For the

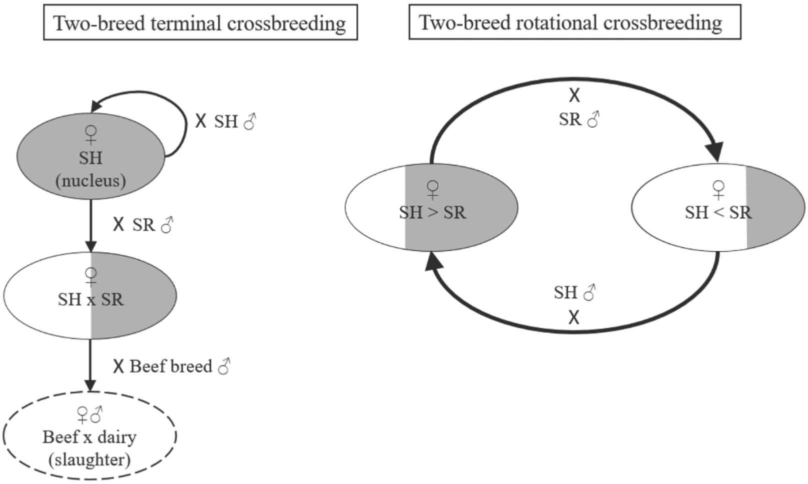

Figure 1. Illustration of 2-breed terminal crossbreeding (left) and 2-breed rotational crossbreeding (right). Terminal crossbreeding requires a nucleus of purebred Swedish Holstein (SH), with some of the females being bred to a sire of the same breed to maintain the size of the nucleus. The remainder of the SH females are bred to a Swedish Red (SR) sire to produce F_1 crossbred production cows. The crossbred SR × SH females are mated to a sire of a beef breed, and all resulting offspring are for meat production only. In rotational crossbreeding, females are rotated between the 2 sire breeds in each generation. Females with a larger proportion of SH than SR are bred to an SR sire and vice versa.

base herd scenarios with a pure-breeding strategy, the general risks of diseases were adjusted so the simulated result continuously reflected the herds we wanted to simulate, as if we had used the original SimHerd model.

SimHerd Crossbred does not model breeding values or genetic change. Therefore, the traits for each individual animal were sampled randomly based on the phenotypic mean of the animals in the herd, which was based on the phenotypic parameters specified in the initial herd and a phenotypic standard deviation. Effect of breed and heterosis were added in accordance with the animal's breed composition and degree of heterozygosity, as described by (Østergaard et al., 2018).

Aside from phenotypic differences between the animals, the 2 production systems differed with respect to 2 management procedures: milk withdrawal period and milk feeding of newborn calves. The milk withdrawal period after medical treatments was twice as long in the organic production system as in the conventional system. Calves in the conventional production system were fed milk replacer, whereas those in organic production were fed bulk tank milk in accordance with KRAV-label regulations (KRAV, 2017).

Breeding Strategies and Reproduction

In the simulations, 2-breed terminal crossbreeding was implemented within a herd, meaning that 2 groups of animals were used for milk production in the herd: a purebred "nucleus" consisting of SH and a group of F_1 SR × SH crossbreds (Figure 1). Terminal crossbreeding with 2 breeds indicates that only purebred animals are selected for the production of replacement heifers, and those females produce both purebred and crossbred replacement heifers. Therefore, all crossbred animals in this system will express 100% heterosis, and they will produce only beef × dairy cross calves.

A 2-breed rotational crossbreeding system implies that females are mated to sires of the breed of the maternal grandsire, and that the breed of the sire therefore "rotates" for each female generation (Figure 1). Approximately 5 generations after the implementation of this system in a purebred herd, individual animals in the herd will constitute of 67% SH or SR and 33% of the other breed. At equilibrium, 67% of the F_1 heterozygosity is expressed in all animals in the herd.

Initially, all females in herds with pure-breeding and rotational crossbreeding were serviced with conventional semen (**CS**). Any purebred virgin heifer in the herds with terminal crossbreeding was serviced with sexed semen (**SS**) to ensure adequate numbers of replacement heifers. To reflect common practice in Swedish dairy herds, 2 attempts were made to impregnate the heifers with SS, and if the attempts were unsuccessful, the heifers were serviced with CS. All purebred cows were serviced with CS. All crossbred females in the herds with terminal crossbreeding were serviced with beef semen (**BS**). It was assumed that all beef × dairy calves would be sold for slaughter finishing in another herd.

The rate of heat observation expressed a combination of the probability of observing heat (by eyesight or heat detection technology) and the cow's ability to show heat signs. Conception rate was defined as the number of positive pregnancy tests over all inseminations. Pregnancy tests were conducted 5 wk after insemination unless heat was observed again before that time point. Initial herd input parameters for chance of conception were 40% for cows and 62.5% for heifers, and the probability of heat observation was 35% for cows and 65% for heifers, corresponding to SH figures obtained from the Swedish cattle database. The 2 production systems did not differ for these 2 parameters. The relative conception probability of SS was 0.85 compared with CS, and the probability of a female calf using SS was 0.90 compared with 0.48 with CS.

Culling Decisions

The model sought to maintain a herd size of between 100 and 105 cows, but it only replaced cows that died or were culled involuntarily (due to disease) or voluntarily (due to infertility or low milk yield). In case no spots were available for a calving-ready replacement heifer, it was sold as a pregnant heifer. In cases in which no calving-ready replacement heifers were available to take an open spot, the model purchased a pregnant heifer from another "fictive" herd.

Cows were voluntarily culled if they produced less milk than average, or if they were unable to become pregnant within a certain period between the voluntary

Table 2. Assumed heterosis estimates for F_1 Swedish Red × Swedish Holstein, based on estimates from Jönsson (2015) and Sørensen et al. (2008)

Trait	Heterosis (%)
305-d kg ECM	3
Mastitis	10
Other diseases[1]	10
Dystocia	7
Fertility	10
Cow mortality	10
Calf mortality and stillbirth	12
Young stock mortality	12

[1] Retained placenta, metritis, milk fever, displaced abomasum, ketosis, digital dermatitis, interdigital hyperplasia, sole ulcers, heel horn erosion, and hock lesions.

waiting period and maximum number of days open. The parameters for these periods differed between production systems and were based on data retrieved from the Swedish cattle database. The cows were inseminated 49 to 324 d after calving in conventional herds and 51 to 331 d after calving in organic herds, regardless of parity number.

Heifers were voluntarily culled if they were unable to become pregnant within the minimum age at first insemination and maximum number of days open. They were inseminated between 470 and 810 d of age in the conventional production system and between 470 and 770 d of age in the organic production system.

Dairy bull calves and beef × dairy bull and heifer calves were sold for slaughter production after a 2-wk rearing period. Dairy heifers reared to become production cows were the only young stock on the farm, and any economic results relating exclusively to young stock accounted for this group of animals.

Health and Mortality

The simulated outcome of disease prevalence was defined as the number of treatments for specific diseases. This number included both first and follow-up treatments each time a cow needed veterinary treatment for a specific disease. In the presentation of results, we pool the simulated diseases into 5 groups: mastitis, hoof and leg diseases, metabolic diseases, reproduction diseases, and dystocia (i.e., calving difficulties requiring veterinary assistance). Mastitis and dystocia only included those specific disorders. Hoof and leg diseases included digital dermatitis, interdigital hyperplasia, sole ulcers, heel horn erosion, and hock lesions. Metabolic diseases included milk fever, displaced abomasum, and ketosis, and reproduction diseases included metritis and retained placenta. The risk of any disease was consistent between production systems but differed between parities and changed during the lactation period (Østergaard et al., 2000). Furthermore, each disease was associated with a risk of involuntary culling.

We defined cow mortality as the proportion of cows that died or were euthanized in response to acute conditions. Calf mortality relates to calves dying within 24 h of calving, including stillbirth. The relative risk of stillbirth when BS was used as compared with dairy bull semen (CS or SS) was 1.05, irrespective of the age of the mother. Young stock mortality included replacement heifers that died between 24 h after birth and first calving. The risk of young stock mortality decreased with the age of the heifer. Replacement rate expressed the annual number of replacement heifers entering the cow herd divided by the number of cow years.

Calibration of Simulations

Before the final simulation, we ran test simulations to ensure the output parameters were reasonable in relation to the input parameters and to make appropriate breeding decisions for the simulated herds.

We decided to retain a surplus of 1 to 3 replacement heifers in each scenario to make the scenarios economically comparable. A large difference in surplus heifers will make any other economic effect vanish in relation to the high value of buying or selling replacement heifers. With the initial breeding decisions described earlier, the herds managing pure-breeding or rotational crossbreeding had a surplus of replacement heifers above 3, and we therefore calibrated sufficient proportions of BS into these scenarios. We continued to service the remaining females in these herds with CS. The calibrated proportions of BS used in these scenarios are presented in the results.

In the terminal crossbreeding strategy, the nucleus of purebred animals had to be maintained at an appropriate size to produce a sufficient amount of purebred and crossbred replacement heifers. When all the purebred females were serviced with CS, the breeding strategy resulted in only 5% crossbred cows in the herd. Adhering to our original decision that all purebred heifers should receive SS, this proportion increased to about 30% crossbreds, which is more substantial. After this calibration step, 75% of all purebred females across age groups were bred to an SH sire for pure-breeding and 25% were bred to an SR sire for crossbreeding. The cows were selected randomly for pure-breeding or crossbreeding, because the SimHerd Crossbred model does not simulate breeding values. The distribution of surplus purebred and crossbred heifers reflected the simulated distribution of purebred and crossbred production cows.

Price Assumptions

The annual contribution margin (**CM**) included income from milk production, slaughter cows, live calves, and surplus replacement heifers, and the costs of feeding the cows and replacement heifers, inseminations (including the service fee), disease treatments, and other costs related to the rearing of the cows and replacement heifers (e.g., bedding, hoof trimming, vaccinations). Labor costs and costs associated with buildings, farming equipment, and other investments were not included.

The price and cost assumptions made in the simulations were based on budgets from Agriwise (2017) and price lists from Växa Sverige (2017), Arla (2017), and HKScan Agri (2017). Essential price and cost assumptions in euros are given in Table 3. Milk and meat were of greater value in organic production, but this production system was also associated with greater feed costs. The ECM produced by crossbreds was assumed to be slightly more valuable as a result of its higher fat and protein content in SR relative to SH (Växa Sverige, 2018). Surplus heifers were sold as pregnant heifers and purebred heifers were assumed more valuable than crossbreds because they would potentially have estimated breeding values. Breeding values for crossbred dairy cattle in Sweden were not estimated at the time of this study. Additionally, heifers pregnant with SS were assumed to be worth 5% more (not shown in Table 3) because of the higher chance of a heifer calf that can be used in future as a replacement heifer.

The slaughter value was assumed to be €0.05/kg live weight higher for an SR cow than an SH cow, due to higher carcass scores (Gård and Djurhälsan, 2018). The benefit was regressed with breed proportion. Thus, a conventional F_1 SR × SH crossbred cow would have a value of €1.325/kg live weight. Likewise, a live calf sold for slaughter was assumed to be more valuable if it was a SR × SH crossbred, as compared with a purebred SH, because SR calves have a faster growth rate and better carcass quality (Gård and Djurhälsan, 2018). In addition, dairy × beef crossbreds were of higher value as a result of the larger growth potential owing to the beef breed genes. The prices for live calves included costs expected to be incurred in a 2-wk rearing period and were adjusted in line with a 3% risk of mortality within that period.

Costs of disease treatments (not shown in Table 3) were based on the price sheet used in Nordic Total Merit Index calculations (Sørensen et al., 2018) and included expenditures on medicine and veterinary fees. In the organic production system, a veterinarian must undertake all the requisite treatments for most diseases. By contrast, farm personnel are permitted to do follow-up treatments for most diseases in the conventional production system. Therefore, the costs were assumed higher for most diseases in the organic production system. Thus, a case of mastitis was taken to cost €125 in a conventional herd and additional €50 in an organic herd, and for hoof and leg diseases, the cost ranged between €15 and €60 plus up to an additional €30 in the organic system. Costs of remaining diseases were between €90 and €225 plus up to an additional €50 in the organic system.

Sensitivity Analyses

Three different sensitivity analyses were carried out to investigate the effect of some of the potentially important assumptions. The sensitivity analyses were only made for the conventional production system, assuming patterns would be the same in both production systems. The first sensitivity analysis investigated the effect of the breed difference in milk yield on CM by changing the relative ratio in SR versus SH to 1.00, 0.975, 0.95, 0.925, 0.90, 0.875, and 0.85, regardless of lactation number. The second sensitivity analysis investigated changes in milk price relative to the current simulated milk price (€372/1,000 kg of ECM) between −20% and +20%. The third sensitivity analysis investigated changes in all feedstuff prices relative to the current (shown in Table 3) between −20% and +20%. All other prices were kept constant for the second and third analyses, including the breed difference in milk price.

Table 3. Assumed income prices and costs for milk production, feeding, slaughter, live animals, and semen services; addition for Swedish Red (compared with Swedish Holstein) in parentheses

Item	Conventional (€)	Organic (€)	Source
Income			
Milk, per 1,000 kg of ECM	372 (+4)	481 (+4)	Arla (2017)
Slaughter cow, per kg of live weight	1.30 (+0.05)	1.34 (+0.05)	HKScan Agri (2017)
Purebred pregnant heifer, per head	1,220	1,220	Agriwise (2017)
Crossbred pregnant heifer, per head	1,100	1,100	—
Dairy bull calf, per head	200 (+25)	200 (+25)	HKScan Agri (2017)
Beef × dairy bull calf, addition per head	70	70	HKScan Agri (2017)
Beef × dairy heifer calf, addition per head	35	35	HKScan Agri (2017)
Costs			
TMR, cows, per kg DM[1]	0.19	0.22	Agriwise (2017)
Concentrate, young stock, per kg of DM	0.27	0.46	Agriwise (2017)
Roughage, young stock, per kg of DM	0.12	0.12	Agriwise (2017)
Conventional semen (including service)	34	34	Växa Sverige (2017)
Sexed semen (including service)	39	39	Växa Sverige (2017)
Beef semen (including service)	34	34	Växa Sverige (2017)

[1] Includes 90 d on pasture with additional TMR feeding.

RESULTS

Herd Dynamics

All simulated herds had 103 cows per year on average during the 10-yr period presented in the results shown in Table 4. As a result of the breeding strategy, the terminal crossbreeding scenarios had 31% crossbred cows and 69% purebred cows, regardless of production system. Given that all crossbreds were 50/50 of each breed, the average breed proportions in the herds were calculated as 84.5% SH (0.31 × 0.5 + 0.69) and 15.5% SR (0.31 × 0.5). In addition, 31% heterosis was expressed across the herds in terminal crossbreeding scenarios. For rotational crossbreeding, the average proportion of each breed was 50%, and because all animals were crossbreds, 67% heterosis was expressed across the herds in these scenarios.

Changing from pure-breeding to crossbreeding led to a decrease in the number of young stock animals in both production systems; the replacement rate was reduced as well due to decreased voluntary culling. The largest effect for both production systems was in the rotational crossbreeding scenarios. Furthermore, crossbreeding altered the age structure among the cows: the proportion of third-parity and older cows in the herd increased.

The crossbreeding strategies allowed for more use of BS as a result of the better reproductive performance of the crossbreds relative to purebreds, and therefore more beef × dairy cross calves were born in these scenarios. In the pure-breeding scenarios, 17% (organic) and 12% (conventional) of all calves sold were beef × dairy crosses. The corresponding proportions were 53 and 54% in terminal crossbreeding and 43% in both rotational crossbreeding scenarios.

Animal Performance

In both production systems, the level of 305-d ECM yield in the pure-breeding and terminal crossbreeding scenarios was similar. In the rotational crossbreeding scenarios, minor reductions occurred in milk yield (115–184 kg, corresponding to 1–2%) as compared with the yield in the pure-breeding scenario. The average daily yield per cow between wk 1 and 24 after calving (not shown in table) in the conventional production system was 28.9 kg of ECM in first-parity cows for both pure-breeding and terminal crossbreeding and 28.7 kg of ECM for rotational crossbreeding. In multiparous cows, it was 38.8, 38.6, and 37.9 kg of ECM for pure-breeding, terminal, and rotational crossbreeding, respectively. The corresponding average daily yield per

Table 4. Simulated herd dynamics at equilibrium in a herd of purebred Swedish Holstein; a herd using a 2-breed terminal crossbreeding system with Swedish Holstein purebreds and F_1 Swedish Red × Swedish Holstein crossbreds; and a herd using 2-breed rotational crossbreeding—all simulations in both organic and conventional production systems

	Organic			Conventional		
Item	Purebred	Terminal	Rotation	Purebred	Terminal	Rotation
Cows (no.)	103	103	103	103	103	103
Crossbred cows (%)	0	31	100	0	31	100
First-parity cows (%)	39	36	30	39	36	30
Second-parity cows (%)	24	23	21	24	23	21
Older cows (%)	37	41	49	37	41	49
Replacement (%)	38.2	36.4	30.3	39.3	35.8	30.1
Young stock (no.)	90	88	73	93	84	72
Surplus heifers sold (no.)	1	2	2	1	1	2
Sexed semen doses, heifers (%)	0	60	0	0	60	0
Beef semen doses, heifers (%)	0	21	0	0	21	0
Beef semen doses, cows (%)	15	30	40	10	30	40
Dairy bull calves sold (no.)	45	27	37	46	26	37
Beef × dairy crosses sold (no.)	9	31	28	6	30	28
305-d ECM yield (kg)	9,148	9,178	9,033	10,007	9,969	9,823
Calving interval (d)	415	409	401	409	406	400
Conception rate (cows)	0.36	0.38	0.43	0.36	0.39	0.43
Mastitis treatments/100 cows	11.5	11.9	12.1	9.7	9.7	9.4
Hoof and leg disease treatments/100 cows	19.2	19.2	18.7	21.7	20.4	18.4
Metabolic disease treatments/100 cows	2.5	2.6	2.6	1.4	1.4	1.4
Reproduction disease treatments/100 cows	5.0	4.8	4.0	1.6	1.5	1.3
Dystocia cases/100 cows	3.7	3.5	3.0	5.9	5.4	4.4
Total disease treatments/100 cows	41.9	42.0	40.4	40.3	38.4	34.9
Cow mortality (%)	6.3	5.7	4.7	6.3	5.8	4.5
Calf mortality (%)	5.8	5.3	4.7	8.6	7.7	6.3
Young stock mortality (%)	3.6	3.5	3.4	3.6	3.5	3.5

cow in the organic production system was approximately 3 kg of ECM less, with more or less the same differences between breeding scenarios, relative to the conventional production system.

Crossbreeding improved fertility in comparison with pure-breeding. The calving interval was shorter and the conception rates were higher in both production systems. The largest effect was in the rotational crossbreeding scenarios.

Hoof and leg diseases accounted for about half of the disease treatments, and mastitis accounted for about a quarter. These rates were followed by low prevalences of reproduction diseases, dystocia, and metabolic diseases. In the organic production system, the number of mastitis treatments per 100 cows slightly increased when crossbreeding was introduced, but it remained at a similar level in the conventional production system. In both production systems, the number of treatments for hoof and leg diseases declined when crossbreeding was implemented. Reproduction diseases and dystocia also declined slightly with the change from pure-breeding to crossbreeding. The number of treatments of metabolic diseases remained virtually unaffected with the change from pure-breeding to crossbreeding.

Total numbers of treatments (including dystocia) per 100 cows in pure-breeding and terminal crossbreeding in the organic production system were similar, but they decreased by 4% in rotational crossbreeding. In the conventional production system, total disease frequency decreased by 5% in the terminal crossbreeding scenario and by 9% in the rotational crossbreeding scenario.

Crossbreeding had a favorable effect on survival rates in the herds. In both production systems, cow mortality fell when the breeding strategy changed from pure-breeding to crossbreeding. Calf mortality (including stillbirths) decreased as well. Regardless of production system, the mortality rate in young stock only decreased (and then only slightly) when crossbreeding was implemented.

Economic Output

Total annual CM in the organic production system increased by 1.9% (€51) and 2.2% (€59) in the terminal and rotational crossbreeding scenarios, respectively, as compared with pure-breeding. In the conventional production system, the corresponding increases were 0.9% (€20) and 1.7% (€39).

More than 90% of the income in all simulated herds derived from milk production; the remaining income came from the sale or slaughter of animals. A 1% increase in annual income per cow from milk production occurred when pure-breeding was replaced by terminal crossbreeding in the organic production system (Table 5). In the rotational crossbreeding scenario, a loss of 1% occurred. In the conventional production system, the losses were 1% for terminal crossbreeding and 2% for rotational crossbreeding. Because of the reduced replacement rate in the crossbreeding scenarios, fewer cows were slaughtered every year, reducing the income from slaughter cows as well. However, a larger proportion of beef × dairy cross calves increased the income from live calves by 20 to 40% (€22–€42), regardless of production system. In the organic production system, the proportional difference between the pure-breeding and crossbreeding scenarios in total annual income per cow was similar to that observed in connection with milk income. In the conventional production system, the total incomes in pure-breeding and terminal crossbreeding were the same, but total income was 1% lower in the rotational crossbreeding scenario.

Most annual costs are feeding costs. Regardless of production system, the feeding costs for the cows were similar in pure-breeding and terminal crossbreeding and 1% less in rotational crossbreeding. The reduced number of replacement heifers saved 3 to 23% of the feed costs and other costs related to young stock. Total costs fell by 4% in the rotational crossbreeding strategy in the organic production system and by 2 to 6% in all crossbreeding strategies in the conventional production system.

Sensitivity Analyses

With a decrease in the relative ratio in 305-d kg ECM yield between SR and SH (increased difference for production performance of SR relative to SH), the CM in the crossbreeding scenarios decreased as well (Figure 2). Between a relative ratio of 1.00 and 0.85, the effect of rotational crossbreeding on CM decreased from +4.7% to −4.1% relative to pure-breeding, while the corresponding effect in the terminal crossbreeding system was from +1.6% to −0.1%.

The relative CM between the pure-breeding scenario and the crossbreeding scenarios increased up to +1.7% for terminal and +3.3% for rotational crossbreeding at 20% reduction in milk price (Figure 3). Increasing the milk price by 20% caused CM to be less favorable for crossbreeding, but it still remained positive at +0.6% and +0.8% for terminal and rotational crossbreeding, respectively.

Changes in feed prices showed an almost opposite trend from changes in milk price (Figure 4). When the feed price was reduced by 20%, the relative CM between the pure-breeding scenario and the crossbreeding scenarios was +0.7% and +0.9% for terminal and ro-

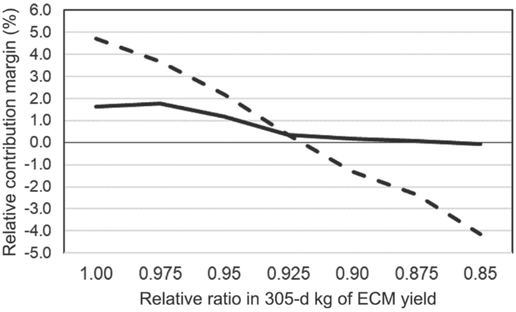

Figure 2. Relative contribution margin between pure-breeding with Swedish Holstein and terminal crossbreeding (solid line) or rotational crossbreeding (dashed line) between Swedish Red and Swedish Holstein when the relative ratio in 305-d kg of ECM yield changes between the 2 breeds.

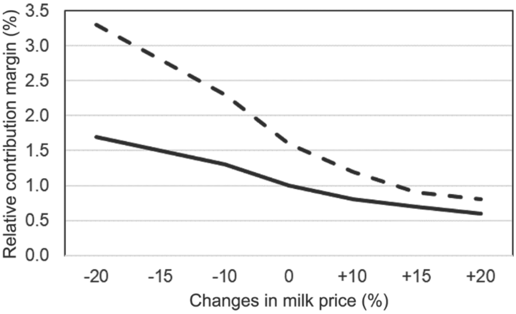

Figure 3. Relative contribution margin between pure-breeding with Swedish Holstein and terminal crossbreeding (solid line) or rotational crossbreeding (dashed line) between Swedish Red and Swedish Holstein when milk price is changed between −20% and +20%.

tational crossbreeding, respectively. The corresponding figures were +1.4% and +2.6% when then feed prices were increased by 20%.

DISCUSSION

To our knowledge, very few studies have investigated crossbreeding performance at the herd level for specific crossbreeding systems and production systems. Indeed, most studies on crossbred performance are on F_1 crosses and conducted at the animal level rather than the herd level. In 2 different production systems in Sweden, organic and conventional, the simulations in the current study showed that improvements in cow replacement rate and profitability especially were secured through a switch from a pure-breeding to crossbreeding strategy in a dairy herd. The results may not directly apply to a specific Swedish herd or a herd from another country because herd parameters, management strategies, and breeds differ within and between countries.

Despite minor reductions in milk yield, which is by far the largest income factor in current dairy production, improved functional traits were key to economic improvement. Beyond that, improved health and reduced mortality were important welfare parameters. This result may ultimately be as important as economic output, because animal welfare and longevity are serious

Table 5. Simulated annual economic consequences (€/cow) in a herd of purebred Swedish Holstein; a herd using a 2-breed terminal crossbreeding system with Swedish Holstein purebreds and F_1 Swedish Red × Swedish Holstein crossbreds; and a herd using 2-breed rotational crossbreeding—all simulations in both organic and conventional production systems

	Organic			Conventional		
Item	Purebred	Terminal	Rotation	Purebred	Terminal	Rotation
Income						
Milk sales	4,360	4,383	4,323	3,730	3,694	3,652
Slaughter cows	269	259	218	270	248	214
Live calves	109	131	150	104	127	146
Surplus heifers	12	26	26	16	16	20
Total	4,751	4,798	4,717	4,093	4,085	4,033
Costs						
Feeding, cows	1,442	1,446	1,431	1,245	1,242	1,230
Feeding, young stock	345	336	281	250	226	192
Inseminations	50	53	46	51	52	45
Disease treatments	55	55	53	35	34	30
Other, cows	142	142	140	144	142	140
Other, young stock	54	52	43	55	50	43
Total	2,078	2,073	1,985	1,780	1,747	1,681
Total contribution margin[1]	2,674	2,725 (+1.9%[2])	2,733 (+2.2%)	2,313	2,333 (+0.9%)	2,352 (+1.7%)

[1] Total economic values are not exactly sums of the subvalues due to rounding of each subvalue.

[2] Percentage increase from the pure-breeding scenario within the same production system.

concerns among Swedish dairy farmers (Röcklinsberg et al., 2016).

The data used as input parameters in our simulations were averages from the whole country. They did not reflect the influence of interactions between, for example, production system and geographical location. These interactions may influence the breed differences used. Some differences are thought to exist between dairy herds in the north of Sweden and those in the south—differences that may be due to herd size and roughage production, as well as the fact that organic production is more common in some regions than others (Jordbruksverket, 2017; Växa Sverige, 2018).

Herd Dynamics

The effect of crossbreeding was strongly expressed in the fertility parameters. This outcome was especially noticeable in the terminal crossbreeding scenarios, in which the crossbred cows managed to improve the overall conception rate and calving interval in the herd, although only 31% of the cows were crossbreds.

When crossbreeding was introduced in the purebred herd, the improved functional traits reduced the number of replacement heifers needed in the herd. Reduction of young stock is favorable because it leads to lower costs in feeding and rearing and may also have other benefits, such as reducing the environmental impact of dairy production (Ondersteijn et al., 2003). Furthermore, costs for labor and the housing of heifers are lower, although this cost effect was not included in the economic results presented here. Reducing the number of young stock animals may allow for an increased number of production cows and thus increase economic gains as well. From an environmental perspective, Ettema et al. (2017) has calculated that a reduction of 32 replacement heifers in a Danish system led to a potential increase of 8.5 production cows with no increase in the number of methane-producing equivalents. However, from either a practical or logistic point of view or both, increasing the number of production cows may not be possible in all herds or production systems.

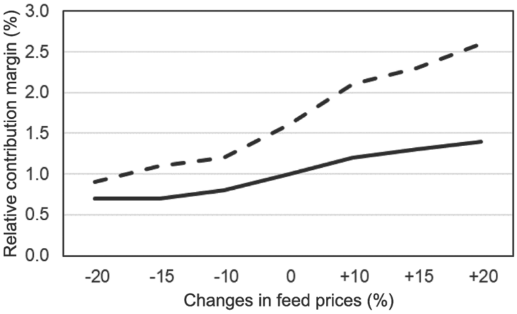

Figure 4. Relative contribution margin between pure-breeding with Swedish Holstein and terminal crossbreeding (solid line) or rotational crossbreeding (dashed line) between Swedish Red and Swedish Holstein when feed prices are changed between −20% and +20%.

A terminal crossbreeding system relies on the provision of enough replacement heifers, both purebreds and crossbreds, which is entirely dependent on an optimal proportion of purebreds. In general, the proportion of purebred animals needed is highly dependent on fertility. Improved fertility allows for smaller nucleus size (i.e., more crossbred animals in the herd), mainly because the calving interval decreases and fewer cows are culled voluntarily in response to infertility. Reduced cow and heifer mortality (including stillbirths) allows for a smaller nucleus size as well. Additionally, the 31% of crossbreds in our simulations can be increased by a different strategy for using SS.

A terminal crossbreeding strategy requires SS to be used to reach an adequate number of crossbreds in the herd to achieve the benefits of crossbreeding. In our simulations, we chose to limit the use of SS to heifers only, which allowed 75% pure-breeding in the nucleus resulting in a nucleus size of 69% purebred cows. But the nucleus size in terminal crossbreeding can be reduced further if SS is used in cows as well. Moreover, using SS at the herd level on the genetically best heifers and cows can increase genetic levels in the purebred cows (Hjortø et al., 2015; Ettema et al., 2017), and this outcome will be reflected in the crossbreds as well. However, the economic value of the increased genetic gain obtained by using SS was not included in the results presented in this study. Sexed semen should not necessarily be limited to pure-breeding; it may benefit crossbreeding as well. We did not investigate the economically optimum proportion of purebreds versus crossbreds in a terminal crossbreeding system, but it may vary with the level of management in the herd and the performance of the purebreds (Clasen et al., 2019).

Sexed semen was not used in the rotational crossbreeding scenarios in this study, but this crossbreeding strategy would also benefit from the use of SS because that would allow for increased use of BS. This approach may improve profitability, because BS increases the average value of slaughter calves. Meat production from beef × dairy crosses may have a smaller environmental impact than production from suckler cow herds (Cederberg and Mattsson, 2000). The combination of BS and SS potentially increases the rate of genetic improvement in the herd (Ettema et al., 2017), although that demands selection tools for crossbred animals, such as breeding values (discussed further in the section about breeding).

Production

Milk yield was expected to decrease when crossbreeding was introduced to a purebred herd, because it is lower in SR than it is in SH. However, the combination of heterosis for milk yield and the larger proportion of older cows in the herd created only a minor reduction in milk yield when rotational crossbreeding was introduced. The relatively low proportion of SR in terminal crossbreeding caused the milk production level to change even less.

Relative to pure-breeding, the average daily kilograms of ECM yield per cow between wk 1 and 24 was, across lactations, ~0.3% less in the terminal crossbreeding scenarios and ~1.5% less in the rotational crossbreeding scenarios. For F_1 crossbreds between SR and SH, Jönsson (2015) estimated an average difference in milk production across 3 lactations. Relative to purebred SH, the crossbreds produced on average 4.6% less 305-d kg ECM. In the United States, Hazel et al. (2017) measured production traits in first-parity Viking Red × Holstein crosses versus purebred Holstein. When converting 305-d milk volume and fat and protein contents to 305-d ECM, they showed just a 0.5% difference in favor of the purebreds. Clasen et al. (2019), however, found no significant ($P > 0.05$) difference in 305-d kg fat plus protein yield between first-parity purebred Holstein and Nordic Red × Holstein crosses.

A comparison between previous studies from Jönsson (2015), Hazel et al. (2017), and Clasen et al. (2019) and the present study is less than straightforward because studies on F_1 crossbred animals do not represent the effects at the herd level, but rather at the animal level, and fail to take herd demography into account. For example, differences in age distribution among production cows between a purebred and crossbred herd are not reflected in those estimates. Furthermore, only 67% heterosis is expressed in rotational crossbred animals, whereas it is fully expressed in F_1 crossbreds. Because SimHerd Crossbred was not programmed to output performances for breed groups (i.e., purebreds and F_1 crossbreds separately) and instead gave performances for the entire herd, comparisons of F_1 crossbreds from our simulated terminal crossbreeding system and studies of F_1 crosses were also impossible.

Health and Survival

The prevalence of most diseases was very low because of the low mean values extracted from the Swedish cattle database that were used as input parameters. Because of the low values, the effect of heterosis when crossbreeding was introduced was hardly visible. Swedish law requires sick animals to be treated, regardless of production system. However, registration of disease treatments in the cattle database is voluntary, and not all veterinarians report treatments very carefully. Consequently, some registrations of treatments may be missing, resulting in assumptions about the level of diseases in the present simulations that are too low. This issue may have caused an underestimation of the effects of crossbreeding in relation to health traits.

The prevalence of mastitis, reproduction diseases, and metabolic diseases simulated in the purebred scenarios are in accordance with Jönsson (2015), who estimated frequencies of diseases in SR and SH. However, frequencies in that study were lower for feet and leg diseases (2.1%) than those in our simulations of hoof and leg diseases. A possible reason for the considerable difference is that Jönsson (2015) only included information from veterinarians, whereas we also included information from hoof trimmers.

Disease risks in dairy cows tend to rise over lactations (Fleischer et al., 2001), which may counteract the benefits of heterosis in health at the herd level when the average age of the cows increases. In the present study, the presence of more older cows when crossbreeding was introduced in a purebred herd may explain why the number of mastitis treatments increased in the organic production system. The favorable breed effect of SR on mastitis risk was stronger in the conventional production system (Table 1), and the number of mastitis treatments therefore decreased in that system. The larger proportion of older cows in the crossbreeding scenarios did not increase the number of other disease treatments, although it may still have counteracted the effect of heterosis.

The age distribution among cows in the scenarios suggests that the cows stayed longer in the crossbreeding herds, which is in accordance with findings from other studies. Heins et al. (2012) estimated +20.1% and 21.4% higher survival rates for third- and fourth-parity Scandinavian Red × Holstein crossbred cows compared with Holstein in 6 Californian commercial herds. Across Danish herds grouped in 3 different production levels, Clasen et al. (2019) found between 7.5% and 15% higher survival rates from first to third calving in F_1 crossbreds between Nordic Red and Holstein compared with Holstein.

Economic Output

Two-breed terminal crossbreeding and rotational crossbreeding, under Swedish conditions and within the selected input parameters, proved to increase annual CM relative to that observed in pure-breeding regardless of production system. Rotational crossbreeding was most beneficial because all animals in the herds were crossbreds, which ensured that a greater benefit of heterosis was achieved at the herd level. Nevertheless, the terminal crossbreeding scenarios showed that, despite only 31% of the production cows in the herd being crossbreds, CM could still be raised by 1 to 2%. The monetary gains were lowest for the terminal crossbreeding scenario in the conventional production system, which was €20 per cow-year. That sums up to €2,000 per year in a 100-cow herd, which essentially only covers small investments. However, none of the scenarios were optimized from an economic point of view. For example, optimized use of SS and BS in both crossbreeding strategies may have led to greater profitability, especially from a genetic perspective. On top of that, with the advantage of having breeding values in purebred animals, the terminal crossbreeding strategy could possibly catch up and cancel the difference in CM between it and rotational crossbreeding.

Changing from pure-breeding to any of the crossbreeding strategies decreased the number of young stock and thus the total number of animals in the herd. This situation permits a saving on resources (e.g., labor, buildings, and farmland), but that was not factored into the economic calculations of this study. Thus, the benefit of crossbreeding may be larger than estimated in the present study. In Sweden, dairy heifers are often used for nature preservation, which is highly subsidized by the European Union and the Swedish government. This practice also means that during the 4- to 6-mo grazing period heifers are relative low or no cost or maybe even profitable. However, that is not the case for all dairy farmers throughout the world, meaning a reduction of young stock may be even more beneficial for herds without this privilege.

Possible heterosis effects on feed efficiency were not considered in this study because heterosis estimates for feed efficiency in dairy cattle are still relatively understudied. However, Shonka-Martin et al. (2019) made comparisons of purebred Holstein with rotational 3-breed crossbred cows (Viking Red, Montbéliarde, and Holstein) and found significantly ($P < 0.05$) higher feed conversion ratios in the crossbred cows during the first, second, and third lactations. Furthermore, the crossbreds produced the same levels of fat and protein on lower feed intake as the purebreds. This outcome suggests that crossbreds may be more profitable because they can generate lower feed costs without a loss in production income. Furthermore, improved feed efficiency potentially reduces the environmental impact from dairy production (Bell et al., 2011).

Studies of the economic outputs of dairy herds differ in various respects, for example, in what they include in income and costs, prices, country studied, management conditions, breeds, and type of study (simulation, commercial or experimental herds). Furthermore, few studies have estimated the economic benefits of crossbreeding between Holstein and breeds similar to SR. In New Zealand, Lopez-Villalobos et al. (2000) simulated a 3.6% increase in net income per cow in a comparison of a 2-breed rotational crossbreeding herd (Ayrshire × Holstein) with a pure Holstein herd. This study was based on somewhat different production from the Swedish system, including lower milk yields, all-year grazing, and seasonal calving. In the study by Heins et al. (2012), the projected daily profit per cow was 4% higher in F_1 crossbreds of Scandinavian Red × US Holstein, than it was in purebred US Holstein. The result in this study was estimated from 6 commercial Californian dairy herds. However, health costs were not included in the economic calculations. In addition, the studies by Lopez-Villalobos et al. (2000) and Heins et al. (2012) did not include beef × dairy crossing. In the first published demonstration of SimHerd Crossbred, rotational crossbreeding between Holstein and Danish Red increased yearly net return per cow by 9.8% compared with pure-breeding with Holstein (Østergaard et al., 2018). This study was based on Danish conditions, which are somewhat similar to those in Sweden. However, the input parameters and breeds differed from the present study. For example, Østergaard et al. (2018) simulated slightly higher milk yield in crossbreeding compared with pure-breeding, and the frequency of disease treatments and replacement rate were somewhat higher.

Sensitivity Analyses

The sensitivity of CM to the difference in production performance between 2 breeds in Figure 2 shows the importance of using economically similar breeds in a crossbreeding system if the goal is to achieve higher profits than pure-breeding. This result can be translated to any breed comparison in any country or region. It is an incentive for breeders of the lowest-producing breed to continue the genetic progress in the breed to keep it attractive for crossbreeding. The change of the relative breed performance had a lower effect on CM for terminal crossbreeding than rotational crossbreeding because the latter included more genes of the inferior breed (i.e., SR). Estimation of proper breed differences is therefore crucial for having the most reliable estimates for simulating the effects of crossbreeding.

Reducing the milk price by 20% had a higher positive effect on the relative CM between the pure-breeding scenario and the crossbreeding scenarios than increasing the milk price by 20% (Figure 3), while changing the feed price had almost the opposite effect (Figure 4). The purebred scenario had the highest income from milk production but also the highest total costs (Table 5). Reducing the milk price while keeping the costs constant led to the CM changing at a relatively faster rate in the purebred scenario compared with the crossbreeding scenarios, making the difference between the scenarios larger. On the other hand, when the feed price, which caused about 85% of the total costs, was reduced without changing the milk price, the relatively higher milk income in the purebred scenario caused a relatively faster increase in CM, making the difference from the crossbreeding scenarios smaller.

The patterns of the sensitivity analyses are in accordance with similar analyses made by Heins et al. (2012). The study compared Holstein with F_1 crossbreds of Normande × Holstein, Montbéliarde × Holstein, and Scandinavian Red × Holstein in 6 commercial herds in California. When the feed costs increased by 37.5%, the difference in projected profit per cow-day increased in favor of crossbreds, showing same tendency as in the present study. Similar to present study's finding, the effect of increasing milk price by 32% was in favor of the purebreds, while the advantage of decreasing milk price by 32% was in the crossbreds. Unlike the present study, feed costs and other costs associated with replacement heifers remained fixed when feed costs (for cows) and milk price changed in the study by Heins et al. (2012). However, they also investigated the effect of increasing costs of replacement heifers by 35%, and the effect was similar to the effect of increasing feed costs for the cows.

The ratio between milk and feed prices has historically switched between favorable and unfavorable within short periods of time (IFCN, 2019). However, within the last decade, feed prices have been rapidly increasing due to higher competition over arable land. This situation provides an incentive for farmers, in Sweden and other countries, to introduce crossbreeding in their herds for reduced feed costs (for both cows and young stock) and potentially improved feed efficiency (Shonka-Martin et al., 2019).

Breeding

The impact of crossbreeding on genetic progress was not simulated in this study. However, breeding decisions concerning the purebred animals in a terminal crossbreeding system should be investigated as a selection strategy. In particular, the use of SS in combination with BS may potentially improve economic benefits (Ettema et al., 2017). Improved genetic levels will benefit the crossbred animals as well. However, breeding values are currently not estimated for crossbred dairy cattle in Sweden. Consequently, selection of the genetically best production cows is easier in a terminal crossbreeding strategy, in which all breeding candidates are purebred animals, than in a rotational system. Estimated breeding values in crossbred animals, or for crossbred performance in purebred animals, would be a valuable tool, enabling farmers to select among females in a rotational crossbreeding system and to select sires for use in a terminal crossbreeding system. As genotyping technologies and genomic selection are currently developing rapidly (VanRaden and Cooper, 2015), breeding values for crossbreeding may be a reality in the near future.

Implementation of Crossbreeding in a Dairy Herd

The implementation of crossbreeding in a herd is a long-term investment. Assuming an optimal breeding and culling strategy, the transition period from having only purebreds in a herd to a 2-breed rotational crossbreeding system may be lengthy: it may be 15 to 20 yr before breed proportions have stabilized. A 2-breed terminal crossbreeding system may have a shorter transition period depending on the desired nucleus size. Effective transition to crossbreeding may require additional use of SS and a strict voluntary culling strategy during the early period. The most effective transition strategy, both economically and in terms of time needed, needs to be investigated.

Most herds in Sweden are mixed herds with SR and SH rather than entirely one breed or the other. With the average herd size currently being around 90 cows (Växa Sverige, 2018), logistical problems with terminal crossbreeding could arise in which 2 (small) nuclei would be present in addition to the crossbred part. The risk of having a shortage of purebred heifers for replacement might lead to maintenance of the status quo or to the use of a rotational system or a suboptimal terminal crossbreeding system with only a small proportion of crossbreds.

In herds with low fertility, poor health, or both, crossbreeding may be a beneficial tool because heterosis is usually largest in functional traits with low heritability (Sørensen et al., 2008). However, studies show that it is not only herds with a low level of management, expressed as level of production, that benefit from crossbreeding (Bryant et al., 2007; Lembeye et al., 2015; Clasen et al., 2019). The economic benefits of crossbreeding at different herd management levels, including herd dynamics, need to be investigated further.

The 2 crossbreeding systems simulated in this study showed strengths and weaknesses in comparison with each other, and the choice between them depends on the farmer's preferences and the current herd situation. Obviously, raised profitability from crossbreeding will be a high priority, but improvements in health, fertility, and production may be highly prioritized as well. Potentially, an improvement in health and fertility resulting in "problem-free" production could be more valuable than is indicated by the individual cost items used here. Farmers empathize with their animals (e.g., Bock et al., 2007) and would rather have healthy animals for ethical reasons. Additionally, sick and subfertile cows create more work and sometimes necessitate special procedures (e.g., milking mastitic cows last). These extra labor costs were not accounted for in our calculations.

CONCLUSIONS

This simulation study showed that terminal and rotational crossbreeding strategies using SR and SH can improve profitability in average Swedish organic and conventional dairy herds with purebred SH only. The main benefits of heterosis were expressed in fertility traits and survival, which ensured that fewer replacement heifers could be kept and that a lower replacement rate was present. The improved fertility in the herds permitted additional use of BS, producing slaughter calves with a higher value. In addition, heterosis on milk yield was favorably expressed in only minor decreases in 305-d production as compared with purebreeding. The largest economic benefits were shown for rotational crossbreeding, in which all animals in the herd were crossbreds and expressed 67% of the full heterosis. In the terminal crossbreeding system, 31% of the animals were crossbreds expressing full heterosis. The 2 crossbreeding strategies were not economically optimized; potentially, they could generate even larger economic benefits. Some aspects of the implementation of crossbreeding in a herd remain to be investigated, such as the economically optimal breeding strategy, genetic improvement, and transition strategies.

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Genetic consequences of terminal crossbreeding, genomic test, sexed semen, and beef semen in dairy herds

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ABSTRACT

The development of breeding tools, such as genomic selection and sexed semen, has progressed rapidly in dairy cattle breeding during the past decades. In combination with beef semen, these tools are adopted increasingly at herd level. Dairy crossbreeding is emerging, but the economic and genetic consequences of combining it with the other breeding tools are relatively unknown. We investigated 5 different sexed semen schemes where 0, 50, and 90% of the heifers; 50% of the heifers + 25% of the first-parity cows; and 90% of the heifers + 45% of the first-parity cows were bred to sexed semen. The 5 schemes were combined in scenarios managing pure-breeding or terminal crossbreeding, including genomic testing of all newborn heifers or no testing, and keeping Swedish Red or Swedish Holstein as an initial breed. Thus, 40 scenarios were simulated, combining 2 stochastic simulation models: SimHerd Crossbred (operational returns) and ADAM (genetic returns). The sum of operational and genetic returns equaled the total economic return. Beef semen was used in all scenarios to limit the surplus of replacement heifers. Terminal crossbreeding implied having a nucleus of purebred females, where some were inseminated with semen of the opposite breed. The F_1 crossbred females were inseminated with beef semen. The reproductive performance played a role in improving the benefit of any of the tools. The most considerable total economic returns were achieved when all 4 breeding tools were combined. For Swedish Holstein, the highest total economic return compared with a pure-breeding scenario, without sexed semen and genomic test, was achieved when 90% sexed semen was used in heifers and 45% sexed semen was used for first-parity cows combined with genomic test and crossbreeding (+€58, 33% crossbreds in the herd). The highest total economic return for Swedish Red compared with a pure-breeding scenario, without sexed semen and genomic test, was achieved when 90% sexed semen was used in heifers combined with genomic test and crossbreeding (+€94, 46% crossbreds in the herd). Terminal crossbreeding resulted in lower genetic returns across the herd compared with the corresponding pure-breeding scenarios but was compensated by a higher operational return.

Key words: sexed semen, genomic selection, beef semen, dairy crossbreeding, herd economy

INTRODUCTION

Dairy cattle breeding has progressed rapidly during the past decades due to new breeding tools, such as genomic selection and sexed semen (**SS**). In less than a decade, genomic selection revolutionized dairy cattle breeding and made it possible to select young bulls with reliabilities of breeding values nearly as high as reliabilities for daughter-proven AI bulls for all kinds of traits. For farmers, genomic testing (**GT**) is an opportunity to more accurately select replacement heifers before they are bred and reduce the genetic lag between the herd and the breeding population (Buch et al., 2012; García-Ruiz et al., 2016). The use of SS enhances the chance of getting female offspring to about 90% (e.g., Borchersen and Peacock, 2009), making it possible for farmers to ensure a sufficient number of future replacement heifers. Also, by ensuring future replacement heifers are born from the best cow dams, genetic lag can be reduced (Weigel, 2004; Sørensen et al., 2011; Ettema et al., 2017). A dose of SS is usually more expensive than conventional semen (**CS**), and the conception rate with SS is 70 to 95% of the conception rate with CS (Borchersen and Peacock, 2009; Butler et al., 2014; Maicas et al., 2020). Combining SS with GT has shown positive interaction effects on genetic gain and thereby economic return at herd level (Calus et al., 2015; Hjortø

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et al., 2015; Bérodier et al., 2019). However, economic and genetic benefits at herd level of using SS and GT differs between farms and management systems and are mainly dependent on reproduction level, rearing costs, and market prices for replacement heifers (McCullock et al., 2013; Hjortø et al., 2015; Newton et al., 2018). Furthermore, by combining SS with beef semen (**BS**), it potentially increases genetic and economic benefits at herd level (Hjortø et al., 2015; Ettema et al., 2017), and additionally, it benefits favorably on the climate footprint by increasing the beef efficiency from dairy farms (Holden and Butler, 2018).

The proportion of dairy herds that use SS and GT differs between countries but generally increases. In Denmark, the proportion of farmers using more than 10% SS on Holstein heifers has increased from 28% in 2011 (SEGES, 2011) to 60% in 2020 (SEGES, 2020). In the United Kingdom, the sales of SS doses have more than doubled between 2012 and 2019. In Sweden, the proportion of SS inseminations is still very low (5%; Växa Sverige, 2019). The number of GT heifers in Denmark, Sweden, and Finland (**DFS**) has increased 5 times between 2012 and 2017 (Nielsen et al., 2019). However, only about 12% of heifers born each year in DFS are genomically tested (Bengtsson et al., 2020).

Crossbreeding between dairy cattle breeds has been known for at least a century as an effective breeding strategy to use complementary traits and heterosis (Touchberry, 1992; Sørensen et al., 2008). However, the frequency of crossbreeding is relatively low in European countries (Dezetter et al., 2017; Clasen et al., 2019a), the United States, and Canada (Norman et al., 2018), whereas crossbreeding has become the primary breeding strategy in New Zealand (DairyNZ, 2021). Studies on the economic benefits of systematic crossbreeding at herd level have been sparse, but more recent studies showed positive economic benefits of crossbreeding (Dezetter et al., 2017; Shonka-Martin et al., 2019; Clasen et al., 2020a).

Several studies have already pointed out genetic and economic consequences of combining GT, SS, and BS, but studies on the effects of combining one or more of these tools with crossbreeding are limited – especially regarding the genetic lag and rate of genetic progress. This simulation study aimed to investigate the operational and genetic return using GT, SS, BS, and crossbreeding at herd level in herds based on Swedish Holstein (**SH**) or Swedish Red (**SR**). Due to the lack of genomic breeding values for crossbred animals, they are not relevant for GT, and therefore we simulated a terminal crossbreeding strategy, where all crossbred and purebred replacement heifers were born from purebred dams. Our long-term goal is to improve the economy of milk production by providing new knowledge on the combined effects of GT, SS, BS, and dairy crossbreeding as a base for decisions at herd level.

MATERIALS AND METHODS

Herd Scenarios

Two base herd scenarios were set up with 100 cows of either purebred SH or SR that resembled average Swedish herds in a conventional production system. The base herds were combined with different scenarios of pure-breeding (**PB**) or terminal crossbreeding (**XB**) with SH or SR and with or without GT. Sexed semen was used on heifers and first-parity cows in some scenarios. An overview of how the breeding tools were combined in 40 different scenarios is presented in Table 1.

The scenarios were simulated using a combination of 2 stochastic models: SimHerd Crossbred (Østergaard et al., 2018) and ADAM (Pedersen et al., 2009). SimHerd Crossbred is a modified version of SimHerd (Østergaard et al., 2005) and was used to simulate the effects of crossbreeding, SS, and BS on herd dynamics. The output from SimHerd Crossbred describing the flow of animals born and culled in the herd was used to specify input parameters in ADAM to simulate breeding values of the animals and genetic progress of the breeding scheme. The combination of SimHerd and ADAM has been used successfully in other studies (Hjortø et al., 2015; Ettema et al., 2017; Clasen et al., 2019b).

Table 1. Herd scenarios having purebred Swedish Red (SR) or Swedish Holstein (SH) combined with sexed semen (SS) used in heifers and first-parity cows, crossbreeding or no crossbreeding, and genotyping or no genotyping

Scenario[1]	Pure breed	SS heifers (%)	SS first parity (%)	Crossbreeding	Genotyping
0:0	SR or SH	0	0	Yes or No	Yes or No
50:0	SR or SH	50	0	Yes or No	Yes or No
90:0	SR or SH	90	0	Yes or No	Yes or No
50:25	SR or SH	50	25	Yes or No	Yes or No
90:45	SR or SH	90	45	Yes or No	Yes or No

[1] Ratios of heifers to first-parity cows that received SS.

Table 2. Phenotypic breed estimates[1] of Swedish Holstein (SH) and Swedish Red (SR) and heterosis estimates in crosses between the breeds for production, risk of diseases, reproduction, and mortality traits used in the model simulating a conventional production system

Trait	SH	SR	Heterosis[2] (%)
305-d kg ECM, first parity	8,822	8,369	+3
305-d kg ECM, second parity	10,508	9,586	+3
305-d kg ECM, later parities	10,957	9,873	+3
Mastitis (%)	10.2	7.8	—
Hoof-related diseases (%)	21.6	16.8	−10
Other diseases (%)	2.7	2.1	−10
Dystocia (%)	5.6	4.6	−7
Cow mortality (%)	6.2	3.5	−10
Calf mortality (including stillbirth, %)	8.7	5.3	−12
Youngstock mortality (%)	3.7	4.1	−12
Conception rate (cows, %)	35	45	+10
Age at first service (mo)	17.6	17.9	—
Calving to first AI (d)	80	77	—

[1] Data from the Swedish milk recording scheme. The data set consisted of 687,828 milk records from SH cows and 440,924 milk records from SR cows.

[2] Based on Jönsson (2015). All estimates are favorable.

SimHerd Crossbred Simulations

Inputs describing breed estimates and heterosis in the crossbred animals were the same as recently used by Clasen et al. (2020a). The breed estimates originated from the Swedish cattle database (managed by Växa Sverige, Uppsala), whereas the heterosis estimates were based on a study by Jönsson (2015), shown in Table 2. The herd management procedures in the simulations were the same as described in Clasen et al. (2020a). We used the same prices for milk, feed, carcass, live animals, and veterinarian expenses. The price for a dose of SS was €35, and the price for a dose of CS and a dose of BS was €20.5, which were approximately the average prices in May 2020 for SR, SH, and beef breed sires, not including AI service (Växa Sverige, 2020).

Terminal crossbreeding in the XB scenarios implied having a herd of partly purebred SH or SR (nucleus), and partly F_1 crosses of SR × SH or SH × SR. The crossbred females were inseminated with BS; thus, the purebred nucleus was essential for providing replacement heifers of both purebreds and crossbreds. The size of the nucleus (i.e., the proportion of the purebreds necessary to keep in the herd to ensure enough replacement heifers) depended on the use of SS in each scenario and the parameters for reproduction and mortality in both heifers and cows. Therefore, presimulations were necessary to decide the proportions of the purebred females that should be used for PB and crossbreeding. As part of the breeding strategy, all heifers in the nucleus were selected for PB, whereas the oldest cows were selection candidates for crossbreeding. In the SimHerd Crossbred model, breed and age distinguished the animals. Selection for PB occurred randomly within 3 groups; heifers, first-parity cows, and older cows. Thus, cows in second parity and older were pooled in the same group from where they were randomly chosen for pure-breeding and crossbreeding, which means that a second parity cow was just as likely to be used for pure-breeding as, for example, a fifth parity cow. The proportions of the purebreds used for pure-breeding and crossbreds are presented in Table 3. Figure 1 illustrates the distribution of females in the XB scenario corresponding to SH with 90% SS in heifers and 45% SS in first-parity cows.

Sexed semen was limited to 2 attempts per female bred to SS to simulate standard practice in Swedish dairy herds. Thereafter, CS was used. The a priori rate of conception with CS was set to 0.625 for heifers of both breeds, 0.35 for SH cows, and 0.45 for SR cows regardless of parity number. The chance of conception with SS was assumed to 0.85 the conception rate for CS.

Table 3. Proportions of purebred first-parity cows and older cows used for terminal crossbreeding (XB) in the crossbreeding scenarios, and the proportions of crossbred cows in the herd using different proportions of sexed semen (SS) in purebred heifers and first-parity cows

Pure breed[1]	Scenario[2]	XB first parity (%)	XB older (%)	Crossbreds (%)
SH	0:0	0	10	5
	50:0	10	40	20
	90:0	10	65	27
	50:25	10	50	23
	90:45	10	85	33
SR	0:0	10	60	34
	50:0	10	80	40
	90:0	10	100	46
	50:25	10	85	42
	90:45	15	100	46

[1] SH = Swedish Holstein; SR = Swedish Red.

[2] Ratios of heifers to first-parity cows that received SS.

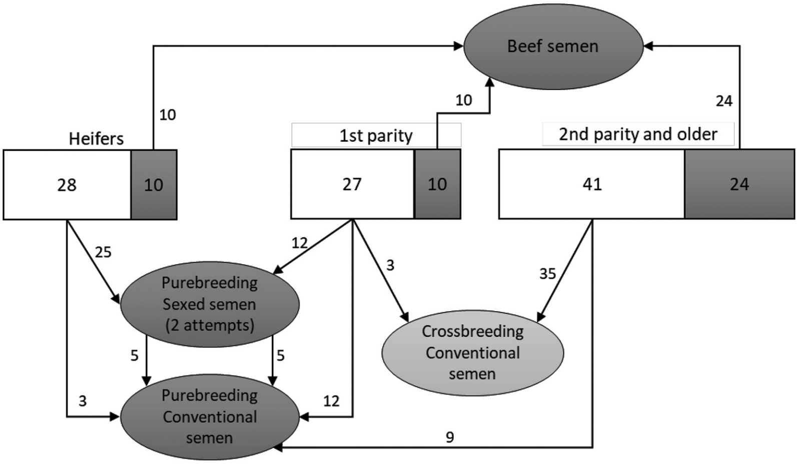

Figure 1. Illustration of the distribution of females in the breeding scheme for the scenario based on terminal crossbreeding with Swedish Holstein in the nucleus, using 90% sexed semen in heifers and 45% sexed semen in first-parity cows. The numbers within the white boxes indicate the number of purebred Swedish Holstein females within the age group. The numbers within the gray boxes indicate the number of crossbred Swedish Red × Swedish Holstein females within the age group. The numbers connected to the arrows indicate the number of females from the respective age group bred to sexed, conventional (pure-breeding or crossbreeding), and beef semen, respectively, in SimHerd Crossbred.

Beef semen was used to limit the surplus of heifers in the PB scenarios. The proportion of BS depended, as did the proportion of crossbreds in the crossbreeding scenarios, on the amount of SS, reproduction, and mortality parameters, and was therefore presimulated for the PB scenarios. In these scenarios, the older cows were selection candidates for BS, pooled in groups of third parity and older cows, with second-parity cows, first-parity cows, and heifers in separate groups. The results of the presimulations of BS in the PB scenarios are presented in Table 4. Figure 2 illustrates the distribution of females in the PB scenario corresponding to SH with 90% SS in heifers and 45% SS in first-parity cows.

In scenarios that included GT, all purebred heifers born in the herd were genotyped. Crossbred heifers were not genotyped, because they were not selected to produce replacement heifers. The price for genotyping was set to €22.5, which corresponds to the lowest price at the time of simulation on the Swedish market using tissue sampling tags to collect DNA samples with ear tagging simultaneously.

In contrast to the previous study by Clasen et al. (2020a), we included labor costs for young stock reared for replacement in the herd. The yearly labor cost per replacement heifer was set to €261.6 (Länsstyrelsen Västra Götaland, 2019). Labor costs associated with cows and capital costs were not included, as they were assumed the same across all scenarios.

ADAM Simulations

Using outputs from the SimHerd Crossbred simulations describing the replacement rate, the distribution of females available in the herd, and females born from different age groups, input parameters for the herd selection scheme were constructed for ADAM. Hence,

Table 4. Proportions of purebred second-parity cows and older cows bred to beef semen (BS) in the pure-breeding scenarios using different proportions of sexed semen (SS) in heifers and first-parity cows

Pure breed[1]	Scenario[2]	BS second parity (%)	BS older (%)
SH	0:0	0	25
	50:0	0	60
	90:0	15	100
	50:25	0	85
	90:45	60	100
SR	0:0	0	90
	50:0	20	100
	90:0	70	100
	50:25	40	100
	90:45	100	100

[1] SH = Swedish Holstein; SR = Swedish Red.

[2] Ratios of heifers to first-parity cows that received SS.

both models simulated the same herd dynamics in each scenario.

Within the simulated herd, females were selected according to the selection scheme composed from the SimHerd Crossbred output and based on EBV or genomic EBV if the scenario included GT. Females not selected for any type of semen (SS, CS, or BS) were culled from the herd. Before selection within each age group, random culling took place to mimic the SimHerd Crossbred output replacement rates.

Besides the simulated herd, ADAM simultaneously simulated a cow population and a breeding population. The cow population represented any other herd in Sweden, and the only function of this population was to provide replacement heifers to the simulated herd, in case needed. However, because the initial simulations in SimHerd Crossbred defined a surplus of heifers, the support from the cow population was only needed in ADAM due to variation between replicates. The breeding population consisted of bull dams and AI bulls that contributed with semen to the simulated herd and the cow population. Each year, 1,000 out of 2,500 young bulls were selected for genotyping, and the 100 bulls with the highest genomic EBV were selected to have semen stored. AI bulls were available up to 4 yr of age, and the top 50 bulls were used for breeding and were mated to a maximum of 200 dams. Because SH and SR were assumed to have similar genetic parameters, the bulls used for pure-breeding and crossbreeding came from the same breeding population in the simulations.

Crossbreeding is not a feature in ADAM, which means that heterosis and breed effects were not included in genetic progress simulations. For that reason, SR and SH were assumed to have the same genetic parameters in the ADAM simulation and the same breeding goal. Even so, heterosis and breed differences were already accounted for in SimHerd Crossbred. Thus, the herd selection schemes differed between breed scenarios (as shown in Tables 3, 4, and 5) due to the differences in herd dynamics. The simulated breeding goal resembled the breeding goal of the Nordic Total Merit Index (**NTM**). Hence, the simulated population had a genetic gain corresponding to the Nordic dairy breeding schemes. This approach has been followed previously and is well described by Buch et al. (2012) and others in previous ADAM simulations. In short, only 2 traits were included in the total merit index simulated in ADAM: one that represented milk production traits and had a heritability of 0.30, and one that represented functional traits and had a heritability of 0.04. The economic weights of the traits were €83 and €82 per genetic standard deviation. These weights were derived to reflect the correlations between milk production traits and functional traits in the NTM. For the simulation of genomic selection, 2 pseudogenomic traits were added

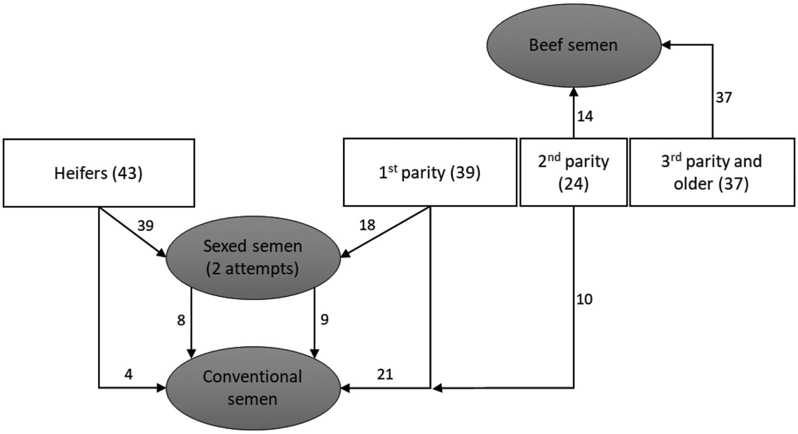

Figure 2. Illustration of the distribution of females in the breeding scheme for the scenario based on pure-breeding with Swedish Holstein using 90% sexed semen in heifers and 45% sexed semen in first-parity cows. The numbers within the white boxes indicate the number of females within the age group. The numbers connected to the arrows indicate the number of females from the respective age group bred to sexed, conventional, and beef semen, respectively, in SimHerd Crossbred.

Table 5. Number of purebred and crossbred heifers born each year in the scenarios with pure-breeding (PB) and crossbreeding (XB) within herds having Swedish Holstein (SH) or Swedish Red (SR) in the purebred nucleus

		Sexed semen scheme (% heifers:% cows)				
Breed	PB or XB	0:0	50:0	90:0	50:25	90:45
SH	PB	43:0	44:0	44:0	43:0	43:0
	XB	42:2	35:6	32:9	32:7	28:10
SR	PB	30:0	31:0	31:0	31:0	31:0
	XB	19:10	19:12	18:13	18:12	17:14

(one for the milk production trait and one for the functional trait) with heritabilities of 0.99 and with correlations to the “true” traits corresponding to a predefined accuracy of the selection index at 0.71. This accuracy reflects the accuracy of the current NTM. See Buch et al. (2012) for a more detailed description of ADAM simulations of the NTM.

Data Analysis

The scenarios were simulated through 50 yr in SimHerd Crossbred to ensure a steady-state equilibrium. Because the SimHerd Crossbred model does not account for genetic progress, steady-state equilibrium occurred when breed proportions were steady between the years. In practice, we do not expect such a long period to implement the crossbreeding strategy fully. We simulated 50 years because the simulated transition period from pure-breeding to crossbreeding is not optimized in SimHerd Crossbred. The analyzed data were means of 1,000 replicates of the last 10 yr of simulation. The data on herd dynamics from the various scenarios were used to calculate the operational return, expressed as €/cow-year. The operational return was calculated as sales income from milk, slaughter, and live animals minus the variable costs associated with cows and replacement heifers, labor costs associated with replacement heifers, and the cost of genotyping heifers in the relevant scenarios.

The scenarios were simulated in ADAM through 30 yr, and the analyzed data were based on means of 1,000 replicates over the last 10 yr of simulation when the yearly genetic progress was stable. The economic value of the genetic level of heifers born each year was interpreted as the genetic return. The difference in genetic returns between scenarios illustrated the genetic lag between the scenarios, which was stable for the last 10 yr of simulation. The total return was calculated as the sum of the operational return and the genetic return, expressed as €/cow-year.

Sensitivity Analysis

A sensitivity analysis was made of the effect of labor costs associated with replacement heifers on the PB and XB scenarios′ operational returns using the SS scheme with 90% SS in heifers and 45% SS in first-parity cows (90:45). Three levels of costs were considered: €0, €130.8, and €261.6 for both SR and SH, where €261.6 corresponded to what we simulated in the main scenarios.

Another sensitivity analysis was carried out on the effect of extreme use of SS on the total return in the XB scenarios within both dairy breeds used for insemination. In these scenarios, SS was used for all females in the purebred nucleus, with unlimited attempts to become pregnant with SS. As we still wanted to limit the number of surplus heifers, the proportion of purebred females used for crossbreeding was presimulated to 50% of the first-parity cows and 100% of the older cows in the SH nucleus, and 65% of the first-parity cows and 100% of the older cows in the SR nucleus.

RESULTS

Economic Returns in SH Scenarios

In the absence of GT, the operational returns decreased by €4–9 relative to the base scenario when SS was applied in the breeding scheme with purebred SH (Figure 3). The genetic returns did, however, increase by €4 to 16 when SS was applied. In the 50:0 SS scheme, the positive genetic return did not compensate for the negative operational return, and the total return was €2/cow-year lower than the base scenario. The positive genetic return for the remaining SS schemes did compensate for the negative operational return; the total returns were between €2 (50:25) and €10 (90:45) higher per cow-year than the base scenario.

The cost of genotyping had adverse effects (−€9 to −€10) on the operational returns in the PB scenarios with SS, evident from comparing the “GT” with “no

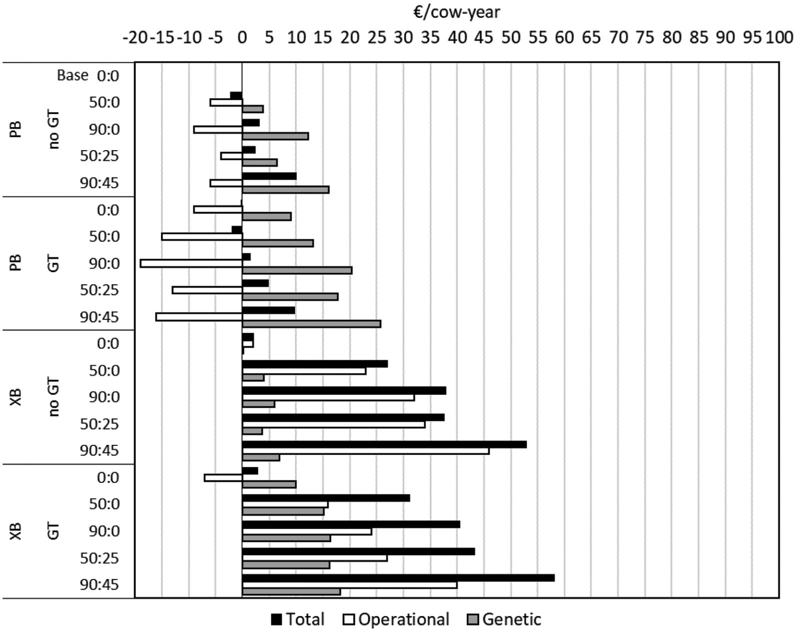

Figure 3. Operational (white), genetic (gray), and total economic returns (black) in €/cow-year for simulated Swedish Holstein scenarios with pure-breeding (PB) or crossbreeding (XB), using genomic selection (GT) or not using genomic selection (no GT) within sexed semen schemes where 0% (0:0), 50% of the heifers (50:0), 90% of the heifers (90:0), 50% of the heifers + 25% of the first-parity cows (50:25), and 90% of the heifers + 45% of the first-parity cows (90:45), were bred to sexed semen.

GT" scenarios within SS schemes. However, the positive effects (+€8–11) of GT on the genetic returns balanced out the total returns, as in the scenarios without GT.

Comparing the XB scenario with PB scenarios within SS schemes, crossbreeding reduced the genetic returns, but genetic returns were equal to or up to €7 larger than the genetic return in the base scenario. The operational returns were higher in the XB scenarios due to breed effects of SR, heterosis, and changes in herd dynamics. Without SS, the effect of crossbreeding (XB scenario 0:0) on the operational return was marginal (+€2) because there were only 5% crossbreds in the herd (Table 3). Excluding GT, the effects on total returns of crossbreeding combined with any other SS scheme were €27 to 53 higher than the base scenario.

The combination of crossbreeding, SS, and GT in the XB scenarios provided the highest total returns. The SH scenario with the highest total return (+€58 higher than the base scenario) was the one with the most use of SS (90:45), which also provided the highest proportion of crossbreds in the herd (33%; Table 3).

Economic Returns in SR Scenarios

Without GT, SS decreased the operational returns by €5 to 7 in the PB scenarios with SR, relative to the base scenario for SR (Figure 4). When 50% SS was used in heifers (50:0), the genetic return was €23 higher than the base scenario, whereas there was no further effect of combining SS in heifers with SS in first-parity cows (50:25). Increasing the use of SS in 90:0 and 90:45 had higher genetic returns (+€24 and +€27, respectively.).

As in the SH scenarios, the cost of GT negatively affected the operational returns, but for SR, the effect was between −€6 and −€7 (i.e., smaller than for SH due to fewer replacement heifers). Except for the PB scenario with SS scheme 90:45 (+€4), GT positively affected the genetic return between +€8 and +€10. In the 90:45 SS scheme with GT, the total return was just €18 higher than the base scenario (i.e., €3 lower than the corresponding scenario without GT). The total returns for the remaining PB scenarios, including GT, were between €17 and €20 higher than for the base scenario, and €1 to €3 higher than for the corresponding PB scenarios without GT.

Without GT, crossbreeding increased the operational return: between +€67 and +€73 relative to the base scenario. Even the XB scenario without SS (0:0), where the proportion of crossbreds was 34% (Table 3), had a larger operational return. Furthermore, the genetic return in this scenario was the same as in the base scenario. The genetic returns in the remaining XB scenarios (without GT) were similar for 50:0 and 50:25 (+€8 relative to the base scenario), but there was a larger effect of crossbreeding comparing 90:0 (+€19) to 90:45 (+€14). The total returns summed between +€69 and +€87 relative to the base scenario, where SS schemes 90:0 and 90:45 had the highest total returns.

The effect of combining crossbreeding with SS and GT in the XB scenarios (with GT) showed similar tendencies as in the XB scenarios without GT. The operational returns were between €61 and €69 higher than the base scenario, despite the cost of GT. The genetic returns gained from GT and were between €10 and €30 higher than the base scenario. The 90:0 SS scheme had higher genetic returns (+€30) than the 90:45 SS scheme (+€24). The total return was highest in the 90:0 SS scheme (+€94), but nearly the same in the 90:45 SS scheme (+€93).

Herd Dynamics

The number of heifers born each year was approximately identical across SS schemes for the PB scenarios but differed between breeds (Table 5). The SH scenarios needed more replacement heifers; thus, 13 more heifers were born each year, compared with SR scenarios. Only 2 crossbred heifers were born each year in the XB scenario with SH without the use of SS (0:0), but the number increased with the increasing use of SS. For SR, there was a considerable reduction of purebred heifers born in the XB scenario without SS (19 in 0:0) than the corresponding PB scenario (30 in 0:0). The number

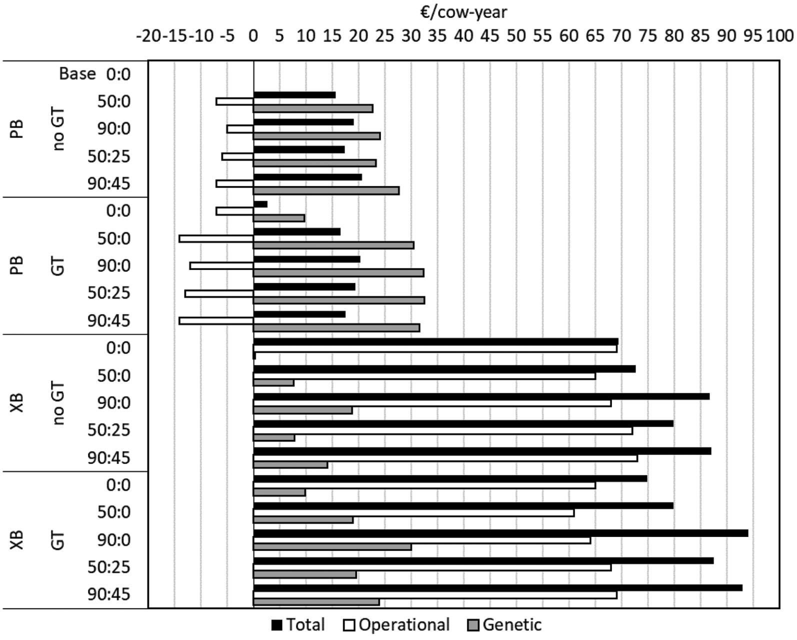

Figure 4. Operational (white), genetic (gray), and total economic returns (black) in €/cow-year for simulated Swedish Red scenarios with pure-breeding (PB) or crossbreeding (XB), using genomic selection (GT) or not using genomic selection (no GT) within sexed semen schemes where 0% (0:0), 50% of the heifers (50:0), 90% of the heifers (90:0), 50% of the heifers + 25% of the first-parity cows (50:25), and 90% of the heifers + 45% of the first-parity cows (90:45), were bred to sexed semen.

of crossbred heifers in the SR scenarios only slightly increased when SS was used.

In the PB scenarios and within the purebred nuclei in the XB scenarios, the age distribution for SH was 39% first parity, 24% second parity and 37% older cows within the herd. The age distribution for SR was 28% first parity, 20% second parity, and 52% older cows. By design, neither SS nor GT affected these distributions. However, there was a marginal effect of crossbreeding toward older cows. Therefore, fewer purebred first- and second-parity cows were available to select from in the SR scenarios compared with the SH scenarios.

Sensitivity Analyses

Applying different labor costs associated with replacement heifers had some effects when changing from the base (PB 0:0) to XB 90:45 in the SH herd scenarios. At no labor cost, the operational return was 1% higher in XB 90:45 relative to the base scenario, whereas it was 2.5% higher at the cost of €261.6/heifer per year. The reason behind this tendency was a considerable reduction (~12%) of young stock when crossbreeding was implemented, as shown in Table 5. In the similar scenarios based on SR, the difference in operational return at no labor cost was 5.6%, but as opposed to the SH scenario, the difference decreased to 4.0% at the highest simulated labor cost due to a small increase in young stock.

In the extreme scenarios simulating 100% use of SS in the XB scenarios, the proportion of crossbreds were 54% in the SH based scenario and 65% in the SR based scenario. Excluding GT, the operational returns were +€290 and +€277 for SH and SR, respectively, compared with the base scenarios within the respective breeds. Correspondingly, the genetic returns were +€11 and +€12; thus, the total returns were +€301 for SH and +€289 for SR. With the addition of GT, operational returns were +€285 for SH and +€276 for SR, whereas genetic returns were +€20 and +€17. Hence, the total returns were +€305 and +€293 for SH and SR, respectively, compared with the base scenarios.

DISCUSSION

Overall, these simulations show positive total economic effects of using SS, GT, terminal crossbreeding, or a combination of them as breeding tools in a dairy herd. Terminal crossbreeding had negative effects on the herd′s genetic return because crossbred animals were out of the oldest purebred dams in the herd. Nevertheless, there was a large and favorable effect of crossbreeding on the operational return, and thus the total return, due to complementation of breed effects, heterosis, and changes in herd dynamics. Disregarding the extreme scenarios simulated for the sensitivity analysis, the SH herd′s best combination was using 90% SS in heifers and 45% SS in first-parity cows, combined with GT and crossbreeding. For the SR herd, the best combination was using 90% SS in heifers (and no SS in cows) and combined with GT and crossbreeding. However, due to differences in mainly reproduction traits between the 2 breeds, there were different effects of using the breeding tools. The simulated scenarios do not necessarily illustrate the best possible breeding schemes and should be interpreted as cases for the use of crossbreeding, SS, BS, and GS and combinations of these tools for 2 different breeds.

SimHerd Crossbred and ADAM did not allow for the best possible breeding scheme, and the economic returns were, therefore, likely a little underestimated. SimHerd Crossbred does not account for each animal′s genetic level, and ADAM was used to study genetic progress. To match SimHerd Crossbred with ADAM, the age distribution obtained in SimHerd Crossbred was used as input parameters for ADAM. The fixed age distribution limited the ADAM model to select the genetically best cow dams within age groups and not across the entire herd. The consequence of this was evident in the PB scenarios with SR and the use of SS, where candidates to be covered with SS were limited to second-parity cows. Thus, potentially better cows from the third or later parities were ignored, and therefore the differences between these scenarios were somewhat limited. Another restriction in the SimHerd Crossbred model was a difference between the input parameters available for BS and crossbreeding; where 4 age groups (heifers, first parity, second parity, and older) were available for BS, just 3 were available for crossbreeding (heifers, first parity, and older). That means, when the SimHerd Crossbred output was used as input for the selection scheme in ADAM, there was an advantage of the selection scheme in the XB scenarios compared with the PB scenarios because in the PB scenarios, the model was “forced” to select among older cows than in the XB scenarios. Thus, the purebred females′ genetic level was likely higher in the XB scenarios than in the PB scenarios due to selection differences.

In general, a high replacement rate is associated with a shorter generation interval, which is favorable for the genetic lag. Our results show that a lower replacement rate (reflected by the number of replacement heifers; Table 5) does not (necessarily) compromise the genetic lag between the simulated herd and the breeding population. Despite having a larger proportion of old cows in the herd, the generation intervals were lower in herds having SR than herds having SH. The SR scenarios needed fewer replacement heifers than SH scenarios, and therefore fewer cows were needed to be inseminated with dairy semen. Thus, the average age of the females producing replacement heifers was lower in the SR scenarios. In a recent review by De Vries (2020), he estimated the cow's economic optimum age at 5 lactations. In a study on the genetic effects of extended lactation, the use of SS and selection prioritized on the youngest females counteracted the negative effects on the genetic lag by having older cows in the herd (Clasen et al., 2019b). Thus, the optimal total economic return lies in the balance between having (older) cows in their most productive age and only selecting the genetically best animals as dams of future replacement heifers (De Vries, 2020).

Sexed Semen and Genomic Selection

Due to the small number of surplus heifers in the simulated scenarios, there was barely any selection among replacement heifers as future cow dams. Therefore, the economic potential of GT was neglected at this stage of selection. However, at the stage of selecting heifers for SS, the benefits of GT were utilized. Calus et al. (2015) concluded that GT was most beneficial when there was a large surplus of heifers, but the additional benefit of SS in the study was largest when the surplus was small. Nevertheless, the use of GT did show some benefits on the genetic return in the present study, despite a small number of surplus heifers. The reason is that the information of GT was used more than once throughout the breeding scheme: at selection of heifers for SS (except for SS scheme 0:0), selection of first-parity cows for SS (in SS schemes 50:25 and 90:45), and selection of cows for BS in second parity and later parities (PB scenarios) or selection of cows for crossbreeding in first and later parities (XB scenarios). The benefit of GT on the genetic return in PB scenarios without the use of SS (0:0) was due only to the selection of cows for BS. However, for the SR scenarios, there was no selection among second-parity and older cows in the 90:45 SS schemes (both PB and XB scenario), which may partly explain why the genetic return in these scenarios was lower than in 90:0. Hjortø et al. (2015) also found a larger benefit of GT when the information was used more than once—they too had only a small surplus of replacement heifers but included SS and BS in their simulation study.

Combining SS with GT had negative interaction effects on the genetic returns comparing SS schemes 90:0 and 90:45 in the SR scenarios. Furthermore, the genetic return was also lower comparing the 90:45 SS scheme with the extreme XB scenario, where SS was used as much as possible. On the other hand, the genetic returns increased throughout the corresponding scenarios for SH. Hjortø et al. (2015) found that herds with average reproductive performance (41% replacement rate) benefited more (genetically) from combining SS and GT than herds with good reproductive performance (38% replacement rate). These findings comply somewhat with our findings, considering SR as having better reproductive performance than SH. From a genetics perspective, it would seem that maximizing the use of SS is not the most optimal breeding strategy at low replacement rates. However, the study from Hjortø et al. (2015) is based on a combination between SimHerd and ADAM as well, thus, this effect is likely due to limitations on the selection scheme when combining the 2 models, as explained earlier.

In the PB scenario with SH without SS (0:0), the cost of GT was only just covered by the genetic return in total return, whereas the similar scenario with SR had +€4 in total return at the same GT cost. The cost of GT was €22.5 in this simulation. A breakeven price for GT (without using SS) was calculated to €21 by Hjortø et al. (2015) when all heifers were genotyped in a herd with average reproductive performance and €30.5 in a herd with good reproductive performance.

Sexed Semen and Beef Semen

The difference in the genetic return between SS schemes 50:0 and 90:0 in the PB scenarios was larger in SH than in SR. The same trend was found in the study by Hjortø et al. (2015) between breeding schemes using 40 and 80% SS in heifers, respectively, in herd scenarios having low versus high reproductive performance. In that study, the proportion of BS increased more between 40 and 80% SS in herd scenarios with low reproductive performance compared with high reproductive performance. Likewise, in the present study, the proportion of cows selected for BS increased more between 50:0 and 90:0 in SH compared with SR. Compared with the SR herd, the heifers in the SH herd had relatively better reproductive performance than the SH cows, which may explain why the herd benefited more from increasing SS on heifers.

The combination of SS and BS has potential economic as well as environmental benefits. Ettema et al. (2017) showed that reducing the number of surplus heifers using BS in combination with SS was economically beneficial if the cost of raising heifers was high compared with the market value. However, in cases where the price of crossbred beef x dairy calves was halved, or the market value of replacement heifers increased, it was more beneficial to produce a surplus of heifers. Therefore, the optimal strategy between producing beef x dairy cross calves versus surplus replacement heifers highly depends on the market situation, which may vary between countries and over time. Knapp et al. (2014) estimated that by reducing the replacement rate from 40 to 30%, the contribution per replacement heifers to the whole-herd enteric methane emissions would be reduced by almost 20%. Additionally, Holden and Butler (2018) estimated a 23% reduction in greenhouse gas emissions from beef production if 75% of the beef was produced from dairy farms (instead of 50%), which can be achieved by using BS in dairy production.

In our simulations, BS was used in all scenarios. However, far from all dairy farms can raise beef x dairy crosses and dairy production. Farms without that capacity depend on sales contracts with beef producers. Furthermore, some beef producers may make demands on beef sire breeds used for crossbreeding, and also, some only accept bull calves.

The relative conception rate of SS versus CS was fixed at 0.85 in our simulations, which may have been a bit conservative. Studies from DFS countries suggests a relative conception rate closer to 0.90 (Borchersen and Peacock, 2009; Tyrisevä et al., 2017), while recent analyses on dairy farms from Italy (Bittante et al., 2020) and the United States (Maicas et al., 2020) suggest relative conception rates above 0.90. In our simulations, 78% of the heifers inseminated with SS were expected to become pregnant after 2 attempts when the assumed conception rate for CS was 0.625, and the relative rate for SS was 0.85 $\{\text{conception rate} = 1- [1- (0.625 \times 0.85)]^2 = 0.78\}$. If the relative conception rate had been simulated at levels of 0.90 or 0.95, the proportion of pregnant heifers with SS after 2 attempts would be expected at 81 and 83%, respectively. However, for the scenarios we simulated, the difference in heifers born from dams inseminated with SS would have been at most 2 additional heifers.

Crossbreeding

The proportion of crossbreds was much higher in the 0:0 scenario having SR than SH because of better reproductive performance and lower calf mortality, allowing for a smaller SR nucleus. However, there were larger increases in the crossbred proportions when SS was introduced in the SH herd than in the SR herd because the SH herd benefited more by increasing SS than the SR herd. Comparing the crossbred proportions in the 0:0 scenarios with the extreme scenarios using 100% SS shows a more considerable increase in crossbreds in the SH scenarios (5 vs. 54% crossbreds) than the SR scenarios (34 vs. 63% crossbreds).

In the XB scenarios based on SR, the crossbred proportion was 46% in 90:0 and 90:45, even though a slight increase was expected in the latter scenario. The explanation is that the scenarios had just a small difference in the proportion of first-parity cows selected for crossbreeding (10 and 15%, respectively; Table 3). Furthermore, because of the low replacement rate in the SR scenarios (reflected by the heifers born; Table 5), the number of first-parity cows to select from was somewhat limited (17–18) and therefore, 10 or 15% would only make a difference of maximum one cow.

As expected, the genetic returns in the XB scenarios were lower compared with the PB scenarios within the same SS schemes because we selected among the oldest purebred cows in the nucleus for crossbreeding. Thus, the crossbred heifers born in the XB herd were at least one generation behind the purebred heifers born in the same herd. However, comparing the genetic returns between PB and XB scenarios should be done with caution because there were differences in the selection scheme due to limitations in the SimHerd Crossbred program described at the beginning of the discussion. Thus, if the selection was made the same way for both PB and XB scenarios, the genetic returns in the XB scenarios would have been expected to be even lower.

As reflected by the number of heifers born in the different scenarios (Table 5), the replacement rate was reduced when crossbreeding with SR was introduced in the SH herd, while it remained the same when crossbreeding with SH was introduced in the SR herd. As discussed previously, reducing the number of surplus replacement heifers has benefits in reducing the cost

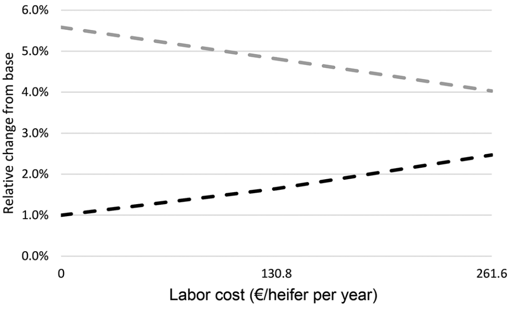

Figure 5. Relative change in operational return (€/cow-year) at different yearly labor costs associated with young stock. Changes are relative to a pure-breeding herd without the use of sexed semen within the breed (Swedish Red or Swedish Holstein) and level of labor cost (€0, 130.8, or 261.6/heifer per year). Scenarios are Swedish Red terminal crossbreeding (dashed gray line), and Swedish Holstein terminal crossbreeding (dashed black line). Both scenarios are using 90% sexed semen in heifers and 45% sexed semen in first-parity cows.

of rearing them—especially when this cost is high, as shown in Figure 5.

The breeds that are used for crossbreeding need to be economically equivalent for crossbreeding to be competitive to pure-breeding (Sørensen et al., 2008). The benefits of crossbreeding SR into an SH herd and vice versa were due to different effects. The SH breed is superior in milk production, whereas the SR breed has better functional traits, making the 2 breeds complement each other well. Thus, for the SH herd, crossbreeding with SR improved functional traits, and milk production was kept almost at the same level as the SH due to heterosis (Clasen et al., 2020a). For the SR herd, crossbreeding with SH improved the milk yield while keeping functional traits almost at the same level as purebred SR (Clasen et al., 2020b).

Our simulations using a terminal crossbreeding strategy cannot be used to determine the genetic effects of other crossbreeding strategies. For example, the crossbred animals were not used as breeding candidates, which is inevitable in rotational crossbreeding. Models for breeding value estimation in crossbreds were not available in ADAM, but are needed. Methods for routine genomic breeding evaluation in crossbred dairy cattle have been suggested (Esfandyari et al., 2015; VanRaden and Cooper, 2015), but until now, the number of genotyped crossbreds within the Swedish dairy cattle population has not been sufficient. This is somewhat a paradox because some (Swedish) farmers hesitate to introduce crossbreeding in their herds without using genomic breeding values (Wallin and Källström, 2019).

The extreme scenarios simulating maximum use of SS in a terminal crossbreeding system clearly showed the largest total economic benefits. The major benefits were increased operational returns, although genetic benefits were lower than the other XB scenarios for SR but slightly higher within the SH scenarios. Nevertheless, the total economic benefits of terminal crossbreeding were boosted in combination with SS and GT.

Improvement of Reproduction

This study's results indicate reproduction as a key trait for improving the genetic and total economic return from SS, GT, BS, and crossbreeding. It is well known that the Holstein breed's reproduction traits have eroded due to inbreeding (Bjelland et al., 2013) and decades of focus on high milk yield (Miglior et al., 2017). For the Nordic cattle breeds, reproduction traits have been included in the breeding goal since 1972 (Berglund, 2008), making it interesting to use SR for crossbreeding with Holstein from other countries. However, reproduction traits in SH are improving (Växa Sverige, 2019). Thus, SR needs to improve in other traits to remain interesting for crossbreeding for farmers with SH herds.

CONCLUSIONS

Breeding tools including sexed semen, GT, BS, and terminal crossbreeding improved the total economic return individually and combined in simulated SH and SR herds. The results indicated that reproduction plays a key role in improving the benefit of any of the tools. The highest total economic returns were found in the scenarios where the breeding tools were used most, whereas the highest genetic returns depended on the breed′s level of reproductive performance. Terminal crossbreeding resulted in a lower genetic return per generation born in the herd than the corresponding pure-breeding scenarios. However, the operational returns gained from terminal crossbreeding compensated for the higher genetic lag, which created higher total returns than pure-breeding. Terminal crossbreeding is but one crossbreeding strategy and does not include crossbred animals as breeding candidates. The genetic effects of other crossbreeding strategies remain to be investigated.

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IV

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Conservation of a native dairy cattle breed through terminal crossbreeding with commercial dairy breeds

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ABSTRACT
Farmers play a key role in conserving native livestock breeds, but without economic support, farms with native breeds may not be viable. We hypothesized that terminal crossbreeding can improve herd economy and decrease the economic support needed from society. Three scenarios were simulated using SimHerd Crossbred: a herd of purebred Swedish Polled Cattle, a herd of purebred Swedish Red, and a herd of 75% Swedish Polled Cattle and 25% F1 crossbreds. The results showed annual contribution margin per cow in the herd can be increased by €181 by crossbreeding compared with pure-breeding with the native breed, giving a 13.6% growth in contribution margin. However, the needed cost in subsidies paid by the government will remain unchanged if the population size of the native breed is to be maintained. Combining a crossbreeding strategy with the marketing of niche products may facilitate the conservation of native cattle.

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Introduction

Over the last few decades, increasing numbers of native cattle breeds all over the world have become endangered, mainly as a consequence of high production demands favouring a few high-performance breeds (Bett et al,. 2013; Upadhyay et al,. 2019) and increasing possibilities to specialize and intensify farming systems. This has led to a loss of genetic diversity, which is a concern, because such diversity may be needed if we are to overcome potential lack of genetic variation (Bett et al., 2013). Furthermore, global climate changes may cause a need for aptitudes specific to some native breeds (FAO, 2015).

Like several other European governments, the Swedish government has initiated a national action plan for animal genetic resources (Swedish Board of Agriculture, 2009) based on global action plans: the Convention on Biological Diversity (UN, 1992), signed in 1993, and FAO's 'Global Plan of Action for Animal Genetic Resources' in the Interlaken Declaration (FAO, 2007), adopted in 2007. The Aichi Target 13 for year 2020in the Convention on Biological Diversity's Strategic Plan for Biodiversity 2011–2020 is that the genetic diversity of domesticated animals is maintained, and 'strategies have been developed and implemented for minimizing genetic erosion and safeguarding their genetic diversity' (CBD, 2020). The main objectives of the national action plan are the conservation and sustainable utilization of domestic animal species native to the country. The Swedish government took responsibility for these objectives when they adopted the global action plans. However, other stakeholders – farmers, breeding organizations, dairies, retailers, etc. – need to be involved as well for the plan to be successful (Oldenbroek & Gandini, 2007; Wurzinger et al., 2011).

Of the nine native Swedish cattle breeds, the Swedish Polled Cattle (*Svensk Kullig Boskap*, **SKB**) is examined in the present study, using it as a model for any European native dairy cattle breed. The SKB breed was created in 1938 by merging the herd books of Swedish Mountain Cattle (*Fjällras*) and Swedish Red Poll (*Rödkulla*) (Johansson et al., 2020). The population of SKB has decreased since the 1970s when changes in the structure of the agricultural sector caused larger but fewer herds, a trend that is ongoing to this day. In 2017, only 735 SKB cows were milk-recorded, as compared with 10 379 in 1970 (Växa Sverige, 2018a). The total number of SKB

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Table 1. Phenotypic breed estimates[a] of Swedish Polled Cattle (SKB; n = 248) and Swedish Red (SR; n = 35 860) kept in an organic production system, and heterosis estimates in crosses between the breeds for production, risk of diseases, fertility, and mortality used in the model

	SKB	SR	Heterosis[b], %
305-d kg ECM, 1st parity	5 309	7 595	+3%
305-d kg ECM, 2nd parity	6 114	8 772	+3%
305-d kg ECM, later parities	6 811	9 087	+3%
Mastitis, %	16.9	9.8	0%
Hoof-related diseases, %	11.5	13.2	−10%
Other diseases, %	10.9	5.6	−10%
Dystocia	3.4	2.3	−7%
Cow mortality	4.5	3.5	−10%
Calf mortality (incl. stillbirth)	13.3	4.5	−12%
Young stock mortality	0.8	4.0	−12%
Conception rate, cows	0.40	0.45	+10%
Age at 1st service, months	17.6	17.9	-
Calving – 1st AI, days	102	93	-

ECM = Energy-corrected milk

[a] Data from the Swedish milk recording scheme from organic herds

[b] Based on Jönsson (2015). All estimates are favourable and based on crossbreds between Swedish Holstein and Swedish Red.

animals in Sweden (including males and young stock) was 2 663 by the end of 2018 (Swedish Board of Agriculture, 2018). Owing to its relatively low milk yield (Table 1) according to the Swedish standards, SKB is not able to compete economically with the two most popular commercial Swedish dairy breeds: Swedish Red (**SR**) and Swedish Holstein. Today, most milk-recorded SKB cows are kept at low proportions (<10%) in mixed herds with SR and/or Holstein cows, as shown in a study of organic production by Bieber et al., (2019). Those farmers who manage to keep mainly SKB cows are often found to have taken specific measures to be competitive on the dairy market, e.g. the promotion of local products, such as cheese, ice cream, and yoghurt, with an added value (Ortman, 2015). However, subsidies for conservation activities are still necessary to keep the farms viable. These subsidies are funded by the government, creating an expense for society. The level of subsidy for native breeds is currently approximately €140 per adult cow per year (Swedish Board of Agriculture, 2019).

Potentially, one way to accommodate the conservation objectives, and to improve the SKB farms' economic sustainability, would be to crossbreed with a high-producing breed. Crossbreeding in dairy cattle has shown favourable effects, especially on functional traits and herd economy, connected with heterosis (Sørensen et al., 2008; Clasen et al., 2020). However, if heterosis is to raise profits, the breeds in the crossbreeding program must be economically similar and complement each other's strengths and weaknesses (Sørensen et al., 2008; Clasen et al., 2020), and this not the case with SKB and SR or Swedish Holstein. The purpose of crossbreeding between a native low-producing breed and a high-producing commercial breed is to gain from the superior milk production performance in the latter (Franklin, 1997) and possibly keep superior functional traits or alleles from the native breed. According to Poulsen et al. (2017), the allele for A2 protein could be an example of a favourable allele found in SKB. Although systematic crossbreeding that utilizes and conserves a native breed has been successful in a few situations (e.g. Lambert-Derkimba et al., 2019), crossbreeding as a conservation strategy is uncommon, as it may be incompatible with the conservation goals for the native breed. Uncontrolled crossbreeding has in some cases threatened the existence of the original breed, as happened with Flemish Red Cattle (Lauvie et al., 2008), or virtually wiped out the original genetics, as was seen with Swedish Lowland Cattle (Bett et al., 2013).

This study simulated the economic outcome of a terminal crossbreeding strategy (sustained crossing; FAO, 2010) using SKB as the example of a native breed crossed with SR as a highly productive breed. The aim was to evaluate how effective such a crossbreeding strategy is in increasing economic sustainability in SKB herds and thus potentially saving the SKB population in dairy production. Some of the potential consequences of the crossbreeding strategy at population-level will be discussed.

The study focuses on organic production. According to the vision of the International Federation of Organic Agriculture Movements, animals used in organic production should be adapted to local conditions and local breeds are preferable (IFOAM, 2014). Organic dairy production in Sweden has a higher proportion of SKB cows (1.2%) than conventional production (0.5%) (Ahlman, 2010), although there are almost five times more conventionally farmed SKB cows than organically farmed ones (Växa Sverige, 2018a).

We hypothesize that the simulated crossbreeding strategy improves production economy at herd level, and reduces the costs per animal for society associated with subsidies paid for conservation of the native breed.

Materials and methods

Herd scenarios

In an organic production system in Sweden, we specified three herd scenarios: purebred SKB alone, purebred SR alone, and two-breed terminal crossbreeding between SKB and SR (**XB**). The terminal crossbreeding implied that only purebred SKB were used as breeding candidates while F1 crossbreds of SR x SKB females were kept as production animals. The F1 crossbreds were bred using beef semen to produce beef x dairy crossbred calves. The terminal crossbreeding system was carried out within the herd, meaning that the simulated crossbreeding herds had both purebreds and crossbreds. We wanted to keep a surplus between one and three purebred heifers in each scenario to ensure they were economically comparable. To do that in the pure-breeding scenarios, we pre-adjusted the number of heifers by breeding some of the purebred cows to beef semen, in the simulation. This adjustment was done on the proportion of purebreds that would produce crossbred animals in the crossbreeding scenario. Considering the reproductive performance, cow longevity, and calf mortality in the simulated herd, 20% of the purebred SKB females were bred to an SR sire after the adjustment.

The three scenarios were simulated using a modified version of the existing SimHerd model, SimHerd Crossbred (Østergaard et al., 2018). SimHerd Crossbred is designed to simulate crossbreeding systems at herd level by tracing breed proportion and heterozygosity for each animal in the simulated herd. The mechanisms of the model are described in more detail in Clasen et al. (2020). The scenarios were simulated for 50 years to ensure that equilibrium was reached. The results in this study are averages of 1 000 replicates over the last 10 years (year 41–50). In practice, we do not expect such a long period to fully implement the crossbreeding strategy; 50 years were simulated because the transition period from pure-breeding to crossbreeding is not optimized in SimHerd Crossbred.

Input parameters

The simulated production system mimicked a Swedish organic production system. The simulated milk withdrawal period after antibiotic treatment was twice (two weeks) that in a conventional production system (European Union, 2018). The effects of other practices in organic production, such as grazing, feeding, health, and housing were reflected in the input parameters (Table 1), management decisions, and prices (Table 2) used.

The input parameters for the breed-specific traits were based on information from the Swedish milk recording scheme. Raw means of data held in the Swedish cattle database (organized by Växa Sverige) on cows with a calving event between 2011 and 2016 were used. The dataset consisted of 248 and 35 860 milk records from SKB and SR cows, respectively, all in organic production. Because there are no available studies on heterosis in SKB crosses, the estimates for direct heterosis effects were based on estimates found in SR x Swedish Holstein crosses (Jönsson, 2015). The breed differences and heterosis estimates for the most important traits are shown in Table 1 (Appendix 1 for the conventional production system).

Table 2. Assumed prices as of 2018 (Clasen et al., 2020) in € for milk production, slaughter value and live calves for organic production

Item	Price, €
Milk, per 1 000 kg ECM	484
Slaughter SKB cow, per kg live weight	1.16
Slaughter SR cow, per kg live weight	1.39
Slaughter SR x SKB cow, per kg live weight	1.29
SKB dairy bull calf, per head	10[a]
SR dairy bull calf, per head	225[a]
SR x SKB dairy bull calf, per head	117.5[a]
Beef x dairy bull calf, addition[b] per head	70
Beef x dairy heifer calf, addition per head	35

ECM = Energy-corrected milk; SKB = Swedish Polled Cattle; SR = Swedish Red

[a] Market price corrected for rearing costs

[b] Added to the price of a dairy calf

The essential price assumptions for these simulations are in Table 2 (Appendix 2 for the conventional production system). All other assumptions regarding prices and costs were identical to the assumptions in Clasen et al. (2020). The milk price per 1 000 kg energy corrected milk (**ECM**) was €1 higher for SR and €0.5 for F1 SKB x SR crosses relative to purebred SKB (not shown in table) as a result of differences in the fat and protein contents of the milk. All dairy bull calves and beef x dairy crossbred calves were sold as live calves for beef production after a two-week rearing period in the simulated herds. The value of purebred SR and beef cross calves was higher than purebred SKB calves because of the higher body weight (Växa Sverige, 2018b). The money received for the live calves was adjusted for the risk of calf mortality, milk feeding, and other costs associated with the rearing period because these costs were not considered for slaughter calves in SimHerd Crossbred.

We chose to simulate a herd size of 100 cows, as this is the number used in previous studies based on SimHerd Crossbred (Clasen et al., 2020). Because we did not include any costs that depend on the herd size, such as labour and buildings, the outcome per cow was expected to be the same regardless of herd size. Thus the results are scalable.

Sensitivity analyses

Some input variables, for example, economic values and breed variables, were fixed in our simulation study. In reality, they are fluctuating between countries, periods, and even herds, which means the total economic result likely fluctuates as well. Therefore, we analysed how sensitive the economic results were to changes in on three of the potentially most fluctuating variables: milk price, milk performance traits in the breeds crosses, and heterosis.

Marketing initiatives promoting the conservation of native breeds have been suggested, such as selling milk or cheese branded as a 'native breed product' for a higher price than conventional products (Swedish Board of Agriculture, 2009). This could lead to an increased milk price being paid, by the dairy plant, to farmers with a majority of the native breed on the farm. The first sensitivity analysis investigated the break-even in milk price that is necessary to pay SKB herds if they are to be economically competitive with purebred SR. The sensitivity analysis was based on the assumption that an additional premium is paid for the milk in herds with cows of a native breed including crossbreds.

The second sensitivity analysis investigated the effect of increasing differences in production level between the breeds on the economic difference between the scenarios. Owing to genetic improvements, SR has increased the 305-day ECM yield by approximately 100 kg per year since 1990, while over the same period the production level in SKB has been almost unchanged (Växa Sverige, 2018a). The analysis assumed an annual increase of 100 kg in 305-day ECM over 25 years for SR and no change in SKB. Changes in other traits were ignored, mainly because the trends for them are unknown in the SKB breed. Five simulations were made to represent the changes every 5 years.

Given the absence of heterosis estimates for crosses between SKB and SR, the assumed heterosis in the simulations may differ from the true heterosis for SKB-crosses. Heterosis estimates in crosses between native and modern breeds in other countries can also be different from our assumed estimates. Therefore, the third sensitivity analysis investigated the effect of changing heterosis on the economic difference between the scenarios. The effects analysed were heterosis estimates of −50%, +50%, and +100% relative to the default heterosis estimates based on crosses between SR and Swedish Holstein given in Table 1.

Results

Herd scenarios

Table 3. Simulated herd dynamics at equilibrium in a herd of purebred Swedish Polled Cattle (SKB); a herd using a two-breed terminal crossbreeding system with SKB purebreds and 25% F1 Swedish Red x SKB crossbreds (XB); and a herd of purebred Swedish Red (SR), all in an organic production system

	SKB	SR	XB
Crossbred cows (%)	0	0	25
Replacement (%)	31.9	29.3	30.1
Replacement heifers in the herd/cow	0.81	0.74	0.72
Dairy bull calves sold/cow	0.37	0.37	0.33
Beef x dairy crosses sold/cow	0.14	0.28	0.23
305-d kg ECM yield (kg/cow)	5 743	8 433	6 091
Calving interval (days)	417	405	413
Conception rate (cows)	0.40	0.45	0.42
Disease treatments/cow	0.39	0.37	0.38
Cow mortality (%)	4.2	3.5	4.0
Calf mortality (incl. stillbirth) (%)	13.3	4.5	11.7
Young stock mortality (%)	1.1	4.1	1.2

The effect of applying crossbreeding to 20% of the purebred SKB cows was 25% F1 crossbred cows within the herd in the XB scenario (Table 3), primarily as a result of better fertility and less calf mortality. Thus, in a 100-cow herd, 75 of the milk-producing cows would be purebred SKB, and 25 would be F1 crosses. The major effects of terminal crossbreeding on herd dynamics were increased milk yield and a reduced number of young stock. The 305-day ECM production per cow increased by 348 kg relative to SKB. With the reduced calving interval (–4 days) and reduced calf mortality (–12%), the number of replacement heifers that should be raised in the herd was also reduced by approximately 12% in the XB scenario.

As an effect of having 25% crossbreds in the herd, the total contribution margin per cow-year increased by €181 (+13.6%) in XB compared to SKB (Table 4). The increases were mainly due to increased income from milk production, increased income from the sale of live calves, and reduced costs associated with young stock. Income from milk production increased by 6.1% in XB in comparison with the purebred SKB herd, but the higher milk production also increased feed costs. The dairy bull calves and beef x dairy crossbred calves sold from the farm at the age of two weeks had on average a higher value in the crossbreeding scenario than in

Table 4. Simulated annual economic results (€/cow) in a herd of purebred Swedish Polled Cattle (SKB); a herd using a two-breed terminal crossbreeding system with SKB purebreds and 25% F1 Swedish Red x SKB crossbreds (XB); and a herd of purebred Swedish Red (SR), all in an organic production system

	SKB	SR	XB
Income			
Milk production	2 754	4 055	2 922
Slaughter cows	120	227	121
Live calves	13	157	29
Total income	2 887	4 469	3 073
Costs			
Feeding cows	943	1 369	992
Feeding young stock	308	273	275
Inseminations	48	44	46
Disease treatments	62	49	59
Other costs	192	182	186
Total costs	1 552	1 918	1 557
Total contribution margin	1 334	2 552	1 515
Difference to SKB		+1 218	+181

the SKB scenario as a result of the influence of SR and beef breed. This created higher income from the sale of live calves in the crossbreeding scenario.

Appendices 3 and 4 show results for the conventional production system. These are similar to those obtained in the organic production system; the crossbreeding scenario earned +€179 per cow-year relative to the SKB scenario. However, the relative gain was slightly larger (+16.1%), mainly as a result of the larger differences in milk yield between the breeds and lower prices in the conventional production system.

Sensitivity analyses

Figure 1 shows the effect of increasing the milk price for a herd that has at least some SKB cows, i.e. the SKB scenario and the crossbreeding scenario, compared to the SR scenario. The break-even in milk price cow-year was €696 per 1 000 kg ECM paid for milk originating from herds with SKB cows to obtain the same contribution margin per cow-year as SR. This corresponds to a 43.8% increase from the initial milk price (€484). In the XB scenario, the break-even was estimated at €656 (+35.6%) for XB to obtain the same contribution margin per cow-year as SR.

When the production level was increased due to genetic progress for SR but not for the SKB breed, the difference in production level between SKB and crossbreds of SKB and SR increased as well. This caused the total contribution margins per cow-year to increase in the XB scenario (Figure 2). From year 0 to year 25, the difference in total contribution margin per cow-year between SKB and XB increased from €186 to €307 (€4.8/year). Other traits were kept at a fixed level, and therefore there were no changes in other variables.

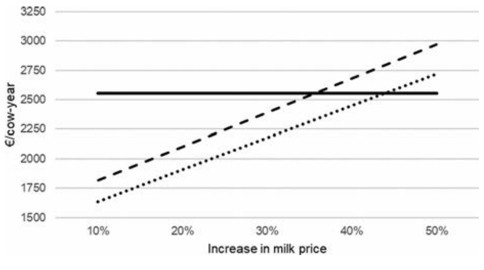

Figure 1. Effect of increasing milk price in a herd of purebred Swedish Polled Cattle (SKB; dotted line) and a herd using a two-breed terminal crossbreeding system with SKB purebreds and 25% F1 Swedish Red x SKB crossbreds (XB; dashed line) compared with a herd of purebred Swedish Red (solid line; no increase in milk price) in an organic production system with current milk price.

Changing the heterosis estimates had some effects on herd dynamics and herd performance, and a substantial effect on the total contribution margins in the XB scenario (Table 5). Doubling the heterosis allowed more crossbreds to be introduced into the herd: 27% relative to 25% in the initial scenarios (default heterosis estimates). This was mainly due to improvements in production, fertility and calf mortality, and a reduced replacement rate, thus fewer purebred cows were needed to ensure enough replacement heifers. The crossbred cows survived longer in the herd with higher heterosis estimates; thus the need for purebred cows to produce crossbred replacement heifers was reduced. Relative to the initial scenarios, the total contribution margin per cow-year increased €36 in XB when the heterosis estimates were doubled. Halving the heterosis estimates had the opposite effect, resulting in 24% crossbreds in XB, and fewer benefits in production and other traits, relative to the default scenario. The total contribution margin per cow-year was €20 less than the default scenario when heterosis was halved.

Discussion

The simulated crossbreeding scheme does not necessarily represent an optimal strategy for conserving a native breed and obtaining higher contribution margins from terminal crossbreeding with modern breeds. Nevertheless, it points to a potential economic way to conserve dairy herds with native breeds, and one that can benefit both farmers and society, if it is assumed that all animals on the farm include some native breed genes.

Financial subsidies were not included in the economic calculations, as the size of any such subsidy and the regulations under which it is offered may differ between countries and breeds. Currently, the Swedish regulations for endangered livestock breeds only allow subsidies for animals owned by farmers who follow breed-specific (pure-)breeding plans (Swedish Board of Agriculture, 2019). The purpose of this regulation is obviously to promote the pure-breeding of native breeds. However, the conservation of native breeds may be more attractive to farmers if it can be combined with higher contribution margins in alternative breeding strategies such as terminal crossbreeding with modern dairy breeds or beef breeds. Thus, the regulations governing subsidies may need to be changed to allow crossbreeding plans – at least, if it is confirmed that crossbreeding promotes the conservation of the breed.

Farmers play an important role in the conservation of dairy cattle. But if the economic benefit is too small, they might as well convert to SR or Holstein or another high-

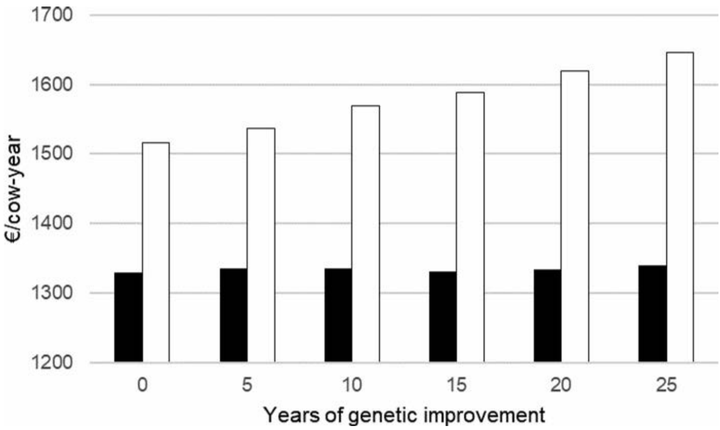

Figure 2. Effect on total contribution margin after 5, 10, 15, 20 and 25 years when 305-day kg ECM yield increases by 100 kg/year in the Swedish Red breed in a herd of purebred Swedish Polled Cattle (black bars) and a herd using a two-breed terminal crossbreeding system with SKB purebreds and 25% F1 Swedish Red x SKB crossbreds (white bars). All herds in an organic production system.

profit breed and phase out any native breed cows in the herd. The estimated herd contribution margin was €2 552 per cow-year for purebred SR which is €1 218 more than purebred SKB. This difference indicates the subsidy that will be needed from society for SKB to be economically competitive with SR herds, given the parameter inputs in our simulations. The difference in contribution margin between the SKB herd and the SR herd can be reduced to €1 037 by having 25% crossbreds in the SKB herd (XB). The farmer will still need economic support from society, but the ability to create higher profits from some of the cows may motivate more farmers to keep the native cows. However, if subsidies are paid only for purebred cows, the crossbred cows will be insufficiently profitable to cover the difference in subsidies between the SKB and XB herds needed to match the profit of a purebred SR cow. A mixed herd with purebred cows of SKB and SR, i.e. without any crossbreeding, would provide a higher contribution margin (+8%) than that obtained in the XB scenario if the proportion of SKB cows is the same. This is because the SR breed is economically superior to SR x SKB crossbreds, despite heterosis effects. However, such a mixed herd may present management challenges as a consequence of the large breed differences (e.g. cow size, energy requirements, and robustness under extensive conditions), which is why farmers may be reluctant to adopt this strategy and rather choose the XB scenario if they intend to include another breed in the herd.

Table 5. Effect of changing heterosis estimates on simulated herd dynamics at equilibrium in a herd using a two-breed terminal crossbreeding system with SKB purebreds and 25% F1 Swedish Red x SKB crossbreds (XB) compared to a herd of purebred Swedish Polled Cattle (SKB) in an organic production system

Change in heterosis	Default[a]	−50%	+50%	+100%
Crossbred cows (%)	25	24	26	27
Replacement (%)	30.1	30.4	29.8	29.3
305-d kg ECM yield (kg/cow)	6 091	6 054	6 134	6 156
Calving interval (days)	413	414	412	410
Calf mortality (incl. stillbirth) (%)	11.7	12.0	11.5	11.3
Total contribution margin	1 515	1 495	1 537	1 551
Rel. SKB	*+13.6%*	*−12.2%*	*+15.1%*	*+16.2%*

[a] Please see Table 1 for default heterosis estimates

In our simulations of the conventional production system, the crossbreeding scenario's economic gain in comparison to the SKB scenario (Appendix 4) was similar to the corresponding gain in organic production system. Thus, from an economic perspective, the consequences of crossbreeding between SKB and SR are similar regardless of the production system. However, that may not be the case in other countries or between other native and modern dairy breeds, and from the perspective of conserving the genetics of the native breeds, the production system does not matter. However, from the socio-economic perspective, the incentive of conserving the native breeds in organic rather than conventional systems is enhanced by the EU commitment to increase organic farming in Europe ('The European Green Deal'; European Commission, 2019).

The main characteristics of organic dairy production include pasture-based feeding and the utilization of local feed sources. This may benefit breeds that are adapted to these practices (IFOAM, 2018). Studies have suggested that local breeds or crossbreds, rather than modern high-producing breeds, are better suited to organic production (Ahlman, 2010; Bieber et al., 2019;

Rodríguez-Bermúdez et al., 2019). The studies point out that the high-producing breeds have been intensively selected under high-input production conditions, and have become less fit for organic conditions. Given this, having crossbreds and native breeds in the same herd may be preferable to keeping purebreds of both the native and modern breed in the same herd. Additionally, milk from native breeds in combination with grass-based diets shows favourable compositions of minerals and fatty acids (Poulsen et al., 2020).

Niche products from local breeds have been a major key in efforts to increase the population of endangered local breeds (e.g. Gandini et al., 2007). The first sensitivity analysis showed that the break-even in milk price that must be paid for herds to become economically competitive with SR is lower for XB (+35.6%) than SKB (+43.8%). This additional milk price could, for instance, be met through the marketing of niche products. In Sweden, there is no additional price paid by the large dairies, although some farmers of native breeds run on-farm dairies and manage to create a local market for the milk they produce. Milk from native Swedish cattle breeds has shown better properties for cheese and cream-based products, compared with high-yielding Swedish Red cows (Poulsen et al., 2017). In France, there is a large market for dairy products labelled PDO (Protected Designation of Origin; INAO, 2019), which is based on EU legislation on quality control for agricultural products (European Union, 2012;2013). For each specific product, there are regulations on the origin of the milk used to manufacture it. For example, some cheeses from the Normandy region, such as the *Livarot*, require milk from herds with 100% Normande cows, while the *Neufchâtel* cheese allows milk from herds having at least 60% Normande cows (the remainder may be crossbreds or other breeds), and the *Camembert de Normandie* and *Pont-l'Evêque cheeses* allow milk from herds having at least 50% Normande cows (Association de Gestion des ODG Laitiers Normands, 2020). The PDO incentive has turned out to be an effective motivation for farmers to keep local breeds, as they will then benefit from higher prices for their products (Verrier et al., 2005).

Where a specific (minimum) number of purebred native cows are maintained the cost of government subsidies for society should not change with crossbreeding. However, if dairy plants, retailers, and consumers were willing to pay more for products from herds in which purebred native cows are kept together with crossbred cows, economic support from the government directly to farmers could eventually be scaled down.

Milk yields from modern breeds in Sweden have increased substantially, which makes the native breeds even less competitive (Växa Sverige, 2018a). Faster improvement of modern breeds makes crossbreds with native breeds more profitable than the native breed, as was shown in the second sensitivity analysis (Figure 2). However, the sensitivity analysis here assumed that only milk yield improved genetically in the modern breed, and an almost linear relationship in total contribution margin per increase in milk yield emerged. Most breeding indices, such as the Nordic Total Merit Index (NTM; Sørensen et al., 2018) that is used in the selection of breeding candidates in Nordic dairy cattle, are constructed to improve all desired traits simultaneously. Given this, the sensitivity analysis may have underestimated the effects of other traits as well, such as improved fertility and health.

The information on SKB in organic production was very limited in comparison with that available for SR. This is explained by the small SKB population size, and the fact that approximately 17% of the milk-recorded cows (across all breeds) are organic (Växa Sverige, 2018a). Bieber et al. (2019) also used a rather limited number of SKB cows in their study on German and Swedish breeds under organic conditions. The low number of records for SKB cows means that the relative breed differences shown in Table 1 may not show the true characteristics of the breed, especially for the health traits.

The heterosis estimates in Table 1 were based on SR x Swedish Holstein crosses (Jönsson, 2015) because, to our knowledge, heterosis has not been estimated in SKB crosses. Therefore, the values we used may not accurately reflect heterosis for SKB crosses. A recent study of the genomic relationships between Swedish cattle breeds suggests that SR and SH are genetically closer than are SKB and SR or Swedish Holstein (Upadhyay et al., 2019). Thus, the heterosis when SKB is crossed with SR could, theoretically, be larger than that involved in the crossing of SR and Swedish Holstein. Furthermore, the heterosis estimates between native breeds and modern breeds in other countries may be different. The third sensitivity analysis (Table 5) showed how the results changed with changing heterosis estimates. It implied that the greater the heterosis effect is, the larger the contribution margin obtained from crossbreeding will be as compared with pure-breeding. Nevertheless, the increase in contribution margin from doubling heterosis effects would still be insufficient to compare to purebred SR.

Bull calves of pure SKB are smaller and grow at a slower rate than the larger dairy breed calves and beef x dairy crosses (Växa Sverige, 2018b). They are therefore not very attractive to beef producers, hence the low value assumption. We did not simulate the alternative for farmers to keep the SKB males as steers and eventually sell them for slaughter at an older age. The number of dairy bull calves produced (both purebred and crosses) was slightly reduced when crossbreeding was introduced, while the number of beef x dairy crossbred calves increased as a result of the increased use of beef semen. The production of dairy bull calves can be minimized through the use of X-sorted sexed semen. Sexed semen is usually not available in native breeds, but sexed semen from modern breeds to produce crossbred heifers can make crossbreeding more efficient (van Arendonk, 2011), and would also lower the number of purebred cows needed in the herd, i.e. allow for more crossbreds. Beef semen was used in the purebred SKB scenario to reduce the surplus of replacement heifers. Production of beef x SKB calves is probably more beneficial than raising purebred SKB bulls and heifers for beef production unless there is a reasonable market to sell replacement heifers.

The number of young heifers needed to be raised as replacements decreased when crossbreeding was introduced. This not only reduces associated costs but also creates more free resources, such as labour time, stable space, and pasture space – resources that were not taken into account in the economic calculations. Such resources could, for instance, be used to increase the herd size or to raise slaughter calves instead of selling them. The simulated results are based on a 100-cow herd, but the economic figures are scalable to any herd size, because the costs of labour, buildings, equipment, etc. are not included in the calculations. However, most herds with native dairy cows are usually small, and one can question if the effect of having 25% crossbreds in a 30-cow herd really would remain the same as in a 100-cow herd. The effect of herd size was not studied in this simulation. If the benefits of crossbreeding are dependent on expanded herd size, they may be less obtainable for some farmers. Furthermore, to keep the current population size of SKB, today's SKB farmers will need to increase their herd sizes if a terminal crossbreeding scheme of the sort studied here is widely adopted. Alternatively, of course, more farms with SKB cows need to be established.

As a part of FAO's global plan of action on animal genetic resources, guidelines including issues such as for crossbreeding programs have already been published (FAO, 2010, 2012). However, before implementing a terminal crossbreeding strategy in a native dairy herd, the actual effects on the conservation of the breed in question should be investigated and a thorough breeding plan on population-level needs to be prepared. Improving herd economy might 'conserve the farm', but how many farms are needed to implement the crossbreeding for the actual breed to be conserved? According to Upadhyay et al., (2019), the SKB breed still has a high genetic diversity, which confirms the conclusion from Bett et al. (2013) that this breed is not at risk. Nevertheless, the population size of SKB is decreasing (Växa Sverige, 2018a), and in case crossbreeding is implemented, it is of high importance to develop a breeding plan that conserves the genetic diversity a nucleus of the breed. A control system for crossbreeding and conservation needs to be put in action, to avoid the risk of inappropriate crossbreeding practices that threaten the pure breed, as what happened to the Flemish Red Cattle (Lauvie et al., 2008) and the Swedish Lowland Cattle (Bett et al., 2013). Furthermore, the terminal crossbreeding strategy that we propose, requires a well-managed purebred population, which potentially benefits from playing a key role in a crossbreeding strategy (FAO, 2012). Additionally, the crossbred animals in this strategy are omitted from the breeding populations, which minimizes the risk of loss of valuable gene combinations unique to the native breed.

Using SKB as an example, this study shows improved herd contribution margins of 13.6% in a herd with 25% crossbreds between a native and modern breed, as compared with a herd with the native breed alone. However, a mixed herd containing purebred cows of SKB (75%) and SR (25%) and no crossbreeding would generate contribution margins 8% higher than those obtained in the corresponding XB scenario. Even though crossbreeding may not reduce the monetary cost per native breed cow to be carried by society, it could keep the farms viable, thus helping to succeed in conservation plans. From a societal perspective, not only the number of purebred native cows matters but also the number of farmers engaged in the conservation scheme. Crossbreeding alone cannot compensate for the economic gap between native and modern breeds. However, combining crossbreeding with other conservation incentives, such as marketing niche products, may improve the economic benefits of having native cows on the farm, meaning that eventually the economic support from society can be scaled down. This study only examines economic potentials, and further investigations of the genetic and conservation effects of this strategy are highly recommended before any such crossbreeding with native breeds is implemented. The conservation strategy presented in this study may apply to breeds of interest in other European countries. However, its benefits, when its application is extended in this way, may differ depending on the national prices and costs, differences between breeds, and heterosis expressed by crossbreds.

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Appendices

Appendix 1. Phenotypic breed estimates[a] of Swedish Polled Cattle (SKB) and Swedish Red (SR) kept in a conventional production system, and heterosis estimates in crosses between the breeds for production, risk of diseases, fertility, and mortality used in the model

	SKB	SR	Heterosis[b], %
305-d kg ECM, 1st parity	5 360	8 369	+3%
305-d kg ECM, 2nd parity	6 572	9 586	+3%
305-d kg ECM, later parities	6 856	9 873	+3%
Mastitis, %	8.1	7.8	-
Hoof-related diseases, %	11.1	16.8	−10%
Other diseases, %	2.6	2.1	−10%
Dystocia	6.4	4.6	−7%
Cow mortality	4.5	3.5	−10%
Calf mortality (incl. stillbirth)	8.8	5.3	−12%
Young stock mortality	0.8	4.1	−12%
Conception rate, cows	0.40	0.45	+10%
Age at 1st service, months	19.7	17.9	-
Calving – 1st AI, days	74	77	-

SKB = Swedish Polled Cattle; SR = Swedish Red; ECM = Energy-corrected milk

[a] Data from the Swedish milk recording scheme. The dataset consisted of 789 milk records from SKB cows and 440 924 milk records from SR cows

[b] Based on Jönsson (2015). All estimates are favorable.

Appendix 2. Assumed prices as of 2018 (Clasen et al., 2020) in € for milk production, slaughter value and live calves for conventional production

Item	Price, €
Milk, per 1,000 kg ECM	375
Slaughter SKB cow, per kg live weight	1.12
Slaughter SR cow, per kg live weight	1.35
Slaughter SR x SKB cow, per kg live weight	1.24
SKB dairy bull calf, per head	10[a]
SR dairy bull calf, per head	225[a]
SR x SKB dairy bull calf, per head	117.5[a]
Beef x dairy bull calf, addition[b] per head	70
Beef x dairy heifer calf, addition per head	35

ECM = Energy-corrected milk; SKB = Swedish Polled Cattle; SR = Swedish Red

[a] Market price corrected for rearing costs

[b] Added to the price of a dairy calf

Appendix 3. Simulated herd dynamics at equilibrium in a herd of purebred Swedish Polled Cattle (SKB); a herd using a two-breed terminal crossbreeding system with SKB purebreds and 25% F1 Swedish Red x SKB crossbreds (XB); and a herd of purebred Swedish Red (SR), all in a conventional production system

	SKB	SR	XB
Crossbred cows (%)	0	0	30
Replacement (%)	31.4	28.1	29.4
Replacement heifers in the herd/cow	0.75	0.69	0.67
Dairy bull calves sold/cow	0.36	0.35	0.33
Beef x dairy crosses sold/cow	0.22	0.32	0.29
305-d kg ECM yield (kg/cow)	6 124	9 205	6 624
Calving interval (days)	412	399	409
Conception rate (cows)	0.40	0.45	0.42
Disease treatments/cows	0.22	0.32	0.22
Cow mortality (%)	4.2	3.5	4.0
Calf mortality (incl. stillbirth) (%)	9.0	5.4	8.0
Young stock mortality (%)	1.1	3.9	1.3

Appendix 4. Simulated annual economic results (€/cow) in a herd of purebred Swedish Polled Cattle (SKB); a herd using a two-breed terminal crossbreeding system with SKB purebreds and 25% F1 Swedish Red x SKB crossbreds (XB); and a herd of purebred Swedish Red (SR), all in a conventional production system

	SKB	SR	XB
Income			
Milk production	2 292	3 441	2 479
Slaughter cows	73	209	71
Live calves	17	24	37
Total income	2 382	3 836	2 587
Costs			
Feeding cows	800	1 179	856
Feeding young stock	206	185	185
Inseminations	47	44	45
Disease treatments	31	28	30
Other costs	186	180	181
Total costs	1 271	1 615	1 296
Total profit	1 111	2 221	1 290
Difference to SKB		+1 110	+179

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This thesis aimed to explore the benefits of dairy cattle crossbreeding at herd level and form recommendations for dairy farmers, advisors, and breeding companies. The results showed that crossbreeding in a dairy herd is economically beneficial, and can be combined with beef semen, sexed semen, and genomic testing to increase the genetic level and economic return in the herd. Furthermore, it may be a useful breeding strategy for conserving native dairy breeds.

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