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GENERAL INTRODUCTION

Crossbreeding is a method used for improvement in agricultural industries such as pigs, beef cattle and poultry but it is not usual for dairy cattle in most temperate countries, due to the high milk production of the Holstein-Friesian breed. The exception is New Zealand where widespread adoption of crossbreeding has been a feature of the recent history of the dairy industry and now more than one third of the replacement cattle are crossbred.

Under New Zealand pastoral conditions where the objective is to maximize the net income per hectare, crossbreeding can provide a good opportunity. Moreover, it allows to improve composition of milk that is an important feature since farmers are paid on the basis of quantity of milk solids (fat and protein) and not of milk yield. Thus, crossbreeding permits to increase the farm net income

Since 1996, an across-breed genetic evaluation system for milk, fat and protein yields, using a two-step test-day model, has been used to compare animals nationally and within herd regardless of breed.

Actually, a test-day random regression model is under development for the genetic evaluation of somatic cell count and will be implemented in 2005. A random regression test-day model allows to model more correctly the shape of lactation by use of polynomials of time, so it provides a better representation of the biological lactation curve.

The objective of this work was to contribute to development of such a model for the genetic evaluation of production traits (milk, fat and protein) in New Zealand and allowing to take breed differences in an optimal manner into account. In order to do this a advanced model was developed allowing breed specific additive genetic effects. Needed (co)variance components were estimated first inside purebreds then across breeds. Based on this model, breeding values were estimated and rankings of sires compared. The results provided a first test of the feasibility and the usefulness of a random regression test-day model with breed specific additive genetic effects.

LITERATURE REVIEW

1. Dairy farming in New Zealand

1.1. A pastoral dairy farming system

Breeding of dairy cows in New Zealand consists in an extensive grazing system, with pastures of several hectares where cows are largely fed on grass. The New Zealand climate allows that cows to spend their entire lives outside in most of the areas, therefore they must be able to perform at temperatures ranging from below zero to 40 degrees Celsius, and continue to produce milk from often minimal pasture. But in colder areas of New Zealand (next to the Southern Alps for example), they may be sheltered or fully housed during the winter months. They must also have a good conformation with strong legs, excellent feet and udders that are well developed and strongly supported because they walk daily long distances to be milked. Thus cows must settle quickly into their milking routine, have a mild temperament and are fast through the milking shed. Cows that do not exhibit these traits or a good conformation are quickly culled as are the bulls that sired them [Meadows, 1996].

In this system the main component of cows diet is grazed pasture and pasture products; concentrate is rarely fed and the quantities of hay and silage (maize or grass) fed per cow are low in comparison with European and North American dairying systems. This is due to unfavorable grain prices compared to milk prices [Harris and Kolver, 2001]. Approximately fourteen million tonnes of pasture dry matter is utilized annually for conversion into thirteen million tonnes of milk [Montgomerie, 2003].

Their first calving happens often when they are around two years old and they continue to calve each year for life. The seasonal nature of the farming system demands that every cow should have a calving interval close to 365 days, cows not respecting this interval are culled resulting in an indirect selection on cows fertility at the farm level. Most of calving take place in a window of eight weeks in the late winter or early spring, generally between July and September-0ctober coincident with the period of rapid grass growth (Figures 1 and 2). But a small number of farmers choose to be “winter milk farmers”, their cows calving in the late summer and autumn (March to May) to produce milk through the winter months. Moreover, sometimes cows in New Zealand can have induced lactation[1] that is the pregnancy is terminated up to four weeks before planned calving date [Harris, 1994].

[1] This practice yields an unfavorable effect, the milk yield depression due to this is close to 4-5% of the annual yield. [Harris et al., 1996]

As the average New Zealand dairy farmer need to calve over 250 cows in an eight week period, it is obviously essential to minimize calving difficulties [Meadows, 1996]. The cows are dried off in late summer or autumn, depending on climatic conditions such as rainfall, so that the reduced feed requirements of dry cows coincide with winter when pasture growth is at its slowest [Harris and Kolver, 2001] (see Figures 1 and 2).

Thus on average, the term of lactation is 225 to 250 days that is due to New Zealand dairy grazing system. Figures 1 and 2 represent this seasonal farming system based on pastures.

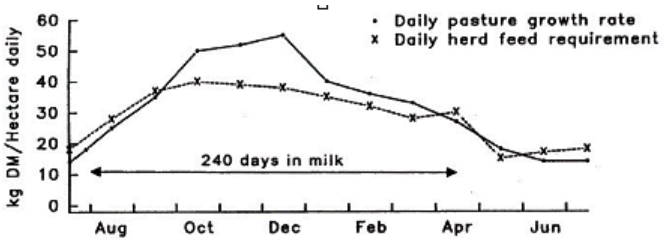

Figure 1: Representation of daily pasture growth and daily herd feed requirement in function of months [Pryce and Harris, 2004].

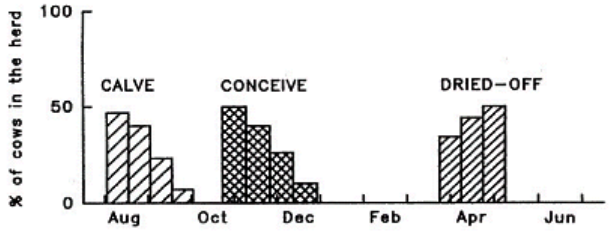

Figure 2: Representation of seasonal farming system in New Zealand [Pryce and Harris, 2004].

1.2. Economic view of the pastoral dairy farming system

The objective of pasture based farming is to maximise the net income per hectare rather than per cow [Harris, 1998]. In fact, income per cow as a measure fails to account for the large variation between achievable stocking rates for herds with substantially different live weight and milk yield characteristics. Stocking rate[2] is the number of milking cows per hectare of productive land. So, the total milk production per unit of feed consumed in this pastoral system is a function of the average animal production, genetic improvement and stocking rate. In the current situation, the stocking rate is 2.61 cows per hectare and the average herd size is 285 cows by herd [Montgomerie, 2003].

Thus, the net farm income is related to production per hectare of available grazing land. This low-cost system is supported by a climate that allows pasture to grow year round, even if it is a marked seasonal pattern.

[2] Computed as the ratio of utilizable pasture per hectare to the total dry matter requirement (including replacements) per cow per year. [Lopez-Villalobos and Garrick, 1996]

1.3. Breeds found in New Zealand

The most common breed in New Zealand is Holstein-Friesian but more than one third of the replacement cattle bred for the dairy industry are crossbred and is increasing. So, the percentages of breeds and crosses in the current dairy population, which counts approximately 3.7 million of cows, are 52% Holstein-Friesian, 24% Holstein-Friesian×Jersey crossbred, 15% Jersey, 6% other crosses (include three breed crosses) and 3% other breeds mainly Ayrshire. [Montgomerie, 2003; Harris, 2004]

Most of the dairy herds in New Zealand are a mixture of purebred and crossbred cows [Lopez-Villalobos et al., 2000c].

1.4. Economic situation of the dairy industry in New Zealand

In New Zealand, the dairy industry is oriented towards export production; 90%-96% of the milk is manufactured into a range of dairy products and exported to many countries. Few cows are required to supply fluid milk to domestic consumers [Harris, 2004; Montgomerie, 2003].

Low cost systems for conversion of pasture into protein and fat (milk solids) provide the basis for the industry to survive [Lopez-Villalobos et al., 2000a, 2000c]. Generally, farmers are rewarded for the amount of protein and fat produced, with a penalty made for milk volume produced. This penalty allows the dairy industry to face up to transporting, storing and processing costs [Montgomerie, 2003]. Moreover, the value of payment is determined by the prices for which milk products are sold to the world market minus costs of processing and marketing. Often, the milk price for producers is typically around half the producer price received by EU and USA producers [Montgomerie, 2002].

In the face of the low milk prices, most operators achieve acceptable profitability by spending only small amounts on purchased feed, and by managing high numbers of cows for each staff member (around 150-200 cows per staff member) [Montgomerie, 2003].

1.5. Consequences for dairy cattle breeding in New Zealand

This special situation has obviously repercussions on dairy cattle breeding in New Zealand and leads to different breeding objective and favors the selection of animals that are well adapted for this type of management (e.g. easy calving, high fertility). Another method to improve the value of milk is provided by crossbreeding and selection which allow to modify yield of milk and its components (fat and protein). Indeed, farm costs can be reduced if the same amount of milk solids is produced per hectare by a smaller number of cows. Milk collection and manufacturing costs can be reduced too if the same amount of milk solids is processed from a smaller volume of milk. Thus, crossbreeding is an option to increase farm profit [Lopez-Villalobos and Garrick, 1997b; Lopez-Villalobos et al., 2002].

Several studies done in New Zealand over the past few years [e.g. Lopez-Villalobos and Garrick, 1996; Lopez-Villalobos et al., 2002; Lopez-Villalobos and Garrick, 2002] evaluated the effect of selection and mating strategies on industry production of milk components and dairy industry net income (see part Profitability of crossbreeding).

2. Mating strategies in New Zealand

Mating strategies affect breed composition in New Zealand and therefore productivity of the whole dairy industry. There are three kinds of mating strategies in New Zealand involving Holstein-Friesian (**HF**), Jersey (**JE**) and Ayrshire (**AY**) breed : straight breeding, upgrading or grading-up and crossbreeding. These mating strategies influence gene combinations received by the progeny; they were evaluated for several breed combinations in different studies.

2.1. Straight breeding strategy

The goal of this strategy is to avoid crossbreeding and allows to maintain purebred (HF, JE and AY) composition of national herd. Moreover, straight bred herds produce their own replacements by mating the cows to bulls of the same breed [Lopez-Villalobos and Garrick, 1997b]. This mating system is important because it allows to supply purebred bulls and cows of high genetic merit used in crossbreeding and upgrading strategies [Lopez-Villalobos et al., 2000a].

According to Dairy statistics for the 2002-2003 season in New Zealand, HF cows produced more milk, fat and protein than JE cows. However, milk from JE is more concentrated in fat and protein for a smaller volume of milk.

2.2. Upgrading strategies

The aims of these strategies are to create one dominant breed in the population by continuous mating of females to males of the expected dominant breed. After five generations, the progeny theoretically have 96.9% of their genes from dominant breed [VanVleck et al., 1987].

2.3. Crossbreeding strategies

The use of crossbreeding is common in agricultural industries such as pigs and poultry but has been widely ignored in dairying in most of temperate countries. Indeed, crossbreeding in dairy cattle has not been widespread in temperate climates, largely because of the notable merit of the HF breed for liquid milk production [Touchberry, 1992].

The exception is in New Zealand, where crossbreds are now the second largest “breed type” at approximately 25% of the dairy cow population. Since 1985, crossbreeding is actively practiced by dairy farmers and the interest in crossbreds is so strong in New Zealand that crossbreds bulls are now being progeny tested (Kiwicross bulls) [Montgomerie, 2002].

2.3.1. Crossbreeding benefits

Crossbreeding is a system of mating individuals from different breeds; it is a kind of process in which the gene flow is very important and therefore it produces positive results due to two main effects.

First, it is the ability to utilize **complementarity**, a well-designed crossbreeding system allows the producer to combine the desirable characteristics of the breeds involved in the cross while masking some of the disadvantages of the breeds. For example, HF produce a high milk volume and JE produce high milk components; by crossing these two breeds the producer aims to produce an animal that produces a large volume of milk that also contains a high component content [Falconer, 1989]. Breed complementarity can generate economic advantage in crossbred animals even in the absence of heterosis for individual traits [Lopez-Villalobos and Garrick, 2002].

The second effect arises from **heterosis or hybrid vigor** and it can lead to economic gains through heterosis [Swan and Kinghorn, 1992] (see part about heterosis).

Crossbreeding also takes advantage of the increase of heterozygosity that it produces and so it can be considered as a solution to increasing levels of inbreeding within each of the major dairy breeds [Swan and Kinghorn, 1992]. Indeed, according to VanRaden [1992], crossbreds are more heterozygous and less inbred than purebreds, only crossbreds may have an inbreeding coefficient of zero.

Moreover, the crossbreeding strategies can provide an opportunity to make progress in one generation that would require generations of selection to obtain it and can allow the introduction of a new breed in a herd [Bidanel, 1992].

In conclusion, all these reasons can lead to an increase of overall productivity. Nevertheless, crossbreeding is not a cure for inferior management and cannot replace the need for continued selection policies in the “purebred” herds.

2.3.2. Heterosis

When two different populations are crossed causing an increase in heterozygosity in F1 generation, the level of inbreeding in the hybrid falls to zero and there is an improvement in the traits which suffered from inbreeding depression in the parents populations. This improvement is called heterosis or hybrid vigor, it is the phenomenon in which progeny of cross is better than the expected average of the two populations for a particular trait [VanVleck et al., 1987].

According to VanRaden [1992] heterosis can be considered being the opposite of inbreeding depression, therefore the extra performance observed through heterosis is simply

the recovery of losses that occurred through inbreeding depression over time in the parental breeds. In this way, inbreeding and heterosis can be modeled on the same scale.

Biological explanations

Heterosis is usually attributed to non-additive genetic interactions within loci (dominance) and interactions between loci (epitasis). Indeed, it is mainly caused by dominance complementation or over dominance due to pleitropic effects. Dominance is present if the heterozygous individual is not exactly intermediate between the two homozygotes [Falconer, 1989]. The amount of heterosis gain depends on the difference in gene frequencies at loci where dominance effects exists in the two breeds. However, epistasis may also play a part in heterosis, the consequence of these epistatic effects is that the prediction of heterosis level due to heterozygosity will be biased because it is difficult to model the epistatic effects and so to predict them [Panicke and Freyer, 1992; VanVleck et al., 1987].

Measurement

Heterosis is typically measured as a deviation from the average of the parental breeds, and it is expressed on a percentage of their parent's performance [VanVleck et al., 1987]:

$$\%\,\text{Heterosis} = \frac{\text{Crossbred average} - \text{Parent average}}{\text{Parent average}} \times 100 \quad (1)$$

According to preceding equation, heterosis is measured as the deviation of crossbred progeny from what is expected from a completely additive genetic model, thus it is the non-additive component of crossbreeding. Not all traits express the same degree of heterosis, there is a considerable improvement in traits due to the heterosis, most noticeably in low heritability traits like fertility and survival than in moderate heritability traits like milk production [VanRaden, 1992]. Furthermore, the degree of heterosis for the same trait varies between strains, breeds and environments [Swan and Kinghorn, 1992]. It is very difficult to predict accurately just how much heterosis to expect from a given cross. But the mean performances of a crossbred can be predicted knowing the performance and degree of heterosis of the breeds crossed.

Heterosis in New Zealand

Several studies [Ahlborn-Breier, 1989; Ahlborn-Breier and Hohenboken, 1991; Panicke and Freyer, 1992; Harris et al., 1996] on the national data have revealed positive heterosis effects for production traits, for live weight, for fertility and for survival, these facts can explain the increase of crossbreeding in New Zealand. Expressed in percentage terms, the average first cross heterosis effects estimated from the New Zealand national data 1986-1995 are shown in Table 1.

Table 1: Heterosis effects in percentage.

Traits	HF×JE	HF×AY	JE×AY
Fat yield	4.3	1.8	5.0
Protein yield	4.2	1.9	4.7
Milk volume yield	4.1	1.8	4.8
Liveweight	1.7	0.8	3.1
Fertility	6.8-10.1*	NA	NA
Survival (1st to 2nd lactation)	3.4-8.8*	2.6	4.7

* estimated heterosis effects for local HF strain × JE and for overseas HF strain × JE
(Source: Montgomerie, 2002)

Loss of heterosis

First generation crossbred animals express 100% of the heterosis. In the next generation, these favourable combinations of genes from each breed will be mixed up with genes from the other breed(s). So, subsequent crosses will still produce some heterosis but to a less extent. This decrease of heterosis is called recombination loss or heterosis loss and it due to dominance for a part but epistasis may lead to increase or decrease this loss. This loss is one reason why second and later generation crosses usually do not perform as well as the first generation cross. Estimates for recombination loss vary widely over literature, but generally the effect is negative and smaller than the effect of heterosis in absolute value [Van Der Werf, 1990; Lopez-Villalobos, 1998].

However, some crossbreeding schemes can maintain high levels of heterosis such as rotational crossing schemes. Indeed, the average milk solids yields of the first reciprocal crosses and of the ¾ HF backcross cows exceeded the average milk solids yield of the HF cows [Lopez-Villalobos and Garrick, 1997; Montgomerie, 2002].

2.3.3. Specific crossing schemes

These schemes indicate mainly first-cross or **F1** between two purebred animals. The F1 contains 50% of genes of the two parental breeds and expresses 100% of the heterosis [Lopez-Villalobos and Garrick, 1997b].

The high productivity of F1 cows comprising HF and JE breeds have been identified by several studies in New Zealand [Ahlborn-Breier, 1989; Ahlborn-Breier and Hohenboken, 1991; Lopez-Villalobos and Garrick, 1997b; Lopez-Villalobos et al., 2000c]. Ideally the whole herd should be made up of first-cross animals but these animals cannot produce their own replacements unless some purebred animals are maintained. Thus, one approach for

exploiting heterosis in a self-replacing herd is by the way of rotational crossbreeding [Lopez-Villalobos et al., 2000a].

2.3.4. Rotational crossing schemes

Purebred bulls of different breeds are mated to crossbred cows from alternate generations. Rotational crossbreeding allows to exploit additive and heterosis effects in self-replacing herds and to maintain high levels of heterosis in animals [Lopez-Villalobos and Garrick, 1996, 1997b; Lopez-Villalobos et al, 2000a].

In a **two-breed rotational scheme** with HF and JE, starting with a JE herd, cows are mated to HF bulls to produce F_1 HF × JE cows. Half of the F_1 cows are mated to HF bulls to produce ¾ HF ¼ JE cows, and the other half are mated to JE bulls to produce ¼ HF ¾ JE cows. Next, ¾ HF ¼ JE cows are mated to JE bulls and ¼ HF ¾ JE cows are mated to HF bulls. After three more generations, half of the herd will be 2/3 HF 1/3 JE and the other half will be 1/3 HF 2/3 JE. This strategy can retain two thirds (67%) of the original heterosis expressed by the F_1. Similar approaches can be followed for two-breed rotation with HF and AY and with JE and AY [Lopez-Villalobos et al., 2000a].

In **a three-breed rotational scheme** with HF, JE and AY, starting with an AY herd, cows are mated to JE bulls to produce F_1 JE × AY cows. These F_1 cows are mated to HF bulls to produce ½ HF ¼ JE ¼ AY, which will be mated to AY bulls to produce ¼ HF 1/8 JE 5/8 AY, and so on. After several generations, the herd will comprise three groups of animals: 4/7 HF 2/7 JE 1/7 AY, 2/7 HF 1/7 JE 4/7 AY and 1/7 HF 4/7 JE 2/7 AY. Heterosis decreases also in each generation but at equilibrium 86% of the original heterosis can be observed [Lopez-Villalobos et al., 2000a].

2.3.5. Crossbreeding: performances

Results from different studies [Lopez-Villalobos and Garrick, 1996; 1997b; Lopez-Villalobos, 1998; Lopez-Villalobos et al., 2000a, 2000b] indicated that crossbred cows are more productive than purebred cows. On average, HF×JE crossbred cows produce less milk volume but with high concentrations of fat and protein than purebred HF. The body size and live weight of these crossbred animals is smaller than HF animals therefore stocking rate increases but it is smaller than JE stocking rate [Montgomerie, 2002]. These animals are also more adapted to an extensive system than HF and so have a better efficiency to convert pasture into prime milk.

Moreover, according to some studies [Grosshans et al., 1997; Harris and Winkelman, 2000; Lopez-Villalobos et al., 2000b] crossbred cows had a better fertility.

According to the milk recording statistics, for the main breeds and crosses in the 2002-2003 season, crossbred cows produced more fat than both parent breeds and than AY cows

while HF cows produced more protein and a higher volume of milk. Table 2 shows these milk recording statistics.

Table 2: Breed average for milk recorded cows in 2002-2003.

Breed	Number	Milk (litres)	Fat (kg)	Protein (kg)
HF	1,110,878	4038	175.4	142.9
JE	374,409	2839	162.6	116.9
HF×JE *	612,868	3610	179.1	137.3
AY	25,880	3571	154.9	128.6

* includes backcrosses.

(Source: Dairy Statistics 2002-2003)

Most authors observed clear benefits for first-cross HF x JE cows and for profitable use of rotational crossbreeding systems [e.g. Lopez-Villalobos and Garrick, 2002].

2.3.6. Profitability of crossbreeding

Results from several studies [e.g. Lopez-Villalobos and Garrick, 1996, 1997b; Lopez-Villalobos et al., 2002; VanRaden and Sanders, 2001] have suggested that crossbreeding could increase net returns of the farm.

According to Lopez-Villalobos and Garrick [1997a] crossbred cows tended to be more profitable than purebred cows because they fitted the milk payment system and showed favourable heterosis for milk traits. So, net income per hectare was higher for crossbred cows than for purebred HF or JE cows.

In a study, investigators in New Zealand have sought to evaluate the profitability of alternative breeding systems under pastoral conditions. Lopez-Villalobos et al. [2000a] developed a comprehensive deterministic model based on a 25 year planning horizon which on an annual basis simulated nutritional, biological and economic performance of straight breeding and rotational crossbreeding using two or three New Zealand breeds. Breed additive effects and heterosis for milk, fat and protein yields, body weight and survival were taken from analyses of field data in New Zealand. The economic analysis revealed the largest advantage in net income per hectare[3] for a HF-JE rotational cross which was only slightly larger than that for a HF-JE-AY rotational cross. Results were similar for net income per cow. For milk income, HF and the rotational cross groups were nearly identical. Results of this study suggested that, under New Zealand conditions, the use of rotational crossbreeding systems could increase profitability of dairy herds under the conceivable market conditions. Moreover, the two-breed rotational scheme with HF and JE seems to be an alternative mating

[3] Net income per hectare is a more important measurement of economic effiency than is net income per cow for New Zealand dairy farmers.

strategy to exploit variation within and between breeds for milk production through a stratified breeding scheme combining selection and crossbreeding as methods of genetic improvement. These results were confirmed by a recent study realized by Lopez-Villalobos and Garrick in 2002.

However, future costs and prices of dairy products (economic circumstances) have major impact on profit of mating strategies. More information are available in Lopez-Villalobos et al. [2000c] and in Lopez-Villalobos and Garrick [2002].

Furthermore, crossbreeding can benefit traits such as reproduction (fertility), health and survival, which sometimes have large influences on farm profit [e.g. Touchberry, 1992; Lopez-Villalobos et al., 2000b; White, 2002].

2.3.7. Crossbreeding between HF strains

Crossbreeding between the local HF strain (**NZHF**) and the overseas HF strain (**IHF**) has occurred since 1980 as artificial insemination companies introduced North American genes into their breeding schemes. However, this crossbreeding program within the HF breed is not deliberately followed by farmers in opposition to crossbreeding between HF and JE purebreds [Montgomerie, 2002]. Moreover, heterosis from crossbreeding between IHF and JE is more important than heterosis from NZHF×JE because IHF strain is more genetically different of the JE breed [Harris and Kolver, 2001; Pryce and Harris, 2004].

2.3.8. Crossbreeding: Future consequences

Lopez-Villalobos et al. [1997; 2000b] carried out some studies evaluated the effects of simultaneous selection and mating strategies (upgrading and rotational crossbreeding) on the rate of genetic improvement and productivity of the New Zealand dairy cattle with a deterministic model based over a 25 year planning horizon. For all mating strategies, the size of active cow population affected the within-breed average annual genetic gain. Therefore, the adoption of rotational crossbreeding reduced the size of the potential purebred bull mothers[4] population with only minor changes in the annual genetic gain of bulls compared to upgrading strategies. However, annual recruitment of new active cows should be regularly monitored to ensure long term gain will be maintained [Lopez-Villalobos and Garrick, 1997b].

Therefore, in the long term, crossbreeding can be used in combination with selection to exploit the effects of heterosis while maintaining genetic diversity to cover changes in market conditions [Lopez-Villalobos et al., 2000b].

[4] Also known as active cows that may be registered (pedigree) or not (grade), provided that they are the result of at least three generations of artificial breeding to sires of one breed.

3. Genetic models

Dairy cattle breeding aims to reduce the production costs of milk, improve animal health and welfare, thus to increase farm profitability by improving the genetic level of livestock. This is most effectively achieved by selection of animals with the highest genetic merit, using accurately breeding values which allow to compare and to classify animals between them. Breeders operate on these breeding values, which are solutions to mixed model equations (**MME**) established by Henderson.

3.1. General notation of mixed models

Henderson adapted theories of linear models to quantitative genetic. According to Henderson [1984] a mixed linear model can be written in matrix notation as:

$$\mathbf{y}=\mathbf{Xb}+\mathbf{Zu}+\mathbf{e} \qquad (2)$$

where **y** is the vector with all the observations; **b** is the vector with unknown fixed effects; **u** is the vector with unknown random effects; **X** is the incidence matrix which relates observations to corresponding fixed effects; **Z** is the incidence matrix which relates observations to corresponding random effects; **e** is the vector of the residuals. With this model, the mean of **y** is represented by **Xb** since both random effects and residuals have a mean of zero and the covariance between its observations by Var(**y**)=Var(**Xb**) + Var(**Zu**) + Var(**e**). However, V(**Xb**)=0 since b is a fixed effect, Var(**u**)=**G** and so Var(**Zu**)=**ZGZ'** and Var(**e**)=**R** then Var(**y**)=**V**=**ZGZ'** + **R**, with the assumption that the random effect and the residual are not correlated, thus Cov (**u**, **e**)=0.

The resolution of equation (2) provides the following solutions [Henderson, 1984]:

$$\hat{\mathbf{b}}=(\mathbf{X'V^{-1}X})^{-1}\mathbf{X'V^{-1}y} \qquad (3)$$

$$\hat{\mathbf{u}}=\mathbf{GZV^{-1}(y-Xb)} \qquad (4)$$

However, this resolution requires the inversion of **V** (= the (co)variance matrix of observations), which is not computationally feasible. Nevertheless, Henderson [1984] presented MME, these including both fixed and random effects. So, these equations allow to estimate **b** and predict **u** simultaneously, without the need for computing $\mathbf{V}^{-1}$.

$$\begin{bmatrix} \mathbf{XR^{-1}X} & \mathbf{XR^{-1}Z} \\ \mathbf{ZR^{-1}Z} & \mathbf{ZR^{-1}Z+G^{-1}} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{XR^{-1}y} \\ \mathbf{ZR^{-1}y} \end{bmatrix} \qquad (5)$$

or

$$\mathbf{Cs=r} \qquad (6)$$

where **R** is the residual (co)variances matrix and **G** is the genetic (co)variances matrix. These equations require the inversion of **G** and **R** matrices. The purpose of using those models in quantitative genetic is to sort animals by their genetic merits, and then to do controlled matings.

In a single trait model, the residuals can be supposed no correlated and $\mathbf{R} = \mathbf{I}\sigma^2_e$; and **G** is equal to $\mathbf{A}\sigma^2_a$ where **A** is the relationship matrix and σ^2_a the additive genetic variance. Henderson [1976] and Quaas [1976] have developed a method to inverse directly the relationship matrix **A**.

3.2. Animal model

The principle of the animal model is to apply MME in order to include all the relationship links to evaluate simultaneously dairy cows and sires allowing to increase the accuracy of evaluations. This is possible by the use of the relationship matrix **A**. The basic animal model is so according to Gengler [2003] in direct use of equations (5) :

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu}_a + \mathbf{e} \qquad (7)$$

$$\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z} \\ \mathbf{Z'X} & \mathbf{Z'Z} + \mathbf{A}^{-1}\lambda_a \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u}_a \end{bmatrix} = \begin{bmatrix} \mathbf{X'y} \\ \mathbf{Z'y} \end{bmatrix} \qquad (8)$$

$$\text{with } \lambda_a = \frac{\sigma^2_e}{\sigma^2_a}$$

In this model, the performance of an animal is described genetically according to its additive genetic value ($\mathbf{u}_a$) in (7). The estimates of σ^2_a and σ^2_e are given for the whole population with the analysis of appropriate samples of the population by advanced methods (see material and methods).

The model (7) is a simplified approach and can be transformed to contain several random effect for example.

3.3. Repeatability model

When there are repeated records of the same trait on the same animal (e.g.: milk yield in successive lactations), a second random effect appears in the models : the permanent environmental effect ($\mathbf{u}_{EP}$). A repeatability model is used to analyse these situations, it is a transformed animal model [Ducrocq, 1992; Gengler, 2003].

This model always assumes a genetic correlation close to unity between all pairs of records, an equal variance for all records and an environmental correlation between all pairs of records [Mrode, 1996]. The correlation between records of an individual can be expressed by the repeatability [VanVleck et al., 1987]:

$$r=\frac{Var(\mathbf{G})+Var(\mathbf{Ep})}{Var(\mathbf{P})} \qquad (9)$$

$$0 \le r \le 1$$

The estimate of permanent environmental effect for an animal represents environmental influences and a non-additive genetic effect, and they are proper to the animal and affect its performance for life. The model is written as:

$$\mathbf{y}=\mathbf{Xb}+\mathbf{Zu}_a+\mathbf{Zu}_{Ep}+\mathbf{e} \qquad (10)$$

or

$$\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z} & \mathbf{X'Z} \\ \mathbf{Z'X} & \mathbf{Z'Z}+\mathbf{A}^{-1}\lambda_a & \mathbf{Z'Z} \\ \mathbf{Z'X} & \mathbf{Z'Z} & \mathbf{Z'Z}+\mathbf{I}\lambda_{Ep} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u}_a \\ \mathbf{u}_{Ep} \end{bmatrix} = \begin{bmatrix} \mathbf{X'y} \\ \mathbf{Z'y} \\ \mathbf{Z'y} \end{bmatrix} \qquad (11)$$

$$\text{with } \lambda_{Ep}=\frac{\sigma^2_e}{\sigma^2_{Ep}}$$

Thus, there are a large number of possible animal models, depending upon the characteristics of the data being analysed. Several traits can be analysed simultaneously (milk, fat and protein for example) taking correlation between traits into account, this is a multiple trait model. Finally, the incidence matrix **Z** can be make up of 0 and variables for the random regressions rather than 0 and 1. This kind of matrix is used in the random regression models that are often used in Test-Day Models.

3.4. Test-day models

Test-day records conventionally have been used in aggregated forms as lactation records which used in a lactation model like traditional 305-day approaches. For some years, in order to account for some of the problems in the lactation statistical model, Test-Day Models (**TDM**) have been developed where each test-day record is included in the models as an observation and no used in aggregated forms [Swalve, 1998].

The TDM are defined as a model that considers all genetic and environmental effects directly on a TD basis, therefore they include better modelling of factors affecting yields, no need to extend records, and possibly greater accuracy of evaluations [Ptak and Schaeffer, 1993].

3.4.1. Why use TDM?

There are some reasons for the use of TD records rather than lactation records [Swalve, 1998; Swalve, 2000; Borremans, 2001]:

The reduction of the costs of recording dairy cattle performance, thus there is a trend to go to an extensification of data collection schemes with very few tests per lactation.

The decrease of the generation intervals with the aim to increase the genetic progress in dairy cattle breeding schemes by the rapid use of every single TD record.

The conventional methods of aggregating TD records to form lactation records are less useful compared with the methods used when evaluating the TD records. A TDM is a model considering several test-days directly per individual lactation.

TDM are more flexible and present numerous advantages over the traditional 305 days models allow:

- more accurate estimation of genetic merit;
- more information about the cows and on environmental effects like herd management which allow to assist every day decisions on the farm;
- accounting for time-dependent variation in the course of the lactation, which is done by defining the HTD as the contemporary group but also by the expression of days in milk (**DIM**);
- and an economic advantage by the flexibility in handling records from different recording schemes: some herds may only contribute milk yields while in others fat and protein contents are also sampled. Every piece of information about a performance can be used in TDM.

3.4.2. Types of TDM

TDM may be separated in two approaches [Swalve, 2000]:

1. One-step methods

These methods, directly producing breeding values for dairy production, have been derived from repeatability animal models under which the TD records within a lactation are taken as repeated measurements.

Two sort of these:

➔ Fixed Regression Models (**FRM**) account for the curvilinear pattern of the lactation curve by using suitable covariates which are regression of milk yield in function of DIM or rather a function of these DIM. The genetic variation during the lactation is assumed to be

constant. FRM has been extended to a multiple-trait model under which TD records within the lactation are considered as repeated traits and lactations are treated as separate traits:

$$\mathbf{y}=\mathbf{Xb}+\mathbf{Z}(\mathbf{a}+\mathbf{p})+\mathbf{e} \qquad (12)$$

This type of model was used until recently in Germany for evaluation of dairy cattle production traits and for somatic cells.

➔ Random Regression Models (**RRM**) additionally define the animal's genetic effect by using regression coefficients and allowing for covariances among them. In these models, the genetic merit of an individual is allowed to differ for any day in the lactation and therefore decompose the effect of an animal coefficients. They offer the opportunity to express estimated breeding values as curves of genetic merit. In RRM, the genetic variance and 'genetic yields' for each single day of the lactation can be estimated and used to define suitable criteria of persistency which is a trait of economic importance because of its impact on feed costs, health, and fertility.

The matrix notation of this type of model is:

$$\mathbf{y}=\mathbf{Xb}+\mathbf{QZ}(\mathbf{a}+\mathbf{p})+\mathbf{e} \qquad (13)$$

where **y** is a test-day record, **b** are fixed coefficients for different effects (HTD, age, region,…), **a** are random regression coefficients for animal effect (genetic effect), **p** random regression coefficients for the permanent environment, e is the residual, **X** and **Z** are incidence matrices and **Q** is the covariate matrix for the orthogonal polynomials (Legendre polynomials for example).This sort of model is used in Canada for evaluation of dairy cattle (sires and cows).

2. Two-step methods

In these methods, some corrections are carried out at TD level and subsequently corrected TD records are processed in an aggregated form as lactation records. It is this type of TD model that is used in New Zealand since 1996; but also in Australia and in North-eastern United States. Two-step model will be detailed in the part concerning the current genetic evaluation system of production traits in New Zealand.

4. Current genetic evaluation systems for New Zealand dairy cattle

In the 1960's, a system for genetic evaluation of dairy cattle performances was developed in New Zealand; it carried out separate for sire and cow evaluations. Within each of these processes separate methods have evolved for the calculation of lactation yield from individual test-day records. More information about this old system are available in Johnson [1996]. This system remained largely unchanged, except for fine-tuning during the mid 1980's. Major developments in database capability and statistical techniques have since taken place. These developments provided some opportunities to review the procedures for genetic evaluation of dairy cattle in New Zealand [Garrick et al., 1997].

The genetic evaluation system was replaced in 1996 by a new system using an animal model including pedigree records since 1940 and performance records (TD records) since 1986. This replacement concerned evaluation of production traits such as milk volume, fat and protein yields; but also the evaluations of live weight, four survival traits and 16 linear type traits [Harris et al., 1996].

4.1. Genetic evaluation system of production traits

An across-breed genetic evaluation system, using a two-step TDM,. it is divided in two stages; the first is a prediction stage where the TD records are corrected for TD environment. These corrected TD records are then combined into lactation records weighting the individual TD record according to the correlations among them. The second stage is a stage of analysis using an animal model, it is so an indirect use of TD yields [Gengler, 2002].

The genetic evaluation provides breeding values, producing values and lactation values that allow to compare animals of different breeds on the same scale and to select the best animals for the future.

4.1.1. First stage: prediction of lactation yields

The production traits are milk in litres, fat in kg and protein in kg; these records are individual TD records, sampled twice in 24 hours supervised or not. TD records of all cows, having known parents or not, where the date of calving is greater than 590 days after the date of birth and less than 20 years after birth, are considered; they include records obtained in the interval from four days to 305 days after calving. Cows herd are tested four or more times during the milking season [INTERBULL, 2004].

The objective of this stage is to find a function of TD records that has maximum correlation with lactation yield. The procedure is undertaken separately for milk volume, fat and protein yields [Garrick et al.,1997].

Variance structure

Variance components were estimated between nine 30-day intervals of lactation curve with each stage treated as a separate trait. These results are used to obtain a covariance function to calculate the phenotypic co-variance between any two stages of lactation so between any pair of TD records. Accordingly, an individual variance-covariance matrix can be calculated for every cow-lactation. Therefore, the phenotypic correlation depends only on the number of days between stages of lactation [Garrick et al., 1997].

Correction for TD environment

Analysis of TD records within herd-year-season-age contemporary groups, the same groups defined in the animal model, is undertaken after each TD. A linear model is fitted to account for DIM by an extended version of Wood's model, TD yields are so adjusted for stage of lactation, so the correction for TD environment [Harris, 1996]. Let $\mathbf{y}_{ik}$ denote the performance of cow *k* at test *i* for any of the three traits milk volume, fat and protein yields. Then $\mathbf{y}_{ik}$ has expectation μ_{ik} which may be represented by an extended version of Wood's model [Johnson, 1996]:

$$\ln(\mu_{ik}) = m_i + a t_{ik} + b \ln(t_{ik}) \qquad (14)$$

where m is a parameter reflecting the environment of test *i* (= correction of TD), t_{ik} is the number of DIM for cow *k* at test *i* and a and b are shape parameters which model the stage of lactation. The regression in t_{ik} take account of the variation in DIM so that cows can be compared as if they were at the same stage of lactation. Generalised least squares (GLS) is used to estimate the parameters of this model, the GLS estimation takes account of culling. The shape parameters are estimated for each contemporary groups [Johnson, 1996].

This correction is important when combining TD for cows with different combination of valid tests, it allows to eliminate environmental effects that influence the production of all cows on a particular TD.

Lactation yield estimation

The corrected TD records, deviations of observed test-day yields $\mathbf{y}_{ik}$ from their fitted values estimated (μ_{ik}), are accumulated across all TD from one lactation of a cow and are combined linearly to predict a 270-day lactation yield deviation from contemporary average by Best Linear Prediction using the covariance structure appropriate to the individual cow [Garrick et al., 1997]. For the covariance structure, it supposes that the phenotypic correlation depends only on the number of days between stages of lactation. So, the phenotypic correlation between TD yields at days t_1 and t_2 is [Johnson, 1996]:

$$r_p(t_1,t_2) = \tau(1-\rho^{|t_1-t_2|}) \qquad (15)$$

where $\tau<1$ and $\rho>0$ are constants depending on the trait (estimated on raw data, see Variance structure). This correlation is linearly decreasing when days between TD increase! The variance of TD records is modelled by assuming a constant coefficient of variation, independent of stage of lactation, and the function (15) to take account of repeated measures on the same cow. Any combination of tests can be used, allowing for inclusion of records in progress or incomplete lactations [Johnson, 1996].

In conclusion, the first originality of this TDM used in New Zealand is the combination of test-day production records into a measure of lactation yield, which standardises lactation length, for the purposes of genetic evaluation.

4.1.2. Second stage : analysis

The standardized lactation records are then subject to a further analysis, a genetic evaluation using an animal model including pedigree records since 1940 and performance records since 1986. Best Linear Unbiased Prediction (**BLUP**) under an animal model is used to evaluate dairy cattle for breeding and production [Harris, 1995].

The animal model used to evaluate predicted lactation yields is a repeated records, single trait, additive genetic effects and simple repeatability model. It is also an across-breed animal model. This model ignores genetic and phenotypic relationships between traits, and assumes yields are a repeatable trait with the same genes involved in production at all ages [Harris et al., 1996]. It allows simultaneous sire and cow evaluation, which can prevent certain types of selection bias and can increase the accuracy of prediction [Misztal and Gianola, 1987].

Thus, this evaluation system is able to compare animals nationally and within herd regardless of breed to allow farmers to select the most profitable animals for the future [Harris et al., 1996].

Statistical model

The statistical model for analysis of a cow *n* with a production yield *o* is [Harris, 1995]:

$$y_{ijklmno} = hsa_i + \sum_{r=1}^{C_h} w_r h_r + m_j + d_k + ab_{lm} + \sum_{r=1}^{C_g} q_r g_r + a_n + p_n + e_{ijklmo} \qquad (16)$$

where $y_{ijklmno}$ is the production yield *o* adjusted to a constant phenotypic standard deviation for animal *n* in herd-season-age contemporary group *i*, calving in calendar month *j*, in induced lactation class *k*, age-at-calving *l*, and of breed *m*.; hsa_i is the fixed effect for herd-season-age contemporary group *i*; m_j is the fixed effect for period of calving *j*; d_k is the fixed effect for induced lactation *k*; w_r is the contribution of heterosis class *r* to animal *n*; h_r is the fixed

effect for heterosis *r* with C_h classes; ab_{lm} is the fixed effect for age at calving class *l* nested with in breed class *m*; q_r is the contribution of genetic group *r* to the genetic merit of animal *n*; g_r is the fixed effect for genetic group r with C_g classes; a_n is the random additive genetic effect for animal *n*; p_n is the random non-additive genetic and permanent environment effect for animal n and e_{ijklmo} is the random residual.

The herd-season-age classes are assigned as a nested classification of herd which is defined as a herd number at a map location, age is defined in years (2 years up to 8 years and greater than 8 years) and season is defined as spring and autumn calving periods within each year. Period of calving is defined as early, mid and late intervals of calving relative the contemporary group start of calving nested within season and year. Induced lactation is defined as induced or not nested within age. Age at calving is defined in months at partition, with class 1 being less than 22 months, then proceeding in monthly divisions up to class 90 which was older than 109 months. The age at calving effect is nested within breed where breed has five classes HF, JE, AY, JE×HF cross and other breeds. Animals with greater than 0.75% of their genes originating from one breed were classified as that breed for nesting the age at calving effect within breed. This nest within breed allows to account for different rates of maturity of the breeds, for example JE cattle mature at a faster rate than other breeds, so the rate of decline in the effects with age is greater for the JE breed [Harris et al., 1996]. The contribution *q* of the group *r* to the observation *y* is weighted by the proportion of genes of the ancestors in the group passed on to animal with record. Heterosis coefficients are calculated for all animals based on five breed classes (HF, JE, AY, non-AY Red Breeds, Other (beef) Breeds); the heterosis coefficient for breed i×j is computed as [Harris, 1995]:

$$\mathbf{het}_{i\times j}=[\mathbf{ps}\times\mathbf{pd}']_{ij}+[\mathbf{ps}\times\mathbf{pd}']_{ji} \qquad (17)$$

where het is the vector of heterosis coefficients and ps (pd) is the vector containing the percent of genes of each of the eight breeds present in the sire (dam). The total heterozygosity for an individual is $(1-\mathrm{ps'pd})$ according to VanRaden [1992]. Heterosis is included as a fixed effect in the animal model [Harris et al., 1996].

Matrix notation

In matrix notation the animal model for production traits is expressed as [Harris, 1995]:

$$\mathbf{y}=\mathbf{Xb}+\mathbf{ZWh}+\mathbf{Za}+\mathbf{Zp}+\mathbf{ZQg} \qquad (18)$$

where **y** is the vector of records; **b** is the vector of fixed effects; **h** is the vector of heterosis fixed effects; **a** is the vector of random additive genetic effects; **p** is the vector of random non-additive genetic and permanent environment effects; **g** is the vector of genetic group effects; **Z, X, W** and **Q** are incidence matrices associating records with the elements of **a, b, h** and **g**

respectively. (The ith row elements of **W** contain the proportion of heterosis expected for animal *i* for the appropriate breed combination. The ith row elements of **Q** contain the contribution of each genetic group to the genetic merit of animal *i*.)

The MME for model in equation (19) are [Harris, 1995]:

$$\begin{bmatrix} \mathbf{X'R^{-1}X} & \mathbf{X'R^{-1}Z} & \mathbf{X'R^{-1}Z} & \mathbf{X'R^{-1}ZQ} & \mathbf{X'R^{-1}ZW} \\ \mathbf{Z'R^{-1}X} & \mathbf{Z'R^{-1}Z}+\mathbf{A^{-1}}\lambda_g & \mathbf{Z'R^{-1}Z} & \mathbf{Z'R^{-1}ZQ} & \mathbf{Z'R^{-1}ZW} \\ \mathbf{Z'R^{-1}X} & \mathbf{Z'R^{-1}Z} & \mathbf{Z'R^{-1}Z}+\mathbf{I}\lambda_p & \mathbf{Z'R^{-1}ZQ} & \mathbf{Z'R^{-1}ZW} \\ \mathbf{Z'Q'R^{-1}X} & \mathbf{Z'Q'R^{-1}Z} & \mathbf{Z'Q'R^{-1}Z} & \mathbf{Z'Q'R^{-1}ZQ} & \mathbf{Z'Q'R^{-1}ZW} \\ \mathbf{Z'W'R^{-1}X} & \mathbf{Z'W'R^{-1}Z} & \mathbf{Z'W'R^{-1}Z} & \mathbf{Z'W'R^{-1}ZQ} & \mathbf{Z'W'R^{-1}ZW} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{a}} \\ \hat{\mathbf{p}} \\ \hat{\mathbf{g}} \\ \hat{\mathbf{h}} \end{bmatrix} = \begin{bmatrix} \mathbf{X'R^{-1}y} \\ \mathbf{Z'R^{-1}y} \\ \mathbf{Z'R^{-1}y} \\ \mathbf{Z'Q'R^{-1}y} \\ \mathbf{Z'W'R^{-1}y} \end{bmatrix} \quad (19)$$

$$\text{where } \lambda_e = \frac{\sigma_e^2}{\sigma_a^2} = \frac{\text{Var}(\mathbf{e})}{\text{Var}(\mathbf{a})} \text{ and } \lambda_p = \frac{\sigma_e^2}{\sigma_p^2} = \frac{\text{Var}(\mathbf{e})}{\text{Var}(\mathbf{p})}$$

This model can be adjusted to take lactation expansion factors into account when the vector **y** includes both partial and complete lactation yields.

4.1.3. Lactation expansion

The animal model for production traits uses records based on partial lactation information and/or records based on complete lactation information for genetic evaluation [Harris et al., 1996].

For partial lactation information, we must predict some records to complete the lactation period (length). But the predicted records based on partial lactation information have less genetic and phenotypic variance than “true” records based on complete lactation information [Johnson, 1996]. Indeed the variance of the prediction depends on the number of tests available and stage of lactation at each test. Therefore, the predicted lactation yield is expanded and weights are used in the animal model equations to account for the differences in the variances and to account for the prediction error [Harris, 1995].

Two approaches can be considered, the first it is to expand the predicted record [VanRaden et al., 1991] and the second it is to modify the MME [Weller, 1988]. It is better to include the expansion factor values directly in the MME rather than to use expanded record in the animal model that expands also the fixed effects which is undesirable according to Harris [1995].

If $\mathbf{y}_c$ denotes a completed lactation records and $\mathbf{y}_p$ its prediction based on partial lactation information (TD records) then it is assumed that the true yield ($\mathbf{y}_c$) is the best predictor of the expanded record ($b_p\mathbf{y}_p$):

$$E(b_p\mathbf{y}_p|\mathbf{y}_c)=\mathbf{y}_c \quad (20)$$

where $\mathbf{b}_p$ is the theoretical expansion factor based on phenotypic information [Johnson, 1996]. This factor is used to equate the genetic and permanent environmental variances of $\mathbf{y}_c$ and $\mathbf{y}_p$; and it is given by [Harris, 1995]:

$$b_p=\frac{Var(\mathbf{y}_c)}{Var(\mathbf{y}_p)}=\frac{1}{[Corr(\mathbf{y}_p,\mathbf{y}_c)]^2} \qquad (21)$$

which is the inverse squared correlation between predicted and true value. To compensate for this expansion, the temporary environmental variance or error variance is higher and so expanded records receive less weight in the animal model.

The variance of completed records can be decomposed as :

$$Var(\mathbf{y}_c)=rVar(\mathbf{y}_c)+(1-r)Var(\mathbf{y}_c) \qquad (22)$$

where r is the repeatability between lactation and $(1-r)Var(\mathbf{y}_c)$ represents temporary environmental variance.

The variance of prediction of $\mathbf{y}_c$, $\mathbf{y}_p$ can be also decomposed as [Harris, 1995]:

$$Var(\mathbf{y}_p)=\frac{rVar(\mathbf{y}_c)}{b_p^2}+\frac{b_pVar(\mathbf{y}_c)-rVar(\mathbf{y}_c)}{b_p^2}=\frac{Var(\mathbf{y}_c)}{b_p} \qquad (23)$$

where the second term is the temporary environmental variance of the partial lactation record.

The ration of the temporary environmental variances is the lactation weight:

$$\lambda_e=\frac{(1-r)b_p^2}{(b_p-r)} \qquad (24)$$

which is the factor for the diagonal elements of the inverse error matrix $\mathbf{R}^{-1}$ in the MME.

Thus, the model (19) can be modified to include the lactation weights (λ_e) and the values of b_p^{-1} when the vector of records includes both partial and complete lactation yields. Indeed, the inverse error matrix R^{-1} contains λ_e values on the diagonal and the incidence matrix Z contains the values of b_p^{-1} [Harris, 1995]. Table 3 gives the contributions for solving the MME by iteration on data methods.

Table 3: Contributions for solving the MME by iteration on data methods.

Description	Element	Value
Fixed effects x Fixed effects	$\mathbf{X'R^{-1}X}$	λ_e
Fixed effects x Heterosis effects	$\mathbf{X'R^{-1}Z_hW}$	$w \times \lambda_e$
Fixed effects x Genetic Group effects	$\mathbf{X'R^{-1}ZQ}$	$b_{\bar{p}}^{-1} \times \lambda_e$
Fixed effects x Animal effects	$\mathbf{X'R^{-1}Z}$	$b_{\bar{p}}^{-1} \times \lambda_e$
Fixed effects x PE effects	$\mathbf{X'R^{-1}Z}$	$b_{\bar{p}}^{-1} \times \lambda_e$
Heterosis effects x Heterosis effects	$\mathbf{Z_h'W'R^{-1}Z_hW}$	$\lambda_e \times w^2$
Heterosis effects x Genetic Group effects	$\mathbf{Z_h'W'R^{-1}Z_hQ}$	$b_{\bar{p}}^{-1} \times \lambda_e \times w$
Heterosis effects x Animal effects	$\mathbf{Z_h'W'R^{-1}Z}$	$b_{\bar{p}}^{-1} \times \lambda_e \times w$
Heterosis effects x PE effects	$\mathbf{Z_h'W'R^{-1}Z}$	$b_{\bar{p}}^{-1} \times \lambda_e \times w$
Genetic Group effects x Genetic Group effects	$\mathbf{Z'Q'R^{-1}ZQ}$	$b_{\bar{p}}^{-2} \times \lambda_e \times q^2$
Genetic Group effects x Animal effects	$\mathbf{Z'Q'R^{-1}Z}$	$b_{\bar{p}}^{-2} \times \lambda_e \times q$
Genetic Group effects x PE effects	$\mathbf{Z'Q'R^{-1}Z}$	$b_{\bar{p}}^{-2} \times \lambda_e \times q$
Animal effects x Animal effects	$\mathbf{Z'R^{-1}Z}$	$b_{\bar{p}}^{-2} \times \lambda_e$
Animal effects x PE effects	$\mathbf{Z'R^{-1}Z}$	$b_{\bar{p}}^{-2} \times \lambda_e$
PE effects x PE effects	$\mathbf{Z'R^{-1}Z}$	$b_{\bar{p}}^{-2} \times \lambda_e$
Fixed effects RHS	$\mathbf{X'R^{-1}y}$	$y \times \lambda_e$
Heterosis effects RHS	$\mathbf{Z_h'W'R^{-1}}y$	$y \times \lambda_e \times w$
Genetic Group effects RHS	$\mathbf{Z'Q'R^{-1}y}$	$y \times b_{\bar{p}}^{-1} \times \lambda_e \times q$
Animal effects RHS	$\mathbf{Z'R^{-1}y}$	$y \times b_{\bar{p}}^{-1} \times \lambda_e$
Perm. Env. effects RHS	$\mathbf{Z'R^{-1}y}$	$y \times b_{\bar{p}}^{-1} \times \lambda_e$

(Source: Harris, 1995)

4.2. Genetic evaluation system of live weight

The animal model used for live weight is the same model as the one used for production traits: it is a repeated records, single trait, additive genetic and simple repeatability model.

The statistical model is the same as for production except the effects for induction and period of calving are replaced with an effect for stage of lactation when weighed nested within age [Harris, 1995; Harris et al., 1996].

4.3. Genetic evaluation systems of the linear type traits and survival

The models are single record, single trait, additive genetic models according to Henderson [1988].

The statistical model for analysis of a cow with linear type scores includes effects for herd-season contemporary group, stage of lactation class when scored and age at first calving class in months nested within breed, heterosis, genetic group, random animal genetic merit and the random residual [Harris, 1995; Harris et al., 1996].

The statistical model for survival is the same as for linear type except there is no effects for stage of lactation or age at calving. The herd-season-age for survival is assigned as the herd-season-age immediately prior to the survival record [Harris, 1995; Harris et al., 1996].

4.4. Use of genetic groups and relationships

A grouping strategy developed by Westell et al. [1988] in which a genetic group for each animal is derived from the genetic group effect of the animal's ancestors is used. For each animal with unknown ancestors, phantom parents without records are created and are assigned to appropriate genetic groups; the relationship matrix is augmented to include those. The genetic group effects represent the average genetic merit of the phantom animals selected to be parents to their descendants that do have records available. Phantom parents are assumed to be unrelated to one another [Harris et al., 1996]. More information about the transformation and the absorption of the augmented MME are available in Quaas and Pollack [1981], Westell et al. [1988], and Wiggans et al. [1988].

In a multibreed animal model genetic groups are assigned by breed; in the case of an animal who is ¾ breed A and ¼ breed B with a known pure breed parent, the phantom parent would be a ½ A x ½ B crossbred. Therefore, the animal would be assigned to both the genetic groups for A and B with values of ½ for the unknown parent. More details about computation rules can be found in Harris [1995].

Thus, genetic groups are assigned by sex (male or female missing parent), birth year, country of origin and breed (eight classes). So, when both parents are known there is no need to assign genetic groups; genetic groups must be assigned if one or more parents are unknown. Genetic groups are assigned in 5 years intervals after 1960 to 1980 then yearly with the first group being prior to 1960 [Harris, 1995].

After merging small groups across years and across countries, in which there is a insufficient number of animals assigned, there are 125 genetic groups. There is no clustering across breed or sex [INTERBULL, 2004].

4.5. Inclusion of overseas information

Provision within the animal model have been made to include foreign information for sires for the production traits. This is achieved by creating phantom daughters with the level of performance which equals the value of the foreign information in New Zealand with the number of phantom daughters being computed from the New Zealand reliability of the foreign information in New Zealand [Harris et al., 1996].

So, the number of overseas phantom daughters and the overseas phantom daughter deviation are derived from the difference between the animal model results using only New Zealand data and the Interbull proof, that is retained at subsequent New Zealand evaluations unless there is New Zealand daughter data [INTERBULL, 2004]. The interested reader can find more details in Harris [1995] and in Harris et al. [1996].

4.6. Computational methods

Methods for solving animal models have been discussed in details by Quaas and Pollack [1981], Schaeffer and Kennedy [1986], Misztal and Gianola [1987] and Westell et al. [1998].

The MME are solved iteratively for the fixed effects **b** and using block iteration for the random effects, with the groups being solved as one block and each animal has a block for **a** and **p.** Solutions for **a** and **p** are solved simultaneously by iterating on data.

The animal evaluation for yields traits is undertaken every three weeks, with computations carried out on a different computer from that used for maintaining the database. Daily recordings for milk yield from the farm are sent directly to central computing center of Livestock Improvement for further processing. A temporary calculation (within-herd update) is run every night, to process herds as test-day records are entered into the database. The continuous evaluation allows sires of high genetic merit to be identified earlier in the season on the basis of partial lactation evaluations and permit to use younger sires for generating cows and future sires thus reducing the generation interval and increasing the rate of genetic gain! [Harris et al., 1996]

4.7. Breeding values, producing values and lactation values : results of genetic evaluations

Breeding values, which are the sum of the additive animal genetic effect and the genetic group effect, are the genetic merit of the animals. Producing values, which are the sum of the breeding value, non-additive genetic, permanent environment and average heterosis effects, are the lifetime productive merit [Harris et al, 1996]. Lactation values, which correspond to production values but just for one lactation, represent current season productive ability [Harris, 2004].

These values are reported in units of measurement (litres milk, kg fat and protein, kg live weight, fertility and longevity) relative to an across-breed base defined by 1985-born cows, a group of 30,000 cows with all traits measured. The average breeding value of the base cows is zero for all traits and the averages for the different breeds are directly comparable. [Harris et al., 1996]

4.8. Productive efficiency: economic indexes

Three selection indexes have been developed to identify the most economically efficient animals under New Zealand pasture based farming systems.

To compare individual animals on net farm profitability for breeding and production two indexes exist: **Breeding Worth** (**BW**) and **Production Worth** (**PW**), these economic indexes are calculated to reflect profit per unit feed consumption and they are expressed in terms of profit per 4.5 tonnes[5] of feed on dry matter basis [Garrick et al., 1997]. BW and PW are based on future price predictions for milk components.

The BW index is the sum of the breeding values for fat, protein, milk volume, live weight and survival each weighted by an economic weight [Lopez-Villalobos et al., 1997]:

$$BW=\sum v_i EBV_i \qquad (25)$$

where v_i is the economic weight in dollars of trait *i*, which is the net income per unit of feed from breeding replacements with one unit of genetic improvement, and EBV_i is the estimated breeding values of the individual for trait *i*. This index measures the ability or the expected ability of the cow to breed replacements which are efficient converters of feed into profit (= milk solids), so it allows to identify the best animals for breeding herd replacements in the future; it is a selection index. The BW is based mainly on the performance of close relatives [Livestock Improvement Corporation, 2004].

The PW index is the sum of the production values for fat, protein, milk volume and live weight each weighted by an economic weight.

$$PW=\sum u_i EPV_i \qquad (26)$$

where u_i is the economic weight for the trait *i*, which is the net income per unit of feed from milking cows with one unit of genetic improvement, and EPV_i is the estimated producing values of the animal for trait *i* [Harris et al. 1996]. This index measures the ability of the cow to convert feed into profit over her lifetime, therefore it allows to rank cows on lifetime profitability and to make purchasing and culling decisions [Livestock Improvement

[5] This value corresponds to the annual intake of the average cow in New Zealand. [Harris, 1998]

Corporation, 2004]. This index is useful for the dairy farmers with mixed breed and crossbred herds, in which there are large ranges of cow size, to rank the usefulness of the cows in their herds because it takes account of the extra costs associated with cows with higher live weight or higher volume than their herd mates but without additional protein or fat [Montgomerie, 2002; 2003].

The third economic index measures the expected ability of the cow to convert feed into profit in the current season and allows to rank cows on current lactation profitability. It is the **Lactation Worth** (**LW**) that is based on predicted end of season prices [Livestock Improvement Corporation, 2004].

The economic weights, which used in indexes, are calculated from a farm model using economic methods to value technological change [Ladd, 1982]. This farm model takes into account the future revenue and cost streams to rank the animals on net income per unit of feed and it is timetabled for annual update[6,] with facility for inclusion of new traits. Thus, the economic weights are partial derivatives of the net income function with respect to the trait measure and represent the marginal net income per unit improvement. [Harris et al., 1996] Fat, protein and herd-survival have positive economic weights, and milk yield and live weight have negative economic weights. In New Zealand, there is a penalty for milk volume to account for cartage and processing costs [Garrick et al., 1997; Harris, 1998].

The indexes are reported with an associated reliability that indicates how likely the index is to change as extra information is gathered [Livestock Improvement Corporation, 2004].

The true efficiency advantage of the crossbred cows is underestimated in the PW index because production values are not available for cow fertility and longevity. Even so, the HFxJE crossbred group has had the highest average index of any of the breed groups for every year for which the production worth has been available according to Dairy statistics referred by Montgomerie [2003]; thereby encouraging further crossbreeding.

[6] The economic weights are reviewed annually and therefore may change from year to year.

5. Conclusion

Selection across breeds and crossbreeding in New Zealand go on to be used to improve the genetic ability of cows to convert grazed pasture into milk solids, so to improve the quality of milk. These methods have already proved their efficiency to increase the net income of dairy farmers and go on it to do.

The current genetic evaluation system of production traits is an across-breed genetic evaluation system, using a two-step TDM, that provides breeding values and production values. From these values, three indexes are created allowing farmers to compare and to select the best animals for the future regardless for breed.

For some years, investigators in New Zealand have been trying to improve the genetic evaluation system of production traits and to go up to one-step TDM. This could allow to use directly TD records and so to produce directly breeding values and producing values for dairy production.

In this way, the objective is to contribute to the development of a one-step TDM adapted to the crossbred dairy cattle of New Zealand.

MATERIAL AND METHODS

1. Introduction

Data preparation and computations were done on LINUX workstations using FORTRAN, OCTAVE, PERL and Statistical Analysis System (**SAS**) programs and procedures. The following chapter will give additional details how data was prepared and analysed and about the models and algorithms used.

2. Data preparation

2.1. Introduction

The data preparation consisted in the fusion of the initial data sets, the elimination of abnormal values with some filters, the definition of effects included in the models and the creation of data files necessary for the computations.

The research consisted in three parts:

- Estimation of (co)variance components for purebred HF and JE cattle using a number of random samples and a simple single-breed model.
- Estimation of (co)variance components for purebred HF and JE and crossbred HF×JE cattle using a number of random samples the complete multi-breed model.
- Estimation of breeding values using estimated (co)variance components and the complete multi-breed model.

2.2. Initial data files

Data was provided by Livestock Improvement Corporation situated in Hamilton in New Zealand and included a production file, a lactation yield details file, a pedigree file and a breed file.

2.2.1. Lactation yield details file

This file consisted in 852,910 records from 223,141 animals and included the season of the first parturition of the animal; the animal key; the sire proving scheme (**SPS**) animal status code (1 = SPS, 0 = non-SPS); the birth date; the herd number the animal born in; the map reference the animal born in; the number of lactations the animal has in its lifetime; the map reference the animal lactated; the herd number the animal lactated; the parturition date; the fat yield deviation; the fat yield deviation reliability; the protein yield deviation; the

protein yield deviation reliability; the milk volume yield deviation; the milk volume yield deviation reliability. The map reference and the herd number provided a unique herd location.

2.2.2. Production file

Test-day data was collected from 1989 until 2003 by the Herd Testing service of Livestock Improvement Corporation. The production file included 3,035,670 observations from 223,141 animals and provided additionally the animal key; the map reference of the herd-test took place; the herd number of the herd-test took place; the date of herd-test; the fat percentage; the protein percentage; the milk volume; the somatic cell count. Again, the map reference and the herd number allowed a unique herd location where the herd-test took place.

2.2.3. Breed file

This file provided the breed composition of the 223,141 animals in production, with additional information as the animal key; the birth year; the HF proportion; the JE proportion; the AY proportion; the Guernsey (**GU**) proportion; the Shorthorn (**SH**) proportion and the Brown Swiss (**BRS**) proportion.

2.2.4. Pedigree file

This last file contained identification number of animal, its birth date and its parent's identification number. Pedigree records started in 1940 until 2001. There was a total of 500,134 animals in the pedigree. The pedigree file provided also the breed origin and the major breed of the animal. Animal was considered belonging to a major breed when its breed proportion was at least 81.25%. Animals having no single breed proportion over this level were considered crossbred (e.g., HF×JE, HF×AY, JE×AY)

2.3. Preparation of data

2.3.1. Selection of lactations

Given the time frame we had to limit our study to first lactations which were selected from the data sets.

2.3.2. Stratification of herds

Sampling of data was done on a herd base. Average "breed" proportion of herds were computed using cows with a known first lactation. Herds were then classified in ten classes:

- Class 1= herds with a % HF $\geq$0.95
- Class 2= herds with a % HF between 0.5 and 0.95
- Class 3= herds with a % JE $\geq$0.95
- Class 4= herds with a % JE between 0.5 and 0.95

- Class 5= herds with a % AY $\geq$0.95
- Class 6= herds with a % AY between 0.5 and 0.95
- Class 7= herds with a % GU between 0.5 and 0.9
- Class 8= herds with a % SH between 0.5 and 0.9
- Class 9= herds with a % BRS between 0.5 and 0.9
- Class 0= other herds.

These classes allowed to make intermediate files from which samples to estimate (co)variance components were obtained. On these intermediate files, some additional filtering was done to eliminate the inconsistent records and the length of lactation was limited from 4 to 305 DIM.

2.3.3. Data for estimation of (co)variance components for purebred HF and JE

Using herds in classes 1 or 3, animals whose proportion of HF or JE genes were ≥ 0.95 were selected. Doing this allowed us to obtain, using a random function, samples of purebred animals in purebred herds. Three samples, with about 45,000 records each, were created for HF and two samples, with about 30,000 records each, for JE.

2.3.4. Data for estimation of (co)variance components across HF and JE

Using herds in classes 2 and 4, animals whose the proportion of HF + JE genes was equal to 1.00 were selected. Thus, samples of crossbred herds were composed of purebred and crossbred animals. Table 4 shows the composition of samples for purebred and crossbred herds.

2.3.5. Data for genetic evaluation

For this estimation, animals in first lactation whose the proportion of HF + JE genes was equal to 1.00 were considered. So 792,204 TD records of 208,164 animals were used in the genetic evaluation to estimate breeding values of these animals. These data have undergone the same preparation than for the estimation of (co)variance components: application of some filters, addition of data, extraction of pedigree and renumbering of effects and animals.

Table 4: Composition of samples.

Data sets	Number of herds.	Number of animals in production.	Number of records.
HF 1	160	11,721	44,531
HF 2	166	11,952	45,326
HF 3	165	11,748	45,324
Je 1	107	7,703	29,512
Je 2	105	7,671	30,605
HF×JE 1	64	4,966	19,048
HF×JE 2	48	4,918	19,769
HF×JE 3	44	4,990	19,486
HF×JE 4	60	4,959	18,305
HF×JE 5	64	4,968	18,017
Genetic evaluation	3,539	208,164	792,204

2.3.6. Additional data preparation steps

Several other data preparations steps were done adding the following items:

- Constant, linear and quadratic modified Legendre polynomials: $I_0 = 1$, $I_1 = 3^{0.5}$ x and $I_2 = (5/4)^{0.5}$ $(3x^2-1)$ where $x = -1 + 2[(DIM-1)/(305-1)]$, which are the third order Legendre polynomials (see model for purebred herds);
- Classes of calving years, different classes of DIM, classes of calving months, for fixed effects (see models for purebred and crossbred herds);
- Classes of calving years, for herd period random effect (see model for purebred and crossbred herds);

2.3.7. Pedigree extraction and renumbering of effects

For each sample, extraction of pedigree was done using hash matrix techniques [Auvray, 2000]. Pedigrees were limited to 1940 for purebred samples and to 1970 for crossbred samples. This limitation were necessary as the number of ancestors of crossbred was too high.

Renumbering of production and pedigree files was done to allow the use of standard (co)variance estimation and genetic evaluation programs.

3. Estimation of (co)variance components

Study of quantitative traits and genetic evaluations require the knowledge of parameters such as heritabilities, genetic correlations and variances. In the following section we will describe the methods and models used in our study.

3.1. (Co)variance component estimation

(Co)variance components were estimated using Restricted Maximum Likelihood (**REML**). This method allows to get the (co)variance components that maximise the likelihood of a function of the data, the model and the current (co)variance components. REML algorithms are therefore iterative. Different implementations exist. We used the expectation-maximization algorithm (**EM**) with acceleration EM-REML. This algorithm finds the estimates by indirect approximation of the first derived of the likelihood function. EM-REML is very stable but the convergence rate is very slow [Misztal, 2002]. Therefore we also used the average information (**AI**) algorithm. AI-REML uses approximate second derivatives, is computationally more demanding and needs less iterations to convergence. Unfortunately convergence problems appeared when the (co)variance matrices were not positive definite [Meyer, 1997; Misztal et al., 2000] and most of the computations needed to be done by EM-REML. More information about the methods of variance components estimation are available in Searle et al. [1992] and in Gengler [2003].

3.2. Models used for estimation

Models used to estimate (co)variance components of purebred and crossbred her were similar to test-day models used currently in the Walloon region of Belgium [Auvray and Gengler, 2002]. As explained earlier we limited our research to one trait (milk) in first lactation.

3.2.1. Model for estimation of (co)variance components for purebred HF and JE

In matrix notation the model (**model P**) used was:

$$\mathbf{y}=\mathbf{Xb}+\mathbf{Q}\left(\mathbf{Wh}+\mathbf{Z}_a\mathbf{a}+\mathbf{Z}_p\mathbf{p}\right)+\mathbf{e} \qquad (27)$$

where **y** is a vector of milk test-day records, **b** is a vector of fixed effects included herd * test-day date, lactation stage, gestation stage and lactation period * calving season * calving period regressed on age at calving, **h** is a vector of herd * period of calving random regression coefficients, **a** is a vector of additive genetic random regression coefficients, **p** is a vector of permanent environmental random regression coefficients, **e** is a vector of random residual;

X, W, $\mathbf{Z}_t$ are incidence matrices linking respectively **b**, **h**, **a** and **p** to **y**.

Q is the covariate matrix for the third order Legendre polynomials.

The herd * period of calving effect was defined like a combination between herds and seven periods of two years of calving from 1989 to 2002.

3.2.2. Model for estimation of (co)variance components across HF and JE

Transformation matrices for crossbred herds

In order to simplify the estimation of (co)variance components across breeds the following strategy was used.

Correlations across polynomials were considered known from single breed analysis and polynomial regressions were transformed inside breeds using the following algorithm:

Let H_i and J_i be (co)variance matrices for the HF and JE breeds for trait i. For every breed a transformation matrix can be defined as $\mathbf{T}_{Hi}$ and $\mathbf{T}_{Ji}$ that diagonalize $\mathbf{H}_i$ and $\mathbf{J}_i$:

$$\mathbf{D}_{Hi}=\mathbf{T}_{Hi}\mathbf{H}_i\mathbf{T}'_{Hi} \quad (28) \text{ and } \quad \mathbf{D}_{Ji}=\mathbf{T}_{Ji}\mathbf{J}_i\mathbf{T}'_{Ji} \quad (29)$$

The transformation matrices were obtained from

$$\mathbf{T}_{Hi}=(\mathbf{U}_{Hi}\mathbf{L}_{Hi})^{-1} \quad (30) \text{ and } \quad \mathbf{T}_{Ji}=(\mathbf{U}_{Ji}\mathbf{L}_{Ji})^{-1} \quad (31)$$

where the **U** matrices contain the eigenvectors and the **L** matrices are diagonal matrices with the square-root of the eigenvalues of the (co)variance matrices for the HF and JE breeds for trait i:

$$\mathbf{H}_i=\mathbf{U}_{Hi}\mathbf{L}_{Hi}\mathbf{L}'_{Hi}\mathbf{U}'_{Hi} \quad (32) \text{ and } \quad \mathbf{J}_i=\mathbf{U}_{Ji}\mathbf{L}_{Ji}\mathbf{L}'_{Ji}\mathbf{U}'_{Ji} \quad (33)$$

The use of transformation matrix permit to reduce the rank of equations in the estimation of variance components for crossbred animals.

If **r** is a vector of initial polynomial regression coefficients then **t** is a vector of uncorrelated transformed regression coefficients where:

$$\mathbf{t}_i=\begin{bmatrix}\mathbf{t}_{Hi}\\ \mathbf{t}_{Ji}\end{bmatrix}=\begin{bmatrix}\mathbf{T}_{Hi} & \mathbf{0}\\ \mathbf{0} & \mathbf{T}_{Ji}\end{bmatrix}\begin{bmatrix}\mathbf{r}_{Hi}\\ \mathbf{r}_{Ji}\end{bmatrix}=\mathbf{T}_i\begin{bmatrix}\mathbf{r}_{Hi}\\ \mathbf{r}_{Ji}\end{bmatrix}=\mathbf{T}_i\mathbf{r}_i \quad (34)$$

and therefore:

$$\mathrm{Var}(\mathbf{t}_i)=\mathbf{T}_i\mathrm{Var}(\mathbf{r}_i)\mathbf{T}'_i=\mathbf{T}_i\mathbf{G}_i\mathbf{T}'_i=\begin{bmatrix}\mathbf{D}_{Hi} & \mathbf{T}_{Hi}\mathbf{G}_{HJi}\mathbf{T}'_{Ji}\\ \mathbf{T}_{Ji}\mathbf{G}_{HJi}\mathbf{T}'_{Hi} & \mathbf{D}_{Ji}\end{bmatrix}=\begin{bmatrix}\mathbf{D}_{Hi} & \mathbf{C}_i\\ \mathbf{C}'_i & \mathbf{D}_{Ji}\end{bmatrix} \quad (35)$$

The regressions variables were transformed using : $\mathbf{Q}_i\mathbf{r}_i=\mathbf{Q}_i\mathbf{T}_i^{-1}\mathbf{t}_i=\mathbf{Q}_{Ti}\mathbf{t}_i$ (36) where the $\mathbf{Q}_i$ matrices contain the Legendre polynomials.

Under the hypothesis that $\mathbf{C}_i$ is diagonal, the (co)variances components of transformed scales ($\mathbf{t}_i$) were estimated. So, the **D** and $\mathbf{C}_i$ matrix are assumed to be diagonal and their elements (= regression coefficients) are not correlated between them within a matrix and are just correlated between them for the same sort of regression coefficients across matrix.

The (co)variances estimates of t_i were then back transformed to find the (co)variances estimates of $\mathbf{r}_i$:

$$\mathbf{r_i} = \mathbf{T_i}^{-1}\mathbf{t_i} \qquad (37)$$

thus:

$$\mathrm{Var}(\mathbf{r_i}) = \mathbf{T_i}^{-1}\begin{bmatrix}\mathbf{D}_{Hi} & \mathbf{C}_i \\ \mathbf{C}_i' & \mathbf{D}_{Ji}\end{bmatrix}(\mathbf{T_i}')^{-1} = \mathbf{T_i}^{-1}\mathbf{M_i}(\mathbf{T_i}')^{-1} \qquad (38)$$

Mi is a 6×6 matrix that can be represented by the following symbolic matrix for every random effect.:

$$\begin{bmatrix} \mathbf{HF} & \mathbf{HF} & \mathbf{HF} & \mathbf{HF\times Je} & \mathbf{HF\times Je} & \mathbf{HF\times Je} \\ \mathbf{HF} & \mathbf{HF} & \mathbf{HF} & \mathbf{HF\times Je} & \mathbf{HF\times Je} & \mathbf{HF\times Je} \\ \mathbf{HF} & \mathbf{HF} & \mathbf{HF} & \mathbf{HF\times Je} & \mathbf{HF\times Je} & \mathbf{HF\times Je} \\ \mathbf{HF\times Je} & \mathbf{HF\times Je} & \mathbf{HF\times Je} & \mathbf{Je} & \mathbf{Je} & \mathbf{Je} \\ \mathbf{HF\times Je} & \mathbf{HF\times Je} & \mathbf{HF\times Je} & \mathbf{Je} & \mathbf{Je} & \mathbf{Je} \\ \mathbf{HF\times Je} & \mathbf{HF\times Je} & \mathbf{HF\times Je} & \mathbf{Je} & \mathbf{Je} & \mathbf{Je} \end{bmatrix} \qquad (39)$$

Models : definition

A first model (**model I**) was defined and used to estimate (co)variance components of crossbred herds. The first estimates obtained from model I allowed to develop another model (**model II**).

Model I was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Q}_{HF}(\mathbf{Wh} + \mathbf{Z}_t\mathbf{a} + \mathbf{Z}_t\mathbf{p}) + \mathbf{Q}_{JE}(\mathbf{Wh} + \mathbf{Z}_t\mathbf{a} + \mathbf{Z}_t\mathbf{p}) + \mathbf{e} \qquad (40)$$

It was the same model than the model P (27), but there are two differences: the first in the fixed effects where the effect regressed on age at calving is defined like breed * lactation period * calving season * calving period where breed is HF, JE or HF×JE. The second difference is $\mathbf{Q}_{HF}$ and $\mathbf{Q}_{JE}$ matrices that are the covariate matrices for the third order Legendre polynomials inside breed composition. Thus, this model took account of the differences between breeds.

In model II, a weight was used in order to standardize residual variance[7]. With the assumption that the covariance between residual of environments was 1, the weight was defined as:

$$\text{weight}_x = \left[\frac{HF_p \times \sqrt{Var(\mathbf{e}_{HF})} + JE_p \times \sqrt{Var(\mathbf{e}_{JE})}}{HF_x \times \sqrt{Var(\mathbf{e}_{HF})} + JE_x \times \sqrt{Var(\mathbf{e}_{JE})}} \right]^2 \qquad (41)$$

where HF_p and JE_p are the average breed proportion for breed HF and JE of population used for the estimation; $Var(\mathbf{e}_{HF})$ and $Var(\mathbf{e}_{JE})$ are the residual variances estimated from purebred herds (see point 3.2.1); and HF_x and Je_x are the breed proportion for breed HF and JE of each animal x in production.

The fixed effect regressed on age at calving, milk yield and Legendre polynomials were weighted by this weight. The model was the same as the model I (40), but it allowed to model better residual variance.

3.3. Estimation

Programs used were developed by I. Misztal, S. Tsuruta and T. Druet.

[7] Residual variance of the animal is replaced by the expected one.

4. Estimation of breeding values

4.1. (Co)variance components and model.

(Co)variance components were average from samples from Model II. The model used was based on Model II and can be written as:

$$\mathbf{y}=\mathbf{Xb}+\mathbf{Q}_{HF}(\mathbf{Wh}+\mathbf{Z}_t\mathbf{a}+\mathbf{Z}_t\mathbf{p})+\mathbf{Q}_{JE}(\mathbf{Wh}+\mathbf{Z}_t\mathbf{a}+\mathbf{Z}_t\mathbf{p})+\mathbf{e} \qquad (42)$$

where **y** is a vector of milk test-day records, **b** is a vector of fixed effects (heterosis, recombination loss, herd * test-day date, lactation stage, gestation stage and lactation period * calving season * calving period * breed regressed on age at calving), **h** is a vector of herd * period of calving random regression coefficients, **a** is a vector of additive genetic random regression coefficients, **p** is a vector of permanent environmental random regression coefficients, **e** is a vector of random residual;

X, W, $\mathbf{Z}_t$ are incidence matrices linking respectively **b**, **h**, **a** and **p** to **y**.

$\mathbf{Q}_{HF}$ and $\mathbf{Q}_{JE}$ matrices that are the covariate matrices for the second order Legendre polynomials inside breed composition.

The coefficient of heterosis measures the expression of the dominance effect, plus half of the additive by additive interaction between the breeds. It can be expressed as:

$$het_{ij}=s_i\times d_j+s_j\times d_i \qquad (43)$$

where s_i is the breed proportion for breed i in the sire and d_i is the breed proportion for breed i in the dam. For this genetic evaluation four breed classes were assigned for the calculation of heterosis and recombination effects, namely, HF, JE, AY, and other breeds.

The coefficient of recombination loss is twice the coefficient of additive by additive interaction expression minus the coefficient of heterosis:

$$r_{ij}=2AA_{ij}-het_{ij} \qquad (44)$$

where $AA_{ij}=2(p_i\times p_j)$ with p_i that is the individual breed proportion for breed i. The recombination loss was included to account for the possible effects of the break-up of coadapted gene complexes that may occur in F_2 or later breed crosses. Heterosis and recombination coefficients were summed across breed combinations.

4.2. Estimation of effects

Equations were solved using Preconditioned Conjugate Gradient and iteration on data [Tsuruta et al., 2001]. Estimation of effects was realized:

- with the (co)variance components estimated from model II;
- regardless of differences between breeds (**model III**);

For the last step, a reference animal was defined according to the proportion of HF and JE genes in the population used for the genetic evaluation. This allowed to take not into account of the differences between breeds for the estimation of breeding values.

4.3. Breeding values estimated: analysis

With random regressions, a breeding value is estimated for every DIM. Breeding values from first to 270th DIM for each animal were calculated and then were added together in order to obtain an overall value for lactation. The particularity of this work is to consider each animal as a potential mate within each of the two breeds. In this way, two overall breeding values were calculated for each animal, one for HF breed and one for JE breed as:

$$VAL_{HF}gen = (VAL_{HF}C*270) + (VAL_{HF}L*-53.8417) + (VAL_{HF}Q*-51.7466) \quad (45)$$

$$VAL_{JE}gen = (VAL_{JE}C*270) + (VAL_{JE}L*-53.8417) + (VAL_{JE}Q*-51.7466) \quad (46)$$

where **VAL C**, **VAL L** and **VAL Q** are estimated values of an animal by the model, used for genetic evaluation, for each of the three Legendre polynomials and VAL gen is the global breeding value.

RESULTS AND DISCUSSION

1. Introduction

In this chapter, only results useful for understanding are presented, other results are put in the annexes.

2. Description of the dairy population

In this part, the populations used for estimation of (co)variance components and for genetic evaluation are described and characterized.

2.1. Population of animals in first lactation

The results showed in Table 5 confirm the values of literature concerning the composition of the dairy population in New Zealand.

Table 5: Mean breed compositions of population of animals in first lactation.

Breed	Animals in first lactation (%)
HF	64.43
JE	33.01
AY	2.39
GU, SH and BRS	0.17

From this population, only animals of HF and JE breed were kept to estimate (co)variance components of purebred and crossbred herds.

2.2. Population used for genetic evaluation

Table 6 shows the breed composition of the cows used for the genetic evaluation. As expected in New Zealand, the percentage of crossbred animals was important. Our results were similar to the % reported by Montgomerie [2003].

Table 6: Composition of population used for the genetic evaluation.

Breed	Animals (%)
HF purebred	53.68
JE purebred	20.84
HF×JE crossbred	25.48

Figure 3 shows the average milk production as a function of DIM during the lactation for the two main breeds and their crosses. Peak of the lactation occurred around 25 DIM for all the three breed types with a more pronounced peak for HF cows. After peak, production of milk decreased and followed the same trend for all breeds. This general pattern can be explained by the extensive dairy breeding system, based on pastures, in New Zealand since quantity of feed decreases with time and production follows this closely.

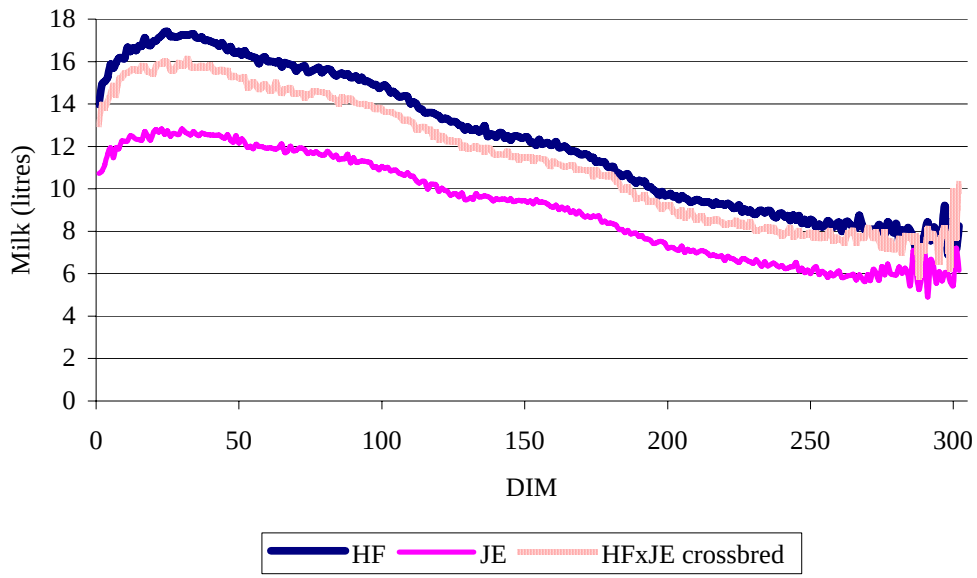

Figure 3: Average milk yield during the lactation for animals used for genetic evaluation.

As expected, the milk production of crossbred animals is closer to milk production of HF purebred animals than JE purebred animals. We can also notice that persistency of JE cows, defined as rate of decline, was higher than the one of HF cows.

3. Estimation of (co)variance components for purebred herds

This step has been realized only for milk trait for the animals in first lactation. (Co)variance components for milk yield were estimated using the Model P described in point 3.2.1 of Material and Methods.

3.1. Results

3.1.1. (Co)variance components estimation

The components were estimated for each HF samples and from these estimations a average of three samples was calculated. This average is presented in Table 7. The same was done for JE and the average of the two JE samples is shown in Table 8. VAL C, VAL L and VAL Q are variables of Legendre polynomials.

This results are difficult to analyze directly but we can notice that permanent environment effect accounted for the largest part of the variability, followed by additive genetic effect in both cases.

Table 7 : (Co)variance components (litres²) for milk estimated for HF purebred herds.

		(Co)variance components		
Residual variance ($\times 10^{-1}$)		17.771		
		VAL C	VAL L	VAL Q
Herd × calving period (co)variance ($\times 10^{-1}$)	VAL C	8.137		
	VAL L	- 4.035	3.945	
	VAL Q	- 0.365	-0.499	0.414
Permanent environment (co)variance ($\times 10^{-1}$)	VAL C	17.537		
	VAL L	-7.943	4.172	
	VAL Q	1.674	-1.971	3.268
Additive genetic (co)variance ($\times 10^{-1}$)	VAL C	12.355		
	VAL L	-2.414	1.810	
	VAL Q	-0.499	0.013	0.484

Table 8: (Co)variance components (litres²) for milk estimated for JE purebred herds.

		(Co)variance components		
Residual variance ($\times 10^{-1}$)		8.674		
		VAL C	VAL L	VAL Q
Herd × calving period (co)variance ($\times 10^{-1}$)	VAL C	6.623		
	VAL L	-3.833	2.430	
	VAL Q	1.503	-0.919	0.456
Permanent environment (co)variance ($\times 10^{-1}$)	VAL C	8.433		
	VAL L	-3.701	2.055	
	VAL Q	0. 601	-0.972	1.609
Additive genetic (co)variance ($\times 10^{-1}$)	VAL C	7.455		
	VAL L	-1.136	1.031	
	VAL Q	-0.177	0.218	0.330

Figures 4 and 5 represent variance components of HF and JE purebred animals as function of DIM. These Figures[8] show the effect of the use of random regressions, (co)variances of random effects (genetic, permanent environment and herd period) vary with DIM (see 3.4.2 of the literature review), therefore they were not constant during the lactation:

- Total variability was important at the beginning of the lactation and decreased after;
- Permanent environment and herd×period of calving variances followed the same pattern over the lactation;
- Additive genetic variance did not follow this same trend.

According to these figures, the largest part of the variability was represented by the permanent environment effect as cited before but was not followed by the additive genetic effect during the whole lactation. Indeed, in the start of the lactation herd×period of calving effect followed permanent environment effect during about 70 DIM for HF purebred animals and 110 DIM for JE purebred animals.

The magnitude of additive genetic variances during the lactation was lower than other variances for both breeds.

Residual variances were assumed to be constant for both (Figures 4 and 5) but residual variance of HF purebred herds was greater than the one of JE purebred herds, respectively 1.777 and 0.867 litres².

[8] Shape is specified by the function used in random regressions, Legendre polynomials in this work.

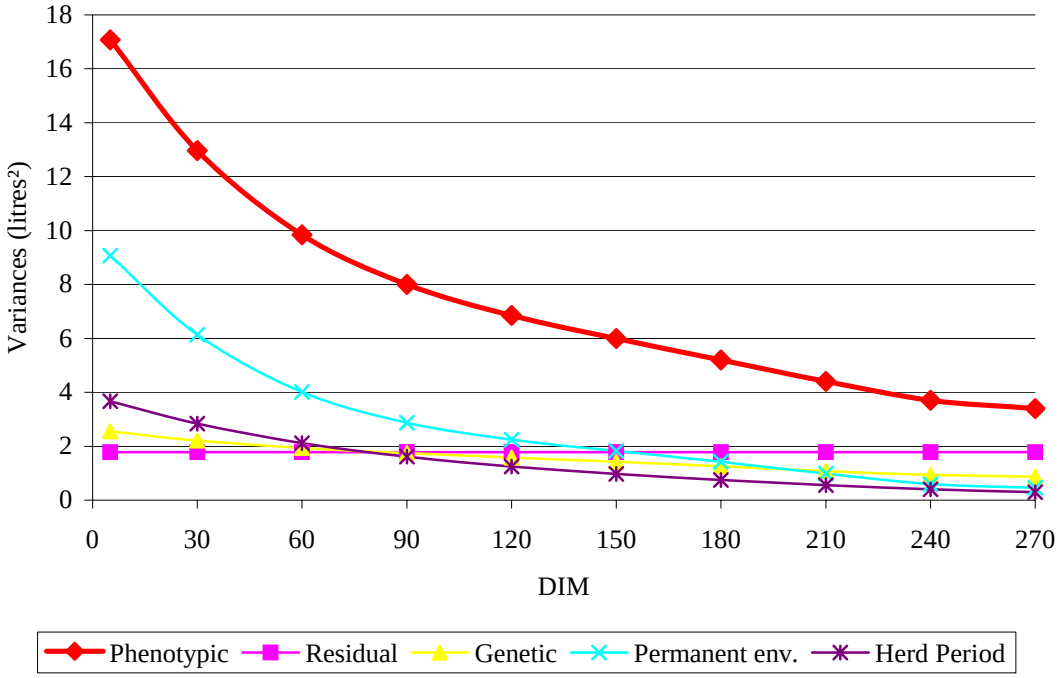

Figure 4: Variance components for milk as function of DIM estimated for HF purebred herds.

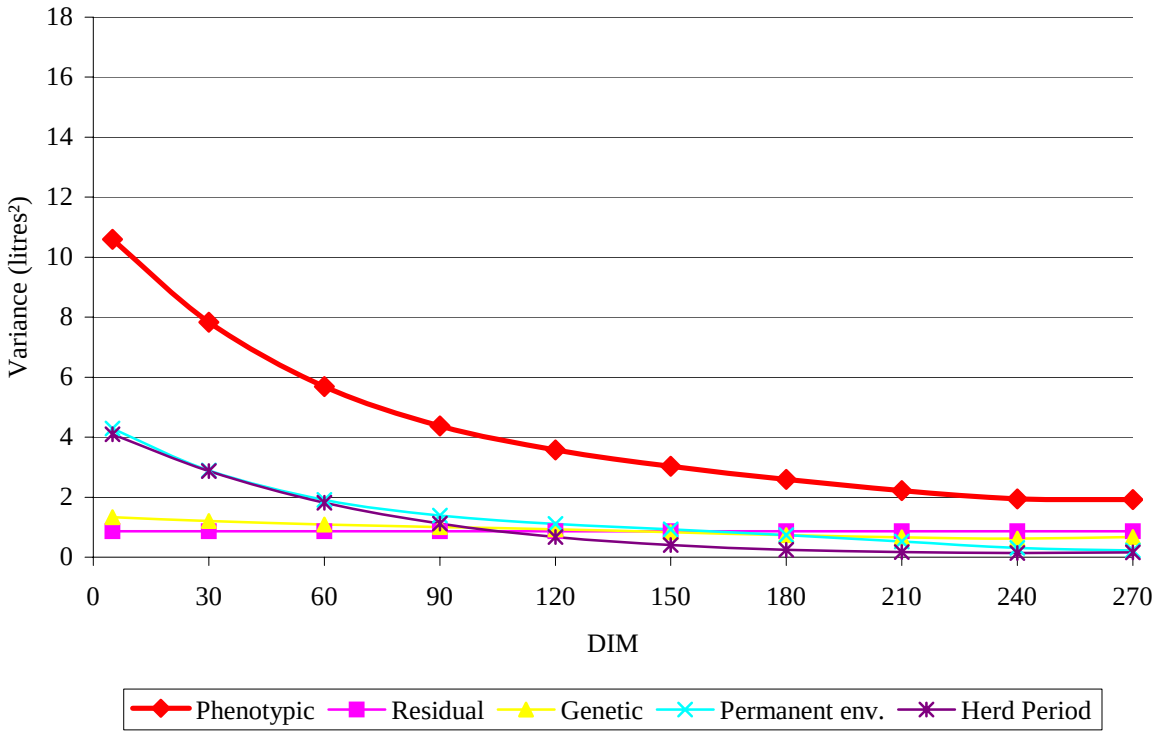

Figure 5: Variance components for milk as function of DIM estimated for JE purebred herds.

From these figures, we can notice that HF purebred animals presented a higher phenotypic variability than JE purebred animals.

At the start of the lactation variability of permanent environment was more important for HF purebreds than for JE purebreds and decreased after considerably (Figures 4 and 5) but the sum of permanent environment variances on 270 DIM for HF was twice the one for JE (Table 9).

Table 9 gives the first lactation variances and heritabilities (**h^2 270**) for milk production computed from estimation of (co)variance components within the HF and JE breeds.

Table 9: Variances and heritabilities calculated on 270 DIM for purebred herds.

Variances on 270 DIM (litres$^2 \times 10^{+6}$)	HF purebreds	JE purebreds
Phenotypic	32.00	18.50
Permanent env.	14.50	7.00
Genetic	9.91	5.87
Herd period	7.31	5.55
Residual	0.05	0.02
h^2 270	0.310	0.316

A comparison between HF and JE purebred herds concerning additive genetic variances and herd period variances is made in Figure 6.

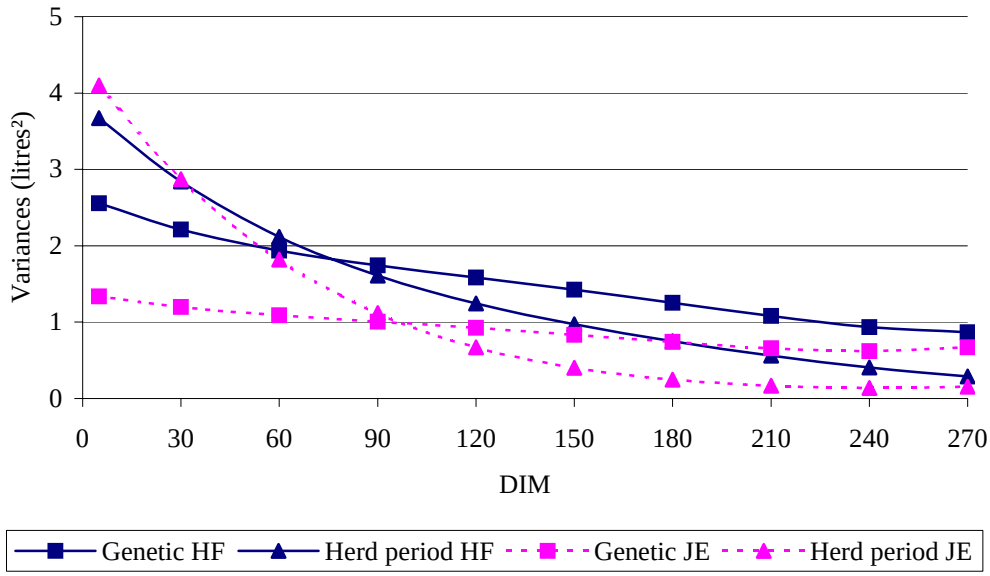

Figure 6: Comparison between additive genetic and herd period variances for milk as function of DIM estimated for HF and JE purebred herds.

According to Figure 6, JE breed showed a lower genetic variability than HF breed, this was confirmed by the genetic variances added on 270 DIM as indicated in Table 9. The same observation can be done for the herd period variances.

3.1.2. Heritabilities

Figure 7 shows evolution of the heritabilities for milk estimated for HF and JE purebred animals. The heritabilities increased from the beginning up to the end of the lactation for JE and remained essentially flat from 150 DIM up to the end for HF.

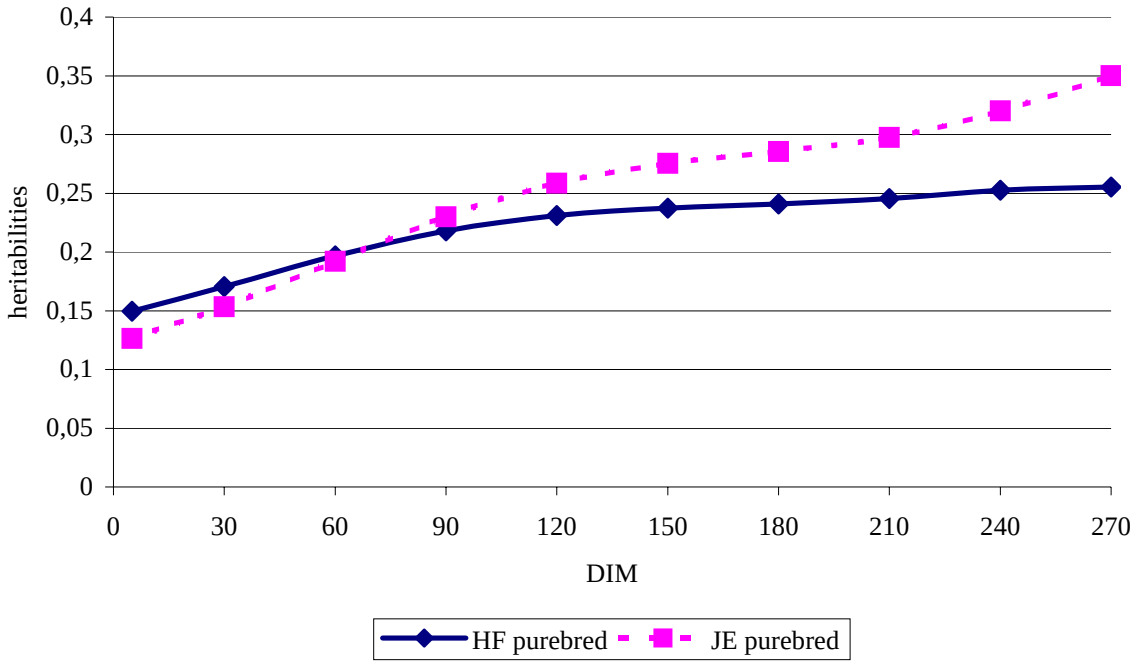

Figure 7: Heritabilities for milk as function of DIM estimated for HF and JE purebred herds.

According to this figure, HF purebred animals had a higher heritability than JE in the beginning of lactation up to 60 DIM. In the second part, the trend reversed. However, the sum of heritabilities on 270 DIM (Table 9) were similar for HF and JE purebred herds (respectively 0.310 and 0.316).

3.1.3. Correlations

In a RRM, variances vary during the lactation, as cited before. Correlation across TD records at different DIM can therefore also vary and this can be represented in graph (Figure 8) as a function of DIM. This graph shows that correlation between different stages of lactation were less than unity and decreased with increasing days between tests. In addition, there was not big differences between HF and JE purebreds.

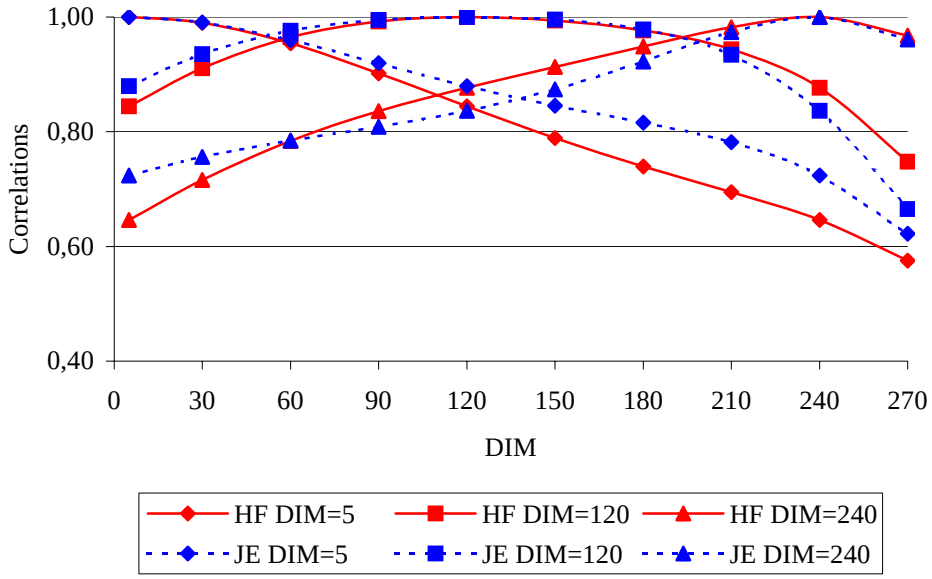

Figure 8: Genetic Correlation curves between DIM (5, 120 and 240) as function of DIM estimated for HF and JE purebred herds.

Tables 10 and 11 contain heritabilities (diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for milk estimated for HF and JE purebred herds.

Table 10: Heritabilities, genetic correlations and phenotypic correlations for milk among first lactation estimated for HF purebred herds.

	Days in milk (DIM)				
DIM	5	60	120	180	270
5	0.150	0.954	0.844	0.739	0.575
60	0.804	0.197	0.965	0.896	0.670
120	0.597	0.719	0.231	0.977	0.747
180	0.415	0.581	0.672	0.241	0.841
270	0.361	0.401	0.408	0.458	0.255

Table 11: Heritabilities, genetic correlations and phenotypic correlations for milk among first lactation estimated for JE purebred herds.

	Days in milk (DIM)				
DIM	5	60	120	180	270
5	0.126	0.960	0.880	0.816	0.622
60	0.840	0.192	0.976	0.925	0.630
120	0.648	0.746	0.259	0.978	0.665
180	0.471	0.608	0.684	0.285	0.782
270	0.466	0.479	0.457	0.447	0.350

On average, genetic and phenotypic correlations decreased as the length of time between intervals increased. Genetic correlations between DIM 5 and DIM 270 were high for HF and JE purebred animals (respectively 0.575 and 0.622), phenotypic correlations were lower (Tables 10 and 11). On average, genetic and phenotypic correlations between DIM were greater for JE animals than for HF animals.

3.2. Discussion and conclusion

As expected, these first results showed a difference between both breeds (Figures 5 and 6). Animals of HF breed had a greater variability than animals of JE breed (respectively, 32.00 and 18.50×10^{-6} litres²).

At genetic level, this could be explained by the great number of importations of HF genetic material from overseas (Canada, US, Europe,…) since the late 1960s. Moreover, the existence of two different HF strains (NZHF and IHF) in New Zealand could account for the higher genetic variability of HF breed. Harris and Kolver [2001] have reviewed the effect of Holsteinization on intensive pastoral dairy farming and discussed the differences between the two HF strains in New Zealand.

The differences of herd period variances between both breeds may be due to a difference of management between HF and JE purebred herds in New Zealand, moreover the higher stocking rates of JE breed could be an explanation of these differences of variability. An other assumption is that the geographical location and so the climate could be influenced the production level of herds but not the same manner for both breeds producing these differences.

Variability of permanent environment effect of HF purebreds was high in the beginning of the lactation and decreased considerably thereafter but stayed higher than the one of JE purebreds. This trend could be explained by the higher production level of HF breed and by the seasonal dairying system in New Zealand. Indeed, as shown in Figures 1 and 2 in

the literature review. In such a system animals express their differences in production level only when feed requirement can be met by grass growth.

However, both heritabilities on 270 DIM are more or less similar whereas some authors [e.g. Ahlborn and Dempfle, 1991] have demonstrated that heritabilities of JE tend to be higher than these of HF during the whole lactation; it was not the case in the beginning of the lactation in Figure 8. This may be explained by the fact that JE herds used in (co)variance components estimations for purebred herds were herds affected by selection. Animals used for selection show a high genetic level, but a low genetic variability. This assumption will be discussed more in details after the analysis of (co)variance components for crossbred herds.

Another residual variances were assumed to be constant during the whole lactation in each estimation and this assumption could lead to bias in heritability.

In conclusion, we can say that there are several differences between the two main breeds of dairy cattle in New Zealand. The genetic parameters for milk production in New Zealand HF and JE were computed within single breed however more than one third of the dairy cattle are composed of crossbred animals. This shows the rational behind our study as it might be useful to develop a model allowing to estimate the genetic parameter across breeds taking the crossbred animals into account.

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4. Estimation of (co)variance components across HF and JE

4.1. Model I

4.1.1. (Co)variance components estimation

The components estimated for each HF×JE sample were average and presented in Table 12. VAL_{HF} C, VAL_{HF} L and VAL_{HF} Q are variables of Legendre polynomials (constant, linear and quadratic) in function of breed (HF or JE).

Table 12: (Co)variance components (litres²) for milk estimated for crossbred herds using model I.

(Co)variance components							
Residual variance ($\times 10^{-1}$)		14.752					
		VAL_{HF} C	VAL_{HF} L	VAL_{HF} Q	VAL_{JE} C	VAL_{JE} L	VAL_{JE} Q
Herd×calving period (co)variance ($\times 10^{-1}$)	VAL_{HF} C	9.718					
	VAL_{HF} L	-4.923	4.603				
	VAL_{HF} Q	-0.425	-0.577	0.364			
	VAL_{JE} C	3.562	-1.572	-0.252	2.111		
	VAL_{JE} L	-1.595	1.794	-0.355	-0.274	1.610	
	VAL_{JE} Q	0.579	-0.781	0.055	0.074	-0.558	0.552
Permanent environment (co)variance ($\times 10^{-1}$)	VAL_{HF} C	20.776					
	VAL_{HF} L	-8.806	6.068				
	VAL_{HF} Q	2.079	-1.926	4.287			
	VAL_{JE} C	12.245	-5.455	1.446	7.382		
	VAL_{JE} L	-5.352	3.202	-1.067	-3.305	1.815	
	VAL_{JE} Q	1.228	-0.843	1.482	0.800	-0.497	0.585
Additive genetic (co)variance ($\times 10^{-1}$)	VAL_{HF} C	13.133					
	VAL_{HF} L	-2.458	2.382				
	VAL_{HF} Q	-0.474	0.071	1.595			
	VAL_{JE} C	10.856	-2.261	-0.459	10.509		
	VAL_{JE} L	-1.761	0.936	-0.099	-1.757	0.614	
	VAL_{JE} Q	-0.258	0.283	0.341	-0.294	0.101	0.182

The same remarks done in chapter 3.1. about the (co)variance components for purebred herds can apply to the ones of crossbred herds.

4.1.2. Heritabilities

Parameters of milk computed on 270 DIM, for animals of different breed composition are shown in Table 13; these components were estimated for purebred and crossbred animals using model I.

Table 13: Variances and heritabilities calculated on 270 DIM for purebred and crossbred animals using model I (crossbred herds).

Parameters on 270 DIM						
	Phenotypic variance (litres² × 10^{+4})	Permanent env. variance (litres² × 10^{+4})	Additive genetic variance (litres² × 10^{+4})	Herd period variance (litres² × 10^{+4})	Residual variance (litres² × 10^{+4})	h² 270
HF=1 and JE=0	36.6	17.3	10.5	8.75	0.04	0.288
HF=0 and JE=1	16.1	6.16	8.28	1.63	0.04	0.514
HF=0.5 and JE=0.5	24.1	11.0	9.03	4.11	0.04	0.374
HF=0.75 and JE=0.25	29.8	13.9	9.69	6.16	0.04	0.325
HF=0.25 and JE=0.75	19.6	8.37	9.56	2.60	0.04	0.437

4.1.3. Correlations

The correlation between both breeds was calculated for each Legendre polynomial in each effect, these correlations are presented in Table 14.

Table 14: Correlations between HF and JE breeds estimated from model I.

Correlations between HF and JE breeds		
Herd period effect	VAL C	0.786
	VAL L	0.659
	VAL Q	0.123
Permanent environment effect	VAL C	0.989
	VAL L	0.965
	VAL Q	0.936
Additive genetic effect	VAL C	0.924
	VAL L	0.774
	VAL Q	0.633

4.2. Model II

The aim of this model was to standardize residual variance, for that a weight using residual variances estimated for purebred herds was calculated in function of breed proportions.

4.2.1. (Co)variance components estimation

The average estimates of (co)variance components calculated from the same five samples which those used with model I and are presented in Table 15.

Table 15: (Co)variance components (litres²) for milk estimated for crossbred herds using model II.

(Co)variance components							
Residual variance ($\times 10^{-1}$)		15.154					
		VAL_{HF} C	VAL_{HF} L	VAL_{HF} Q	VAL_{JE} C	VAL_{JE} L	VAL_{JE} Q
Herd × calving period (co)variance ($\times 10^{-1}$)	VAL_{HF} C	9.331					
	VAL_{HF} L	-4.841	4.299				
	VAL_{HF} Q	-0.357	-0.468	0.334			
	VAL_{JE} C	3.172	-1.395	-0.228	1.890		
	VAL_{JE} L	-1.424	1.590	-0.349	-0.159	1.548	
	VAL_{JE} Q	0.497	-0.725	-0.020	0.034	-0.449	0.702
Permanent environment (co)variance ($\times 10^{-1}$)	VAL_{HF} C	20.289					
	VAL_{HF} L	-8.876	5.415				
	VAL_{HF} Q	1.998	-2.055	3.960			
	VAL_{JE} C	12.617	-5.663	1.371	8.016		
	VAL_{JE} L	-5.552	3.168	-1.280	-3.574	1.953	
	VAL_{JE} Q	1.144	-1.038	1.817	0.776	-0.663	0.903
Additive genetic (co)variance ($\times 10^{-1}$)	VAL_{HF} C	12.690					
	VAL_{HF} L	-2.409	2.162				
	VAL_{HF} Q	-0.479	0.046	1.155			
	VAL_{JE} C	11.047	-2.290	-0.467	11.225		
	VAL_{JE} L	-1.778	1.011	-0.092	-1.864	0.727	
	VAL_{JE} Q	-0.261	0.301	0.296	-0.310	0.129	0.208

The same observations can be made about estimates of variances: the largest part of variability was accounted for by permanent environment effect, followed by additive genetic effect and by herd period effect. Records were weight in order to allow breed differences for

residual variances. The reported residual variance is therefore the residual variance of an animal with a mean breed composition.

Figure 9 represents the variances by DIM for milk estimated for animals whose the proportion of genes were 100% HF or JE (**HF=1 and JE=0 or HF=0 and JE=1**); these components were estimated from TD records of crossbred herds data (i.e. herds composed of purebred and crossbred animals) using Model II. This figure shows that the permanent environment, genetic and herd period variances were higher for HF purebred animals, thus HF animals had a greater variability than animals of JE purebred animals as found in previous chapter.

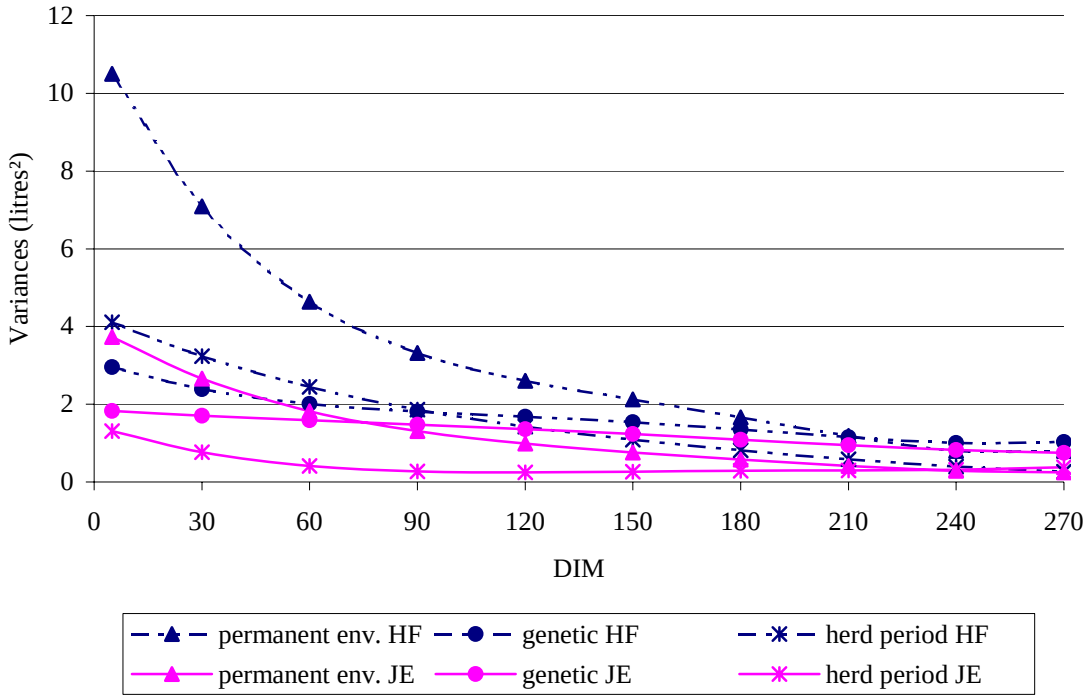

Figure 9: Variance components for milk as a function of DIM estimated for HF=1 and JE=1 (purebred) animals using Model II (crossbred herds).

From (co)variances matrices (Table 15), variances for milk as function of DIM were estimated for HF×JE crossbred animals. These animals were defined as first-cross (F1) between two purebred animals (**HF=0.5 and JE=0.5**) and second-cross (**F2**) between F1 and purebred animals (**HF=0.75 or 0.25 and JE=0.25 or 0.75**). The results were similar, only phenotypic variances for milk are represented as function of DIM in Figure 10 for these crossbred animals but also purebred animals.

Phenotypic variances for HF×JE crossbred animals were in-between both purebred animals and followed the same trend than purebred animals. Values of phenotypic variances presented in Table 16 provided confirmation of this fact. This seems consistent seeing that crossbred animals are combinations of both breeds.

The heritabilities for milk, represented in Figure 11, followed the same pattern over the lactation as did the phenotypic variances. Values of Table 16 confirmed this observation.

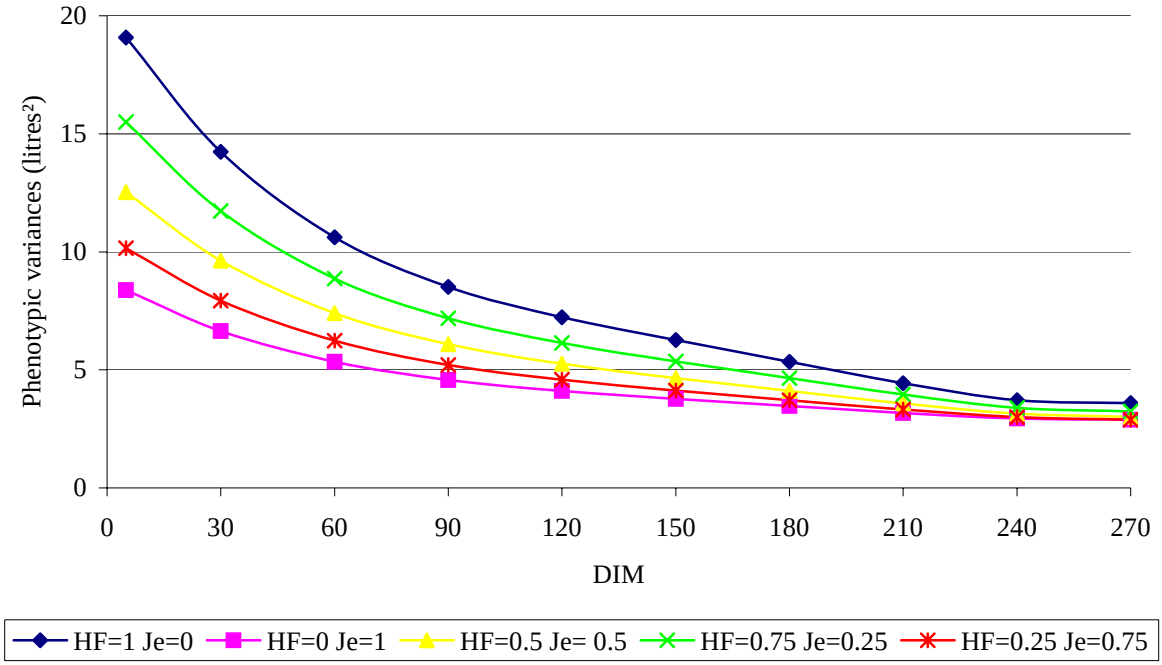

Figure 10: Phenotypic variances for milk as function of DIM estimated for purebred and crossbred animals using Model II (crossbred herds).

Table 16 contains first lactation variances and heritabilities for milk computed on 270 DIM using estimates of (co)variance components from Model II.

Table 16: Variances and heritabilities calculated on 270 DIM for purebred and crossbred animals using Model II (crossbred herds).

	Parameters on 270 DIM					
	Phenotypic variance (litres² × 10^{+4})	Permanent env. variance (litres² × 10^{+4})	Additive genetic variance (litres² × 10^{+4})	Herd period variance (litres² × 10^{+4})	Residual variance (litres² × 10^{+4})	h² 270
HF=1 and JE=0	35.6	17.0	10.2	8.42	0.04	0.286
HF=0 and JE=1	17.0	6.71	8.85	1.45	0.04	0.519
HF=0.5 and JE=0.5	24.2	11.2	9.15	3.82	0.04	0.378
HF=0.75 and JE=0.25	29.4	13.9	9.58	5.84	0.04	0.326
HF=0.25 and JE=0.75	20.1	8.79	8.91	2.36	0.04	0.443

4.2.2. Heritabilities.

Figure 11 shows that the heritabilities for milk as function of DIM were low at the beginning and the end of the lactation whereas were higher towards mid-lactation for JE purebred and crossbred animals. The change in heritability over the lactation is more a function of changes in the permanent environment and herd period variances over time than a change in the genetic variances (Figure 9).

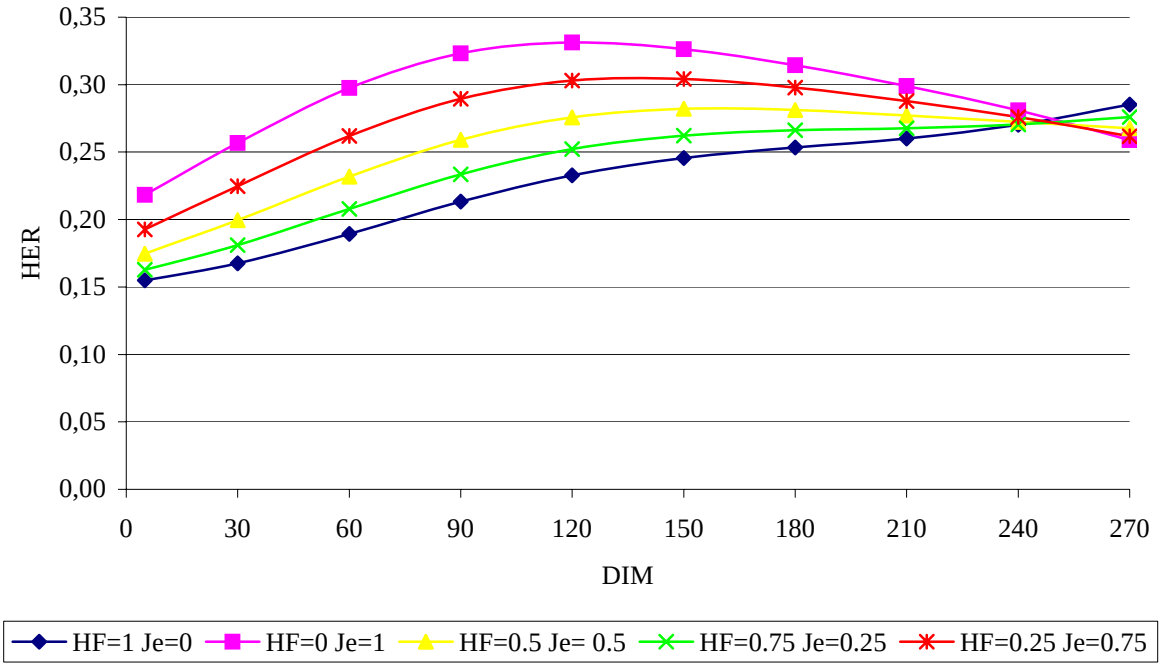

Figure 11: Heritabilities for milk as function of DIM estimated for purebred and crossbred animals using model II (crossbred herds).

According this Figure, JE purebred animals had a higher heritability than HF animals during the whole lactation. Heritability estimated on 270 DIM, as showed in Table 16, confirmed this observation; heritabilities were 0.286 for HF purebred animals and 0.519 for JE purebreds.

4.2.3. Correlations

The heritabilities, genetic and phenotypic correlations obtained from the Model II are shown in Table 17 for HF purebred animals and in Table 18 for JE purebred animals.

Table 17: Heritabilities (diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for milk among first lactation estimated for HF=1 animals.

	Days in milk (DIM)				
DIM	5	60	120	180	270
5	0.155	0.916	0.729	0.604	0.540
60	0.829	0.189	0.941	0.855	0.599
120	0.609	0.755	0.233	0.972	0.632
180	0.420	0.611	0.711	0.253	0.732
270	0.378	0.401	0.397	0.421	0.270

Table 18: Heritabilities (diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for milk among first lactation estimated JE=1 animals.

	Days in milk (DIM)				
DIM	5	60	120	180	270
5	0.218	0.981	0.943	0.918	0.845
60	0.719	0.297	0.989	0.971	0.855
120	0.537	0.625	0.331	0.993	0.865
180	0.391	0.515	0.575	0.314	0.907
270	0.347	0.384	0.397	0.413	0.281

The values of heritabilities are in line with literature, nevertheless slightly lower. Comparison of Tables 17 and 18 shows that the correlations had similar trends throughout the lactation, but some differences were evident in the magnitude of these estimated correlations. The highest difference between the genetic correlations occurred at the 5^{th} and 180^{th} DIM, where the estimated correlation was 60.4% for HF purebred animals and 91.8% for JE purebreds.

In Table 19, genetic and phenotypic correlations estimated for F1 crossbred animals (50% HF 50% JE) are presented. These values were intermediate at the correlations for purebred animals, the same trend was followed by the other crossbred animals.

Table 19: Heritabilities (diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for milk among first lactation estimated for crossbred animals (0.5 HF 0.5 JE).

	Days in milk (DIM)				
DIM	5	60	120	180	270
5	0.175	0.954	0.858	0.789	0.705
60	0.787	0.232	0.971	0.926	0.748
120	0.594	0.698	0.276	0.984	0.774
180	0.426	0.570	0.645	0.281	0.840
270	0.374	0.409	0.414	0.425	0.268

For each polynomial of each effect, correlations between HF and JE breeds were estimated; Table 20 contains these correlations. Correlations of additive genetic effect were below 1 and therefore confirmed the differences between HF and JE breeds, observed from the analysis inside breeds.

Table 20: Correlations between HF and JE breeds estimated from Model II.

Correlations between HF and JE breeds		
Herd period effect	VAL C	0.755
	VAL L	0.616
	VAL Q	-0.040
Permanent environment effect	VAL C	0.989
	VAL L	0.974
	VAL Q	0.961
Additive genetic effect	VAL C	0.926
	VAL L	0.807
	VAL Q	0.604

We can notice that correlations of permanent environment effect between HF and JE breeds were high, close to unity, that seems to be consistent since the environment was the same for both breeds. Herd period correlations were lower.

4.3. Comparison between Models I and II

The comparison of (co)variance components of both models shows there were few differences between results of Models I and II, therefore introduction of the weight produced no great changes among residual, herd period, permanent environment and genetic variances.

These observations were confirmed by the estimation of variances and heritabilities on 270 DIM (Tables 13 and 16).

Model II allowed to replace residual variance of the animal by the expected one and so to model more correctly residual variance in function of breed proportion. However, residual variance estimated using Model I was lower than the one estimated using Model II (respectively, 1.475 and 1.515 litres^2).

Thus, only Model II was used to estimate the (co)variance components in the rest of this work. However, this model didn't consider non-additive genetic variation (dominance, epstasis,…) and therefore this might have biased the estimation of variance components and additive genetic parameters. The predictions of breeding values might be influenced as well. In order to reduce the problem of bias in genetic evaluation, the model used to estimate the breeding values took non-additive effects due to interaction between breeds (heterosis and recombination loss) into account (see Material and Methods).

5. Comparison between results for purebred and across breeds

Variances, heritabilities and correlations estimated for milk using model of purebreds (Model P) and the model across breeds (Model II) are compared in this part.

5.1. Variance components estimation

The evolution of variance components in function of DIM are presented in graphs (Figures 12, 13 and 14) that are easier to analyze than tables (Tables 7, 8 and 15) to compare estimated variance components for purebred animals using Model P and Model II.

Figure 12 shows there were few differences of permanent environment variances between Model P (dotted lines) and Model II (straight lines).

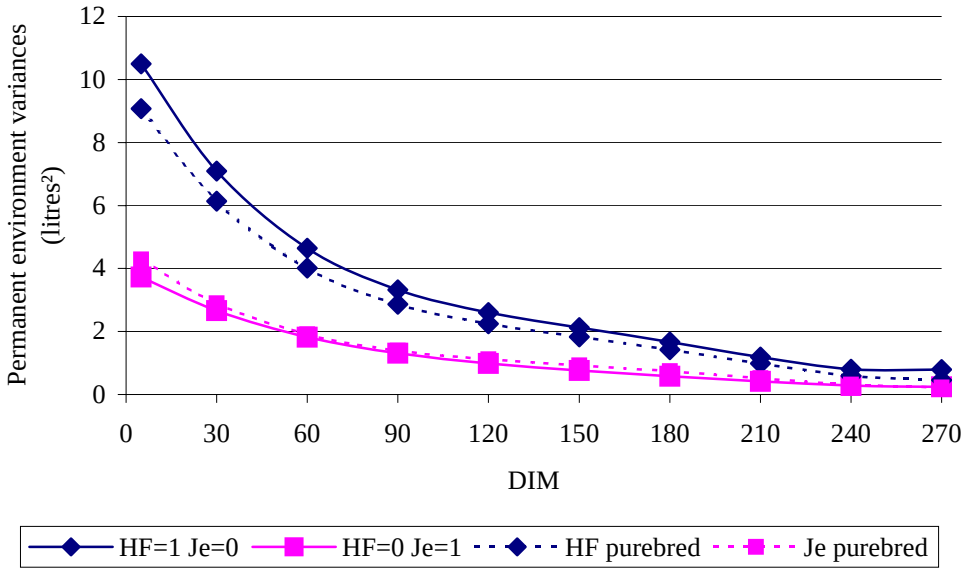

Figure 12: Permanent environment variances for milk as function of DIM estimated for HF and JE purebred animals using Model P and Model II.

By the previous graph, the permanent environment variances of HF purebreds from Model P were lower than HF purebreds from Model II and inverted trend for JE animals. The values of permanent environment variances on 270 DIM confirmed these observations (Tables 9 and 16).

As shown by Figure 13, differences between the herd period variances obtained from Model P and Model II were evident at the beginning of the lactation, especially for JE breed; the variances were higher for the JE purebred animals in the beginning up to 150 DIM.

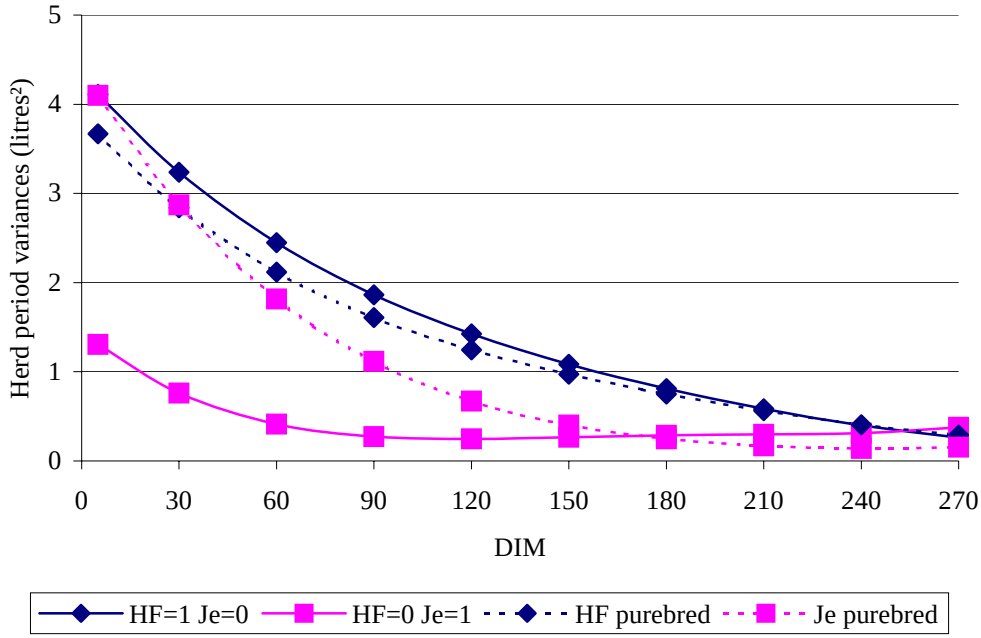

Figure 13: Herd period variances for milk as function of DIM estimated for HF and JE purebred animals using Model P and Model II.

As shown in Figure 14, the genetic variances estimated for purebred animals using Model II were higher than those from Model P, mainly for JE animals. The consequence of this was heritabilities were higher than those calculated from Model P.

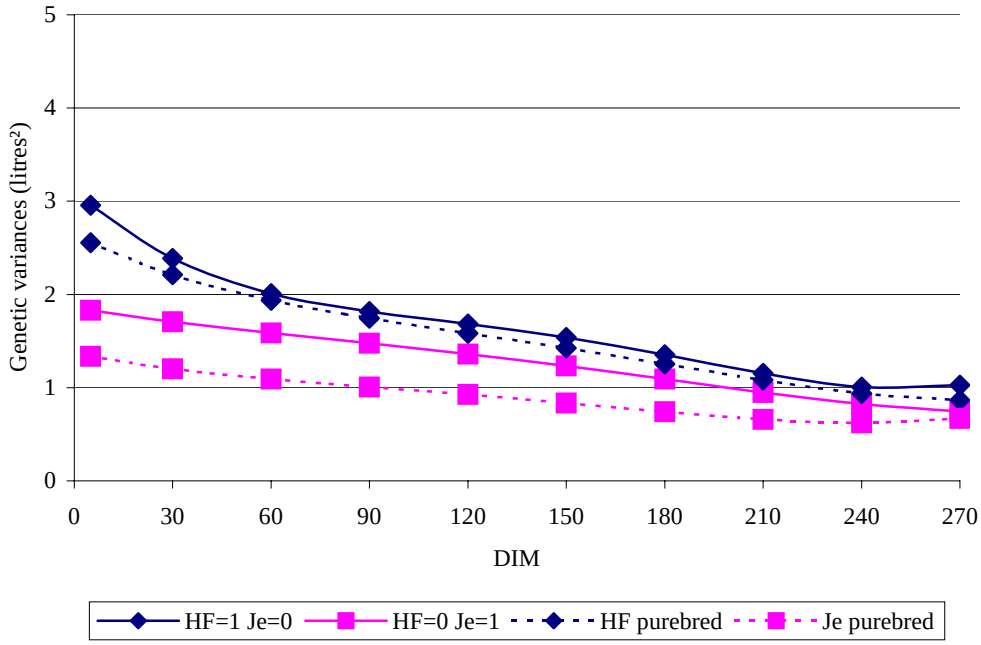

Figure 14: Additive genetic variances for milk as function of DIM estimated for HF and JE purebred animals using Model P and Model II.

Indeed, this difference between heritabilities estimated from purebred herds and estimated from crossbred herds is illustrated in Figure 15.

5.2. Heritabilities

As cited before, the heritabilities estimated for JE purebred animals using Model II were higher than those obtained from Model P but the heritabilities for HF purebred animals were similar for both models (Figure 15). Moreover, heritabilities from Model II for HF purebreds were lower than for JE purebreds during the whole lactation excepted at the end.

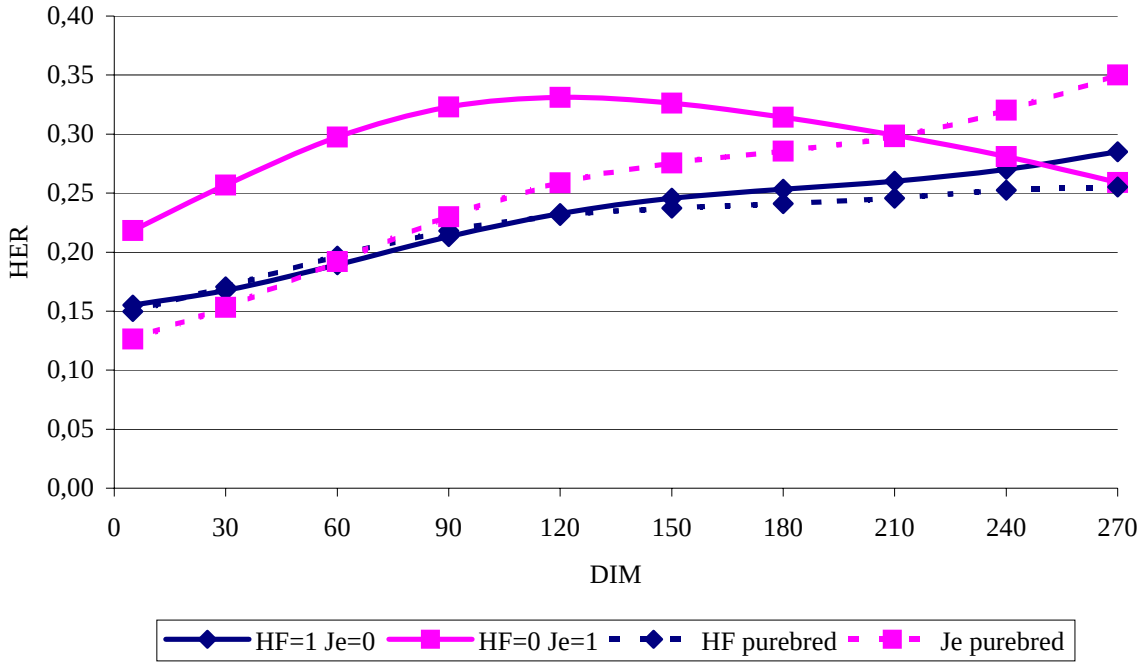

Figure 15: Heritabilities for milk as a function of DIM estimated for HF and JE purebred animals.

5.3. Correlations

Genetic correlations estimated between DIM of the 270-day lactation using Model P were on average higher for HF animals (Table 10) and lower for JE animals (Table 11) than those estimated from Model II (Tables 17 and 18 respectively).

5.4. Discussion and conclusion

The consequence of evolution of variance component was a variability of heritabilties obtained during different stages of lactation. Most of studies on genetic parameters [e.g. Ahlborn and Dempfle, 1991] have shown that the heritabilities of milk in function of DIM were low at the beginning and end of the lactation, whereas were higher towards mid-lactation. The heritabilities estimated for JE purebred and crossbred animals using Model II showed more or less this trend (figure 11). However, the heritabilities computed for purebred

animals using Model P did not show the same trend especially for JE heritabilitity curve (figure 14). Because heritability is a ratio of the additive genetic and phenotypic variances, a difference in heritability could be a result of difference in the numerator, denominator, or both. In this way, the difference between heritability curves of JE breed of both models may be explained by the fact that JE herds used in (co)variance components estimations for purebred herds were herds affected by selection and therefore showed a high genetic level but a low genetic variability. As shown in figure 14, additive genetic variances of JE purebred animals from crossbred herds (Model II) were higher than the ones from purebred herds (Model P). Thus, JE purebred animals from crossbred herds presented higher heritabilities than JE animals from purebred herds. Also, these heritabilities were higher than heritabilities of HF purebred animals (0.519 and 0.286 respectively) which goes in the direction of breed difference found in literature, even if our differences were very large. In order to compare, the heritability for milk estimated across breed using the current national genetic evaluation system of New Zealand is 0.35 [INTERBULL, 2004].

The estimated permanent environment variances were more or less similar and were characterized by high permanent environment variances at the beginning of the lactation and considerably decrease thereafter, for HF purebred animals in both models: Model P and Model II (figure 12). Some explanations of this have been discussed in details in 3.2 of this chapter.

The herd period variances presented some differences between breeds but also between estimates from Model P and Model II. The differences between breeds have been discussed in details in 3.2 of this chapter. Concerning differences between the two models, we sampled in a way that purebred herds were not the same for crossbred herds. Therefore, may be some other factors like the geographical location, the climate, the number of animals in herd, or the kind of herds could have had an influence.

In conclusion, excepted the genetic and herd period variances for JE animals, curves of variances in function of DIM for purebred animals showed few differences between both models. Furthermore, variances calculated on 270 DIM for HF animals using Model II were higher than those using Model P, except residual variance was lower. For JE animals, the opposite trend was observed excepting for genetic variance as explained before. We can think that the model II is an accurate and efficiency model to estimate genetic parameters of dairy cattle in New Zealand.

6. Genetic evaluation

Breeding values were used as a tool to show consequences of the use of a model allowing for breed differences.

6.1. Model II with differences between breeds

Breeding values from first to 270th DIM for each animal were calculated and then were added together in order to obtain two global values for lactation since the particularity of this work was to consider each animal as a potential mate within each of the two breeds. In this way two overall breeding values were calculated for each animal:

- one for HF breed (**BV HF**), that considered the animal like a 100% HF even if the animal was a JE purebred or HF×JE crossbred;
- and one for JE breed (**BV JE**) that considered the animal like a 100% JE even if the animal was a HF purebred or HF×JE crossbred.

Table 21 provides a summary statistics for animals used in the genetic evaluation, for cows in production (from 1987 to 2000). The extreme values observed for minimum of BV HF and maximum of BV JE were a particular case where solutions showed a strange behaviour[9] for an animal.

Table 21: Summary statistic for breeding values (litres) estimated for milk using Model II.

		Number	Mean	Std Deviation	Minimum	Maximum
Cows in production	BV HF	208164	271.004	217.102	-6502.64	1693.77
	BV JE		501.109	256.156	-735.29	5457.82

These breeding values were fitted by mean of breeding values of all animals born in 1995. Table 22 contains some statistics of these fitted breeding values (**fitted BV HF and fitted BV JE**).

[9] A special pattern probably linked to multicolinearity appeared for a single 50% HF, 50% JE cow where a low BV HF was associated to a high BV JE, her average BV staying in a normal range.

Table 22: Summary statistic for fitted breeding values (litres) estimated for milk using Model II.

	Fitted BV	Number	Mean	Std Deviation	Minimum	Maximum
Cows in production	HF	208164	-5.255	217.102	-6778.90	1417.51
	JE		-28.338	256.156	-1264.73	4928.38

Illustrated in Figure 16, the genetic trends for milk by year of birth for cows in production was positive and increased over time for both kinds of fitted breeding values. The HF genetic trend was greater than JE trend, this could be explained by the high production level of HF breed but also by the high selection intensity on the bull-to-cow and the dam-to-bull. We could supposed there was a selection for milk yield too, even if selection for fat and protein yields is more severe.

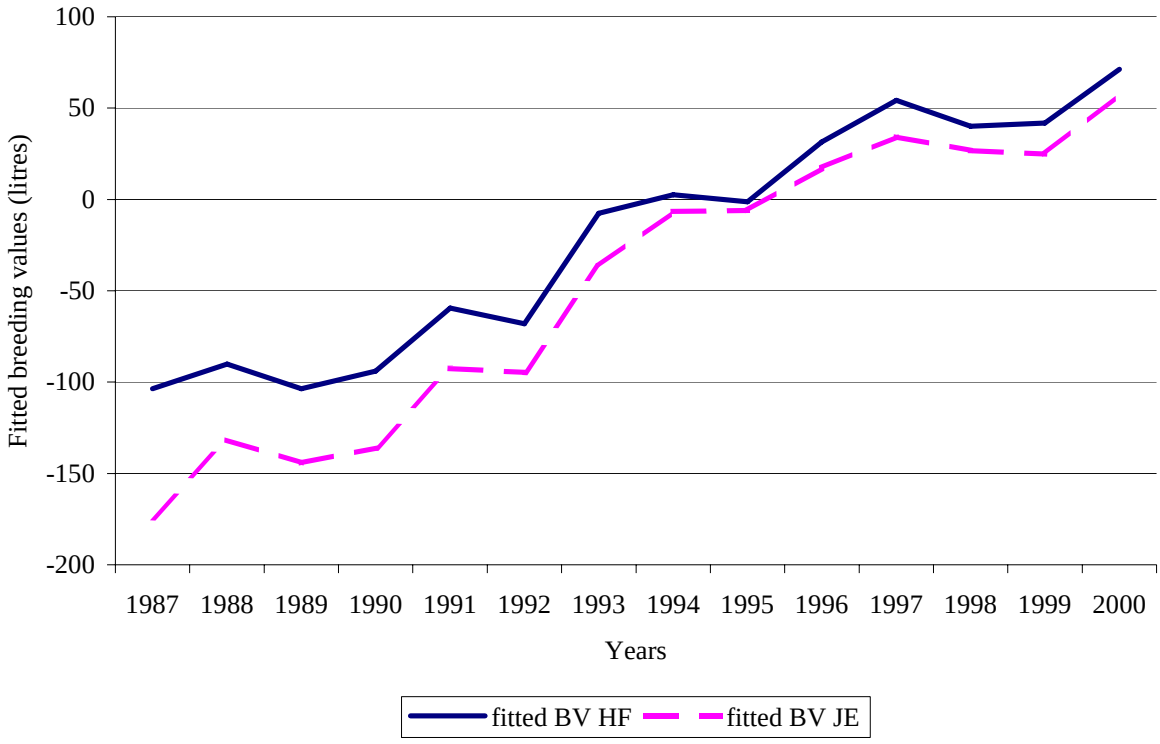

Figure 16: Genetic trend of cows in production computed using Model II.

Table 23 gives within breed summary statistics for cows in production, in which there were 53.95% of HF purebred animals, 20.64% of JE purebred animals and 25.41% of crossbred animals. The genetic trend for milk by breed is showed in Figures 17 and 18.

Table 23: Summary statistics for fitted breeding values (litres) by "breed" for cows in production.

	Fitted BV	Number	Mean	Std Deviation	Minimum	Maximum
HF purebreds	HF	112303	11.769	216.642	-1000.36	1058.64
	JE		84.692	211.076	-825.21	1314.93
JE purebreds	HF	42975	-47.416	205.650	-1590.52	1417.51
	JE		-273.416	205.766	-1264.73	1243.57
HF×JE crossbreds	HF	52886	-7.146	222.326	-6778.90	1205.27
	JE		-69.207	227.270	-1094.07	4928.38

The fitted breeding values were on average greater for HF purebred animals than for JE purebred and HF×JE crossbred animals (Figures 17 and 18), the ones of JE purebred animals were the lowest in both cases.

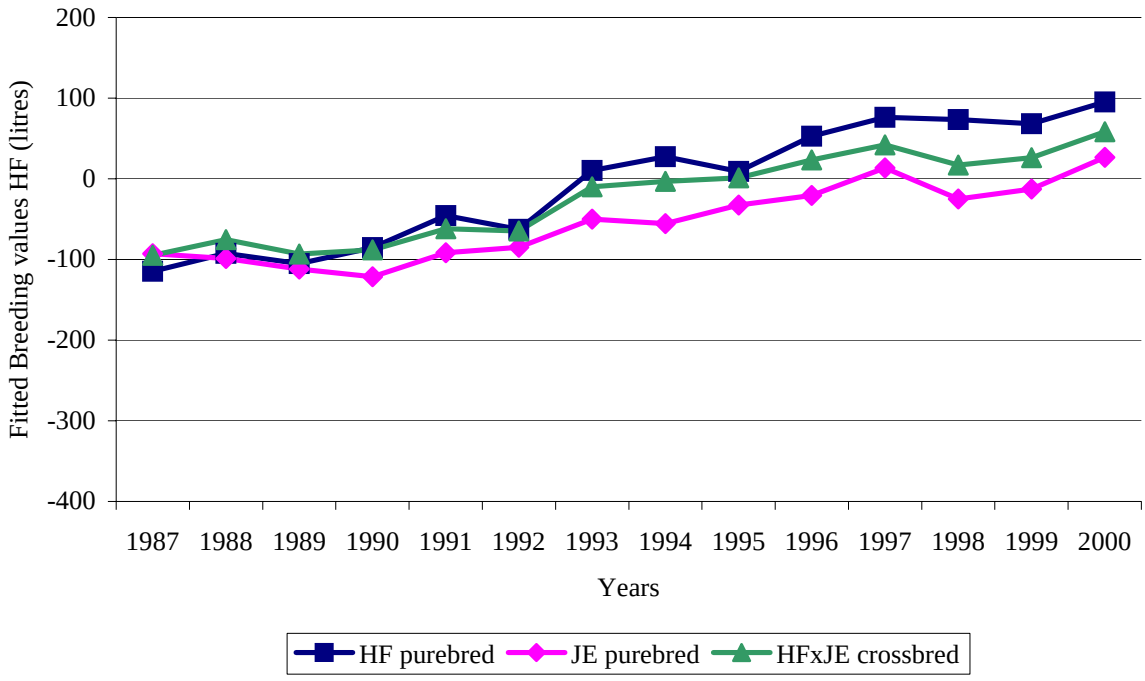

Figure 17: Genetic trend for milk by breed for fitted BV HF.

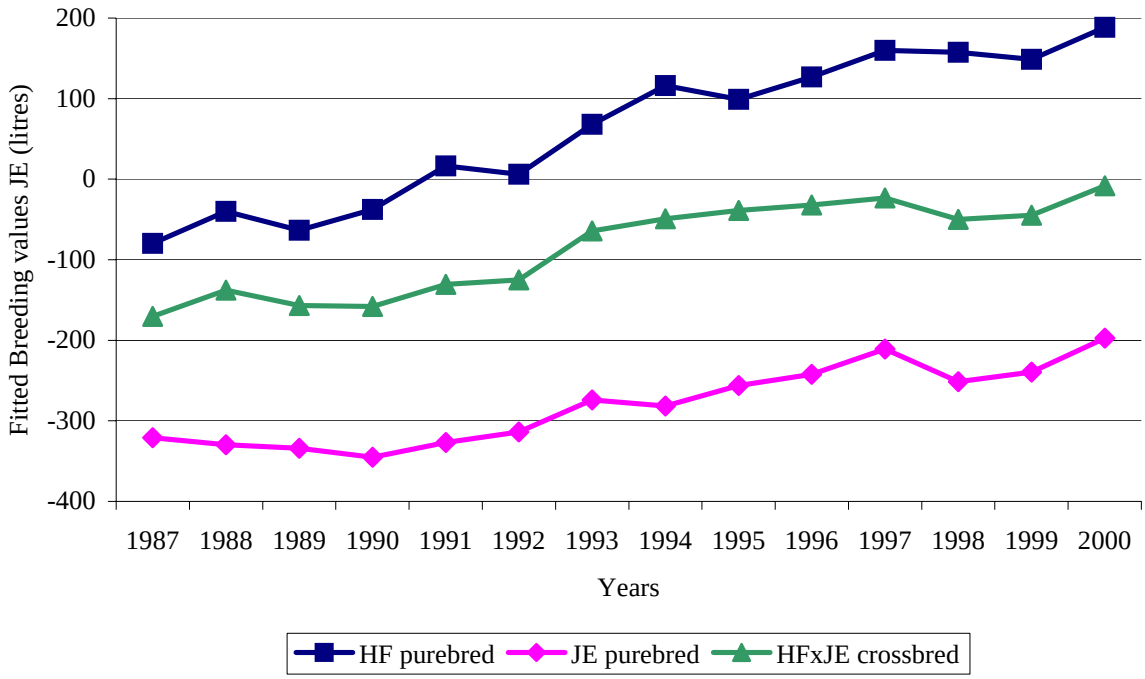

Figure 18: Genetic trend for milk by breed for fitted BV JE.

The comparison between both figures shows some differences in the magnitude of the increase of these fitted breeding values. The highest difference between the values occurred for HF purebred animals where the genetic trend increased of 209,6 litres for fitted BV HF and 267,9 litres for fitted BV JE from 1987 to 2000 and this last value was the highest milk gain during this period. In addition, the high fitted BV JE estimated for HF purebred animals demonstrated the usefulness of upgrading to HF strategy to improve JE cattle. Thus, the HF purebred animals were the best potential mates within both breeds followed by crossbred animals.

Moreover, these results confirmed the superiority of crossbred animals on JE purebred animals, so the HF×JE crossbreeding provides a good opportunities to increase milk production rather than by the selection within the JE breed.

6.2. Model III without differences between breeds

In this model, the assumption was made that there were no differences between HF and JE breeds, thus animals were considered as similar from a genetic point of view. In this way, all animals had 66% genes of HF breed and 33% genes of JE breed which was the racial proportion in the concerned population. Thus, all animals were considered as “crossbred animals” for the estimation of the additive genetic effect.

With this model, the genetic variances of HF purebred animals were lower than the estimated values used in Model II and those of JE purebreds were higher. Therefore, the

heritabilities of HF purebred and crossbred (75 HF 25 JE) animals were "overestimated" whereas the heritabilities of JE purebred and crossbred animals (50-50 and 25-75) were "underestimated" as illustrated in Figure 19.

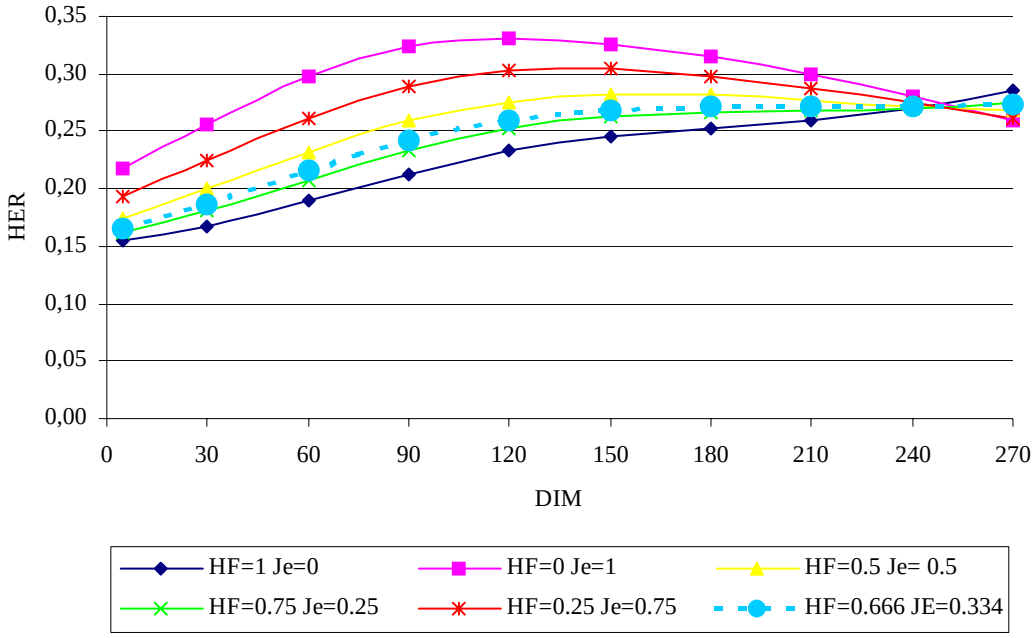

Figure 19: Heritabilities for milk as function of DIM estimated for crossbred herds using Model II and for basis animal using Model III.

Table 24 presents some statistics for fitted breeding values estimated for all animals and cows in production using Model III. The comparison between Tables 22 and 24 shows that with Model III the fitted BV HF decreased and the fitted BV JE increased in comparison with the ones estimated from Model II.

Table 24: Summary statistics for fitted breeding values (litres) estimated for milk using Model III.

	Fitted BV	Number	Mean	Std Deviation	Minimum	Maximum
All animals	HF	403919	-61.220	238.918	-7132.76	1417.51
	JE		-42.338	181.166	-3179.37	2900.29
Cows in production	HF	208164	-14.575	248.163	-1132.72	1278.02
	JE		-6.985	203.800	-989.93	1095.75

However, the genetic trend, illustrated in Figure 20, presented no differences between fitted BV HF and fitted BV JE; and the Spearman's correlation coefficients were high between these both values (Table 27).

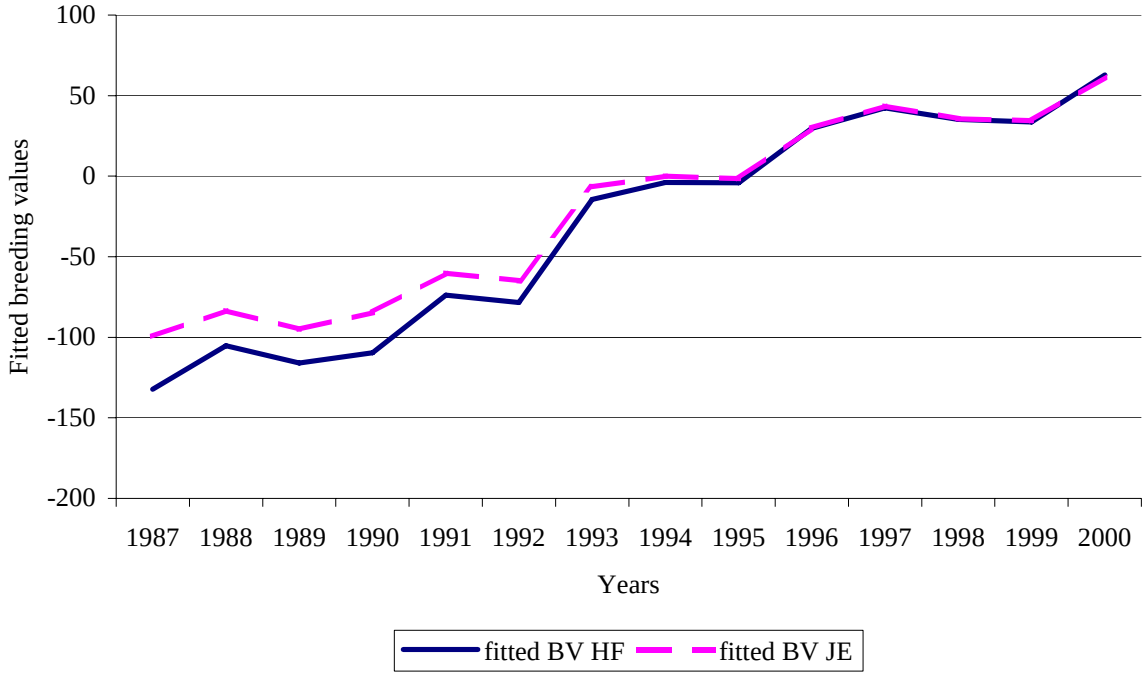

Figure 20: Genetic trend of cows in production computed using Model III.

These statements allowed to assume a "average" breeding value (**average BV**) for each animal which was a combination of these two values according the breed proportion of the considered population. This average BV was calculated for each animals as:

$$\text{average BV} = (0.666 \times \text{BV HF}) + (0.334 \times \text{BV JE})$$

The summary statistics of these average BV are presented in Table 25 for all animals and for cows in production.

Table 25: Summary statistics for "average" breeding values (litres) computed for milk.

	Number	Mean	Std Deviation	Minimum	Maximum
All animals	403919	209.267	217.629	-5548	6229
Cows in production	208164	252.141	232.028	-820.54035	1481

6.3. Sires ranking

Only the sires of cows in production were used and analysed. There were 3,296 sires of 208,164 cows, since their breeding values were estimated from the performance of their daughters and the genetic parameters of their relatives too. Thus, these values were more accurate than the ones of sires without daughters' performances recorded.

The Spearman rank correlation coefficients were computed for breeding values (BV HF and BV JE) for both models, these coefficients were high but not equal to unity (Tables 26 and 27). Therefore, the arrangement of sires was different following the breeding value taken account (BV HF or BV JE).

Tables 26 and 27 give Spearman rank correlation coefficients for sires using Model II and Model III. These coefficients were high between breeding values estimated from Model III and they were higher than the ones for Model II.

Table 26: Spearman rank correlation and breeding values for sires using Model II.

Year of birth	Number of sires	BV	Mean	Std Deviation	Correlation
< 1980	73	HF	140.907	181.614	0.818
		JE	339.965	284.882	
1980-1984	157	HF	224.593	231.593	0.870
		JE	463.645	333.148	
1985-1989	893	HF	233.872	256.799	0.812
		JE	482.261	328.077	
1990-1994	1080	HF	356.675	267.589	0.828
		JE	609.222	339.771	
1995-2000	1093	HF	405.093	274.634	0.840
		JE	633.936	353.548	
All	3296	HF	328.385	274.745	0.830
		JE	570.121	347.927	

Table 27: Spearman rank correlation and "average" breeding values for sires using Model III.

Year of birth	Number of sires	BV	Mean	Std Deviation	Correlation
< 1980	73	HF	149.686	253.670	0.945
		JE	19.864	174.033	
1980-1984	157	HF	260.445	307.155	0.962
		JE	102.605	226.913	
1985-1989	893	HF	267.246	307.089	0.948
		JE	107.670	238.751	
1990-1994	1080	HF	390.329	326.919	0.963
		JE	218.538	257.224	
1995-2000	1093	HF	425.914	339.685	0.966
		JE	258.651	296.891	
All	3296	HF	357.265	331.903	0.960
		JE	191.880	261.673	

From these results (Table 27), the average BV were calculated. According the kind of breeding value, an animal could have a different ranking among the other animals; Spearman rank correlation coefficients allow to give the degree of difference between two rankings. These coefficients were computed for each kind of breeding value, the results were 0.943 between average BV and BV HF and 0.957 between average BV and BV JE. As cited before, it was 0.830 between BV HF and BV JE. Therefore, according to these values, the ranking of sires in function of BV HF or BV JE was not very different from average BV.

According this top 10 (Table 28), we can notice that the first four sires in each ranking were the same but their position changed excepted the fourth sire (in bold). Rankings 1 and 3 had the same ten sires but with different ranks from the fifth rank. In ranking 2, there were 3 sires (in italic) different of those of rankings 1 and 3.

From these rankings, we can conclude that the selection of sires based on an overall genetic value (Model III) is less optimal that a selection based on the breed of the mate. Therefore selection of sires is different should also be a function of the mating strategy.

Table 28: Top 10 of sires for the three breeding values.

	Ranking 1: BV HF		Ranking 2: BV JE		Ranking 3: average BV	
Rank	id sire	Breeding value	id sire	Breeding value	id sire	Breeding value
1	9797446	1341.999	15778567	1612.672	9797446	1393.404
2	15778567	1296.816	9797432	1599.206	15778567	1345.986
3	9797432	1287.821	9797446	1545.419	9797432	1324.399
4	**13567858**	**1267.636**	**13567858**	**1543.256**	**13567858**	**1322.049**
5	12456790	1218.429	13843769	1500.577	13843769	1268.057
6	13843769	1214.607	*10601502*	*1452.837*	12456790	1266.555
7	13833521	1184.198	*10256580*	*1451.935*	15368353	1237.540
8	15368353	1177.695	12531518	1443.685	13833521	1233.679
9	12531518	1170.336	15368353	1439.733	11570551	1209.1098
10	11570551	1160.989	*13463350*	*1422.670*	12531518	1205.833

6.4. Heterosis and recombination loss effects

Table 29 contains the values of heterosis and recombination loss estimated using Model II and Model III.

Table 29: Heterosis and recombination loss estimated using Models II and III.

	Model II	Model III
litres of milk/ DIM per % of heterosis	0.00893	0.01480
litres of milk/ DIM per % of recombination loss	- 0.00376	-0.00666

According values presented in Table 24, heterosis and recombination loss effects were higher for Model III than for Model II. As Model III considered none genetic differences between HF and JE breeds, crossbred animals (0.5 HF 0.5 JE and 0.25 HF 0.75 JE) had their heritabilities “underestimated” (Figure 19) and so their permanent environment and herd period variances were higher than the estimated values used in Model II but heterosis and recombination loss fixed effects too. This increase is illustrated in Figure 21 by the mean heterosis and the mean recombination loss for cows in production.

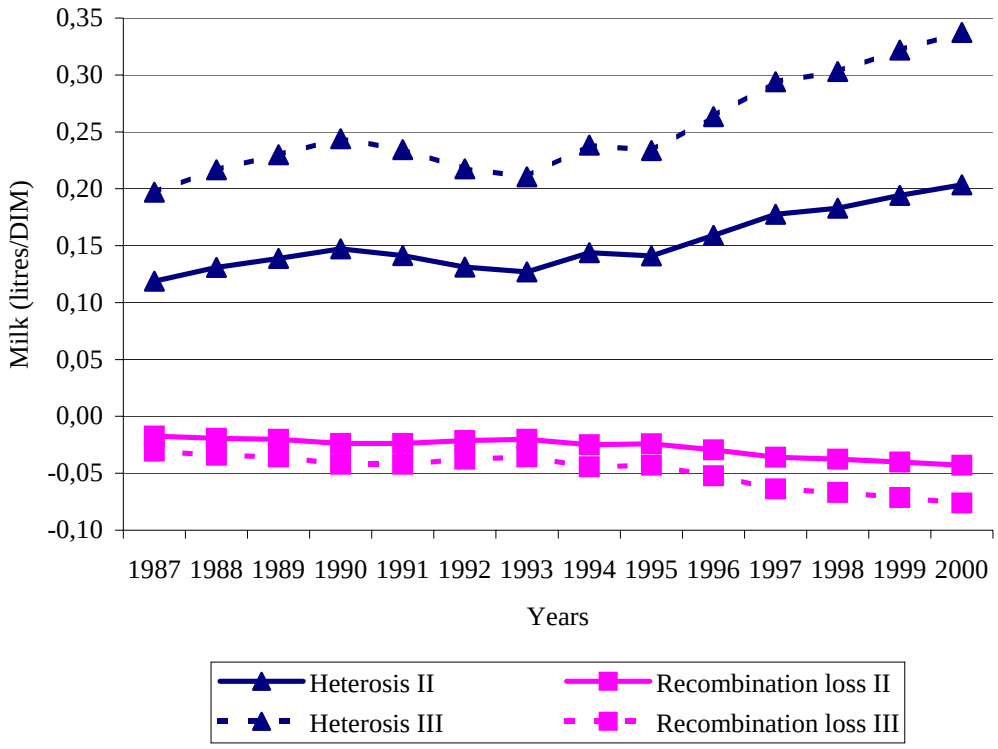

Figure 21: Evolution of mean heterosis and mean recombination loss across years estimated for cows in production using Model II and Model III.

The trend of heterosis, showed in Figure 21, illustrated the rising use of crossbred animals for milk production; so the great interest of dairy farmers for crossbreeding programs in New Zealand during the last twenty years but the increase is very important since 1996.

According to values of heterosis estimated with Model II, the first generation crossbred animals (F_1) can produce about 241 litres of milk in addition to the average production of their parents during the standard lactation length in New Zealand (270 DIM). In a two-breed rotational scheme with HF and JE, 67% of this original heterosis expressed by the first generation should be observed.

Estimates of recombination loss were negative and smaller than the effect of heterosis in absolute value, this was in line with the literature [e.g. Van Der Werf, 1990].

In conclusion, it was necessary to estimate heterosis and recombination loss to reduce the problem of bias in prediction of breeding values and estimation of breed differences.

CONCLUSIONS AND IMPLICATIONS

The main objective of this study was to contribute to the development of a random regression test-day model for the genetic evaluation of production traits in New Zealand permitting an optimal use of crossbred dairy cattle data. The proposed model allowed the estimation of different breeding values according to breed composition.

(Co)variance components and genetic parameters within and across breeds were estimated for HF and JE animals and showed genetic correlations below 1 for breed specific additive genetic effects. The proposed model was able to account for differences in variability too. Results from single breed analysis showed that HF purebred animals had a higher variability than JE purebred animals.

Genetic evaluations showed ranking differences by using the model with breed specific additive genetic effects and a model assuming the same breed composition for all animals. We can therefore conclude that optimal selection of sires and mating decision would need to have advanced evaluations of the performances of crossbred animals. This is true for current purebred sires used in crossbreeding, but especially with regard to crossbred sires (Kiwicross bulls), assuming that they could be a potential mate within each breed. Indeed, such a model could provide solutions to some problems due to an intensive practise of a crossbreeding scheme among dairy cattle, because it will help to choose animals in function of the mating strategy to apply.

This work is the first stage of a long study, which is in progress, and expected to lead to a test-day model allowing to evaluate accurately the crossbred dairy cattle of New Zealand.

Further developments have to be considered. First, the genetic parameters of milk solids (fat and protein) need to be estimated.

The future genetic evaluation model will be multi-lactation and therefore the (co)variances will be extended to next lactations.

The model presented in this study can be improved, especially the use of a reduced matrix for the permanent environment effect can be considered, since the correlations of this effect between HF and JE breeds were high.

Most of crossbred animals are HF×JE however other crosses exist, thus this model will need to be extended to three or more breeds.

In a final genetic evaluation model, heterogeneity of (co)variances due to environment will have to be considered.

Finally, the current model stays additive, however non-additive genetic effects such as dominance or epistasis could be modelled. This type of very advanced models could have theoretical advantages with crossbred data, they are however for the moment technically very difficult to use.

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