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CROSSBREEDING EFFECTS IN DAIRY COWS

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ABSTRACT

Crossbreeding is a common practice in poultry and swine breeding. Conversely, this mating system has not been widely adopted for breeding purposes in dairy cattle in temperate climates (except in New Zealand), mostly because of the superiority of Holsteins for milk yield, the economic relevance of this trait, the strong historical influence of purebred breeders and breed associations, and some biological aspects such as the low reproductive rate and the long generation interval of the cattle species. Recently, the interest in crossbreeding aspects has been growing among dairy producers, and this practice may be used to remove inbreeding depression accumulated in the major dairy breeds, to improve some economically important traits such as fertility, health, longevity, and calving ease, and to increase economic gains in countries where milk pricing systems have put a great emphasis on milk solids. It appears important to estimate the expected level of heterosis for traits of economic interest in dairy cattle in order to evaluate the profitability of crossbreeding.

Objectives of this work were a) to estimate crossbreeding effects for milk yield traits and calving interval in dairy cows (Chapter 2), b) to investigate the influence of the environment on the expression of heterosis for milk yield traits, somatic cell score, and age at first calving in dairy cattle (Chapter 3), and c) to estimate the effect of different genotypes on age, live weight, price, and commercial value of purebred and crossbred calves sold for beef and veal production (Chapter 4). The thesis started with an introduction on crossbreeding in dairy cows (Chapter 1), followed by three contributions.

Chapter 2 provided a study to assess crossbreeding effects for lactation milk, fat, and protein yield, and calving interval in dairy cows reared in Ireland. The analysis showed that breed effects for production traits were in favour of North American Holstein Friesian cows, while for calving interval were in favour of Friesian, Jersey, and Montbéliarde breeds. The highest heterosis estimates for milk yield traits were for crosses between North American Holstein Friesian and Jersey, with first generation cows giving 626 kg more milk, 25 kg more fat and 21 kg more protein than the average of the pure parental breeds. Regarding calving interval, the highest estimate was for crosses between North American Holstein Friesian and Montbéliarde, with first generation cows showing 10 d less calving interval than the average of the parental breeds. Estimates obtained in this study could be considered in the genetic evaluation model currently run in Ireland.

Chapter 3 investigated the effect of the environmental level of production on the expression of heterosis for lactation milk, fat, protein, and fat plus protein yield, somatic cell score and age at first calving in primiparous Black and White dairy cows reared in The Netherlands. Holstein Friesian, Dutch Friesian and first generation crosses obtained from the mating of these strains were studied. The environments (low, medium, high) were defined on the basis of the herd production level. Holstein Friesian produced more than Dutch Friesian. First generation crosses showed comparable productions to Holstein Friesian, especially in the low environment. Estimates of heterosis for production traits ranged between 2.4% for milk yield in the high environment and 5.3% for fat yield in the low environment, with decreasing percentages observed for the traits when moving from the low to the high environment. Overall, heterosis for somatic cell score and age at first calving were moderate. Results emphasized that the highest non-additive genetic effects for yield traits were expressed in the most stressful environment, i.e. low level of production.

Chapter 4 investigated the effect of four purebred genotypes (Brown Swiss and Holstein Friesian as dairy breeds, and Simmental and Alpine Grey as dual purpose breeds), and eight crossbred genotypes derived from mating of previous four dam breeds and two sire breeds (Limousin and Belgian Blue) on age (d), live weight (kg), price (Euro/kg), and market value (Euro/calf) of calves sold for veal and beef production during public auctions. Dual purpose purebred calves were heavier and presented higher price and market value than dairy purebreds (314 and 227 Euro/calf for Simmental and Alpine Grey, and 189 and 203 Euro/calf for Brown Swiss and Holstein Friesian, respectively). Crossbreeding with Limousin bulls increased live weight, price, and market value of calves from dairy and Alpine Grey cows, but had a small influence on price and market value of calves from Simmental cows. Crossbreeding with Belgian Blue bulls increased price and market value of calves much more than Limousin, particularly when used on Brown Swiss and Alpine Grey.

Key words: crossbreeding, dairy cows, heterosis

RIASSUNTO

L’incrocio è il sistema riproduttivo di riferimento delle produzioni avicole e della maggior parte di quelle suinicole. In queste specie l’eterosi è un bonus utile e largamente sfruttato per migliorare la produttività e l’efficienza produttiva degli animali. Al contrario, nei climi temperati gli allevatori di vacche da latte tradizionalmente hanno escluso l’incrocio dalla gestione riproduttiva della loro mandria (produzione della rimonta). L’unica eccezione è rappresentata dalla Nuova Zelanda. I motivi alla base di questa esclusione sono la superiorità della razza Holstein per la produzione di latte, l’importanza economica assunta da questo carattere in molte realtà produttive, la forte influenza esercitata delle associazioni di razza a livello mondiale e alcune considerazioni di carattere biologico come la bassa efficienza riproduttiva e l’intervallo di generazione piuttosto lungo nella specie bovina. Tuttavia, il panorama zootecnico è in continua evoluzione e negli ultimi anni si è assistito ad un crescente interesse da parte degli allevatori nei confronti della possibilità di implementare l’incrocio in allevamento. Tale sistema riproduttivo può essere utilizzato per rimuovere gli effetti negativi della depressione da consanguineità che, nelle maggiori razze da latte, ha agito su diversi caratteri di interesse economico; l’accumulo di omozigosi e la conseguente depressione da consanguineità sono il frutto della forte pressione selettiva esercitata entro le razze pure. Inoltre, l’incrocio può costituire un valido strumento per il miglioramento dei caratteri funzionali a bassa ereditabilità tra cui la fertilità, il fitness, la longevità e la facilità di parto. Infine, può costituire un modo per migliorare la qualità del latte in termini di proteina e grasso in quelle realtà dove i costituenti del latte vengono premiati dai sistemi di pagamento vigenti. La valutazione della redditività di un programma di incrocio deve essere preceduta dalla stima dei livelli di eterosi per i caratteri economicamente rilevanti nelle bovine da latte.

Gli obiettivi della presente tesi sono stati a) stimare gli effetti dell’incrocio per i caratteri produttivi e per l’interparto in vacche da latte (Capitolo 2), b) investigare l’influenza esercitata dall’ambiente sull’espressione dell’eterosi per caratteri produttivi, cellule somatiche ed età al primo parto in vacche da latte (Capitolo 3) e c) stimare l’effetto di diversi genotipi sull’età, il peso vivo, il prezzo ed il valore commerciale di vitelli puri e meticci venduti per la produzione di vitellone e vitello a carne bianca

(Capitolo 4). La tesi inizia con un'introduzione sull'incrocio nel settore bovino da latte (Capitolo 1), seguita da tre contributi sperimentali.

Nel Capitolo 2 sono stati stimati gli effetti dell'incrocio sulla produzione di latte, grasso e proteina, e sull'interparto in bovine da latte allevate in Irlanda. L'analisi ha evidenziato che gli effetti razza per i caratteri produttivi sono stati in favore della razza Holstein, mentre per l'interparto sono stati in favore delle razze Frisona, Jersey e Montbèliarde. Le stime più alte di eterosi per latte, grasso e proteina si sono avute nei meticci Holstein x Jersey: gli incroci di prima generazione hanno prodotto 626 kg di latte, 25 kg di grasso e 21 kg di proteina in più a lattazione rispetto alla media delle razze parentali pure. Per quanto concerne l'interparto, la stima più alta si è avuta nei meticci Holstein x Montbéliarde: gli incroci di prima generazione hanno evidenziato una contrazione di 10 giorni di interparto rispetto alla media delle razze parentali pure. Le stime ottenute in questo studio potrebbero essere considerate nel modello di valutazione genetica attualmente utilizzato in Irlanda.

Nel Capitolo 3 è stato investigato l'effetto dell'ambiente (livello produttivo) sull'espressione dell'eterosi per la produzione di latte, grasso, proteina e materia utile (grasso più proteina), punteggio di cellule somatiche ed età al primo parto in bovine primipare Pezzate Nere allevate in Olanda. I genotipi presi in esame sono stati la Holstein, la Frisona Olandese e gli incroci di prima generazione tra queste due linee. Gli ambienti sono stati suddivisi in bassi, medi e alti sulla base del livello produttivo degli allevamenti. La Holstein ha manifestato produzioni più elevate rispetto a quelle della Frisona Olandese. Gli incroci di prima generazione hanno evidenziato produzioni simili a quelle della Holstein, soprattutto nell'ambiente basso. Le stime di eterosi sono risultate comprese tra il 2,4% per la produzione di latte nell'ambiente alto ed il 5,3% per la produzione di grasso nell'ambiente basso. Si sono osservate percentuali di eterosi decrescenti per latte, grasso, proteina e materia utile passando dall'ambiente basso a quello alto. Complessivamente, i livelli di eterosi per le cellule somatiche e l'età al primo parto sono risultati moderati. I risultati hanno messo in evidenza che gli effetti genetici non additivi per i caratteri legati alla produzione si sono espressi maggiormente nell'ambiente più stressante per tali caratteri, cioè quello basso.

Nel Capitolo 4 è stato analizzato l’effetto del genotipo sull’età (giorni), il peso vivo (kg), il prezzo (Euro/kg) ed il valore commerciale (Euro/vitello) di vitelli venduti nel corso di aste pubbliche e destinati alla produzione di vitellone e vitello a carne bianca. I genotipi puri erano rappresentati da due razze da latte (Brown Swiss e Holstein) e da due razze a duplice attitudine (Simmental e Grigia Alpina), mentre i genotipi meticci erano di otto tipi diversi e sono stati ottenuti dall’accoppiamento delle precedenti quattro razze materne con due razze paterne (Limousin e Bianca Blu del Belgio). I vitelli puri figli di razze a duplice attitudine sono risultati più pesanti e hanno evidenziato un prezzo ed un valore commerciale più elevati rispetto a quelli dei vitelli puri di razze da latte (314 e 227 Euro/vitello rispettivamente per Simmental e Grigia Alpina e 189 e 203 Euro/vitello rispettivamente per Brown Swiss e Holstein). L’incrocio con tori Limousin ha incrementato il peso vivo, il prezzo ed il valore commerciale dei vitelli figli di vacche da latte e della Grigia Alpina, ma ha avuto una modesta influenza sui vitelli figli di vacche Simmental. L’incrocio con tori di razza Bianca Blu del Belgio ha incrementato prezzo e valore commerciale dei vitelli molto più di quanto non abbia fatto la razza Limousin, soprattutto quando la prima è stata utilizzata sulla Brown Swiss e sulla Grigia Alpina.

Parole chiave: incrocio, vacche da latte, eterosi

Chapter 1

Crossbreeding in dairy cattle

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INTRODUCTION

The idea of purebred selection in animal breeding with the aim of obtaining an improvement for different characteristics assumed a great interest in the second half of the 18th century (Wentworth, 1927). In that period, selection was seen not only as a powerful method to unify the characteristics desired, especially in meat animals, but also to stimulate new variation. This idea was discovered to be wrong in the following years and we know that selection beyond certain limits tends to reduce the genetic variability within a population.

The average heterozygosity in the offspring generation is increased or decreased depending on the type of mating system performed, mainly within or between populations. Increasing the level of homozygosity often leads to a reduction in performance called inbreeding depression. Conversely, improved performance in many cases accompanies heterozygosity. Effects exploited by heterosis and selection are opposite, but theoretical basis may be compared. Selection considers models based on the inclusion of additive genetic effects for the estimation of breeding values, while heterosis requires the use of the dominance model. There could be situations in which neither the simple additive genetic nor the dominance model can explain the data. For this reason, where the simplest conditions are not sufficient, there is need of more comprehensive analyses which consider, for example, interactions with the environment or epistatic effects.

Crossbred animals may lead to an advantage if economically important traits show heterosis, but the mere evidence of non-additive genetic effects is not enough to state that crossbreds are better than purebred individuals. Since genotypes do not perform equally under different production circumstances, including different economic and managerial conditions, it appears important to consider the environment in which genotypes are producing. Falconer (1952) nicely explained this situation, known as genotype by environment interaction. This is a crucial point that has to be borne in mind when deciding the mating strategies to be adopted to maximize the farm profit: the comparison can not be at the individual animal level but at the system level.

One of the most important concepts recently discussed by many geneticists is that crossbreeding does not reduce the need for pure animals. The use of the best purebred stock available is important, and a continuous selection process has to be guaranteed within populations in order to make a crossbreeding program a success (Wentworth, 1927). This leads to the opportunity of exploiting additive genetic effects from high merit individuals and non-additive genetic effects from genes interactions.

THE INTEREST IN CROSSBREEDING DAIRY COWS

Crossbreeding has been widely and historically implemented in poultry (Morley, 1958) and swine (Winters et al., 1937) breeding to generate commercial animals. These species rely heavily on heterosis to improve productivity and efficiency of production (Hansen, 2006). Since the first half of the past century, the practice of combining animals from different genotypes has been also referred to improve the economic value of cattle sold for meat purpose. Phillips et al. (1942) reported results from a two-years experiment in which purebred Shorthorn bulls were mated to Hereford cows. Also, beef sires can be used in crossbreeding schemes to produce crossbred calves from dairy cows with good economic revenues. Fuller (1928) showed this opportunity in his dairy-beef cross experiment, and evidenced that crosses from beef sires x dairy cows had good meat features and were appreciated by the market. A well-known practice in Europe is to breed dairy and dual-purpose cows with beef bulls, adopting a simple two-breed cross on animals not used to produce the purebred replacements in dairy farms. The final cross, known as “industrial cross”, is sold to the commercial producers, with a better economic advantage than that achievable from selling purebred animals. Since heterosis generally occurs when crossbreeding practice is applied, an increase of the commercial value of the offspring is expected.

Crossbreeding of *Bos taurus* dairy breeds with local *Bos indicus* cattle is a well-documented strategy to enhance milk production in the tropics (Cunningham and Syrstad, 1987). On the contrary, in most temperate climates, crossbreeding has not been widespread for breeding purposes in dairy cattle except in New Zealand (Swan and Kinghorn, 1992; Sørensen et al., 2008). A purebred system improved by within breed selection is what the dairy industry has practiced for many years, largely because of the increasing global dominance of Holstein-Friesian types (Cunningham and Syrstad, 1987). The strong historical influence and tradition of purebred breeders and breed associations (Weigel and Barlass, 2003), along with the scarce assistance to farmers from the scientific world, are additive elements to the limited interest in crossbreeding dairy cattle.

The genetic superiority of Holstein-Friesian cows compared with crossbred animals and other breeds has encouraged its adoption in most countries where dairy cattle breeding has covered an important role on livestock production and where milk volume has been of great importance in determining income for the dairy farm (López-Villalobos, 1998). McAllister (2002) underlined that the additive genetic advantage of Holstein animals for milk volume is the main reason to explain the fact that less than 5% of dairy cattle reared in the United States are other than purebred Holstein. In many production systems such as Canada, the United States, New Zealand, and Australia, Holstein genes have been increased at the expense of other breeds. Also, the genetic structure of many European countries such as France (Boichard et al., 1993), The Netherlands (Van der Werf and de Boer, 1989), and the United Kingdom (Akbas et al., 1993) has been changed by the introduction of North American genes.

Despite the considerations above, crossbreeding has become a hot topic at this time in dairy cattle genetics, and the interest is rapidly increasing among dairy farmers, rising questions of practical aspects of breed utilization (McAllister, 2002). A number of studies on the matter have been presented in recent congresses, meetings, and symposia, and scientists have been involved in researches on this field during the last 10-15 years. Several reasons are behind the interest in crossbreeding. First, inbreeding levels within the major dairy breeds are rapidly accumulating (Weigel, 2001) and crossbreeding may be an efficient way to cope with this trend in dairy populations under selection and to reduce the impact of the phenomenon of inbreeding depression (Weigel and Barlass, 2003). Second, direct payments for protein as well as fat in many milk pricing systems encouraged some producers of the Holstein herds to consider crossbreeding as a tool to improve milk nutrient content; this enhances the ability of other breeds and breed crosses to compete with the more productive Holstein strains on an economic basis, especially in countries where cheese industry is of great relevance or is gaining importance. Third, easy access to genetic material from almost anywhere in the world, strong competition among breeds like the Holstein, Brown Swiss and Jersey, and standardization of sire evaluations are making crossbreeding viable. Fourth, several temperate countries have changed their breeding criteria in recent years, and animals are now selected on the basis of economic indexes that do not include only milk volume, but also consider functional traits such as fitness, reproductive performance, calving ease, and longevity (López-Villalobos, 1998; Boettcher, 2005; Sørensen et al., 2008). These traits are assuming a central role in reducing farm costs, even if they are still secondary to milk yield (McAllister, 2002). The interest in functional traits is mostly due to their decline over the years, which derives from the strong historical selection for milk volume and the antagonistic genetic correlations between functionality and production (Boettcher, 2005; Sørensen et al., 2008). In particular, problems with fertility has led to a growing need for female replacements in intensive dairy farms, with a consequent increment of cows disposal and a reduction in the herd life of animals. Crossbreeding, along with the economic emphasis given to traits other than production may be useful to keep down the deterioration of secondary traits and to enhance the farm net income.

A well-designed crossbreeding programme allows the producer to combine the desirable characteristics of the breeds involved in the cross and provides a tool to increase health and efficiency in animals (VanRaden and Sanders, 2003). Moreover, a wider demand for purebred animals, a better quality of commercial animals, and a reduction in production costs are expected by implementing an effective crossbreeding strategy. In order to define a profitable programme, it appears important to predict the performance of later generations of crosses from the earlier generations (López-Villalobos, 1998). This implies that heterotic effects for traits of economic relevance in crosses between dairy breeds should be known.

THE THEORY OF CROSSBREEDING

Crossbreeding is known as a type of a larger class of mating systems called outbreeding. It is the mating of animals from different breeds (Falconer and Mackay, 1996) or the mating of individuals less related than the average pair of animals in a population (Cassell, 2007).

McAllister (2002) reported that the total genetic makeup of crossbreds can include additive effects, dominance, maternal effects (both nuclear and cytoplasmic), maternal heterosis, and recombination effects. The theory of crossbreeding has been widely reviewed by several authors in the past (Dickerson, 1973; Sheridan, 1981; Hill, 1982), and comprehensive reviews on practical results obtained in beef cattle (Long, 1980), sheep (Nitter, 1978), pigs (Sellier, 1976), and dairy cattle (Turton, 1981) were also provided.

The main objectives for crossing animals are 1) to obtain individuals intermediate between the two parents (the averaging of breed effects), 2) to exploit the genetic improvement and selection achieved in other populations (“grading-up”), 3) to exploit breed complementarity, 4) to exploit breed differences, 5) to create synthetic/composite breeds/lines, and 6) to exploit heterosis. The attention will be mainly focused on heterosis in the following section.

Heterosis

The practice of combining individuals from different breeds or strains leads to beneficial physiological and production effects in the resulting offspring. This is well-known and long established in animal breeding. Cole (1927), discussing the genetic foundations in crossbreeding, argued that a reliable and logical explanation of the benefits of combining individuals from different breeds is based on the recombination of complementary genes that have become segregated in the breeds themselves by earlier close-breeding or in-breeding. The increasing proportion of homozygous loci in a given population is the result of the mating of highly related animals. Such an increase tends to separate the breeds more and more, and to split animals belonging to the same breed into a number of distinct strains. The main non visible consequence derived from the mating of individuals genetically distant is the increment of “gene richness” in the crosses. This phenomenon conducts to a major possibility of the animal to cope with stress due to environmental changes.

For a long time geneticists used the expressions “hybrid vigour” or “mystical stimulation” to describe the benefits visible in the progeny from different genotypes, but in 1914 Professor Shull, during an invitation lecture in Göttingen (Germany), proposed for the first time the word “heterosis”. In the same period he published a paper in which this term came to the attention of other geneticists and scientists (Shull, 1914). Heterosis is defined as the difference between the average performance of reciprocal crosses and the average of the parents (Willham and Pollak, 1985). The exploitation of this bonus is probably the most important reason for utilising crossbreeding in animals, along with the exploitation of additive effects from improved purebred animals.

From a genetic point of view, heterosis quantifies the amount of non-additive genetic effects occurring in a cross, being the result of interactions between alleles at the same locus (dominance) and among alleles located on different loci (epistasis). Thus, heterosis arises from the effects of gene combinations, that is, the effects of pairs of genes (Cassell, 2007). Gene pairs are unique characteristics of individuals that are broken down and reformed each generation. Also, heterotic effects expected in the crossbred progeny depends upon the differences in the frequencies of the different alleles at each locus that contributes to the trait (McAllister, 2002); larger these differences, greater the heterozygosity and the heterosis effects. This was already established in the first half of the past century by Wentworth (1927), who stated that “the best results from crossbreeding come when strains differing considerably between themselves, but each largely homozygous, have been crossed”. Hence, the genetic cause of heterosis relies on the genetic distance between the animals that are mated, and the exploitation of the “hybrid vigour” depends largely on the “purity” of the lines crossed.

Scientific literature is often supportive of the dominance model to explain heterosis (Cunningham, 1982), and it appears at the same time the one which most generally fits observed data, and is also the simplest. This model assumes a linear relationship between heterosis and heterozygosity (Falconer and Mackay, 1996), so that epistatic effects are neglected and heterosis in first generation crosses (F_1)

depends on the difference in gene frequencies in the parents and on the degree of genetic dominance of the trait. Under these assumptions, second generation crosses (F_2) are expected to retain half of the heterosis shown by the F_1. However, deviations from the dominance conditions were highlighted in the past, and Cole (1927) reported that “the increase is only roughly proportional inversely to the degree of relationship; the amount that may be expected cannot be predicted for different matings, but must be determined by test”. These considerations, formulated more than 80 years ago bring with them two important concepts developed in the following years: 1) the relationship between heterosis and heterozygosity is not always straightforward, especially when second generation crosses are considered, and 2) the prediction of crossbreeding effects is not simple, and often requires specific experiments to be properly estimated. The deviation from linear relationship between the crossbred performance and heterosis is defined recombination loss, and describes the average fraction of independently segregating pairs of loci in gametes from both parents which are expected to be non-parental combinations (Dickerson, 1969, 1973). Authors such as Sheridan (1981) and Hill (1982) investigated models in which epistatic gene actions were included to offer partial explanations of heterosis in those cases where dominance model does not appear to fit well. Moreover, it is worth mentioning that deviations from the dominance conditions are not only due to interactions between alleles at different loci, but also to the interaction between heterosis and environment (Barlow, 1981; Bryant et al., 2007).

Several studies estimated non-additive genetic effects for milk yield traits and productive life in dairy cattle. Estimates of general heterosis in the USA conditions were 3.4%, 4.4%, and 4.1% for milk, fat, and protein yields, respectively, and 1.2% for productive life, a measure of longevity (VanRaden and Sanders, 2003). A Canadian study conducted on the Holstein x Ayrshire cross population (McAllister et al., 1994) provided heterosis estimates ranging from 16.5% to 20% for lifetime milk productive traits and estimates greater than 20% for the composite influence of these characteristics and growth, health, and reproductive traits on lifetime annualized discounted net returns (ADNR) (McAllister, 2002). In a French study on the Holstein x European Black and White cattle, heterosis reached 2 to 2.5% for yield traits (Boichard et al., 1993). Under New Zealand current market values for milk, López-Villalobos et al. (2000) demonstrated the superior profitability of the rotational crossbred herds per hectare when compared to purebred herds.

CROSSBREEDING SCHEMES IN DAIRY CATTLE

In general, the type of crossbreeding to be adopted depends on the reproductive rate of the population. Animals such as pigs, rabbits, and poultry are characterized by medium-high reproductive rates and short generation intervals, thus the application of stratified schemes (the popular pyramidal structure) and the exploitation of crossbreeding effects have been successful to obtain the improvement of reproductive performance in maternal lines and productive characteristics in terminal lines. The top of the pyramidal structure is represented by nucleus herds managed by breeding companies that produce high genetic merit individuals, mainly through within breed/line selection. Genetic resources so improved are replicated by breeders at the multiplier level. At last, commercial producers take advantage from the genetic improvement occurring at the higher levels and from crossing genetic resources. Crossing systems such as three- and four-breed crosses are common, and this implicates that the breeding companies have to maintain a proportion of purebred animals.

The situation becomes more difficult in dairy cattle. The low reproductive rate and the long generation interval of cows, along with the need of increasing female replacements derived from reproductive problems in dairy herds, made impossible the application of a stratified breeding scheme, because of the enormous number of purebred animals that should be maintained. Also, the application of crossing systems such as three- or four-breed crosses would be very difficult, so rotational crossbreeding systems are required to exploit breed and heterotic effects. These schemes allow commercial farmers to produce crossbred female replacements from their own herds. Moreover, the advantage of rotational crossing is that only purebred sires are required, as crossbred dams are self-replacing (López-Villalobos, 1998). This simplifies herd management.

Figure 1. Two-breed rotational crossbreeding scheme.

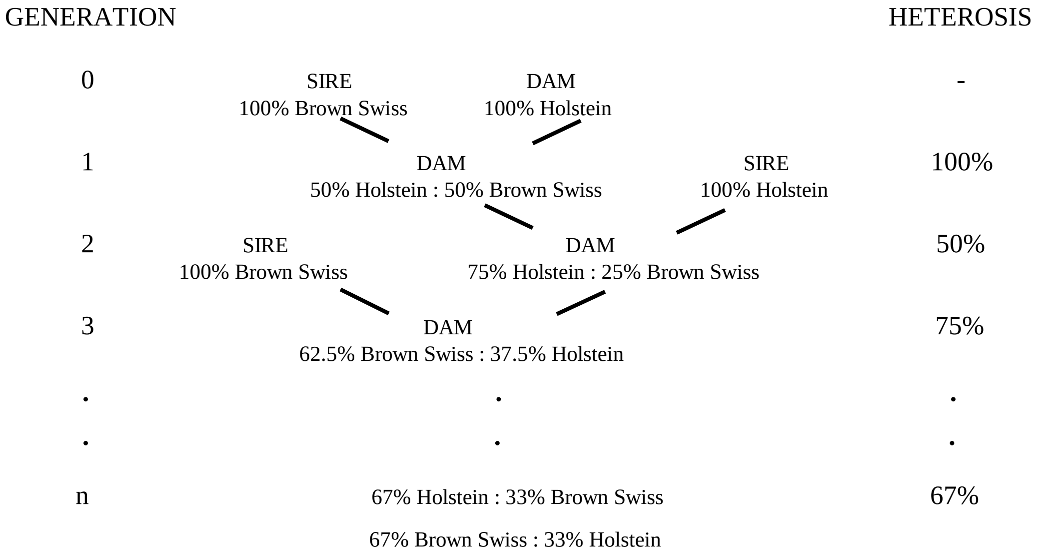
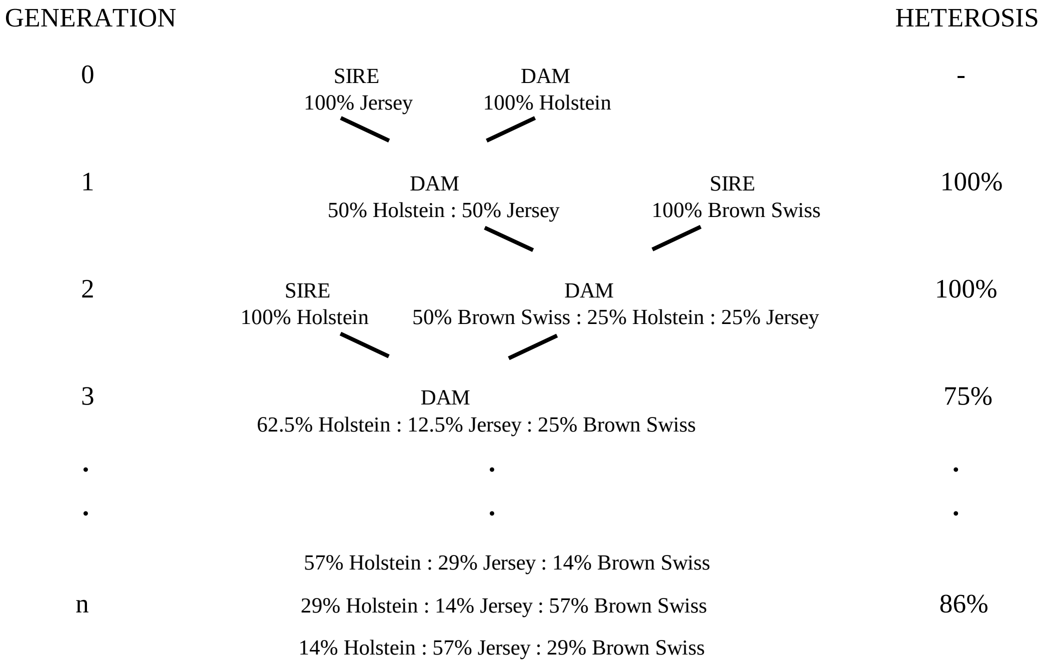


Figure 2. Three-breed rotational crossbreeding scheme.



For example, a two-breed rotational crossbreeding scheme between Brown Swiss and Holstein breeds proceeds by making a first cross with a Brown Swiss sire and a Holstein cow (Figure 1). In the next generation a backcross is made using a Holstein sire, in the third generation a Brown Swiss sire is used again. This alternate use of straightbred Brown Swiss and Holstein sires continues and at equilibrium the breed composition stabilises at 2/3 of the sire breed and 1/3 of the maternal grandsire breed. Such a systematic crossbreeding system exploits 67% of the heterosis expressed in the first Brown Swiss x Holstein cross. A similar approach can be followed in the three-breed rotational crossbreeding system using Jersey, Holstein and Brown Swiss straightbred sires to exploit 86% of the heterotic effects (Figure 2).

Rotational crossbreeding systems can increase the profitability of commercial herds, but wide implementation of crossbreeding in the dairy industry may reduce the number of bull mothers over the years, penalising the rate of genetic gain of the entire population (López-Villalobos, 1998). The most popular example where crossbreeding has been widely adopted is New Zealand. In this country, Holstein-Friesian x Jersey crosses show higher net income than purebred Holstein-Friesian and Jersey cows, so that dairy farmers mate their cows to bulls from another breed to generate crossbred replacements with the aim of exploiting the effects of breed and heterosis (López-Villalobos, 1998), regardless of the fact that the cross has different characteristics from the purebreds.

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Chapter 2

Crossbreeding effects on milk yield traits and calving interval in spring-calving dairy cows

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ABSTRACT

The aim of the study was to assess crossbreeding effects for 305-d milk, fat, and protein yield, and calving interval (CI) in Irish dairy cows (parities 1 to 5) calving in the spring from 2002 to 2006. Data included 188,935 records for production traits and 157,125 records for CI. The proportion of genes from Friesian (FR), North American Holstein Friesian (HO), Jersey (JE), and Montbéliarde (MO) breeds, and coefficients of expected heterosis for HOxFR, HOxJE, and HOxMO crosses were calculated from the breed composition of cows' parents. The model used to obtain estimates of crossbreeding effects accounted for contemporary group, age at calving, linear regression on genes proportions for FR, JE, and MO, and linear regression on coefficients of expected heterosis for HOxFR, HOxJE, and HOxMO crosses, as fixed effects, and cow and residual as random. Breed effects for production traits were in favour of HO and very different from JE, while for CI were in favour of breeds other than HO. The highest heterosis estimates for production were for HOxJE, with first generation crosses giving 626 kg more milk, 25 kg more fat, and 21 kg more protein than the average of the parental breeds. Regarding CI, the highest estimate was for HOxMO, with first generation crosses showing 10 d less CI than the average of the parental breeds. Estimates obtained in this paper could be applied in the genetic evaluation system of Ireland.

Key words: breed effects, calving interval, dairy cattle, heterosis, production traits

INTRODUCTION

Cattle breeding in Ireland relies on a multiplicity of breeds and crosses, and the main genotypes are North American Holstein Friesian (**HO**), Friesian (**FR**), Jersey (**JE**), Montbéliarde (**MO**), and crosses among them. During the last decades, the HO cows have become popular around the world because of their notable genetic merit for milk production. The popularity of this breed is massive in countries where milk volume has been of primary relevance in determining income for the dairy farm (López-Villalobos, 1998).

In Ireland, the percentage of HO genes in young bulls entering artificial insemination progeny testing in 1980 was 8% (Cunningham, 1983), but this proportion in sires increased up to 80% at the end of 1990s (Simm, 1998). The introduction of HO breed at the expenses of FR genes has been identified as a contributor to the declined reproductive performance in spring-calving dairy herds (Evans et al., 2006). It is well-established that cows' fertility is of primary relevance in seasonal-pasture systems where breeding and calving are restricted to a limited time period of the year; failure to conceive during the breeding season determines important economic losses and often leads the cow to be culled (Holmes et al., 2007). Hence, suitable economic indexes have been developed to help dairy farmers identify the most profitable animals for breeding dairy herd replacements, and milk production and fertility are the key drivers of profit.

The exploitation of breeds other than HO or crosses involving HO and other genotypes may be a valuable solution to meet the requirements of a pasture-based system and to cope with fertility problems. Use of crossbreeding in dairy cattle is attracting dairy farmers in many countries including Ireland, New Zealand, Australia, and the United States, and the interest is mostly in the benefits for functional traits (Weigel and Barlass, 2003).

In the case of mixed-breed populations it appears important to estimate breed and heterosis effects, and use this information to assess the profitability under purebred and crossbred scenarios. It is well-known that a genotype ranking the best under certain production and economic circumstances may rank differently when the conditions change (Kahi et al., 1998). So, the choice of the breeds and/or crossbreds to be adopted in a country is strongly related to the local conditions and should be carefully assessed.

Genetic evaluations across breed are routinely computed by the Irish Cattle Breeding Federation (ICBF, Cork, Ireland). The current genetic evaluation of dairy cattle adjusts for a coefficient of general heterosis as fixed effect. Using general heterosis means that the coefficient for each animal is calculated on the basis of its total heterozygosity, without investigating the effect of specific breeds. The inclusion of coefficients of specific heterosis in the model allows the assignment of heterozygosity effects according to the specific combinations of genes from sire and dam. The objective of this study was to estimate breed and specific heterosis effects for milk yield traits and calving interval in Irish spring-calving dairy cows.

MATERIALS AND METHODS

Data and editing procedure

Lactation records on 305-d milk, fat, and protein yield, and information on calving interval (**CI**) for parities 1 to 5 were obtained from the cattle breeding central database operated by ICBF. Records on cows calving in the spring (January to June) from 2002 to 2006 were extracted, and animals with unknown parents were not considered. Also, parents with any fraction of unknown genes, without any information on their breed composition or having any percentage of beef genes were discarded. Because a high number of sires and dams had a percentage of unknown genes, their removal greatly reduced the number of exploitable records in subsequent analyses. Inconsistent production records were removed as well as lactation lengths less than 90 or greater than 450 d, and CIs between 1 and 280 or greater than 510 d. Records on cows that failed to calve again (i.e. with a subsequent CI equal to 0) were treated as missing values in the analysis for production traits, while were omitted in the analysis for CI. Calving intervals were available for lactation 1 to lactation 2, lactation 2 to lactation 3, lactation 3 to lactation 4, lactation 4 to lactation 5, and lactation 5 to lactation 6. Ages at first, second, third, fourth, and fifth calving were restricted to between 20 and 40 months, 30 and 60 months, 45 and 76 months, 50 and 80 months, and 60 to 100 months, respectively as in Evans et al. (2006). Age at calving was grouped into the following classes: <24, 24, 25-26, 27-33 and >33 months for parity 1, <36, 36, 37-38, 39-43, 44-48 and >48 months for parity 2, <48, 48, 49-50, 51-56, 57-61 and >61 months for parity 3, <61, 61-63, 64-71 and >71 months for parity 4, and <73, 73-75, 76-84 and >84 months for parity 5. Contemporary groups (**CG**) were defined as cows calving in the same herd-year, and CGs with less than 5 animals were removed. This requirement was imposed both for production and CI datasets.

Table 1. Number of records, herds, and contemporary groups (CG) for milk yield traits, and distribution of records across years, months, and classes of age at calving, for parities 1 to 5.

Item		Parity				
		1	2	3	4	5
Records[1]		58,338	48,346	36,984	26,202	19,065
Herds		2846	2838	2748	2616	2453
CG		8947	8968	8493	7598	6670
Year of calving	2002	8674	7732	5792	4349	3204
	2003	9895	8743	6918	4835	3673
	2004	11,558	9547	7368	5140	3717
	2005	13,163	10,165	7893	5570	3982
	2006	15,048	12,159	9013	6308	4489
Month of calving	January	11,387	8436	5919	3868	2753
	February	22,712	16,521	11,553	8073	5658
	March	15,463	12,312	9725	6805	5060
	April	6062	7106	6001	4473	3321
	May	2019	2984	2865	2219	1683
	June	695	987	921	764	590
Age at calving (classes)	1	6976				
	2	14,114				
	3	15,964				
	4	13,713				
	5	7571				
	6		4750			
	7		8517			
	8		11,624			
	9		10,331			
	10		7736			
	11		5388			
	12			2738		
	13			5370		
	14			8106		
	15			8065		
	16			7752		
	17			4953		
	18				5644	
	19				7459	
	20				6447	
	21				6652	
	22					3877
	23					5119
	24					5416
	25					4653

[1] Number of records for milk yield traits = 188,935 (104,163 cows).

Table 2. Number of records, herds, and contemporary groups (CG) for calving interval, and distribution of records across years, months, and classes of age at calving, for parities 1 to 5.

Item		Parity				
		1	2	3	4	5
Records[1]		51,035	40,887	30,463	20,636	14,104
Herds		2646	2643	2537	2394	2206
CG		8292	8252	7680	6754	5685
Year of calving	2002	7647	6643	4869	3489	2400
	2003	8917	7531	5769	3867	2817
	2004	10,116	8114	6083	4020	2743
	2005	11,504	8580	6474	4335	2885
	2006	12,851	10,019	7268	4925	3259
Month of calving	January	10,129	7389	5104	3226	2173
	February	20,181	14,461	9921	6673	4439
	March	13,420	10,357	8049	5459	3841
	April	5112	5716	4725	3273	2250
	May	1654	2240	2049	1516	1054
	June	539	724	615	489	347
Age at calving (classes)	1	6180				
	2	12,613				
	3	14,027				
	4	11,860				
	5	6355				
	6		4220			
	7		7575			
	8		9918			
	9		8595			
	10		6408			
	11		4171			
	12			2432		
	13			4742		
	14			6871		
	15			6528		
	16			6333		
	17			3557		
	18				4843	
	19				5955	
	20				5024	
	21				4814	
	22					3225
	23					3956
	24					3942
	25					2981

[1] Number of records for calving interval (CI) = 157,125 (88,097 cows).

Following editing of the data as above and some other individual cow edits, 188,935 records from 104,163 cows for milk yield traits and 157,125 records from 88,097 cows for CI were available for further analyses. The number of records, herds, and CGs, and the distribution of records across years, months, and classes of age at calving, for parities 1 to 5, are in Table 1 for milk yield traits and in Table 2 for CI.

Breeds proportions and coefficients of specific heterosis

Thirteen dairy breeds were identified in the Irish population and the proportion of genes was calculated for each cow using the simple identity:

$$\alpha_i^p = (\alpha_i^s + \alpha_i^d) / 2,$$

where α_i^p is the proportion of genes from breed i in the progeny, α_i^s is the proportion of breed i in the sire, and α_i^d is the proportion of breed i in the dam. Breeds fractions were expressed in increments of 1/32 by ICBF. Four dairy breeds (FR, HO, JE, and MO) were chosen among others to estimate breed effects because the distribution of cows across classes of genes proportions was better than that for other breeds, both for production traits (Table 3) and CI (Table 4).

Table 3. Distribution of cows across classes of breeds proportions for milk yield traits.

Class[2]	Breed[1]			
	HO	FR	JE	MO
1	3345	12,672	102,783	101,814
2	2901	67,774	535	14
3	6449	15,741	185	202
4	18,880	4959	10	6
5	28,407	1224	1	---
6	44,181	1793	649	2127

[1] HO (North American Holstein Friesian), FR (Friesian), JE (Jersey), MO (Montbéliarde).

[2] Classes of genes proportions for a given breed were defined as: 1 = 0%, 2 = from 1 to 25%, 3 = from 26 to 50%, 4 = from 51 to 75%, 5 = from 76 to 87.5%, 6 = from 88 to 100%.

The proportion of FR, HO, JE, and MO genes within sire and dam was required to add up to one. Classes of genes proportions for a given breed were defined as: 1 = 0%, 2 = from 1 to 25%, 3 = from 26 to 50%, 4 = from 51 to 75%, 5 = from 76 to 87.5%, 6 = from 88 to 100%.

Table 4. Distribution of cows across classes of breeds proportions for calving interval.

Class[2]	Breed[1]			
	HO	FR	JE	MO
1	2909	10,465	86,874	86,086
2	2527	57,136	470	11
3	5597	13,520	165	169
4	16,162	4331	7	6
5	24,088	1069	1	---
6	36,814	1576	580	1825

[1] HO (North American Holstein Friesian), FR (Friesian), JE (Jersey), MO (Montbéliarde).

[2] Classes of genes proportions for a given breed were defined as: 1 = 0%, 2 = from 1 to 25%, 3 = from 26 to 50%, 4 = from 51 to 75%, 5 = from 76 to 87.5%, 6 = from 88 to 100%.

Coefficients of specific heterosis were calculated between any pair of the 13 dairy breeds using the following identity (Dickerson, 1973; Lidauer et al., 2006):

$$het_{ij}^{p} = \alpha_i^s \alpha_j^d + \alpha_j^s \alpha_i^d ,$$

where het_{ij}^{p} is the coefficient of expected heterosis between fractions of breeds i and j in the progeny, α_i^s and α_j^s are proportions of breeds i and j in the sire, respectively, and α_i^d and α_j^d are proportions of breed i and j in the dam, respectively. In total 78 breed combinations were tested in order to identify the most representative crossbreds in Ireland, and three of them (HOxFR, HOxJE, and HOxMO) were chosen among others to estimate specific heterosis effects because the distribution of cows across classes of coefficients of expected heterosis was better than that for other breeds crosses, both for production traits (Table 5) and CI (Table 6). No distinction was made about reciprocal crosses, and maternal effects (if present) were not estimated. Classes of coefficients of heterosis were defined as: 1 = 0, 2 = from 0.01 to 0.24, 3 = from 0.25 to 0.49, 4 = from 0.50 to 0.74, 5 = from 0.75 to 1.

Recombination effects were not investigated in this study and a linear relationship between heterozygosity and heterosis (the dominance model) was assumed (Falconer and Mackay, 1996).

Table 5. Distribution of cows across classes of coefficients of expected heterosis for milk yield traits.

Class[2]	Breed cross[1]		
	HOxFR	HOxJE	HOxMO
1	13,580	103,440	103,952
2	37,124	513	5
3	32,154	28	30
4	15,021	72	65
5	6284	110	111

[1] HOxFR (North American Holstein Friesian x Friesian), HOxJE (North American Holstein Friesian x Jersey), HOxMO (North American Holstein Friesian x Montbéliarde).

[2] Classes of coefficients of heterosis are: 1 = 0, 2 = from 0.01 to 0.24, 3 = from 0.25 to 0.49, 4 = from 0.50 to 0.74, 5 = from 0.75 to 1.

Table 6. Distribution of cows across classes of coefficients of expected heterosis for calving interval.

Class[2]	Breed cross[1]		
	HOxFR	HOxJE	HOxMO
1	11,263	87,462	87,920
2	31,195	451	5
3	27,376	20	27
4	12,898	64	55
5	5365	100	90

[1] HOxFR (North American Holstein Friesian x Friesian), HOxJE (North American Holstein Friesian x Jersey), HOxMO (North American Holstein Friesian x Montbéliarde).

[2] Classes of coefficients of heterosis are: 1 = 0, 2 = from 0.01 to 0.24, 3 = from 0.25 to 0.49, 4 = from 0.50 to 0.74, 5 = from 0.75 to 1.

Statistical analysis

A univariate model was applied to milk yield traits and CI using a direct sparse solver implemented in the PEST package (Groeneveld et al., 1990) instead of an iterative procedure so that the standard errors for the covariates would be produced. The model was the following:

$$y_{\mathrm{ijkl}} = \mathrm{CG}_{\mathrm{i}} + \mathrm{age}_{\mathrm{j}} + \sum_{m=1}^{4} \beta_m \, \mathrm{breed}_{\mathrm{m}} + \sum_{n=1}^{3} \beta_n \, \mathrm{het}_{\mathrm{n}} + \mathrm{cow}_{\mathrm{k}} + \varepsilon_{\mathrm{ijkl}},$$

where y_{ijkl} is the l*th* 305-d milk, fat, or protein yield, or CI of animal *k*, of age *j* and contemporary group *i*; CG_{i} is the fixed effect of contemporary group *i*; $\mathrm{age}_{\mathrm{j}}$ is the fixed effect of age class *j* within parity; β_m is the fixed linear regression coefficient of *y* on additive genetic breed effects for FR, JE, or MO; β_n is the fixed linear regression coefficient of *y* on coefficients of expected specific heterosis effects for HOxFR, HOxJE or HOxMO; $\mathrm{cow}_{\mathrm{k}}$ is the random effect of cow *k*; and $\varepsilon_{\mathrm{ijkl}}$ is the random residual associated with observation ijkl. The regression on HO breed proportion was omitted from the model, in order to avoid linear dependencies and so that all other breeds would be compared with HO. Random residual effects were assumed to be identically, independently, and normally distributed with mean zero and variance σ_e^2. The random cow effect would actually account for permanent environment plus genetic effects that are not accounted for by the fixed breed effects. The PEST package (Groeneveld et al., 1990) requires the definition of additive genetic and residual variances for the traits in order to obtain reliable standard errors of the BLUEs. Values of additive genetic variances were assumed 215,055 kg^2, 303 kg^2, 177 kg^2, and 75 d^2 for milk, fat, protein, and CI, respectively, and values of heritability were assumed 0.35 for production traits and 0.04 for CI (Interbull, 2008).

RESULTS AND DISCUSSION

Descriptive statistics for milk yield traits and CI for parities 1 to 5 are summarized in Table 7. Differences between first and fifth lactation cows were in magnitude of 1395, 49, and 46 kg of milk, fat, and protein yield, respectively, and between second and fifth lactation cows were 434, 18, and 13 kg, respectively. Third, fourth and fifth parities animals highlighted similar levels of production. Calving intervals did not appear to differ across parities, with an average value of 378 d. Age at first, second, third, fourth, and fifth calving was 27, 41, 54, 66, and 79 months, respectively.

Table 7. Mean and standard deviation (SD) for 305-d milk, fat, and protein yield, calving interval (CI), and age at calving, for parities 1 to 5.

Item		Parity				
		1	2	3	4	5
Milk (kg)	Mean	6002	6963	7320	7423	7397
	SD	1215	1385	1424	1405	1414
Fat (kg)	Mean	228	259	273	277	277
	SD	45	52	55	56	57
Protein (kg)	Mean	201	234	246	249	247
	SD	38	43	45	44	45
CI (d)	Mean	379	379	377	377	378
	SD	38	38	38	38	38
Age at calving (mo)	Mean	26.9	40.6	54.0	65.7	78.8
	SD	4.1	5.5	6.5	5.9	7.4

Crossbreeding effects for 305-d milk, fat, and protein yield are in Table 8. Estimates of breed effects for these traits were all in favour of HO, the genotype reference in our study. The only estimate close to zero was found for fat yield in JE, but this breed produced 1723 kg less milk and 33.5 kg less protein than HO. Production levels were similar comparing FR and MO, and these breeds performed better than JE for milk and protein yield. On average, JE produced 1000 kg less milk and 12 kg less protein than FR and MO, but around 25 kg more fat. Hoekstra et al. (1994) estimated positive breed effects of 506, 14.6, and 12.8 kg of milk, fat, and protein yield, respectively, of HO over Dutch Friesian first lactation cows. Under New Zealand conditions, Ahlborn-Breier and Hohenboken (1991) reported additive genetic breed differences for lactation milk and fat yield between first lactation HO and JE cows of 908 and 9.6 kg, respectively, in favour of the first breed. Estimates obtained in Ahlborn-Breier and Hohenboken (1991) and Hoekstra et al. (1994) were lower than those reported by our research; however, they considered only primiparous cows while we accounted for parities 1 to 5. These results seem to confirm that JE is not comparable to HO for milk yield, but fat yield was of similar magnitude in the two breeds and JE may be rewarded in milk-pricing systems where emphasis is put on milk-solids. In a recent survey by Weigel and Barlass (2003), dairy producers reported that fat and protein percentages are much higher in JE than in other breeds and breed crosses.

Table 8. Breed and heterosis effects (SE) for milk yield traits and calving interval (CI).

	Milk (kg)	Fat (kg)	Protein (kg)	CI (d)
Breed effects[1,2]				
- FR	-735 (22)	-23.2 (0.8)	-22.6 (0.6)	-10.3 (1.2)
- JE	-1723 (61)	-0.7 (2.3)	-33.5 (1.8)	-10.4 (3.4)
- MO	-764 (42)	-27.8 (1.6)	-19.9 (1.2)	-5.2 (2.3)
Heterosis effects[3]				
- HOxFR	+193 (16)	+9.1 (0.6)	+8.0 (0.5)	-1.6 (0.8)
- HOxJE	+626 (80)	+24.9 (3.0)	+21.4 (2.3)	-1.3 (4.4)
- HOxMO	+468 (73)	+15.8 (2.7)	+11.5 (2.1)	-10.5 (4.0)

SE, standard error.

[1] Breed effects of HO were set to zero for comparison.

[2] FR (Friesian), JE (Jersey), MO (Montbéliarde).

[3] HOxFR (North American Holstein Friesian x Friesian), HOxJE (North American Holstein Friesian x Jersey), HOxMO (North American Holstein Friesian x Montbéliarde).

Specific heterosis effects for milk yield traits were all positive (favourable) in the different breeds crosses, with the highest estimates for HOxJE (Table 8). Coefficients of regression indicated that first generation crosses between HO and JE produced +626 kg of milk, +24.9 kg of fat, and +21.4 kg of protein compared to the average of their purebred parents. The lowest estimates were for HOxFR, while for HOxMO were between those of HOxFR and HOxJE. Results from HOxFR were expected since they are strains from the same breed. In fact, the magnitude of heterosis depends on the degree of genetic dominance of the trait analyzed, but it is also related to the genetic distance between the parental breeds, so that, in general, the higher this genetic distance the higher the heterosis effects (Mäki-Tanila, 2007).

Several studies investigated crossbreeding effects between strains of Black and White cattle populations. Van der Werf and de Boer (1989) reported heterosis of +123 kg of milk, +6.0 kg of fat, and +4.4 kg of protein in first lactation HO and Dutch Friesian crossbred cows. Similar estimates were assessed by Boichard et al. (1993) who found heterosis of +135 kg of milk, +5.6 kg of fat, +4.3 kg of protein in HO x French Black and White cattle using records from parity 1 to 3, and by Akbas et al. (1993) who reported values of +104 kg of milk, +4.3 kg of fat, and +2.9 kg of protein in first lactation HO and European Friesian crossbred cows. In our study, heterotic effects for 305-d milk, fat, and protein yield in HOxFR were in the magnitude of +193 kg of milk, +9.1 kg of fat, and +8.0 kg of protein, respectively. These estimates appeared higher than those found in past researches conducted on crosses between HO and European Black and White cattle populations, maybe indicating that under pasture-based systems the percentage of heterosis is higher than under more intensive conditions. This trend agrees with the review of Barlow (1981) that reported that percentage of heterosis is generally greater in a stressful than in a supportive environment. It is also worth noting that most of the studies considered only primiparous cows. The parity of cows has an influence on the expression of heterosis even if the relationship is not clear yet. Touchberry (1992) reported that heterosis effects for milk and fat yields in HO x Guernsey crossbreds were higher for second than for first lactation. In Donald et al. (1977) these effects for 305-d milk and total solids yields in British Friesian x JE crosses increased from first to second lactation. In a study on HO x Brown Swiss cows, Dechow et al. (2007) found that heterosis for fat plus protein daily yield increased across lactations. Opposite trends were reported by McAllister (1986) for lactation yields of milk and fat in HO x Ayrshire cows.

Regarding the effect of crossbreeding in crosses other than HOxFR, Ahlborn-Breier and Hohenboken (1991) estimated heterosis of +171 kg of milk and +10.3 kg of fat for lactation milk and fat yield between first lactation HO and JE cows under New Zealand conditions. Heins et al. (2008) analysed first lactation yields in pure HO and crossbred cows from JE sires and HO dams. From the study, crossbred animals produced 558 kg less milk, 3 kg less fat, and 15 kg less protein than pure HO. In a study conducted by VanRaden and Sanders (2003) in the United States, fat yield was slightly higher in JExHO crosses than in pure HO cows. Another research by Heins et al. (2006) determined differences between pure HO and crossbred cows of MO sires and HO dams during first lactation for

305-d production traits. Results revealed that crossbred animals produced 596 kg less milk, 12 kg less fat, and 12 kg less protein than pure HO cows.

Breed effects for calving interval indicated all breeds had shorter intervals (favourable) than HO (Table 8). Calving interval in FR and JE was 10 d shorter than in HO cows, while it was 5 d shorter in the case of MO. Also, estimates of heterosis effects for CI were all negative (favourable). Coefficients of regression indicated that first generation crosses between HO and MO had a reduction in CI of 10 d when compared to the average of their purebred parents, while for HOxFR and HOxJE these coefficients were close to zero (-1.6 and -1.3 d, respectively). A recent study by Wall et al. (2005) highlighted that heterosis for CI in crosses between HO and British Friesian cows was -1.6 d. In the past, Donald et al. (1977) reported heterosis estimates of -3.7% for CI in British Friesian x JE, -1.6% in Ayrshire x British Friesian, and -1.7% in Ayrshire x JE crosses, while Vesely et al. (1986) found a value of -0.9% in HO x Ayrshire crosses in Canada, and a difference of 5 d between pure HO and Ayrshire cows. A large and unfavourable heterosis estimate of +13 d for CI was found in HO x Guernsey crosses involved in the Illinois trial (Touchberry, 1992).

CONCLUSIONS

Our results suggested that breed and specific heterosis effects exist in the Irish dairy cattle population. Estimates for HOxJE and HOxMO should be interpreted with caution because of the low number of animals available to assess crossbreeding effects. Results seem to confirm that HO is the breed of choice if the breeding objective emphasizes milk yield traits, while crosses involving HO and JE or HO and MO may perform better than pure HO for fat and protein yields. In the case of Ireland a great emphasis is given to fertility traits, and CI has been found to be better in breeds other than HO. Estimates obtained in this paper could be considered to account for specific effects in the current model of genetic evaluation run in Ireland. The knowledge of specific heterosis along with estimated breeding values routinely calculated by the ICBF, and random permanent environmental effects would provide the farmer with producing value, a useful tool for making culling decisions.

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Chapter 3

Heterosis effects of two Friesian strains of dairy cows in different production environments

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ABSTRACT

The effect of the environmental level of production (ENV) on the expression of heterosis for milk, fat, protein, fat plus protein (FP) yields, somatic cell score (SCS), and age at first calving (AFC) was investigated in first lactation Black and White dairy cows reared in The Netherlands, and officially enrolled in the Dutch herd-book. Holstein Friesian (HF), Dutch Friesian (DF), and first generation crosses obtained from the mating of HF sires and DF dams (HD) were involved in the study, and data from animals with a first calving date between 1990 and 2000 were used. The edited dataset accounted for 22,930 cows with production information distributed in 3549 herds, and 11,055 cows with SCS information distributed in 2071 herds. Adjusted primiparous milk yield for each herd was obtained using a model that accounted for fixed effects of herd, year and month of calving, genotype, and age at first calving. The overall average of all adjusted milk productions was computed, and 3 ENV (low: 5389 kg of milk, medium: 6307 kg of milk, and high: 7337 kg of milk) were defined on the basis of the overall mean ± 0.5 SD. Once environments were defined, all the traits were analyzed with a model that accounted for fixed effects of ENV, herd nested within ENV, age at first calving (except for AFC), year and month of calving, genotype, and the interaction between ENV and genotype. Least squares means for the interaction effect were used to estimate heterosis and to evaluate its magnitude across ENV. Holstein Friesian achieved productions higher than DF. First generation crosses showed levels of production close to HF, especially in the low ENV. Estimates of heterosis for yield traits ranged between 2.4% for milk in the high and 5.3% for fat in the low ENV, with decreasing percentages observed for all production traits when moving from the low to the high ENV. Overall, heterosis for SCS and AFC appeared moderate, with the exception of SCS in the high ENV. Results emphasized that the highest non-additive genetic effects for yield traits were expressed in the most stressful ENV, i.e. low level of production.

Key words: Friesian strains, heterosis by environment interaction, production, somatic cell score

INTRODUCTION

A number of studies reported experiments with crossbreeding of dairy cattle in temperate climates (Pearson and McDowell, 1968; Turton, 1981; Touchberry, 1992), and a review on heterosis and recombination effects for several traits of economic relevance has been provided by López-Villalobos (1998). An increasing curiosity in the application of this mating system has grown among dairy producers, raising questions of breed utilization (McAllister, 2002). Countries such as New Zealand, The Netherlands and, more recently, USA have implemented national genetic evaluation schemes including data from crossbred animals.

Well-designed crossbreeding programs may lead the farmer to exploit desirable characteristics of the breeds or strains involved, and to take advantage of heterosis for traits of economic relevance (López-Villalobos, 1998). The mating of different genotypes increases health and efficiency in animals, and the improvement of reproductive and fitness traits such as fertility, survival, and calving ease, seems to be an important aspect for implementing crossbreeding in dairy cows (Heins et al., 2006a,b), together with an achievable economic advantage in milk pricing systems where fat and protein are rewarded (Weigel and Barlass, 2003).

However, genotypes do not perform equally under different production and managerial conditions. An interesting approach in evaluating the phenotypic performance of animals is to consider the environment in which they are producing (Bryant et al., 2005). Recent papers have emphasized the existence of genotype by environment (**G x E**) interaction for production traits (Boettcher et al., 2003; Fikse et al., 2003), somatic cell score (Calus et al., 2006), and reproductive traits (Boettcher et al., 2003; Kearney et al., 2004). In general, G x E interaction arises when performances of different genotypes are not equally influenced by different environments (Falconer and Mackay, 1996). The scaling effect is one of them, and occurs when differences among animals for a given trait are larger in one environment than in another.

Similarly, in the past, several scientists discussing theoretical aspects of mating animals with different genetic makeups (Sheridan, 1981; Cunningham, 1982; Hill, 1982) highlighted that environmental factors may influence the expression of heterosis in a crossbred population. Because of this possible influence, the assessment of crossbreeding performance becomes more complicated. Hill (1982), described heterosis by environment (**H x E**) interaction as a special case of G x E interaction.

Sheridan (1981), citing the concept of genetic homeostasis proposed earlier by Lerner (1954), stated that "…the degree of heterosis shown by a particular cross can be influenced by the environment, since crossbred animals are expected to be both more uniform and less influenced by environmental factors than their purebred parental lines." This implies that heterozygotes are expected to be less susceptible to external changes than homozygotes. Barlow (1981), in a comprehensive review on the matter, reported that heterosis for most traits appears to be greater in stressful rather than in favorable conditions, and the nature of interactions depends on the species and trait considered in the analysis. On the whole, H x E interaction has to be evaluated in relation to the specific conditions in which animals perform, so that it would be possible to better understand where crossbred animals can positively interact with the environment. This approach may be of interest from an economic point of view.

A recent study has been conducted in New Zealand to establish the influence of environmental conditions on the expression of heterosis for production traits (Bryant et al., 2007). Results evidenced a variation of non-additive genetic effects for crosses from different genotypes and for the same type of cross in different environments. However, literature on H x E interaction for these traits is not extensive, and is scarce for somatic cell score (**SCS**) and age at first calving (**AFC**).

Aim of this study was to investigate the effect of the environment on the degree of heterosis for milk, fat, protein, fat plus protein (**FP**) yields, SCS, and AFC using the Black and White population reared in The Netherlands as case study.

MATERIALS AND METHODS

Data

Data were obtained from the Dutch milk recording database provided by the Nederlands Rundvee Syndicaat (NRS, The Netherlands). Herd-year (**HY**) groups with at least one crossbred and one purebred primiparous cow were extracted. Holstein Friesian (**HF**), Dutch Friesian (**DF**), and F_1 crosses obtained from these two strains of Black and White dairy cattle were the genotypes considered in the study. In particular, only F_1 primiparous crosses from HF sires x DF dams (**HD**) were used, because the reciprocal crosses (DF sires x HF dams) were represented by a very low number of heifers.

Despite the common origin, during the period considered in this research, the DF and HF populations in The Netherlands were different. When looking at the average breeding values for cows born in 2000, it can be highlighted that the genetic difference between HF and DF for lactation milk, fat, and protein yield was +335, +9, and +10 kg, respectively, in favour of HF (de Jong, personal communication). Production statistics by NRS (2006) evidenced differences in average 305-d milk, fat, and protein yield for HF and DF cows (all parities) of 2252, 84, and 72 kg, respectively. Harbers (1997), underlined the need for the Netherlands to adjust the genetic evaluation for heterosis and recombination losses of North American Holsteins crossbred with Dutch Friesians, meaning that a genetic differentiation of the two Black and White genotypes still existed. Hence, even if the American strain is substituting the original Dutch one, it appears appropriate to consider DF and HF as two different genotypes on which the effect of different rearing conditions (production levels) can be investigated.

In The Netherlands, breed/strain codes from each animal are stored on database as well as the proportions of the genes from each breed/strain. The proportions of the genes from each breed are given in classes from 1 to 8, so that each class represents 12.5% of genes (Harbers, 1997). Pure animals from HF and DF, and F_1 crosses were identified.

Production data comprised 305-d milk, fat, and protein yields, and average within 305-d SCS recorded on first lactation cows calving between 1990 and 2000. Only cows with sire and dam information were retained in the dataset. Incomplete lactations of 100 d or more extrapolated to 305 days by NRS were retained, as well as lactations with valid milk, fat, and protein yields produced on the same herd. Also, 305-d fat plus protein (FP) yield was derived by adding the corresponding fat and protein yields for each cow, and age at first calving (AFC) was calculated as the difference between the first calving date and the birth date. Heifers with AFC less than 520 d or greater than 1070 d were not considered in the subsequent analyses. At the end of editing procedure, a total of 22,930 cows distributed in 3549 herds were available.

Collection of SCS data started during the 1990s in The Netherlands, thus there were many cows without SCS information. Average within 305-d SCS was obtained from the mean of the individual SCC calculated as $\log_2(SCC/1000)$. Only cows with 3 to 15 SCC measurements within the 305 days were kept. At the end of the editing procedure, a total of 11,055 SCS cows distributed in 2071 herds were available for statistical analyses of SCS.

Environmental production level (ENV)

Environmental levels of production were defined using the adjusted 305-d milk yield estimate for each herd. These were determined through the use of the GLM procedure of SAS (SAS Institute, 2004) using a model that accounted for fixed effects of herd, year and month of calving, genotype (HF, DF, and HD), and age at first calving. Least squares means (**LSM**) for each adjusted herd were used to create 3 environments (**ENV**) according to the overall average milk yield of first lactation herds LSM ± 0.5 SD. On this basis, herds were defined as low ($x \leq 5980$ kg), medium ($5980 \text{ kg} < x < 6780$ kg), and high ($x \geq 6780$ kg). Since available SCS data were less than production, different ENV were created for the analysis of this trait: low ($x \leq 5990$ kg), medium ($5990 \text{ kg} < x < 6820$ kg), and high ($x \geq 6820$ kg) level of production.

Statistical analysis

Data were analyzed using the GLM procedure of SAS (SAS Institute, 2004) according to the following model:

$$y_{ijklmno} = ENV_i + herd_{j:i} + CY_k + MC_l + G_m + (ENV*G)_{im} + age_n + \varepsilon_{iiklmno},$$

where $y_{ijklmno}$ = 305-d milk, fat, protein, FP yields, average within 305-d SCS, or AFC; ENV_i = fixed effect of the *i*th environment (*i* = low, medium, high); $herd_{j:i}$ = fixed effect of the *j*th herd (*j* = 1,…,3549 for yield traits and AFC; *j* = 1,…,2071 for SCS) nested within the *i*th environment; CY_k = fixed effect of the *k*th year of calving (*k* = 1,…,11); MC_l = fixed effect of the *l*th month of calving (*l* = 1,…,12); G_m = fixed effect of the *m*th genotype (*m* = HF, DF, HD); $(ENV*GC)_{im}$ = fixed effect of the interaction between the *i*th ENV and the *m*th genotype; age_n = fixed effect of the *n*th class of age at first calving (*n* = 1,…,8, with classes of 30 days, and the first and the last being open classes of <720 and >900 d, respectively); $\varepsilon_{ijklmno}$ = random residual ~ N $(0, \sigma^2_\varepsilon)$. The analysis of AFC did not include the age at first calving effect. Least squares means of the interaction effect were used to estimate heterosis as $[(LSM_{F1} - LSM_{AB}) / (LSM_{AB})] \times 100$, where LSM_{F1} is LSM for F_1 crosses (HD), and LSM_{AB} is the average LSM for the purebred parents (HF and DF) involved in the cross. Since only one of the two reciprocal crosses (HF sires x DF dams) were available, heterosis was calculated as the deviation of the first cross from the mean of the parents. Confidence intervals at the 95% level were referred to for testing if differences in heterosis effects were significantly different from zero.

RESULTS AND DISCUSSION

Descriptive statistics for 305-d lactation traits and AFC for each ENV are in Table 1, along with the number of cows of each genotype. The number of animals per genotype was fairly low for DF, particularly in the high ENV, while HF and HD accounted for the highest number of heifers. An average difference of 1948, 71, 66, and 137 kg between the high and the low ENV was observed for 305-d milk, fat, protein, and FP yields, respectively. Moreover, production evidenced a greater variation in the high than in the low ENV when expressed in kg but not as percentage of the mean. Concerning AFC, a reduction in 9 d was observed between the two extreme ENVs, and between the low and the medium ENVs.

Table 1. Means (SD) for first lactation milk yield traits and age at first calving (AFC), and corresponding number of herds and cows for each environmental level of production (ENV).

ENV[c]	Trait[a]					Herds (n)	Cows[b] (n)			
	Milk (kg)	Fat (kg)	Protein (kg)	FP (kg)	AFC (d)		Total	HF	DF	HD
Low	5389 (907)	243 (41)	185 (30)	428 (69)	806 (83)	1064	6111	1660	1322	3129
Medium	6307 (930)	280 (40)	217 (30)	498 (67)	797 (77)	1457	10344	3947	1263	5134
High	7337 (1094)	314 (43)	251 (34)	565 (73)	797 (74)	1028	6475	3523	299	2653

[a] FP = fat plus protein yield; AFC = age at first calving.

[b] HF = Holstein Friesian; DF = Dutch Friesian; HD = F_1 crosses between Holstein Friesian sire and Dutch Friesian dam.

[c] ENV = Classification of herds based on their average first lactation milk production corrected for herd, year of calving, month of calving, genotype (HF, DF, and HD), and age at first calving (low: $x \leq 5980$ kg, medium: 5980 kg $< x <$ 6780 kg, high: $x \geq 6780$ kg).

Table 2 shows the descriptive statistics for average lactation SCS. Decreasing values were evidenced when moving from the low to the high ENV, with a reduction of 0.38 points between the extremes. This trend can be probably considered a dilution effect, i.e. the somatic cells were ejected in a higher volume of milk.

As expected, HF achieved higher milk, fat, protein, and FP yields than DF cows in all ENVs, while for SCS no relevant differences between the two strains were observed, with the exception of a higher value for DF in the high ENV (Figure 1). Estimates for SCS in crossbred cows were lower (favorable) than HF across ENVs. For AFC, the lowest values were found for HF, with a reduction of 29 and 36 d when compared to DF in the medium and high ENVs, respectively. Concerning milk yield traits and AFC, differences among genotypes were greater when compared within the high than within the low ENV (Figure 1), indicating that they were not equally influenced by the environment and that a G x E interaction existed. Probably, HF cows were more sensitive to the limitations to production imposed by the low ENV, characterized by inadequate managerial conditions in relation to their needs, and/or DF cows were not able to fully exploit the advantages of the high ENV. In a recent study from New

Zealand, Bryant et al. (2007) observed a scaling effect for milk, fat, and protein yields comparing overseas HF and New Zealand Jersey breeds over nutritional environments, suggesting that HF animals were more adapted to an intensive feeding system, i.e. an environment where nutritional requirements of animals can be better met.

Table 2. Means (SD) for first lactation average within 305-d SCS and corresponding number of herds and cows for each environmental level of production (ENV).

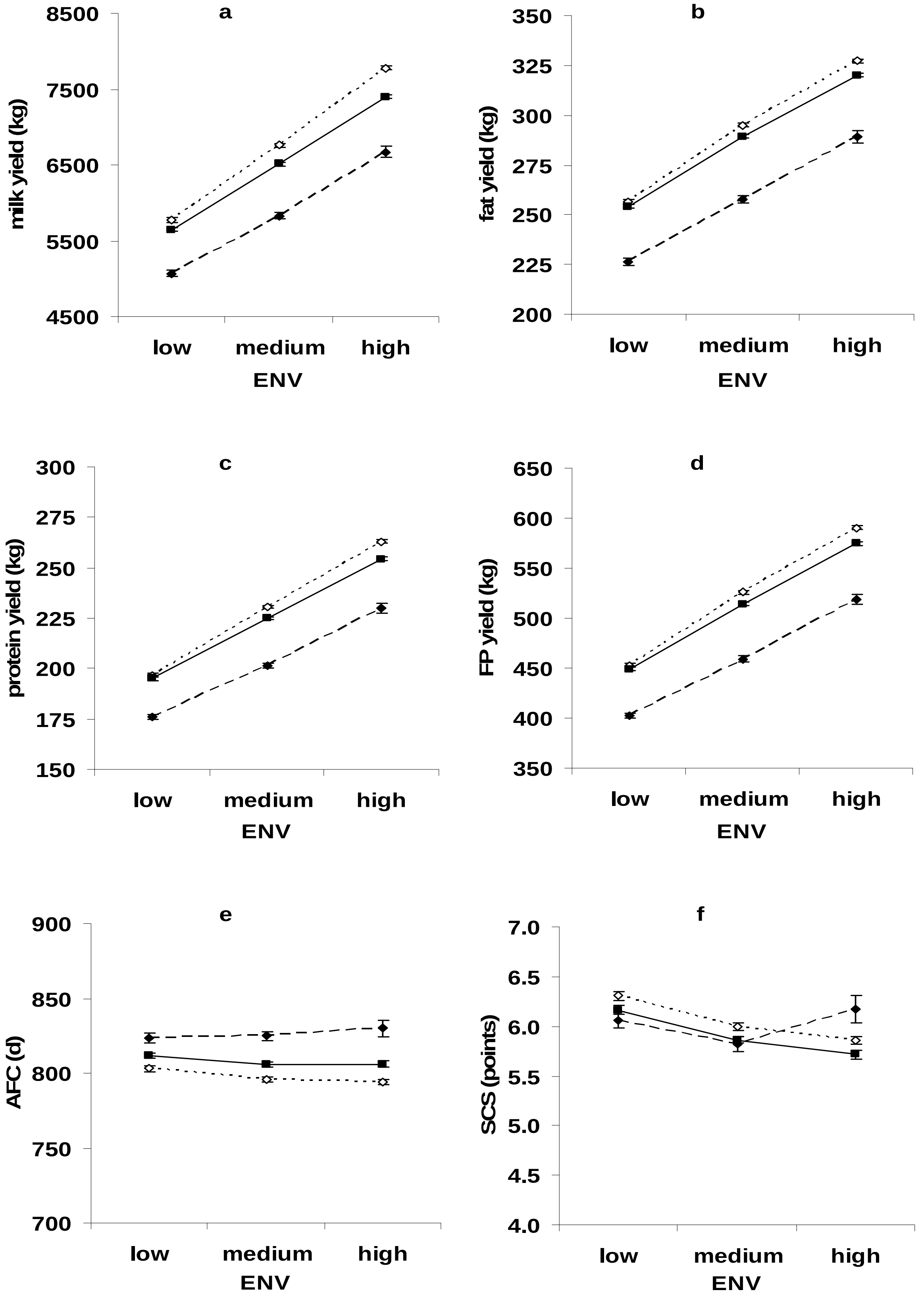
ENV[b]	SCS (points)	Herds (n)	Cows[a] (n)			
			Total	HF	DF	HD
Low	6.21 (1.18)	627	3137	1088	650	1399
Medium	5.96 (1.16)	837	4758	2130	508	2120
High	5.83 (1.18)	607	3160	1791	125	1244

[a] HF = Holstein Friesian; DF = Dutch Friesian; HD = F_1 crosses between Holstein Friesian sire and Dutch Friesian dam.

[b] ENV = Classification of herds based on their average first lactation milk production corrected for herd, year of calving, month of calving, genotype (HF, DF, and HD), and age at first calving (low: $x \leq 5990$ kg, medium: 5990 kg $< x <$ 6820 kg, high: $x \geq 6820$ kg).

Heterosis estimates and 95% confidence intervals for milk yield traits, SCS, and AFC in each ENV are displayed in Figure 2. Overall, all production traits revealed positive but decreasing levels of heterosis when moving from the low to the high ENV, with estimates ranging from 5.3% (fat yield in the low ENV) to 2.4% (milk yield in the high ENV). This could be explained if we consider that the low ENV is stressful for production traits because management does not meet the need of genetically highly productive cows such as HF. Thus, the highest heterosis values were expressed in the most stressful environment. Barlow (1981), summarizing the effects of H x E interaction in animals, debated that sub-optimal conditions let heterosis be better expressed. For SCS, heterosis effects were negative (favorable) but significantly different from zero only in the case of the high ENV. In the case of AFC, heterosis estimates were always very low and significantly different from zero in the medium and high ENVs.

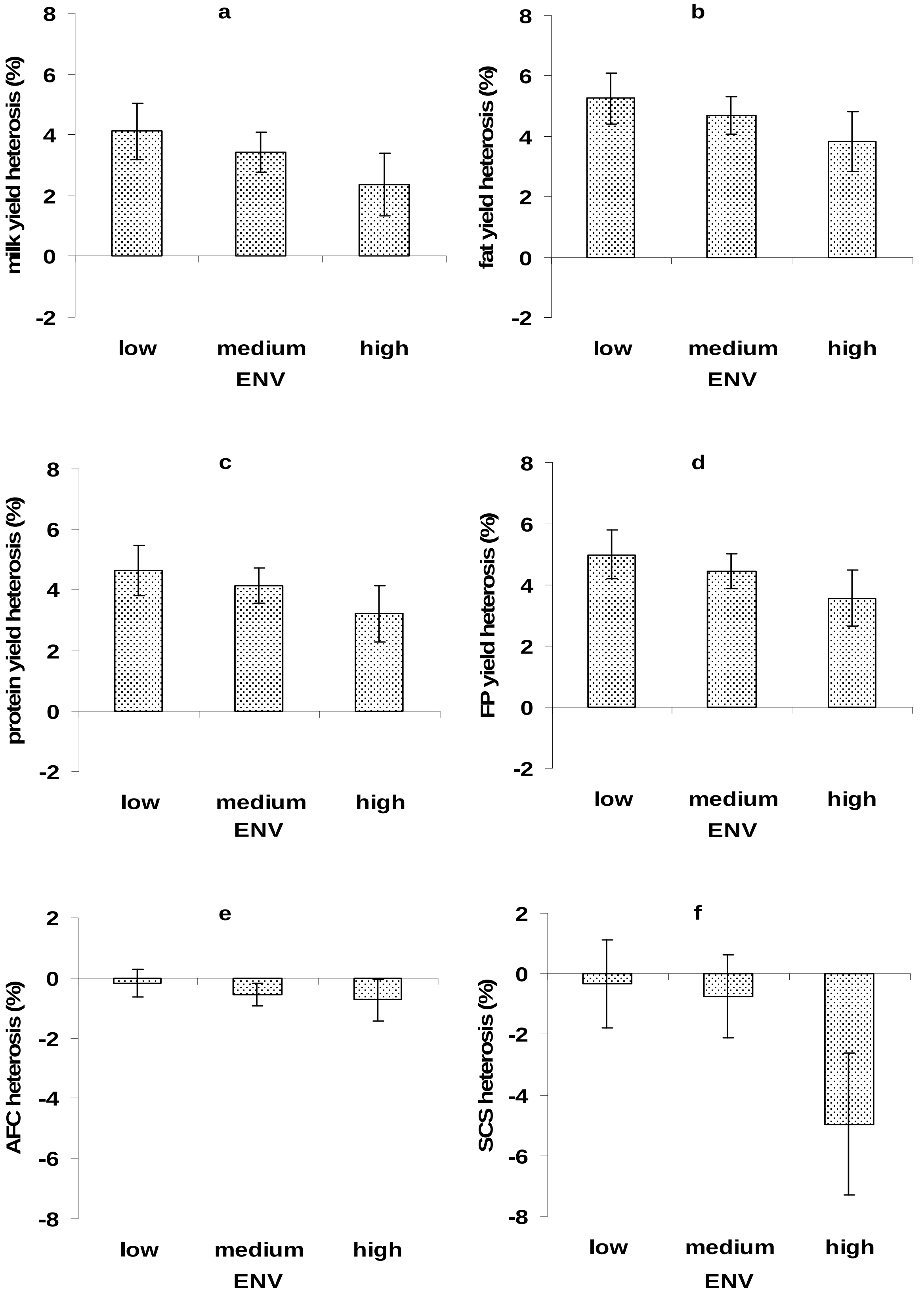
Figure 1. Least squares means and standard errors for (a) 305-d milk, (b) fat, (c) protein, (d) fat plus protein (FP) yields, (e) age at first calving (AFC), and (f) average within 305-d SCS for Holstein Friesian (HF, ◊), Dutch Friesian (DF, ♦), and F_1 crosses between Holstein Friesian sire and Dutch Friesian dam (HD, ■) in each environmental level of production (ENV).



Heterosis effects for lactation yield traits are very variable, ranging from slightly negative values to up to 10% (López-Villalobos, 1998). Ahlborn-Breier and Hohenboken (1991) reported estimates of 6.1 and 7.2% for milk and fat yield, respectively, using data from primiparous HF, Jersey, and crossbred cows. McAllister (1986) found estimates of 3.7, 3.9, and 4.0% for milk, fat, and protein yield, respectively, using data from HF, Ayrshire, and crossbred primiparous cows. Heterosis estimates for 305-d milk yield traits using first lactation records were significant and about 2.5% in a study conducted on DF x HF crosses between 1983 and 1986 by van der Werf and de Boer (1989). In the present research only first lactations were available for the analysis. However, the parity of cows seems to play an important role in the expression of heterosis as reported by several authors (Donald et al., 1977; McAllister, 1986; Touchberry, 1992; Dechow et al., 2007), but the relation is not clear yet. Touchberry (1992) and Dechow et al. (2007) reported an increase of heterosis for production traits across lactations, while opposite trends were evidenced by Donald et al. (1977) and McAllister (1986). Anyway, these studies used different type of crosses, and this can have played an important role in the expression of heterosis across lactations. Regarding H x E interaction, Bryant et al. (2007) estimated heterosis effects ranging between 5.0 and 9.5% for production traits in overseas HF x New Zealand Jersey crosses, and trends of heterosis that were almost opposite compared to those obtained in the present research. However, the average level of production in the study by Bryant et al. (2007) was much lower than that in the present research.

In general, AFC showed very low estimates of heterosis and significantly different from zero in the medium and high ENVs, but without an appreciable trend (Figure 2). Crossbreeding parameters for AFC are known to be low and it is important to bear in mind that this trait depends more on farmers' decisions than on physiological aspects. Touchberry (1992) reported heterosis effects of 1.1% for AFC. More recently, Dechow et al. (2007) observed estimates close to 2.1 and 3.5% (favorable) using least squares techniques. In the latter study, heterosis effects for AFC varied across lactations and varied depending on the breed of sire.

Figure 2. Heterosis estimates and confidence intervals ($P < 0.05$) for F_1 crosses (HD) between Holstein Friesian (HF) sires and Dutch Friesian (DF) dams for (a) 305-d milk, (b) fat, (c) protein, (d) fat plus protein (FP) yields, (e) age at first calving, and (f) average within 305-d SCS in each environmental level of production (ENV).



Heterosis effects for SCS were negative (favorable), close to zero in the low and medium ENVs, and significantly different from zero only in the high one, with a value close to 5% (Figure 2). However, this result should be interpreted with caution because of the fairly low number (n=125) of DF cows available in the high ENV for the estimation of heterosis effects. Values close to zero for this udder health indicator were provided by VanRaden and Sanders (2003) in the United States. Cassell (2007) discussed that traits not much influenced by inbreeding depression are expected to show less non additive effects, and SCS could be recognized as one of these traits. However, Dechow et al. (2007) reported heterosis effects close to 8% (favorable) for SCS using least squares techniques.

CONCLUSIONS

Genotype effect for traits analyzed in Friesian strains of dairy cattle showed changes across environments, and HF appeared to be better suited to intensive conditions. Estimates of heterosis varied across ENVs, with the largest effects observed in the low ENV for production traits and in the high ENV for SCS. The low ENV was the most stressful for production. Hence, the highest heterosis was expressed in the worst environment. Because evidence of H x E interaction emerged from this research, it can be argued that an advantage could derive from the exploitation of genotypes positively interacting with the environment in which they are producing.

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Chapter 4

Use of crossbreeding with beef bulls in dairy herds: effect on age, live weight, price, and market value of calves sold at livestock auctions

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ABSTRACT

The aim of this study was to investigate the effect of different breeds and breed crosses on age (AC, d), live weight (LW, kg), price (PR, Euro/kg), and market value (MV, Euro/calf) of purebred and crossbred calves sold for veal and beef production. The Kovieh wholesale cattle organization (Bolzano, Italy) grouped calves from several dairy herds located in the Trentino-Südtirol region in Italy, and sold them by public auctions. Data on AC, LW, PR, and MV from 96,458 calves were recorded from January 2003 to December 2007, and consisted of 4 pure breeds (two dairy, Brown Swiss (BS) and Holstein Friesian (HF), and two dual purpose, Simmental (SI) and Alpine Grey (AG)), and 8 crossbreds by crosses of Limousin (LI) and Belgian Blue (BB) with the 4 dam breeds. Least squares means for AC, LW, PR, and MV were calculated for breeds and breed crosses with a model that included fixed effects of herd of birth, age (except for AC), sex, and breed of the calf, year and season of auction, and interactions between the main effects. The coefficients of determination of the models were 0.41, 0.51, 0.84, and 0.82 for AC, LW, PR, and MV, respectively. Sex, age, and breed were the most relevant sources of variation for LW ($P < 0.001$) while breed and sex were the most important sources of variation for AC, PR, and MV ($P < 0.001$). Also, PR and MV were significantly influenced ($P < 0.01$) by all the effects included in the model, except for season by age interaction in the case of MV. Market value of male was higher ($P < 0.001$) than that of female calves, with the exception of BS (-21 Euro/calf) and HF (-15 Euro/calf) purebred males. Dual purpose purebred calves were heavier ($P < 0.001$) and presented higher ($P < 0.001$) PR and MV than dairy purebreds (MV of 314 and 227 Euro/calf for SI and AG, and 189 and 203 Euro/calf for BS and HF, respectively). Calves from SI and AG dams had greater ($P < 0.001$) LW, PR and MV than calves from BS and HF dams. Calves from SI cows had greater ($P < 0.001$) LW, PR and MV than calves from AG cows. Crossbreeding with beef bulls increased ($P < 0.001$) LW, PR, and MV of calves from dairy and dual purpose dams. Crossbreeding with BB bulls increased PR (+1.90 ± 0.03 Euro/kg; $P < 0.001$) and MV (+140.5 ± 2.7 Euro/calf; $P < 0.001$) of calves much more than LI.

Key words: beef and dairy breeds, calves, crossbreeding, live weight, market value, price

INTRODUCTION

One reason for crossbreeding is to combine favorable attributes of two or more breeds that are genetically different from each other, but have complementary qualities (Cartwright, 1970). A common practice by farmers in the Alps is the use of beef bulls for mating dairy cows not used to breed replacements for the herd (25-30% of cows). This practice has been decreasing in the more specialized herds because of fertility (Dal Zotto et al., 2007) and longevity (Boettcher, 2005) problems, but in the near future it will be increased by the use of sexed semen (Hohenboken, 1999; Cerchiaro et al., 2007).

Crossbreeding between dairy and beef cattle breeds has been investigated by several authors in the past (Cundiff, 1970; Nelson et al., 1982) and, more recently, there has been a major research on this subject in the US (Cundiff et al., 2001). In a very recent study, Wolfovà et al. (2007) confirmed that carcasses from beef x dairy crosses were much more valuable than carcasses from purebred dairy animals. Moreover, crossbreds showed better eating characteristics of the meat (Davies et al., 1992) and greater dressing percentage (Güngör et al., 2003) than purebreds.

In the Trentino-Südtirol region (northeast Italy) the majority of purebred and crossbred calves from dairy herds are sold at about 3 weeks of age by wholesale cattle organizations that carry out public auctions (about 500 calves per week). Purebred calves from dairy breeds (mainly Brown Swiss (**BS**) and Holstein Friesian (**HF**)) are destined to veal production (Cozzi, 2007). These calves are fed a milk replacer and a small amount of roughage, and are slaughtered at 5-6 months of age. On the contrary, the majority of the purebred dual purpose (mainly Simmental (**SI**) and Alpine Grey (**AG**)) and crossbred calves are destined to beef production as young entire bulls and heifers using high concentrate diets.

The objective of this study was to compare the effect of different breeds and breed crosses on age at auction (**AC**, d), live weight (**LW**, kg), price (**PR**, Euro/kg), and market value (**MV**, Euro/calf) of purebred and crossbred calves sold for veal and beef production.

MATERIALS AND METHODS

Data

Data were provided by Kovieh, a wholesale cattle organization located in Bolzano province (Italy) close to the Austrian border. Information available was AC (d), LW (kg), PR (Euro/kg), and MV (Euro/calf) from 4 pure breeds: BS, HF, SI, and AG, and 8 crossbred types derived from mating the 4 dam breeds (BS, HF, SI, and AG) with two sire beef breeds: Limousin (**LI**) and Belgian Blue (**BB**). According to the European Union legislation, each animal is provided with a passport since birth, and information on sire and dam is registered. Only calves with registered breeds of sire and dam, AC between 7 and 50 d, and LW between 29 and 126 kg have been considered. Following editing of the dataset as above, 96,458 calves sold during 239 weekly auctions from January 2003 to December 2007 were analyzed.

Statistical Analysis

An ANOVA was performed on AC, LW, PR, and MV with the GLM procedure (SAS Inst. Inc., Cary, NC) using the following linear model:

$y_{ijklmno} = \mu + \text{herd}_i + \text{year}_j + \text{season}_k + \text{sex}_l + \text{age}_m + \text{breed}_n + (\text{breed}_n \text{ x } \text{sex}_l) + (\text{breed}_n \text{ x } \text{year}_j) + (\text{breed}_n \text{ x } \text{season}_k) + (\text{breed}_n \text{ x } \text{age}_m) + (\text{sex}_l \text{ x } \text{year}_j) + (\text{sex}_l \text{ x } \text{season}_k) + (\text{sex}_l \text{ x } \text{age}_m) + (\text{year}_j \text{ x } \text{season}_k) + (\text{year}_i \text{ x } \text{age}_m) + (\text{season}_k \text{ x } \text{age}_m) + e_{ijklmno}$,

where $y_{ijklmno}$ is observation ijklmno for AC, LW, PR, or MV; μ is the overall mean; herd_i is the fixed effect of the *i*th herd of birth of the calf (*i* = 1 to 8,634); year_j is the fixed effect of the *j*th year of auction (*j* = 2003 to 2007); season_k is the fixed effect of the *k*th season of auction (*k* = Spring, Summer, Autumn, Winter); sex_l is the fixed effect of the *l*th sex of the calf (*l* = female and intact male); age_m is the fixed effect of the *m*th class of age of calf at auction (young: 7-15d, intermediate: 16-31d, and old: 32-50 d); breed_n is the fixed effect of the *n*th breed (*n* = BS, HF, SI, AG, LIxBS, LIxHF, LIxSI, LIxAG, BBxBS, BBxHF, BBxSI, BBxAG); and $e_{ijklmno}$ is the random residual associated with observation ijklmno. Also, first order interactions between the main effects were considered. Random residual effects were assumed to be identically, independently, and normally distributed with mean zero and variance σ^2e. The effect of age at auction was not included in the analysis of AC.

Contrast estimates (±SE) for AC, LW, PR, and MV within sire and dam breeds, and their interactions were also estimated, and a 5% level was referred to for testing if estimates were significantly different.

RESULTS AND DISCUSSION

The number of calves from different breeds and breed crosses sold at weekly auctions are displayed in Table 1. Purebred calves represented 62.9% of the total data set and ranged from 10% (9,610 animals) for AG to 27.1% (26,133 animals) for BS. The number of calves sired by beef bulls represented the remaining 37.1% of the total data set and varied from 3.8% for AG to 18.1% for BS cows, reflecting the different use of crossbreeding by farmers of the different breeds of cows. The number of calves sired by LI bulls was always less than calves sired by BB bulls. This is particularly true in the case of SI dams, with 285 calves sired by LI and 7,990 by BB bulls.

Table 1. Number of calves[1] of different breeds and breed crosses[2] sold at auctions.

Sire breed	Dam breed			
	BS	HF	SI	AG
BS	26,133			
HF		10,395		
SI			14,516	
AG				9,610
LI	1,563	526	285	285
BB	15,929	5,845	7,990	3,381

[1] 100% = 96,458 calves.

[2] BS = Brown Swiss, HF = Holstein Friesian, SI = Simmental, AG = Alpine Grey, LI = Limousin, BB = Belgian Blue.

Results from the ANOVA are summarized in Table 2. The coefficients of determination were 0.41, 0.51, 0.84, and 0.82 for AC, LW, PR, and MV, respectively. All the main effects included in the model significantly explained the variability of the 4 traits ($P < 0.001$). The two genetic effects (breed and sex) were the most important, with the addition of age for LW. Also, the main effects of year and season were relevant in explaining the variability for PR and MV. Due to the high number of data analyzed, the majority of the interactions was highly significant ($P < 0.001$). Among them, breed by sex was the most important for all the traits and is discussed.

Table 2. ANOVA for age at auction (AC, d), live weight (LW, kg), price (PR, Euro/kg), and market value (MV, Euro/calf).

		Trait							
		AC		LW		PR		MV	
R^2		0.41		0.51		0.84		0.82	
RMSE[1]		6.87		7.21		0.84		67.62	
Effects	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Herd	8,633	6.43	<0.001	5.91	<0.001	1.88	<0.001	3.48	<0.001
Year	4	31.35	<0.001	16.19	<0.001	285.39	<0.001	216.95	<0.001
Season	3	13.68	<0.001	45.14	<0.001	210.62	<0.001	207.53	<0.001
Sex	1	202.11	<0.001	957.64	<0.001	1,496.47	<0.001	2,194.06	<0.001
Age	2	-	-	450.51	<0.001	124.31	<0.001	13.11	<0.001
Breed	11	66.14	<0.001	343.97	<0.001	6,665.37	<0.001	5,509.82	<0.001
Breed*Sex	11	21.18	<0.001	13.45	<0.001	273.94	<0.001	263.96	<0.001
Breed*Year	44	1.63	0.005	2.79	<0.001	55.24	<0.001	53.96	<0.001
Breed*Season	33	3.25	<0.001	3.28	<0.001	39.21	<0.001	16.63	<0.001
Breed*Age	22	-	-	8.26	<0.001	12.32	<0.001	7.39	<0.001
Sex*Year	4	0.78	0.537	1.07	0.368	131.89	<0.001	86.76	<0.001
Sex*Season	3	2.21	0.084	1.48	0.216	14.68	<0.001	8.08	<0.001
Sex*Age	2	-	-	5.84	0.003	18.96	<0.001	17.87	<0.001
Year*Season	12	9.81	<0.001	6.65	<0.001	248.52	<0.001	156.54	<0.001
Year*Age	8	-	-	3.74	<0.001	3.24	0.001	4.91	<0.001
Season*Age	6	-	-	4.17	<0.001	3.01	0.006	1.98	0.064

[1] RMSE = root mean square error.

Age of calves at auction varied, on average, from 23 for BBxBS and LIxBS to 26 d for AG calves (Figure 1), LW ranged from 61 for HF to 69 kg for BBxBS and BBxSI (Figure 2), PR from 2.89 for BS to 7.00 Euro/kg for BBxSI (Figure 3), and MV from 189 for BS to 488 Euro/calf for BBxSI (Figure 4).

Figure 1. Least squares means (with SE whiskers) of age at auction (d) of calves of different breeds and breed crosses.

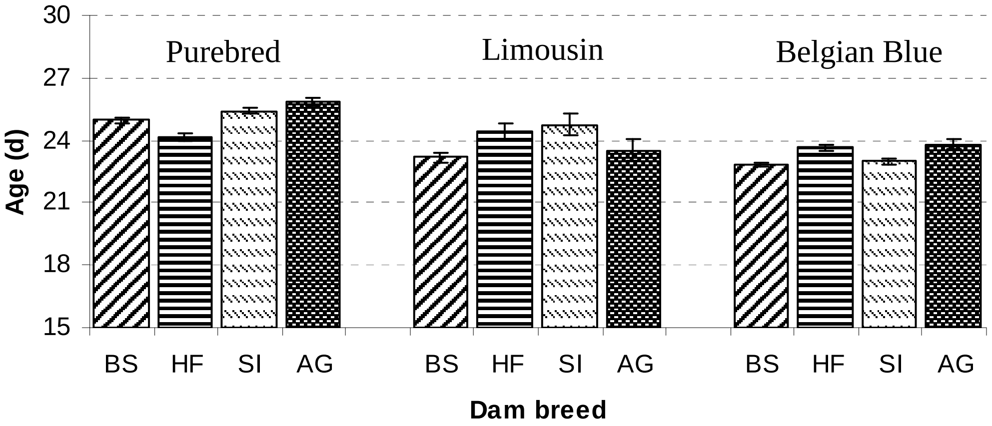
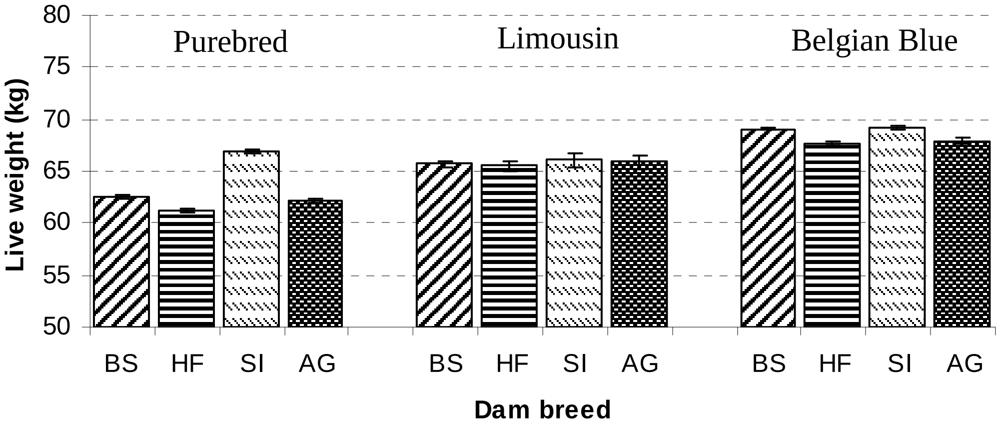


Figure 2. Least squares means (with SE whiskers) of live weight (kg) of calves of different breeds and breed crosses.



Looking more specifically within the pure calves, dual purpose were heavier ($P < 0.001$) and showed higher ($P < 0.001$) PR and MV than dairy. Market values were 189 and 203 Euro/calf for BS and HF, and 314 and 227 Euro/calf for SI and AG, respectively, and SI reached a higher MV compared to the other pure breeds (Figure 4). This is not only due to the more favorable PR but also to the higher LW reached by SI calves. Also, SI calves exceeded the average MV from BS and HF by 118 Euro/calf.

This advantage can counterbalance a lower milk production of 358 kg in terms of income (0.33 Euro/kg was the price of milk in Italy during the period of the study). In terms of income over feed costs, the amount of milk counterbalanced would probably be more than double taking into account the reduction in feed requirements, especially in terms of concentrate consumption. Also, considering the positive effect of longevity, fertility, and somatic cell score that characterize the SI breed, it seems not convenient to keep this breed if not in hard environments which heavily limit the potential of specialized dairy breeds (De Marchi et al., 2007). In the case of the AG breed, the superiority of its calves for MV is much less pronounced than that of the SI breed. Nevertheless, for a correct comparison with specialized dairy breeds from the technical and economical point of view, it is necessary to consider that the AG cows are much lighter than those of the other three breeds; this leads to more cows, calves and lactations per hectare of cultivated land (Bittante et al., 2005). Also, the higher fertility and longevity of the dual purpose and BS breeds respect to HF is responsible for a lower replacement rate, with the opportunity to mate a substantial number of cows with beef bulls. This opportunity is much lower and decreases over time for HF breed. Thus, crossbreeding with beef bulls can further counterbalance a significant part of the higher amount of milk produced by HF cows.

Figure 3. Least squares means (with SE whiskers) of price (Euro/kg) of calves of different breeds and breed crosses.

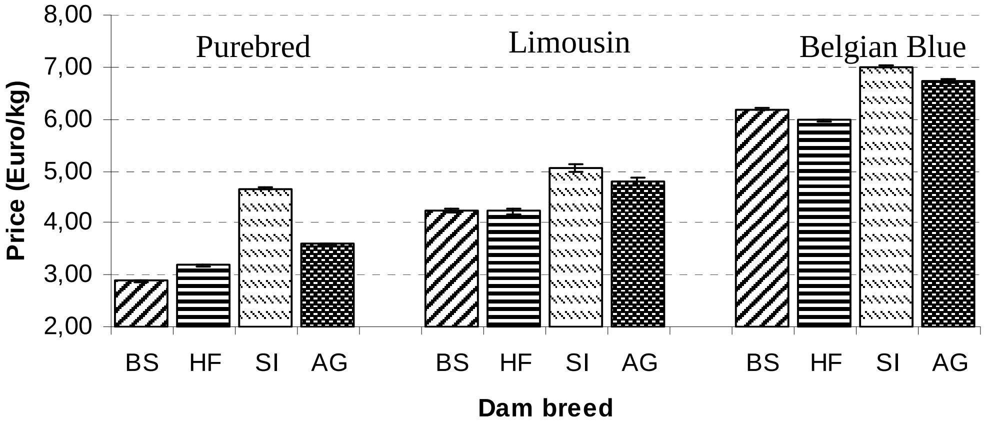
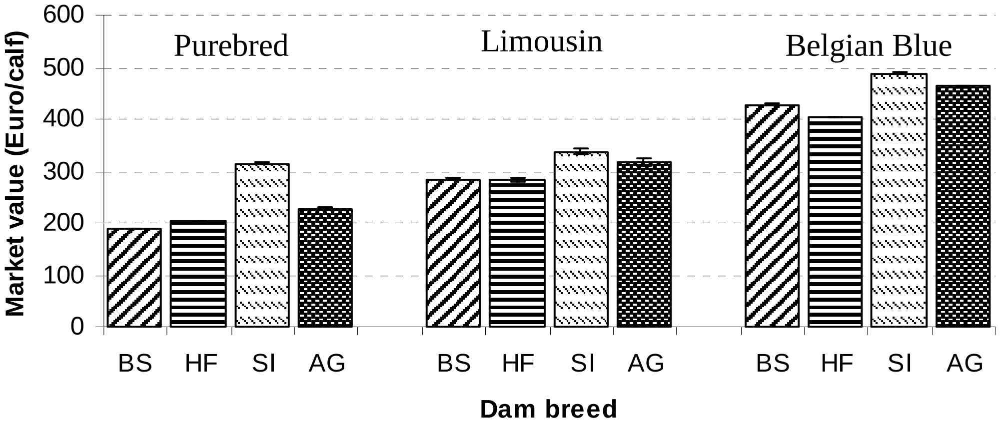


Figure 4. Least squares means (with SE whiskers) of market value (Euro/calf) of calves of different breeds and breed crosses.



Regarding the effect of sire breed (Table 3), crossbred calves highlighted lower AC (-1.45 ± 0.12 d; $P < 0.001$), and higher LW (+3.96 ± 0.16 kg; $P < 0.001$), PR (+1.95 ± 0.02 Euro/kg; $P < 0.001$), and MV (+142.1 ± 1.5 Euro/calf; $P < 0.001$) than purebreds, and among crossbred combinations those from BB were significantly superior than those from LI sires for AC (-0.65 ± 0.21 d; $P < 0.01$), LW (+2.66 ± 0.28 kg; $P < 0.001$), PR (+1.90 ± 0.03 Euro/kg; $P < 0.001$), and MV (+140.5 ± 2.7 Euro/calf; $P < 0.001$). In a recent study, Barham and Troxel (2007) reported that the breed effect was highly significant in explaining the selling price of feeder cattle sold at Arkansas auctions, and a difference of \$33.28 per 45.45 kg was found between the highest (Hereford x Charolais) and the lowest (Longhorn) price. Limousin semen has been widely used because this breed combines a good meat production ability with a small increase of calving difficulty. A study by Comerford et al. (1987) highlighted that the LI breed tended to have heavier calves with less calving difficulty and higher survival rates than other breeds and breeds combinations. More recently, the use of BB semen has exceeded that of LI because the double muscling of the breed is responsible for yielding well-conformed carcasses with reduced fat content (Hanset et al., 1987; Uytterhaegen et al., 1994).

Table 3. Contrast estimates ± SE within sire and dam breeds, and their interactions for age at auction (AC, d), live weight (LW, kg), price (PR, Euro/kg), and market value (MV, Euro/calf).

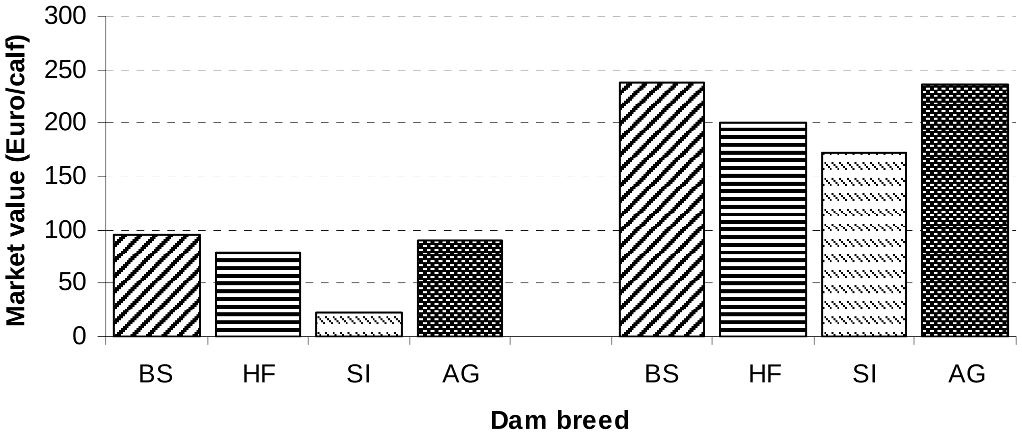
Contrast	Trait			
	AC	LW	PR	MV
	Est. ± SE	Est. ± SE	Est. ± SE	Est. ± SE
Sire breeds				
[1] PB[1] vs (LI+BB)[2]	1.45 ± 0.12***	-3.96 ± 0.16***	-1.95 ± 0.02***	-142.1 ± 1.5***
[2] LI vs BB[3]	0.65 ± 0.21**	-2.66 ± 0.28***	-1.90 ± 0.03***	-140.5 ± 2.7***
Dam breeds				
[3] (BS+HF) vs (SI+AG)[4]	-0.53 ± 0.18**	-1.09 ± 0.23***	-0.85 ± 0.03***	-59.6 ± 2.1***
[4] BS vs HF[5]	-0.42 ± 0.18*	1.00 ± 0.21***	-0.02 ± 0.02	3.6 ± 2.0
[5] SI vs AG[6]	-0.01 ± 0.29	2.09 ± 0.38***	0.53 ± 0.04***	43.7 ± 3.5***
Sire x dam breeds				
[1] x [3]	-0.41 ± 0.12***	-1.19 ± 0.16***	-0.17 ± 0.02***	-11.4 ± 1.5***
[1] x [4]	0.92 ± 0.14***	0.31 ± 0.17	-0.20 ± 0.02***	-13.4 ± 1.6***
[1] x [5]	-0.35 ± 0.19	1.95 ± 0.27***	0.40 ± 0.03***	32.9 ± 2.5***
[2] x [3]	-0.09 ± 0.21	-0.09 ± 0.28	0.05 ± 0.03	7.9 ± 2.6**
[2] x [4]	-0.23 ± 0.21	-0.54 ± 0.27*	-0.09 ± 0.03**	-10.8 ± 2.5***
[2] x [5]	1.01 ± 0.35**	-0.57 ± 0.49	0.00 ± 0.06	-2.7 ± 4.6

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[1] PB = purebred calves, [2] PB vs (LI+BB) = contrast between purebred and crossbred calves, [3] LI vs BB = contrast between crossbred calves from the two beef breeds, [4] (BS+HF) vs (SI+AG) = contrast between calves from dairy and dual purpose dams, [5] BS vs HF = contrast between calves from dairy dams, [6] SI vs AG = contrast between calves from dual purpose dams.

The impact of the two beef breeds on MV of crossbred calves is displayed in Figure 5. The use of LI semen on BS and AG dams increased the value of crossbreds by 100 Euro with the only exception of those obtained from SI cows, whose value was marginally higher (+22 Euro) than that of their purebred counterparts. On average, the value of BB-sired calves was 140 Euro higher than LI calves, and 212 Euro higher than purebred calves. When compared to the purebred counterparts, the use of BB bulls on BS and AG cows enhanced the value of crossbreds 250 Euro, and 200 Euro when used on HF dams. Also, BBxSI crossbreds largely exceeded SI purebred calves (+173 Euro), i.e. much more than the case of LIxSI calves. In general, with both the beef breeds the beneficial effect of crossbreeding from the economical point of view was maximum with BS and AG, and minimum with the SI cows. It is possible that crossbreeding the dairy breeds, especially with BB, increased largely the proportion of calves weaned and fattened for beef production versus veal, while this cannot be done in the case of SI because both the purebred and crossbred calves are mainly used for beef and not for veal.

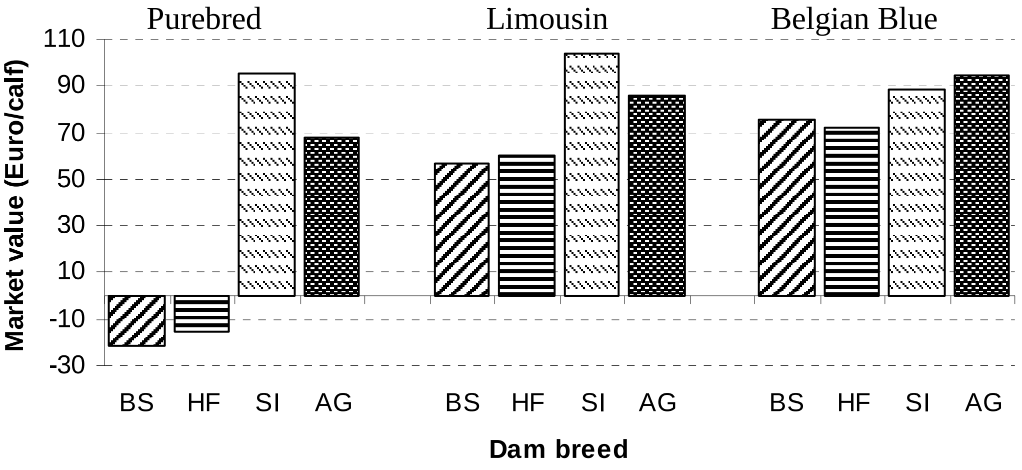
Figure 5. Increase of market value (Euro/calf) of crossbred respect to purebred calves.



Regarding the effect of dam breed (Table 3), calves from the two dual purpose breeds (SI and AG) were superior than those from the two specialized dairy breeds (BS and HF) for LW (+1.09 ± 0.23 kg; *P* < 0.001), PR (+0.85 ± 0.03 Euro/kg; *P* < 0.001), and MV (+59.6 ± 2.1 Euro/calf; *P* < 0.001). Within the dairy breeds, BS and HF produced calves with comparable PR and MV (*P* > 0.05). Nevertheless, calves from BS had lower AC (-0.42 ± 0.18 d; *P* < 0.05) and higher LW (+1.00 ± 0.21 kg; *P* < 0.001) than those from HF dams. Within the dual purpose breeds, SI produced calves heavier (+2.09 ± 0.38 kg; *P* < 0.001), and with higher PR (+0.53 ± 0.04 Euro/kg; *P* < 0.001) and MV (+43.7 ± 3.5 Euro/calf; *P* < 0.001) than those from AG dams. In general, these results confirmed that dual purpose breeds produced calves with better commercial values than specialized dairy cows, because of heavier calves and particularly higher price achieved at auction (Bittante et al., 2005). Also, this increase in value depends on the fact that the majority of dual purpose calves are weaned and used for beef production while dairy calves are almost all used for veal production.

Looking at the interactions between the sire and dam breeds for the traits (Table 3), it is worth noting that, as expected, crossbreeding with beef bulls reduced differences between dairy and dual purpose dam breed effects because dam breeds represent only the 50% of the genome of crossbred calves respect to the 100% of the purebred. Even if purebred BS calves presented higher AC, and lower PR and MV than purebreds HF, crossbred calves from BS cows presented lower AC, and higher PR and MV than those from HF. While purebred SI calves are characterized by superior LW, PR, and MV than AG, in the case of crossbred calves the differences between the two dual purpose dam breeds are almost negligible. The superiority of crossbred calves from dual purpose respect to those from dairy dams was more pronounced for BB-sired than LI-sired calves in the case of MV, but not for LW and PR. The superiority of crossbred calves from BS dams compared to HF was more pronounced for BB-sired than LI-sired calves for LW, PR, and MV. Finally, the breed of sire showed significant interactions with the two dual purpose breeds only in the case of AC.

Figure 6. Average differences between the market value (Euro/calf) of male and female calves of different breeds and breed crosses.



The sex effect showed that male calves were younger at auction (-1.85 ± 0.13 d; $P < 0.001$) and had greater LW (+4.49 ± 0.15 kg; $P < 0.001$), PR (+0.65 ± 0.02 Euro/kg; $P < 0.001$), and MV (+63.8 ± 1.4 Euro/calf; $P < 0.001$) than female calves. Figure 6 illustrates the interaction between sex and breed of calves for MV. In the case of purebred calves from the two specialized dairy breeds, the average value of males was slightly lower than females (-21 and -15 Euro/calf for BS and HF, respectively). This seemed to be due to a negligible gender effect for calves destined to veal production, considering that the production ceases before animals reach the puberty. Moreover, it is possible that part of the purebred heifer calves was bought by dairy farmers for replacements and not for beef production. In all other cases, male exceeded female calves from 57 (LIxBS) to 104 Euro (LIxSI). While sex has a strong impact on MV of LI and purebred calves, the superiority of males in BB-sired calves is not largely influenced by the breed of the dam. Barham and Troxel (2007) highlighted a significant influence of calf sex in determining the selling price.

In conclusion, purebred calves from dual purpose breeds were heavier and obtained higher PR and MV than purebred calves from dairy breeds. Thus, they contributed positively to the farm income. While calves from BS and HF were characterized by a similar MV, those from SI exhibited superior LW, PR, and MV than those from AG, but it should be considered that cows of the latter breed are lighter than cows of the former and the stocking rate is higher. Crossbreeding with LI bulls increased LW, PR, and MV of calves from dairy and AG breeds, but had a low impact on SI cows. Crossbreeding with BB bulls increased PR and MV of calves of both dairy and dual purpose breeds much more than LI bulls. The highest increase in MV was produced when BB semen was used on BS and AG cows and the lowest when used on SI cows. Market value of male was higher than that of female calves in the case of dual purpose pure breeds and all crossbred calves but not in the case of purebred dairy calves. This could be due to the different proportion of calves used for veal and beef production. Results highlighted that breed complementarity (Cartwright, 1970) occurred and the use of crossbreeding to exploit surplus replacements in dairy herds can guarantee a greater economic revenue from selling crossbred calves. In the more specialized dairy herds the use of crossbreeding has been decreasing because of fertility and longevity problems. However, this practice is expected to become more popular in the next years as there is an increasing interest in the use of sexed semen among dairy producers. This perspective would lead to more dairy cows available for mating with beef bulls.

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General conclusions

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Crossbreeding effects in dairy cattle have resulted to be evident (Chapters 2 and 3), particularly for milk yield traits and calving interval.

The Irish study confirmed that the Holstein breed is the most productive, and it should be preferred if the breeding goal gives relevant economic emphasis on milk yield. On the contrary, crosses involving Holstein and Jersey or Holstein and Montbéliarde may be better than pure Holstein for fat and protein yields. Calving interval has been found to be shorter in breeds other than Holstein; this trait is very important in Ireland because of the seasonal pattern of milk production. The knowledge of these effects along with estimated breeding values, and random permanent environmental effects are the three elements to build an index called producing value, useful for making culling decisions.

In the Dutch study, crossbreeding effects changed across environments, and the Holstein Friesian strain resulted more adapted to intensive conditions. Heterosis values varied across the environments; the highest effects were observed in the low environment for milk yield traits and in the high for SCS. Because evidence of heterosis and environment interaction emerged, an advantage may derive from the exploitation of genotypes positively interacting with the environment in which they are producing.

The study in Chapter 4 has shown a strong influence of the genotype on the commercial value of calves. This was very important to know because a large quota of the meat in Europe comes from purebred dairy and beef x dairy crossbred calves. Crossbreeding with Limousin and Belgian Blue bulls increased live weight, price and market value of calves from dairy and dual purpose breeds. The highest market values were obtained in calves sired by Belgian Blue bulls. The use of crossbreeding with beef bulls to exploit surplus replacements in dairy herds can be a viable system to provide the farmer with an extra economic revenue.

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