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**QUANTIFYING GENETIC VARIATION IN  
ENVIRONMENTAL SENSITIVITY OF NEW ZEALAND  
DAIRY CATTLE TO APPLY IN THE DEVELOPMENT  
OF A DAIRY CATTLE SIMULATION MODEL FOR  
PASTORAL SYSTEMS**

A thesis presented in partial fulfilment  
of the requirements for the degree of

*Doctor of Philosophy*  
*in Animal Science*

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# ABSTRACT

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The objectives of this research were firstly, to investigate if dairy cattle genotypes in NZ exhibit genetic variation in environmental sensitivity and to determine if this genetic variation is statistically significant from a genetic evaluation perspective, and secondly, to use genetic information including environmental sensitivity data to simulate dairy cattle responses to changes in nutritional regime and variation in climate.

A comprehensive review identified that simulation models either overlook, or do not represent environmental sensitivity information where genotypes and breeds respond differently when exposed to variations in environment. A large dataset of daily and total lactation records (yields of milk, fat and protein) from herds participating in the progeny testing of sires from 1989 to 2002 was obtained to test for differences in the environmental sensitivity of dairy cattle in New Zealand. Production data was matched with environmental data relating to climate, herd size, altitude and herd average production levels (a proxy for feeding level). The statistical analyses applying univariate and bivariate multibreed models to environmental character states identified minimal sire re-ranking between environmental character states as measured by genetic and rank correlations. However, differences in yields of milk, fat and protein between New Zealand Jersey and overseas Holstein Friesian systematically diverged with production level, in herds expected to use different levels of supplements. These results suggest New Zealand Jersey cattle are best suited to a grassland-type environment, and overseas Holstein Friesian cattle are more suited to an intensive-type environment. A phenotypic analysis identified thermal environment (cold and hot conditions) significantly affected the expression of production traits in Holstein Friesian, New Zealand Jersey and Holstein Friesian x New Zealand Jersey cattle. Holstein Friesian dairy cattle were more susceptible to the effects of heat conditions than New Zealand Jersey cattle with yields of milk, and concentrations of fat and protein of the former compromised at a lower value for temperature humidity index. Dairy cattle performance is likely to be compromised by heat more frequently than cold conditions in New Zealand.

A simulation model that considers how dairy cow genotypes respond to different environments, incorporating the results presented above, was then developed. An initial estimate of feed intake is used to define cow genetic potential based on estimated breeding values for total yields milk, fat and protein, and environmental sensitivity information. A mammary gland module then predicts daily yields of milk, fat and protein based on the cow's genetic potential after considering her age, stage of lactation, body condition score, nutritional status and thermal environment. Live weight change is also predicted via a body energy stores module, which considers the effect of age, stage of lactation, current body condition score, nutritional status, and an estimated breeding value for body condition score. Feed intake is predicted from the requirements for maintenance, growth and pregnancy, and the genetic drive for yields of milk, fat and protein and body fat change. The predictive ability of the model was tested using information from a prior study with two Holstein Friesian genotypes managed in a pasture-based system. The model simulated to a high degree of accuracy, mean values for yields of milk, fat and protein, and concentrations of fat and protein of each genotype. Various tests identified the major source of error between simulated and observed values were due to a lack of simulated variation.

In conclusion, the extent of genetic variation in environmental sensitivity for total lactation yields of milk, fat and protein within the range of New Zealand environments are not sufficient to warrant the formation of separate breeding schemes for distinct environments. However, New Zealand Jersey cattle are best suited to a grassland-type environment, and overseas Holstein Friesian cattle are more suited to an intensive-type environment. Genetic variation in the suitability of different breeds for specific environments existed within breeds. A simulation model was developed that was able to simulate the effect of genotype, environment and genotypic differences in environmental sensitivity on daily cow performance.

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## LIST OF ABBREVIATIONS

Abbreviation	Full Description
<b>BCS</b>	Body condition score
<b>BGT</b>	Black globe temperature
<b>CNCPS</b>	Cornel Net Carbohydrate and Protein System
<b>CSI</b>	Cold stress index
<b>DIM</b>	Days in milk
<b>E</b>	Environment
<b>EBV</b>	Estimated breeding value
<b>EI</b>	Economic index
<b>E<sub>p</sub></b>	Permanent environmental effects
<b>E<sub>t</sub></b>	Temporary environmental effects
<b>G</b>	Genotype
<b>G<sub>max</sub></b>	Global maximum
<b>GxE</b>	Genotype by environment interaction
<b>HF</b>	North American, European Holstein Friesians or New Zealand Friesian
<b>HGM</b>	High genetic merit
<b>HLI</b>	Heat load index
<b>HYS</b>	Herd-year-season
<b>LCI</b>	Lower confidence interval
<b>LGM</b>	Low genetic merit
<b>ME</b>	Metabolisable energy
<b>MGM</b>	Medium genetic merit
<b>MS</b>	Milk solids
<b>NZ</b>	New Zealand
<b>NZF</b>	New Zealand Friesian
<b>NZJ</b>	New Zealand Jersey
<b>OHF</b>	North American or European Holstein Friesians
<b>RH</b>	Relative Humidity
<b>r<sup>2</sup></b>	Coefficient of determination
<b>r<sub>e</sub></b>	Expected correlation
<b>r<sub>s</sub></b>	Spearman's rank correlation
<b>T</b>	Temperature
<b>THI</b>	Temperature humidity index
<b>UCI</b>	Upper confidence interval
<b>WS</b>	Wind speed



# CHAPTER 1

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## General Introduction

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## INTRODUCTION

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The phenotypic expression of traits in dairy cattle is determined by three components: genotype, environment and the mechanisms by which genotype and environment interact. Genotype is the combination of alleles at different loci that determines a specific characteristic or trait. In quantitative genetics, genotype is most often represented by an estimated breeding value (Falconer, 1989). Environment, both permanent and temporary (see chapter 2 for a more full description), refers to all non-genetic factors affecting gene expression (West-Eberhard, 1989). The ways in which genotype and environment interact determine the phenotypic value of a trait exhibited by an individual. The trait responses, in terms of phenotype or estimated breeding values (y-axis), of a genotype to changes in environment (x-axis) are represented through reaction norm functions (West-Eberhard, 2003). Significant variations in reaction norm trajectories are referred to as genotype x environment (GxE) interactions.

### **An introduction to the New Zealand dairying system**

The New Zealand (NZ) dairying system is based primarily on efficient conversion of pasture into milk by grazing cows (Holmes et al., 2002). The NZ dairy cow diet generally consists of pasture with minimal use of supplements. Consequently, the amount and quality of feed available is strongly influenced by seasonal variations in climate, and as a result the yields achieved by NZ herds are considerably lower than those of many overseas countries (International Committee for Animal Recording, 2005).

The NZ dairy cattle population in the 2004/2005 season was comprised of 48.6% Holstein Friesian, 14.8% Jersey, 28.3% Holstein Friesian x Jersey, and 8.3% of other breeds, including Ayrshire, Milking Shorthorn and Guernsey (Livestock Improvement, 2005). To account for the different breeds, a multi-breed evaluation was introduced in 1995 allowing the comparison of all breeds on a common scale (Harris *et al.*, 1996). The common scale is Breeding Worth (a selection index of profit per 4.5 t dry matter [DM] of feed), which combines estimated breeding values for milk volume, yields of fat and protein, live weight, fertility, somatic cell count

and residual survival weighted by their relative economic weights (Anonymous, 2006). Protein yield receives the greatest economic emphasis in the Breeding Worth index (Miglior et al., 2005).

**The potential importance of GxE interactions**

In recent times, the production environment in NZ has diversified with an increase in the differential for fat plus protein (milk solid; MS) yields between average and top herds (Table 1). A survey of NZ dairy farms in the 2001/2002 season identified that 37% of farms fed their cows more than 500 kg dry matter (DM) per cow (average of 943 kg DM per cow) of imported supplements (pasture hay, pasture silage, maize silage, meals and grains). This compares to 22% of farms feeding greater than 500 kg DM per cow in the 1998/99 season (Silva-Villacorta et al., 2005). If GxE interactions exist across these wider environmental ranges, different genotypes or breeds may be needed for specific environments.

Few studies have investigated whether GxE interactions occur within the typical range of NZ dairying environments. Kolver et al. (2002) identified a significant GxE interaction for MS yields when comparing the performance of NZ and overseas Holstein Friesian in a high production level pasture-based system or a total mixed ration system. However, the pasture-based system adopted by Kolver et al. (2002) achieved very high yields of around 460 kg MS per cow for both NZ and overseas Holstein Friesian, much higher than the 308 kg MS per cow achieved in average NZ systems (Livestock Improvement, 2005). The total mixed ration system achieved yields of 600 to 700 kg MS per cow. While these yields are common overseas, few NZ commercial herds reach these production levels.

**Table 1:** Summary of yields of fat plus protein (kg/cow/year) for average and top New Zealand herds over a 12-year period

	Season*		
	1992/93	1998/99	2004/05
<b>Average Herd</b>	259	256	308
<b>Top herds</b>	376	409	>500
<b>Differential</b>	+117	+153	>+192

\*data obtained from Livestock Improvement (1993; 1999; 2005)

## Chapter 1 .....

Environment may also affect the expression of breed effects for production traits. Oldenbroek (1988) in The Netherlands found differences in milk yield between Friesian and Jersey cattle of 991 and 1791 kg on diets of high (60% grass silage, 40% corn silage) or low (50% concentrates, 30% grass silage and 20% corn silage) roughage content, respectively with Friesian cattle achieving the highest milk yields in both systems. Thomson et al. (2001) in New Zealand also observed greater difference in milk yields between Jersey and Friesian cattle on a diet of pasture plus concentrates than a diet of pasture only, although the interaction between breed and environment was not significant. There is also some evidence Jersey cattle are more tolerant to the effects of heat stress than Holstein Friesian cattle (West et al., 2003). Consequently a study of commercial herds in New Zealand is warranted, which analyses whether GxE interactions occur within the typical range of herd environments experienced in NZ. Studies of this nature could provide valuable insights into the suitability of breeds and sires of different genetic origins for specific environments.

If significant GxE interactions were identified in commercial environments, it would be appropriate to include their effects in a simulation model used to predict dairy cattle performance. Dairy cattle simulation models have been used mainly for research purposes, with only UDDER (Larcombe, 1999), used to any extent on commercial farms in NZ. An accurate simulation model can be used to identify and screen potential research projects, estimate parameters that are difficult or expensive to measure and interpret and evaluate experimental results (Bywater and Cacho, 1994). In a commercial context, an accurate simulation model could be used to test the feasibility of different management scenarios, such as determining if the addition of extra feed is likely to be profitable. A dairy cattle simulation model including the effect of genotype and GxE interactions could be used to identify optimal feeding regimes based on knowledge of environment and animal genotype, and how they interact.

## THESIS OUTLINE

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The primary objectives of this body of research were twofold; firstly, to investigate if dairy cattle genotypes in NZ exhibit genetic variation in environmental sensitivity and to determine if this genetic variation is statistically significant, and secondly, to use genetic information including environmental sensitivity data to simulate dairy cattle responses to changes in nutritional regime and variation in climate.

To achieve these objectives, a comprehensive review of the literature summarised in Chapter 2, which outlines the environmental influence on performance of different genotypes or breeds, approaches currently adopted to model dairy cattle performance and potential new strategies to account for GxE interactions in future models.

Chapters 3 to 6 utilise a dataset of yields of milk, fat and protein obtained from herds participating in the progeny testing of young sires matched with environmental data for each herd. This dataset was used to assess if GxE interactions could influence genetic evaluation procedures, sire selection or the future distribution of progeny testing herds (Chapters 3 to 5). The production and environment data was also used to define cold and heat thresholds at which performance (yields of milk and MS, and concentrations of fat and protein) is affected in the three major breed groups in NZ (Chapter 6).

Chapter 7, a mechanistic model of the mammary gland was used to identify the effect of feeding level, genetic merit, body condition score and age on mammary gland dynamics. The results from Chapter 7 were used, along with the findings from Chapters 3 to 6, to develop a grazing systems dairy cattle simulation model that accounts for GxE interactions (Chapter 8). The model's predictive ability was tested using data obtained from a farmlet study with two different genotypes managed in a pasture-based system (Chapter 9). The major findings of the thesis are discussed in Chapter 10, highlighting areas for future investigation.

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## CHAPTER 2

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### **Simulation modelling of dairy cattle performance based on knowledge of genotype, environment and genotype by environment interactions: Current Status**

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## ABSTRACT

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Prediction and modelling of the phenotypic performance of dairy cattle is based on knowledge of cattle genotype and the environment in which they are managed. GxE interactions for feed intake and phenotypic performance are becoming increasingly important as cattle genotypes are now being managed in a diverse range of environments worldwide. These GxE interactions are generally classified as scaling effects, where the difference in phenotypic performance between genotypes is larger in one environment than in another environment, or re-ranking, where genotypes are ranked differently according to environment. The objective of this paper was to outline and assess the approaches used in simulation models to account for GxE interactions. The GrazFeed, CamDairy and Cornell Net Carbohydrate and Protein System (CNCPS) simulation models are used as illustrative examples. Each model was used to quantify the phenotypic responses of different genotypes managed in a range of environments. These simulations highlighted the inability of these commonly used models to demonstrate re-ranking of genotypes, and to a lesser extent, to display scaling effects. This was largely due to their design, which resulted either in inadequate specification of animal genotype or a lack of interaction between the genetic and environmental components within each model. An environmental sensitivity trait, which is the derivative of phenotypic performance as a function of an environmental variable, could be a useful tool to develop a better understanding of the phenotypic responses of specific genotypes. The environmental sensitivity trait could then be used, along with traditional estimated breeding values, to more accurately model the responses of animals to different environments.

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## INTRODUCTION

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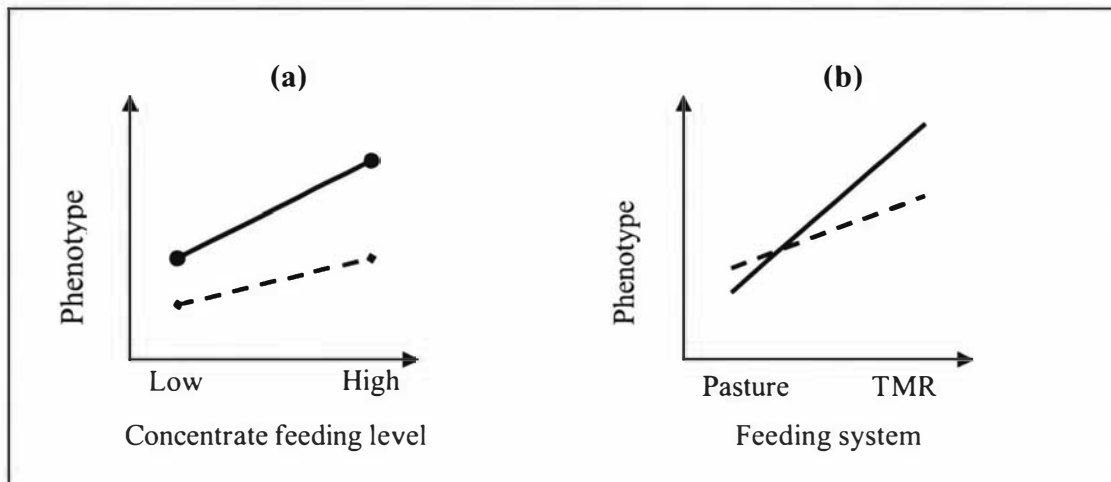
A major research focus in genetics has been the development of methods that predict and model phenotypic performance based on knowledge of the genotype and environment, and interactions between them (Cooper et al., 2002). A GxE interaction occurs when animals differ in their ability to perform in different environments (Falconer, 1989), and a number of studies have detected GxE interactions in dairy production environments (Boettcher et al., 2003; Kolver et al., 2002; Veerkamp et



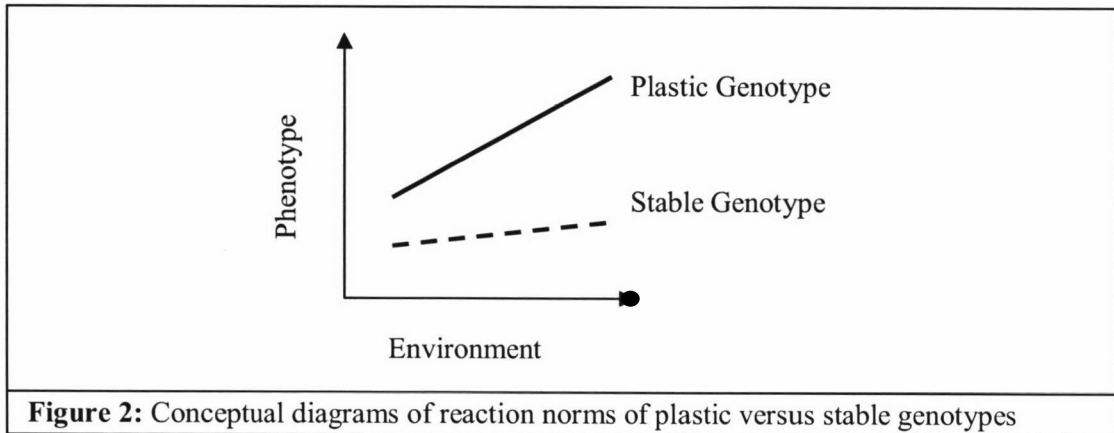
al., 1994). These interactions are becoming increasingly important as animals are being used in environmental conditions which differ greatly from those in which they originated (Luiting, 1999).

There are a number of types of GxE interactions, for example, there may be a “scaling effect” where the difference in the level of performance between two genotypes is smaller at a low feeding level than a high feeding level (Figure 1a), or “re-ranking” where two genotypes rank differently at contrasting feeding levels or feeding systems (Figure 1b), or a combination of both scaling and re-ranking (Cromie, 1999; Podlich and Cooper, 1998).

Interactions between genotype and environment can also be described as differences in the environmental sensitivity of genotypes, or differences in the phenotypic plasticity of genotypes (Via et al., 1995). However, the term environmental sensitivity is used from this point to avoid confusion. **Environmental sensitivity** can be defined as the degree to which the phenotypic expression of a genotype varies under different environmental conditions such as feeding level and temperature (Dutilleul and Potvin, 1995; Kolmodin et al., 2002; West-Eberhard, 2003). This relationship is often represented as a **reaction norm** where the phenotype expressed by a genotype is shown as a function of an environmental parameter. There are two



**Figure 1:** Conceptual diagrams of GxE interactions a. Scaling effect for milk solids yield (kg/year) in high genetic merit (●—●) and low genetic merit (◆--◆) dairy cattle in systems with a low or high concentrate feeding level (Fulkerson et al. 2000). b. Re-ranking for MS yield (kg/day) in NZF (--◆) and OHF (—●) dairy cattle in a pasture-based or total mixed ration (TMR) system (Kolver et al. 2002).



mathematical representations of a reaction norm (Via et al., 1995). Firstly, the character state model (Figure 1) where traits means or breeding values are estimated in a defined number of discrete environments. Secondly, the random regression model where traits means or breeding values are estimated in all environments in a continuous manner (Figure 2). Reaction norms estimated using the character state or random regression approach can be linear as illustrated in Figure 1 and 2 or higher order. In the case of a linear reaction norm, the slope or linear regression coefficient is a direct measure of the degree of environmental sensitivity of a genotype. If different genotypes have significantly different slopes of the reaction norm, then there is a **GxE interaction** or genetic variation in environmental sensitivity. Genotypes that exhibit a wide variation in phenotypes across environments are ‘plastic’ or “sensitive”, whereas genotypes that are relatively constant across environments are ‘robust’ or ‘stable’ as shown in Figure 2 (Bradshaw, 1965; de Jong and Bijma, 2002).

Two classes of genetic mechanisms could be responsible for differences in the environmental sensitivity of genotypes; 1) some alleles may only be expressed in specific environments and 2) gene regulation may change depending on the environment (Schlichting and Pigliucci, 1995; Via et al., 1995; West-Eberhard, 2003). This leads to the theory of specific genes for plasticity, where genes are “switched” on or off depending on the environmental conditions in which the animal is managed (de Jong, 1990; Schlichting and Smith, 2002; Via et al., 1995). Alternatively, environmental sensitivity may evolve due to selection toward different phenotypic values in different environments (Via and Lande, 1985). For instance, West-Eberhard (2003) proposes genomic elements of animals may change due to

indirect selection for genes, which act in specific environments. It is postulated these genetic factors are the underlying cause of the observed GxE interactions for feed intake (Kolver et al., 2002; Linnane et al., 2004), nutrient partitioning (Gordon et al., 1995; Veerkamp et al., 1994) and milk synthesis (Vetharanim et al., 2003b) in studies using *Bos taurus* dairy breeds.

Simulation models to predict animal performance, usually fail to account for GxE interactions because they describe groups as a set of homogeneous individuals with identical phenotypic responses to changes in the environment (Congleton et al., 1997). Yet, the differences in the responses by individuals of varying genotypes to the same nutritional treatment (environment) can be substantial (Kennedy et al., 2002). As the central aim of simulation models is to represent the biological system and all its components as accurately as possible, a model that considers animal genotype and its interaction with the environment is essential. Especially in the case of dairy production environments where wide variations can exist between the genotypes of the animals, and between the environments in which they are managed. Such a simulation model will be a valuable tool, as it will more appropriately represent a real life situation, thereby, providing results that can be used to find the most suitable and profitable feeding regime for each individual genotype.

The objective of this paper was to review the techniques used to predict phenotypic performance in dairy cattle accounting for genotype, environment and their interaction. The ability of some models to account for GxE interactions is assessed. Potential methods to account for GxE interactions in future models are proposed.

## **MATERIALS AND METHODS**

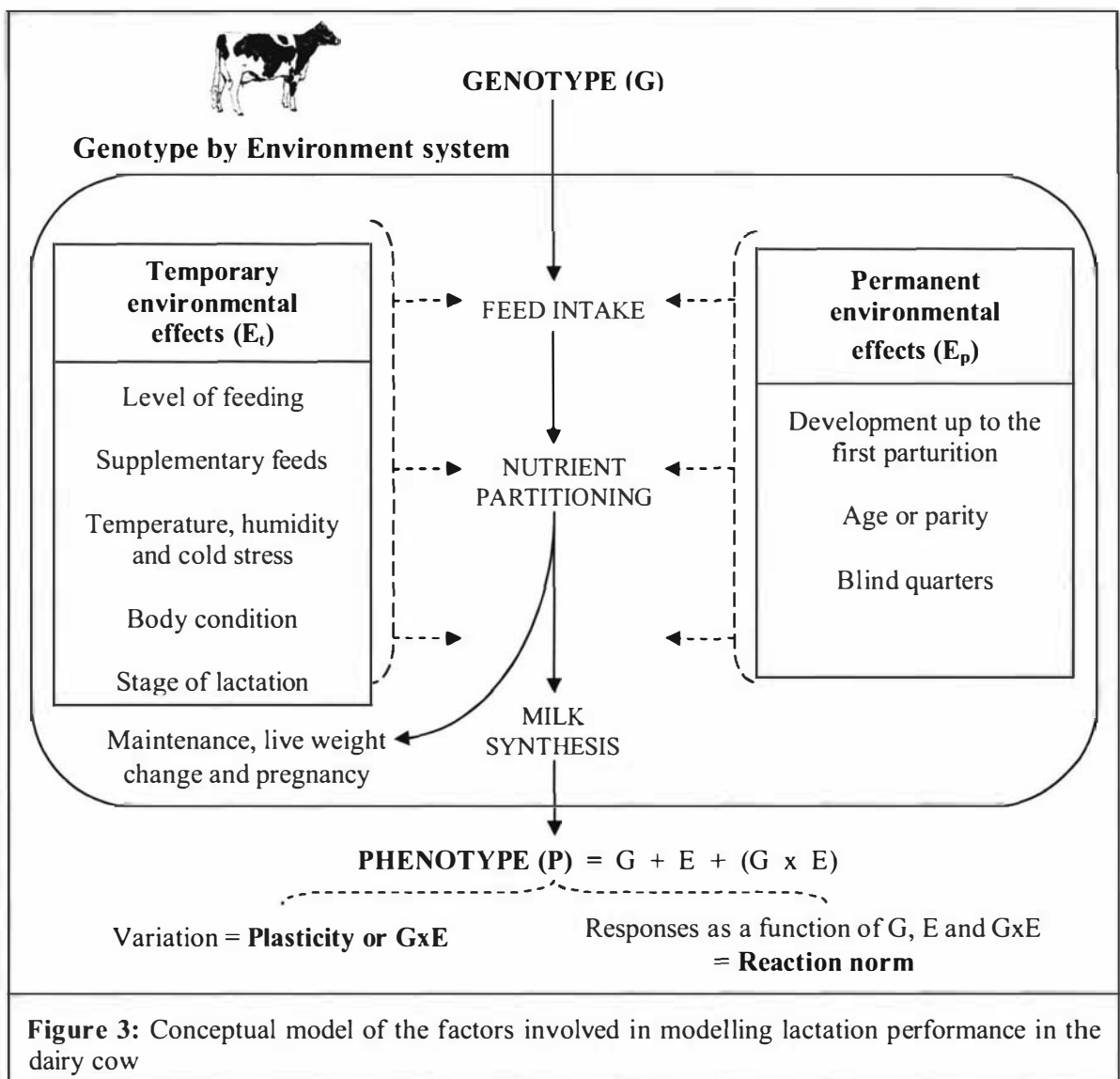
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### **Conceptual diagram of the genotypic and environmental factors determining dairy cattle performance**

The concept map (Figure 3) presented below details the genotypic and environmental factors that determine the phenotypic performance of an individual cow. The phenotypic performance (P) of an individual is a function of its genotype (G), the

environment (E) and the interaction between the two (Cooper et al., 2002):  $P = G + E + (G \times E)$ .

Environmental effects can be classified into 1) permanent, such those that affect development up to the first parturition, and age or parity, or 2) temporary, such as level of feeding, stage of lactation, and health status. Permanent and temporary environmental factors may interact with the genotype of the animal, affecting feed intake and the partitioning of feed, and consequently, the phenotypic expression of traits such as fat and protein production (Ingvarsen et al., 1999; Oldham and Emmans, 1989). The level of environmental sensitivity, described through reaction norms, is a descriptor of how the animal responds to the environmental conditions (Calus et al., 2002; de Jong and Bijma, 2002; Fikse et al., 2003b; Kolmodin et al., 2002).



**Physiological basis for GxE interactions**

Numerous studies have demonstrated scaling effects in the genetic analysis of dairy cattle data (Boettcher et al., 2003; Hill et al., 1983; Lopez-Villalobos et al., 1994; van der Werf et al., 1994). Scaling effects occur where the difference in phenotypic performance between genotypes or degree of environmental sensitivity is greater in a more favourable environment (Figure 1a). An example from an Australian farmlet study by Fulkerson et al. (2000) showed that the difference in MS yield between animals of high genetic merit (HGM) and low genetic merit (LGM) for milk yield performance was smaller at the low concentrate than the high concentrate feeding level (27 vs 51 kg MS/cow/year, respectively; Figure 1a). This study along with studies by Veerkamp et al. (1994), Kennedy et al. (2002), Boettcher et al. (2003) and Bryant et al. (2003a) demonstrate the greater environmental sensitivity of milk production by HGM cows compared to LGM cows, to a common change in environment.

The underlying basis for the exhibition of scaling effect for milk yield is partially due to the higher feed intakes in HGM than in LGM cows i.e. there is a positive genetic correlation between feed intake and milk yield. However, the increase in feed intake above maintenance is not sufficient to account for the increased milk yield in the HGM animals (Veerkamp and Emmans, 1995). Consequently, these HGM cows direct or partition a greater proportion of the feed they consume towards the production of milk to achieve higher yields than LGM cows (Bryant et al., 2003b; Gordon et al., 1995; Veerkamp et al., 1994; Yan et al., 2002).

Veerkamp et al. (1995) also postulated that, with a high proportion of forage in the diet, HGM animals are not capable of eating much more than LGM animals, whereas, on high concentrate diets HGM animals have the advantages of both higher intake and of more body tissue mobilisation. Hence, differences in yield between the genotypes are smaller in grazing systems because intake is limited by constraining factors in the diet such as physical bulk, or by the relative slow rate of intake that can be achieved by grazing cows, when compared with total mixed ration fed cows (Forbes, 1995; Thorne et al., 2003).

An example of re-ranking for MS yield is provided by Kolver et al. (2002). In this study, NZ Friesians (NZF) achieved slightly higher MS yields than North American or European Holstein Friesians (OHF) when both strains were grazed on pasture (465 vs 459 kg MS/cow/year for NZF and OHF, respectively). In contrast, on a total mixed ration the OHF achieved much higher MS yields than NZF (602 vs 720 kg MS/cow/year for NZF and OHF, respectively). Similar re-rankings of Canadian and NZ sires were observed in a study by Peterson (1988), which compared the performance of their progeny in each country. For example, the Canadian sires ranked above the NZ sires in a Canadian total mixed ration system, but ranked below the NZ sires in the NZ pasture-based system.

Re-ranking for milk yield is largely due to re-ranking in the level of feed intake when each genotype is managed in two different environments. For example, in the NZ study by Kolver et al. (2002) they observed intakes of the OHF and NZF animals equivalent to 3.3 and 3.6 % of live weight, respectively on the pasture-based diet in early lactation, whereas on the total mixed ration the OHF animals consumed more feed than the NZF animals in early lactation (4.1 and 4.0 % of live weight, respectively). A subsequent study by Thorne et al. (2003) found the difference in feed intake between OHF and NZF animals fed a total mixed ration was even greater in late lactation (3.3 and 2.9 % of live weight, respectively).

Similar results were observed in an Irish study by Linnane et al. (2004), which compared the feed intakes and performance of first lactation OHF with NZF animals on diets with either high levels of concentrate (1500 kg concentrate/cow/year), or low levels of concentrate (500 kg concentrate/cow/year). In that study, on the low concentrate diet the OHF and NZF animals had intakes equivalent to 3.2 and 3.3 % of live weight, respectively in mid lactation. On the high concentrate diet, the OHF animals consumed more feed than the NZF animals in mid lactation (3.9 and 3.7 % of live weight, respectively).

A potential reason for the difference in feed intake may be a reduced feed consumption ability or genetic-drive of one genotype compared to another genotype when each is subjected to a specific environment (Friggens et al., 2004; Friggens et

al., 1998; Kyriazakis et al., 1999). For example Illius et al. (2002), Kyriazakis et al. (1999) and Yearsley et al. (2001) proposed that animals adapt or evolve to the environment in which they were selected. This environment may involve the feeding of a high proportion of concentrates or where high ambient temperatures are common. The levels of feed intake in these environments are influenced by the animal's genetically pre-determined ability to cope with these conditions. These may include evolutionary adaptations that allow specific genotypes to dissipate heat easily (Bianca, 1965) and/or consume and process concentrates faster than other genotypes.

For example, Linnane et al. (2004) in Ireland observed that, when compared with NZF cows, OHF cows had faster consumption rates on high concentrate diets (59.8 vs 50.5 bites per minute, respectively), and reduced levels of pasture substitution when offered concentrates (0.08 vs 0.50 kg DM reduction in pasture consumption/kg DM of concentrate for OHF and NZF, respectively). This suggests NZF may not be so well equipped to cope with the faster rate of rumen outflow and processes required for the increased supply of metabolites associated with these more readily digestible feeds (Kolver et al., 2002). Conversely, OHF cows may have a greater feeding drive in supplementary feeding systems, and are less able to graze effectively. It seems clear that behavioural, physiological and metabolic changes, such as those reviewed by Forbes (1995), and evolutionary changes are required in order for the animal to achieve high levels of performance on the "foreign" feed. The rate at which this process occurs depends on the extent of the genotypes deficiency and the level of behavioural, physiological or metabolic change required.

### **Accounting for GxE interactions**

In many countries, dairy cattle are selected based on economic selection indexes that combine breeding values for production, reproduction and survival traits weighted by appropriate economic weights. The breeding values for each trait are generally estimated from best linear unbiased prediction procedures (Henderson, 1975) using single or multiple trait animal models. GxE interactions are recognised by adjusting for heterogeneous variances (scaling effect), or by accounting for the genetic correlations (re-ranking) between expressions of the same trait in different countries or environments (Fikse et al., 2003a; van der Werf et al., 1994; Zwald et al., 2003).

The reported breeding values for milk production traits are estimates of the animal's genetic capability in the average environment within the country.

As the range of environmental conditions on farms within a country may be as large as the range that occurs between countries (Hayes et al., 2003), it becomes increasingly difficult to identify a single target genotype (Cooper et al., 2002). For example, the GxE interactions as displayed in Figure 1 highlight the problem of defining a single target genotype. If the type of GxE interaction exhibited is a scaling effect, the HGM animal is selected in all conditions, because it performs best in the range of environmental conditions. If re-ranking occurs, such as that displayed in Figure 1b, the "best" genotype differs between environments; if the animals are fed a total mixed ration, the plastic OHF would be preferred due to its ability to exploit high levels of feeding on a total mixed ration. But, on a pasture-based diet the more stable NZF would be preferred due to superior performance in low input environments.

The widespread use of sire teams at mating in NZ may indirectly limit the effect of GxE interactions. For instance at mating, the sole use of a sire whose daughters perform best in an intensive environment, but not so well in a grassland type environment, may result in a group of daughters who perform below expectations in a farm that uses pasture as the sole source of feed. By using multiple sires, the effect of using this one sire is diluted. Obviously, it would be preferable to have a measure of the ability of an animal, or daughters of a sire, to perform in an environment. Calus and Veerkamp (2003), Hayes et al. (2003), and Kolmodin et al. (2003) propose a breeding value for the slope of the reaction norm - essentially environmental sensitivity - could be treated as a new "environmental sensitivity" trait for inclusion in genetic evaluation models. The environmental sensitivity trait value could be interpreted as being linked to the animal's ability to modify its feeding behaviour, physiological and metabolic mechanisms when in a different environment (Kyriazakis et al., 1999).



Current measures of the environment have included average herd milk or protein yield (a proxy for herd feeding level when this information is not available), the size of the herd, and the temperature and humidity levels (Calus et al., 2002; Fikse et al., 2003a; Hayes et al., 2003; Kolmodin, 2003). However, the most suitable measures of environment have yet to be defined, and may be a combination of the environmental average for herd production level and a meteorological index. Once the correct environmental measures have been determined, the environmental sensitivity traits could be used to extrapolate the predicted performance of a genotype in different environments. Thereby, enabling more accurate simulations of milk production responses by different genotypes to different feeding and climatic conditions.

**Current approaches adopted in simulation models to account for the effects of genotype, environment and their interaction**

A number of simulation models are used to predict dairy cattle performance and these are summarised in Tables 1 and 2. These models can be divided into three main categories based on their general objectives (Table 1):

- Physiological models which simulate the effect of mammary gland growth and regression on the secretion of milk (Vetharanim et al., 2003b). These types of models represent genetics and nutrition by altering physiological factors involved in milk secretion.
- Nutritional models which determine the effect of different nutritional regimes on performance levels (Fox et al., 1992; Freer et al., 1997; Hulme et al., 1986; Larcombe, 1999; Rotz et al., 1989). These models represent the genetics and nutrition of the animal by use of a combination of empirical, deterministic and mechanistic components.
- Genetic models, which simulate the effect of genetics on animal performance (Congleton, 1984; Dijkhuizen et al., 1986; Sorensen et al., 1992). These models represent the genetic variation (stochastic) in animal performance and animal nutrition is represented empirically or deterministically.

The physiological model developed by Vetharanim et al. (2003b) represents animal genotype by altering parameters involved in the secretion of milk and a nutritional buffer factor which determines the ability of the animal to sustain milk production

**Table 1:** Some examples of dairy cattle simulation models and their general objectives.

<b>Model</b>	<b>General objective and purpose</b>	<b>Type of model</b>	<b>Main references</b>
Vetharanim	Investigate the impact of nutrition and genotype on the synthesis of milk in the mammary gland	Physiological - Mechanistic	(Vetharanim et al., 2003a; Vetharanim et al., 2003b; Vetharanim et al., 2001)
Congleton	Simulate discrete, and time-oriented events of the dairy cow and herd	Genetic - Stochastic	(Congleton, 1984; Congleton and Everett, 1980)
Dijkhuizen	Quantify the economic effects of different culling policies with respect to productive and reproductive failure.	Genetic – Stochastic and Deterministic	(Dijkhuizen et al., 1986)
SIMCOW	Simulate the effects of feeding regimes within different calving and culling strategies, herd sizes and milk quotas.	Genetic - Stochastic	(Bruce et al., 1984; Ostergaard et al., 2000; Sorensen et al., 1992)
Lopez-Villalobos	Evaluate the effects of crossbreeding strategies on herd performance and the rate of genetic gain	Genetic – Deterministic	(Lopez-Villalobos, 1998)
CAMDAIRY	Determine the suitability of formulated rations to reach milk yield potentials	Nutritional - Deterministic	(Hulme et al., 1986)
DAFOSYM	Test the adequacy of formulated rations to meet animal performance targets	Nutritional - Deterministic	(Congleton and Everett, 1980; NRC, 1989; Rotz et al., 1989; Rotz et al., 1999)
CNCPS	Diet evaluation tool to predict the ability of a ration to meet specified targets	Nutritional - Deterministic	(Fox et al., 1995; Fox et al., 1992; NRC, 2001; Sniffen et al., 1992)
GRAZFEED	Assess the ability of a specified pasture and supplementary feed allowance to reach desired milk yields	Nutritional - Deterministic	(Freer et al., 1997; SCA, 1990)
UDDER	Predict the expected milk production of a herd under different conditions of management and pasture growth	Nutritional - Deterministic	(Hart et al., 1998; Larcombe, 1999; Uribe et al., 1996)

**Table 2:** Summary of approaches used to model animal genotype, the environment, lactation and live weight in simulation models

Model	Genotype (G)	Environment (E)	Lactation	Live weight
Vetharianiam	Parameters describing mammary gland growth, and regression and a nutritional buffer factor	Energy pool used for milk synthesis	Set of differential equations scaled for G and E	Not modelled
Congleton	BV + MR	Age, LS, cystic follicles, twin calving, mastitis, and pregnancy	Age-specific gamma curves, scaled for the effects of G and E	Logarithmic equation
Dijkhuizen	Stochastic BV's, $\sigma^2_{BV}$ , $r_g$ and MR	LS, Stochastic $E_p$ (constant) and $E_t$ (changes each lactation)	Age-specific standard curves scaled for the effects of G and E	Richards growth curve function
SIMCOW	Input potential milk yield with stochastic variation	Age, level of feeding, and disease. Stochastic $E_p$ (constant) and $E_t$ (changes each lactation)	Age-specific gamma curves scaled for the effects of G and E	Gompertz growth curve function
Lopez-Villalobos	Breed, BV's, heterosis	Year and age effects	Annual yields	Von Bertalanffy growth curve function
CAMDAIRY	Input potential milk yield (daily)	LS, BCS, quantity and quality of feed, supplementary feeds	Breed-specific gamma curves scaled for the effects of G and E	User defined
DAFOSYM	Input milk yield (yearly)	Age, LS, breed, quantity and quality of feed, supplementary feeds	Age-specific gamma curves scaled for the effects of G and E	Range of sources
CNCPS	Input potential milk yield (daily or yearly)	Age, LS, breed, BCS, temperature, type of feed and level of feeding	Age-specific gamma curves scaled for the effects of G and E	Gompertz growth curve function
GRAZFEED	Input potential milk yield (peak/daily)	LS, BCS, Quantity and quality of feed, supplementary feeds, temperature and humidity	Gamma curves scaled for the effects of G and E	Brody function with allometric scaling for time
UDDER	Input milk yield (production data)	Age, LS, BCS, pasture growth, feed quality, supplementary use	Calculated from feed supply and nutrient partitioning	User defined

**Abbreviations:** BV = Breeding value,  $\sigma^2_{BV}$  = breeding value variance,  $r_g$  = genetic correlation between traits, MR = Mendelian recombination,  $E_p$  = Permanent environmental effect,  $E_t$  = temporary environmental effect, BCS = Body condition score, LS = Lactation stage

performance in periods of nutritional stress. An earlier mechanistic model by Neal and Thornley (1983) represented animal genotype by the number and activity of secretory cells in the mammary gland and a similar, but a more biologically advanced approach was used in the model by Dijkstra et al. (1997).

The nutritional models generally represent animal genotype as values for potential peak, daily or yearly milk yield. Genetic models represent genotype with either breeding values (Congleton, 1984; Dijkhuizen et al., 1986; Lopez-Villalobos, 1998), or potential milk yield (Sorensen et al., 1992). Genetic potential or potential milk yield as it will be referred herein, is not implicitly defined in the nutritional or genetic models, but generally refers to the milk production ability of the herd if these animals are given unrestricted access to high quality feed.

In the nutritional models, potential milk yield is entered by the user of the model based on either production records (Fox et al., 1992; Larcombe, 1999; Rotz et al., 1989), or assumed potential milk yield of the herd at peak lactation (Freer et al., 1997) or throughout the lactation (Fox et al., 1992; Hulme et al., 1986). Dijkhuizen et al. (1986) simulated breeding values for each female at birth, as an average of the parents' breeding values, plus Mendelian recombination which is equal to half of the additive genetic variance. Heritability (0.25), repeatability (0.50), and coefficient of variation (15%) for age-herd-year-season-corrected lactation production of milk, fat, and protein are assumed. Values for phenotypic and genetic correlations between milk, fat and protein traits were also considered when calculating performance levels for each trait. An estimate of the production levels for milk, fat and protein for each cow in the herd when they are mature (8 years, 2<sup>nd</sup> month of lactation) is then generated. Sorensen et al. (1992) represented genetic variation between animals in the herd through the use of stochastic simulation. Permanent and temporary environmental effects are imposed, by assigning a random number from a normal distribution at birth, and at the start of a new lactation, respectively.

The values for potential milk yield in each of the models are then used to scale the lactation curve of herd animals (Table 2). The lactation curves, with one exception (Larcombe, 1999) which uses previous herd production records, are based on the

## Chapter 2.....

gamma curve function proposed by Wood (1967). This function has the following form:

$$y_t = at^b e^{-ct}$$

where  $y_t$  = yield (kg milk) on day  $t$ ,  $a$  = scaling factor to represent the yield at the beginning of the lactation,  $b$  and  $c$  are factors associated with the inclining and declining slopes of the curve. A number of the models have specific gamma curve parameters ( $a$ ,  $b$ , and  $c$ ) depending on the age (Congleton 1984, Fox et al. 1992, Sorensen et al. 1992, Rotz et al. 1999), or breed (Hulme et al., 1986) of the cow or herd. These parameters are largely based on the studies by Congleton and Everett (1980) and Wood (1980).

A number of environmental factors in simulation models influence the calculation of potential and actual feed intake, nutrient partitioning, and performance (Table 2). For example, in each model the age of the herd or individual determines the potential milk yield lactation curve relative to mature equivalents. Similarly, lactation stage or days in milk alters the potential milk yield through the simulated lactation curve. Simulated performance is lower if the animal or herd is in thinner body condition in GrazFeed, CamDairy, CNCPS, and UDDER as the animal directs more energy towards live weight gain and less to the production of milk.

In each model, increased levels of feeding (with pasture or with supplementary feeds) increase animal intakes, subsequently lifting levels of performance as more of the feed consumed is used for the production of milk. In GrazFeed (Freer et al., 1997), the potential intake, defined as the amount eaten (kg DM/cow/day) when unrestricted access is allowed to a feed with a dry matter digestibility of at least 80%, at the defined stage of lactation, is calculated. The proportion of the potential intake which is actually achieved, defined as the relative intake, declines with lower values of pasture available (kg DM/ha), supplementary feeds offered and feed digestibility. For any amount of metabolisable energy (ME) available, a logistic function is used to calculate the manner in which energy is partitioned between milk production and body tissue gain or loss, thereby determining the level of milk production that can be sustained. The logistic function reproduces the diminishing response to energy inputs

at high levels of production, while recognising that severely underfed cows will still produce low levels of milk.

The model by Vetharaniam et al. (2003b) demonstrates the effect of nutrition through the use of an energy pool, which corresponds to the energy flux in the blood of an animal. The degree of partitioning of energy towards pregnancy, lactation, or growth is achieved through this pool in terms of relative energy status, which is the ratio of current versus a maximal energy status (which may not be realised because of digestive constraints). Simulated milk yield being higher when the ratio of current versus maximal energy status is closer to 1.

In CamDairy, if a cow's intake reaches 72 % of their potential intake, the amount above that proportion is deposited as fat and the cow will gain weight (Hulme et al., 1986). Potential intake in CamDairy is expressed as a percentage of live weight, ranging from 3.0 to 3.3 % of live weight (Hulme et al., 1986). In CNCPS, nutrient inputs are compared with estimated requirements for target milk production, and differences in ME are accounted for as live weight change (Fox et al., 1992). Alternatively, the level of performance (assuming no live weight change) that can be achieved on the stipulated feed is estimated. In UDDER, the predicted intake based on the feed available is divided among the requirements for maintenance, pregnancy, and growth as suggested by ARC (1980), with residual energy used for milk production or live weight change depending on the condition score of the herd (Uribe et al., 1996).

### **Calculation of phenotypic performance using simulation models**

To assess the capabilities of the respective models to account for genotype, environment and their interaction, simulations were carried out using the readily available GrazFeed (Freer et al., 1997), CNCPS (Fox et al., 1992), CamDairy (Hulme et al., 1986) models. In order to do this, we simulated the phenotypic performance of two genotypes across a range of feeding levels or environments. These phenotypic performance curves (or reaction norms) could then be used to determine the ability of these models to demonstrate either scaling effects or re-ranking of genotypes at two stages of lactation (45 days post-partum and 180 days

**Table 3:** Daily allowances of pasture<sup>1</sup> and maize grain<sup>2</sup> per cow (GrazFeed) or daily intakes of pasture and maize grain per cow (CNCPS and CamDairy) in the four environments which were simulated.

	Allowance model (GrazFeed) kg DM allowance/cow/day	Intake models (CamDairy and CNCPS) kg DM intake/cow/day
<b>Environment 1</b>		
Pasture	25.0	12.0
Maize grain	0.0	0.0
<b>Environment 2</b>		
Pasture	25.0	11.0
Maize grain	3.5	3.0
<b>Environment 3</b>		
Pasture	25.0	10.0
Maize grain	7.0	6.0
<b>Environment 4</b>		
Pasture	25.0	9.0
Maize grain	10.5	9.0

<sup>1</sup>11 MJME/kg DM and 22% crude protein

<sup>2</sup>14 MJME/kg DM and 10% crude protein

post-partum). The ability of the models to account for greater feed intakes in HGM animals was also assessed. It would have been ideal to include a mechanistic and/or genetic model. However, these were not readily available and in most cases, they do not simulate the effect of different levels of nutrition. The genetic-type models are more commonly used in the derivation of economic values for dairy cattle traits such as the model described by Harris (1998).

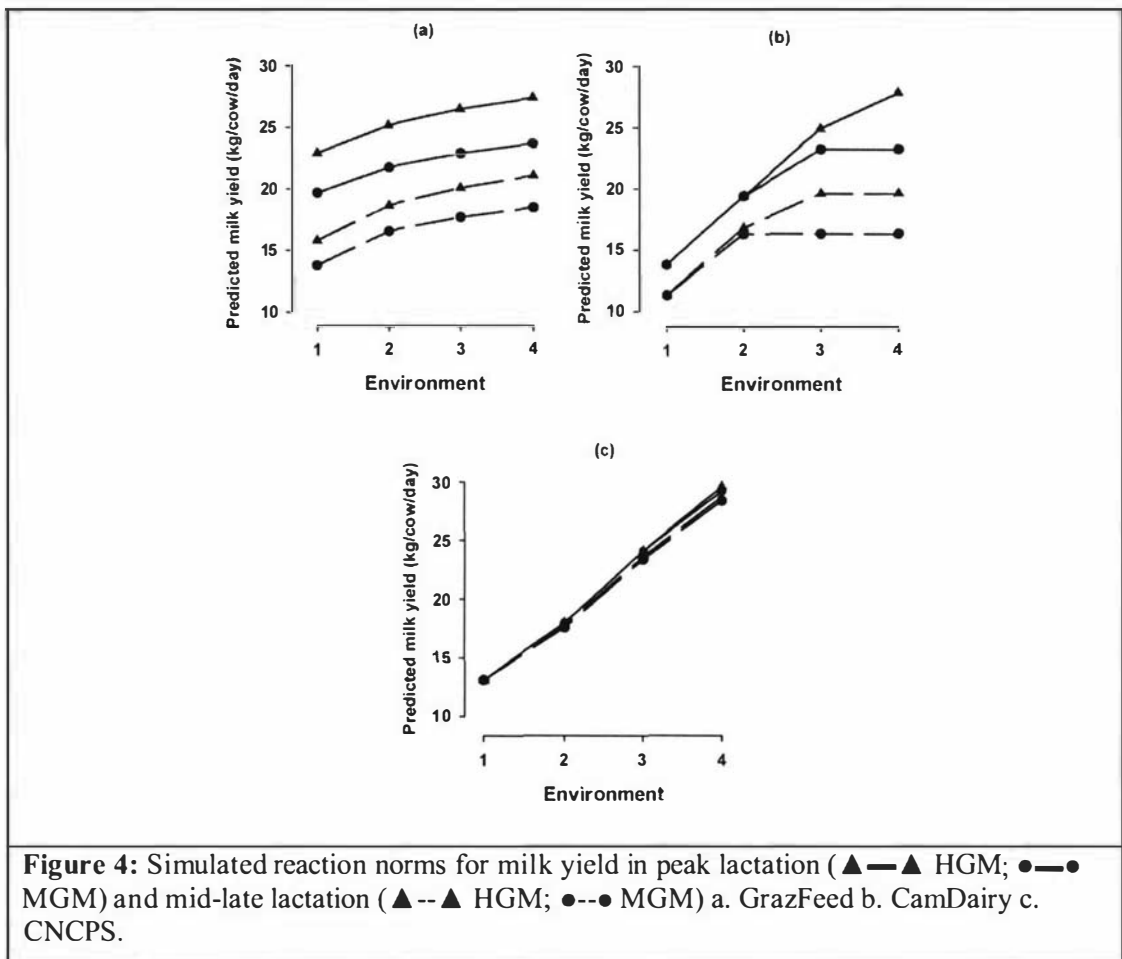
**Assumptions for the exercise**

The simulated medium genetic merit (MGM; 25 kg peak milk yield potential) and high genetic merit (HGM; 30 kg peak milk yield potential) Holstein Friesian genotypes were assumed to be in their 3<sup>rd</sup> lactation, weighing 550 kg and at a body condition score of 5.0 (on the 1-8 scale (Earle, 1976)) at parturition. Two lactation stages were simulated; peak lactation (45 days post-partum) and mid-late lactation (180 days post-partum). Four feeding allowances or intakes (defined as the environments) were specified for input into the allowance-dependent GrazFeed and intake-dependent CNCPS and CamDairy models (Table 3). Feed allowance was defined as the total amount of feed offered to the animal. For animals grazing pasture, feed allowance was the pre-grazing pasture mass including senescent material at the base of the sward, which the animal is unlikely to eat. If supplementary feeds are given to the animal, feed allowance represented the total

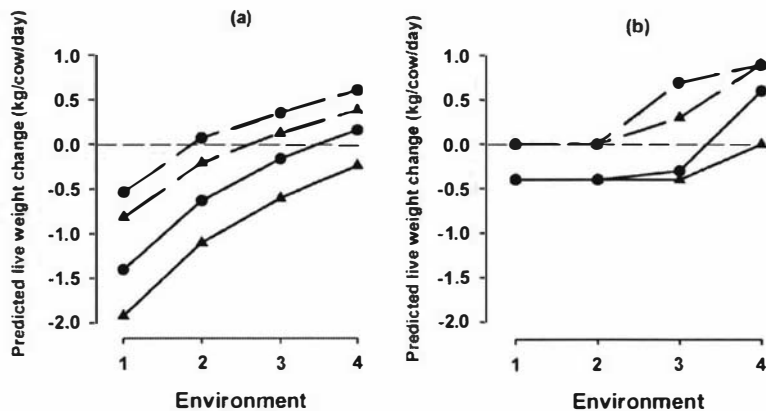
amount offered as pasture and supplementary feeds, not necessarily consumed by the animal.

## RESULTS

In GrazFeed, feed intake is estimated based on an allowance of pasture or supplementary feeds. This results in higher feed intakes in animals of superior genetic merit (Table 4), which has been demonstrated in a number of studies (Buckley et al., 2000; Kennedy et al., 2003; O’Connell et al., 2000). For example, in the four simulated environments the estimated daily intakes of HGM animals were on average 0.2 kg DM/cow/day higher than for the MGM animals.







**Figure 5:** Simulated reaction norms for live weight change in peak lactation (▲—▲ HGM; ●—● MGM) and mid-late lactation (▲--▲ HGM; ●--● MGM) a. GrazFeed b. CamDairy

**Table 4:** GrazFeed simulated feed intakes (kg DM/cow/day) for MGM and HGM dairy cows managed in four different environments in early and mid-late lactation

Environment	1		2		3		4	
Genotype	MGM	HGM	MGM	HGM	MGM	HGM	MGM	HGM
Early lactation								
Pasture intake	12.0	12.0	11.5	11.7	11.2	11.4	10.9	11.1
Maize grain intake	0.0	0.0	2.7	2.8	4.3	4.5	5.5	5.7
Total	12.0	12.0	14.2	14.5	15.5	15.9	16.4	16.8
Mid-late lactation								
Pasture intake	11.7	11.9	11.0	11.2	10.6	10.8	10.3	10.4
Maize grain intake	0.0	0.0	2.6	2.7	4.0	4.1	5.1	5.3
Total	11.7	11.9	13.7	13.9	14.6	14.9	15.3	15.8

The information displayed in Figures 4 and 5 are the simulated phenotypic performance values for milk yield and live weight change generated from each model. The GrazFeed, and CamDairy models predict lower performance levels in mid-late lactation (Figure 4), and this is associated with a reduction in the size of the negative energy balance or live weight change at low feed allowances or intakes in the CamDairy and GrazFeed models (Figure 5). CNCPS, which assumes the diet (above maintenance) is solely used for milk production i.e. no change in live weight, predicts little or no difference in performance between the genotypes. Alternatively, to achieve the milk yield targets for each genotype in CNCPS (results not shown) considerable live weight is lost (>2.0 kg live weight/cow/day) at the lowest feeding level.

## DISCUSSION

There was a curvilinear relationship between phenotypic performance and nutritional environment in the GrazFeed (Figure 4a) and CamDairy (Figure 4b) simulations in

peak and mid-late lactation. That is, as the nutritional environment improves there is a reduction in the marginal responses of milk production, which would be expected in a practical situation. By contrast, CNCPS (Figure 4c) illustrates a linear relationship where phenotypic performance continues to increase as the nutritional environment improves, because the model does not include live weight change. The inability to predict the level of performance and live weight change by a cow on the given diet has been an inherent problem with the CNCPS simulation model. However, a recent study by Reynoso-Campos et al. (2004) applied a dynamic approach to enable prediction of performance and live weight changes within the CNCPS model.

GrazFeed accounts for scaling effects, although marginally, through the higher intakes and greater partitioning of energy to milk in animals with higher peak yields. The CamDairy simulation demonstrates the scaling effect, where the difference in phenotypic performance between genotypes is greater at a higher feeding level. However, at the lowest feeding level there is no difference in the phenotypic performance (Figure 4b) or the level of live weight change (Figure 5b) between genotypes, thereby, suggesting the level of nutrients partitioned to milk is the same for both genotypes. This contradicts the results of Bryant et al. (2003b) who found there was a significant difference in the level of energy partitioned to milk between HGM and LGM Jersey cattle fed at very low levels in early (<60 days in milk) and late (>180 days in milk) lactation. This phenomenon occurs in CamDairy because when the animal or herd reaches their pre-defined milk yield potential they direct the remainder of feed consumed towards fat stores. Consequently, as the HGM animal reaches this point at a higher level of milk production than a MGM animal the former is able to partition more of the feed at a high allowance to the production of milk.

Feed intake or feed consumption is quantified in a number of ways in the illustrated simulation models. For example, GrazFeed and UDDER predict intake based on genotypic and environmental parameters. Initial investigations of GrazFeed found feed intake declined with lower values for pasture mass (kg DM/ha), supplementary feed usage and feed digestibility. UDDER adopts a similar approach where pasture growth, use of supplements and stocking rates are used to predict the feed intake of the herd. In addition, lower intake values for animals of inferior genetic merit were

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observed in the four simulated environments in GrazFeed (Table 4). The remainder of the models requires the input of a feed intake or a nutrient pool rather than estimating intake based on feed allowance, animal genotype, stage of lactation etc. This method prevents any potential Gx $\times$ E interaction for feed intake in different environments.

The simulated phenotypic performance curves (Figure 4) illustrate marginal scaling effects in the simulations using the GrazFeed, CamDairy models. However, none of the simulation results from the illustrated models demonstrated re-ranking of genotypes. This is inevitable, as the user of the model must first define animal genotype as peak, daily, or yearly milk yield for the system in which the animal is managed (Table 2). However, this is actually the phenotypic expression of the animal. Estimation of this value requires significant prior knowledge of the animal genotype, the environmental conditions and the environmental sensitivity of the genotype.

The potential inaccuracy of this method is clearly illustrated in the NZ study by Kolver et al. (2002) where the OHF and NZF animals had the same Breeding Worth (genetic measure of profitability per 4.5 t DM eaten/cow/year; Harris, 1998). Yet, the ranking of these genotypes when they were managed in the pasture-based differed markedly from their ranking on the total mixed ration system (Figure 1b). The greater MS production of the OHF on the total mixed ration system could partly be attributed to these animals having greater breeding values for fat and protein traits. However, this could not account for the 118 kg MS difference in performance between strains on the total mixed ration system. This study highlights the need to clearly identify the genotype of the animal and the particular system, in order to be able to simulate the phenotypic performance of the herd or individual cows correctly.

It would be preferable to use breeding values for milk production and live weight traits to estimate the genetic capabilities of animals as carried out by Congleton (1984), Dijkhuizen et al. (1986) and Sorensen et al. (1992). In these stochastic models, genetic variance and Mendelian recombination were used to generate genotypic variation among animals. The genetic correlation between traits is also used to ensure the phenotypic yield of one trait is correlated to other traits. However,

none of these models can, or were designed to, account for GxE interactions, as they do not use a parameter that quantifies the response of an animal to changes in its environment.

The review of the mechanistic, genetic and nutritional models have clearly illustrated marked differences in the specification of genotype and environment (Table 2), which largely prevents simulation of GxE interactions. Generally speaking the nutritional models are designed to help to assess the adequacy of a diet to reach target levels of production (Table 1), rather than assess the effect of differences in animal genotype. The genetic models take a more detailed view of genetics, for example, the dairy herd is represented by genetic variation around the mean breeding values and phenotypic levels of performance. The nutrition or environment provided to the animals ensures that simulated levels of performance are achieved, as opposed to simulating the effect of different feeding regimes. This is similar to the approach adopted in the mechanistic model by Vetharaniam et al. (2003b). However, the model of Vetharaniam et al. (2003b) defines animal genotype in terms of mammary gland parameters which need to be determined for specific genotypes. Therefore, in each type of model there is a limited capacity to simulate GxE interactions for dairy cattle performance as illustrated in Figure 4. This is due to the lack of interaction between the genotypic and environmental components within the models. This reinforces the view of Oldham and Emmans (1989), who stated “in order to obtain a sufficient genotypic description of the cow’s ability to deal with different feeds there needs to be a closer liaison between geneticists and nutritionist”. This greater interaction would help to facilitate progress in studies simulating and dealing with GxE interactions.

The inability to show GxE interactions for feed intake and performance is contrary to an increasing number of studies (Kolver et al., 2002; Linnane et al., 2004). It seems clear that some genotypes have environmental conditions where they are able to best express their genetic abilities, and other environmental conditions where they have a limited ability to perform to high levels (Illius et al., 2002; Kassen, 2002; Kyriazakis et al., 1999; Yearsley et al., 2001). This information is made available by using the derivative of the reaction norm as an environmental sensitivity trait.

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Kolmodin et al. (2002) stated that breeding values for reaction norm parameters can be estimated, if phenotypic values of a large number of offspring in a reasonably wide range of environments are available. Further investigations need to be undertaken to determine if the shape of the reaction norm for milk production traits are linear, as demonstrated for protein production (Calus et al., 2002; Kolmodin et al., 2002) and fertility (Kolmodin et al., 2002), sigmoidal (Kolmodin, 2003), or polynomial as demonstrated for milk yield in relation to herd size (Calus and Veerkamp, 2003). When the shape of the reaction norm is confirmed, environmental sensitivity trait values and traditional estimated breeding values for individual animals could be used to extrapolate and predict animal intake and ability in the expected range of environments.

For example, the feed allowance approach used by GrazFeed, where a feed allowance of pasture and supplements is specified, could be used to estimate a genetically driven feed intake on the specified feed. The genetically driven feed intake would be based on the animal or herd's genotype, which is represented by live weight and production breeding values, age, the level of heterosis and the environmental sensitivity trait. This method would allow the integration of GxE interactions for feed intake. Based on the estimated feed intake, the level of milk synthesis could be calculated using the most appropriate environmental adjustment techniques of the nutritional and genetic models.

Alternatively, it may be possible to simulate re-ranking of genotypes in different systems with the model of Vetharanim et al. (2003b). This would require quantification of the number of active mammary gland cells or alveoli, and the number of quiescent alveoli for specific genotypes throughout the lactation. Quiescent alveoli are previously active alveoli, which still retain the potential to become "reactivated" and thus secreting alveoli. Quantification of the respective rates of quiescence of active alveoli and reactivation of quiescent alveoli for genotypes in specific environments may indicate differences in the environmental sensitivity of specific genotypes. For instance, Vetharanim et al. (2003b) observed the North American Holstein Friesian group fed pasture had a higher rate of quiescence than NZ Holstein Friesian fed pasture, perhaps reflecting a difference in

the environmental sensitivity between North American and NZ Holstein Friesian cows. Further studies are needed to validate and quantify differences between genotypes managed in a range of systems. In addition, the approach adopted by Vetharaniam et al. (2003b) needs to be integrated with a model that accurately predicts feed intakes of genotypes in different environments. A combined simulation model of this manner would allow the integration of mammary gland and feed intake factors that are causes of GxE interactions.

## **CONCLUSION**

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This study has highlighted the fact that existing dairy cattle simulation models have been designed with a focus either on animal genetics or nutrition, with minimal integration between the two components. This lack of integration makes it difficult to simulate known GxE interactions in dairy production systems using available models. In order to simulate GxE interaction, the use of an environmental sensitivity trait has been proposed which could be used to predict performance in different environments. Using this trait, a model could be constructed that simulates differences in milk secretion and feed intakes between genotypes depending on the environment in which they are managed.

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## CHAPTER 3

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### **Environmental sensitivity in New Zealand dairy cattle of mixed breeds**

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## ABSTRACT

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This study quantifies the extent of sire re-ranking for milk production traits in a range of environments encountered within NZ. Character states of herds were formed within the environmental ranges of herd MS yield, summer heat load index (HLI), herd size and altitude. Single-trait and bivariate sire models across breeds were then applied for estimation of genetic parameters and genetic correlations between extreme character states. A low degree of sire re-ranking occurred, as measured by genetic correlations around 0.9, between herd environments that differed widely in MS yield (227 versus 376 kg MS per cow), and HLI (61.4 versus 69.6). The HLI of 61.4 and 69.6 are approximately equivalent to average summer maximum temperatures of 19 and 25 °C at 80 % humidity. Rank correlations of sire estimated breeding values in the extreme character states were low, but only in one case were they below expected correlations. The results show the environment in NZ is not sufficiently diverse to warrant separate breeding schemes for different environments.

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## INTRODUCTION

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Numerous recent studies have reported genetic variation in environmental sensitivity of dairy cattle sires, as measured by phenotypic responses of their progeny to different nutritional and climatic environments (Hayes et al., 2003; Kadzere et al., 2002; Kolver et al., 2002; Linnane et al., 2004; Ravagnolo and Misztal, 2000). Generally, genetic variation in environmental sensitivity results in an increase in phenotypic differences in milk production between sires associated with increased average performance i.e. a scaling effect (Hill et al., 1983; Visscher and Hill, 1992). However, in some cases where large variations in environment exist, sires may re-rank (Kearney et al., 2004; Zwald et al., 2003a).

Global sales of semen expose progeny of sires to climates and production systems vastly different from their original selection environment. This may cause sire re-ranking as the progeny of some sires are not expected to perform to their optimum in each different environment (Mulder et al., 2005). This fact has been recognised by Canadian producers who use intensive grazing as they are concerned their current

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evaluation system may not rank bulls adequately for their specific needs (Boettcher et al., 2003). The United States also estimated sire genetic merit on a regional and national basis up until 1995 because of the expectation that genotype x region interactions may be important (Norman et al., 2005). In NZ, similar questions exist for those producers who use significant amounts of feeds other than grazed pasture, as these producers often prefer to use sires proven in intensive production environments such as the United States or Canada.

Environmental clusters, or character states, of herds are often formed to reflect similar climatic and production levels, with performance in each character state being treated as genetically distinct traits (Ceron-Munoz et al., 2004; de Jong and Bijma, 2002; Fikse et al., 2003a; Zwald et al., 2003a). The estimated genetic correlations between environmental character states can then be tested to determine whether they depart significantly from 1.0 (unity). Commonly, the estimated genetic correlation between different environments range between 0.9 and unity, indicating minimal re-ranking of sires amongst or within countries (Calus and Veerkamp, 2003; Kolmodin et al., 2004; Weigel et al., 1999; Zwald et al., 2003a). Genetic correlations close to unity are generally observed when comparing average and high production environments, expected to use medium to high levels of concentrate feeds (Calus and Veerkamp, 2003; Cromie, 1999; Kolmodin et al., 2002; Rekaya et al., 2003; Veerkamp and Goddard, 1998). Significant re-ranking of sires has been observed, however, in studies by Hayes et al. (2003), Kolmodin et al. (2002) and Zwald et al. (2003a) with wide variations in environment within and between countries, potentially from different levels of concentrate feed usage. For example, Hayes et al. (2003) observed genetic correlations of 0.70 to 0.83 for yields of milk, fat or protein when comparing the 5<sup>th</sup> and 95<sup>th</sup> percentile of herds in Australia that achieved average test day protein yields of 0.54 and 1.10 kg per cow per day.

Environmental factors that cause re-ranking have been related to nutrition, climate and herd size. Nutritional (or production) environment, in the absence of information on levels and types of feeds offered to the herd, is generally classified on the basis of herd averages or standard deviations for total or peak yields of milk, fat or protein (Calus and Veerkamp, 2003; Fikse et al., 2003b; Zwald et al., 2003a). Climatic environment of the herd can be described using regional measures of rainfall or



temperature (Fikse et al., 2003a; Zwald et al., 2003a), or localised measures such as a temperature-humidity index (THI) (Hayes et al., 2003; Ravagnolo et al., 2000). Herd size may be based on contemporary group size, the number of first lactation animals, or the actual size of the herd.

Production environment, climate and herd size differ greatly among NZ herds. Average herd size is 302 cows but approximately 31 and 13 % of herds have a herd size of less than 200 or greater than 500 cows, respectively (Livestock Improvement, 2004). Average yields of milk are 3,913 kg per cow, much lower than yields in other countries (International Committee for Animal Recording, 2005). Nevertheless MS yields per cow exhibit significant regional differences (Livestock Improvement, 2004). In Northland, the far north of the North Island, average MS yield is 246 kg (2,947 kg of milk) compared to Southland, the far south of the South Island, where average MS yield is 362 kg (4,251 kg of milk; Livestock Improvement, 2004). Mean daily maximum air temperature is 5.0 °C higher in the north of the North Island than in the south of the South Island (National Institute of Weather and Atmospheric Research, 2005). Therefore, to determine if sires can be used with confidence throughout NZ in any environment, it is important to determine if variations in herd size, production environment and climate cause re-ranking of sires.

Genetic evaluation of NZ dairy cattle is undertaken using an animal model, adjusting for scaling effects where phenotypic differences between genotypes are greater in superior environments, analysing all breeds and breed crosses simultaneously. Breeding value estimates are on one scale allowing direct comparison of individual animals regardless of breed (Harris et al., 1996). To ensure the correct selection of the best sires for each environment, it is important to determine if sire by environment interactions are more than a scaling effect, and if they extend to re-rank sires between environments. The objectives of this study were to determine if sire re-ranking for milk yield traits occurred within NZ between different production, heat stress, herd size or altitudinal environments.

## MATERIALS AND METHODS

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### Production data

Initial data comprised 711,096 records of total lactation yields and yield deviations (Johnson, 1996) for milk, fat and protein from animals of various ages in sire-proving scheme herds of the Livestock Improvement Corporation. These herds progeny tested all of the young sires from 1989 to 2003. Herd-year-season (HYS) groups were formed, with season corresponding to calving in either, autumn or spring. HYS with less than 5 animals, and records that were <50 kg protein or <100 days in milk were discarded.

Total lactation yields were calculated from test day records and intervals between tests, with the total lactation comprising the period from day 5 after parturition until fifteen days after the last test. Total 270-day lactation yield deviations for milk, fat and protein were calculated from test day yields, with each test day record weighted according to the number of tests, stage of lactation at test and intervals between tests (Johnson, 1996).

A pedigree file was obtained for all animals in the analysis, traced back to the 1940's where possible. The breed composition of OHF, imported or derived from primarily North America bloodlines (Harris and Kolver, 2001), NZF, NZ Jersey (NZJ) and other which included Ayrshire, Guernsey, Milking Shorthorn were calculated. Heterosis and recombination coefficients were calculated for each of these breed crosses (OHF x NZF, OHF x NZJ, NZF x NZJ, and grouped OHF/NZF/NZJ x other) using the method described by VanRaden and Sanders (2003) and Wolf et al. (1995). Genetic groups for phantom parents were formed based on year of birth and breed (general OHF/NZF, NZJ or other). A genetic group within breed was assigned for all animals born between 1940 and 1970, but thereafter, genetic groups were formed in ten-year blocks. Some small genetic groups, such as 1980-1989 and 1990 onwards where animal recording was common were merged within breeds.

**Formation of environmental character states**

Four environmental factors were considered; 1) adjusted HYS total MS yield, a proxy for feed consumption levels 2) summer heat load index (HLI), a measure of the degree of prolonged heat stress 3) herd size, a reflection of stress imposed by competition and 4) altitude. These environmental factors were chosen due to a high likelihood for interaction between genotype and environment (Fikse et al., 2003a; Kolmodin, 2003; Ravagnolo and Misztal, 2000), or because they have not been studied in a NZ context (i.e. altitude). They are easily calculated and generally known by commercial producers.

Adjusted total lactation MS yield using total lactation data, as opposed to total 270-day lactation yield deviations, for each HYS was obtained using the general linear model procedure of the Statistical Analysis System (SAS) package, version 8 (SAS, 1999). The model included fixed effects of HYS, age (years at calving), breed (OHF/NZF, crossbred, NZJ and other) and lactation length fitted as a covariate. Lactation length was included as there is significant variation in lactation length due to heavy reliance on grazed pasture. Adjusting for breed effects ensured that all character states contained a range of cow breeds. For example, OHF and NZF achieve higher MS yields than NZJ at comparative levels of intakes. Therefore, if an adjustment for breed was not included the high MS yield character state may have contained herds with mainly OHF and NZF cattle. Similarly, the very low MS yield character state may have contained only herds with mainly NZJ cattle.

Summer HLI for each HYS was calculated from meteorological data for 1989 to 2002, obtained from 65 stations by the National Institute of Water and Atmospheric Research. Meteorological station data included map reference, daily measures of maximum and minimum temperature, rainfall, average relative humidity, solar radiation, and wind speed. These data was then used to calculate summer HLI (Castaneda et al., 2004) for each year:

$$HLI = 34.1 + (0.26 \times RH) + (1.33 \times BGT) - (0.82 \times WS)^{0.1} - \text{Log}^{[0.4 \times (0.0001 + WS^2)]}$$

where RH is mean daily relative humidity divided by 100, BGT is black globe temperature (°C) calculated as:

$$(1.33 \times T) - (2.65 \times \sqrt{T}) + [3.21 \times \text{Log}(SR+1)] + 3.5$$

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where  $T$  is air temperature ( $^{\circ}\text{C}$ ) at 1200 hrs and  $SR$  is solar radiation ( $\text{MJ}/\text{m}^2$ ) and  $WS$  is mean daily wind speed ( $\text{m}/\text{s}$ ).

The Livestock Improvement Corporation supplied map co-ordinates for each herd. Herds and meteorological stations were spatially located on a map (Figure 1) using Arc View GIS version 3.2 (ESRI, 1999). The nearest meteorological station with complete climate data (within a 50 km radius), was found using the Nearest Neighbor Script 3.4 (Weigel, 2004), and was used to determine summer HLI for that particular HYS. Some 30% of cow records were lost because farms did not have HLI data within a 50 km radius.

Herd size was based on yearly estimates of the number of lactating animals in each herd that was provided by the sire-proving scheme participants at the start of a season. Herd size data was only available for years in which a herd participated in the sire-proving scheme, resulting in a significant loss (60 %) of data. Farm altitude was estimated in Arc View GIS 3.2 (ESRI, 1999), by aligning a map with the spatial location of farms and a digital elevation map where altitude was estimated every 100 metres.

Character states of HYS were formed for each environmental parameter using the FASTCLUS procedure of SAS (SAS, 1999), based on the k-means algorithm. This procedure finds natural partitions in the data, as opposed to a quartile analysis where very similar herds may be assigned to different character states. The number of character states was dependent on the amount of data with matching environmental information. At least 40,000 records were needed to ensure a reasonable number of sires had a sufficient number of daughters ( $>20$ ) in each environmental character state for meaningful genetic correlation estimates. Four character states were considered for MS yield and HLI, and three characters states for herd size and altitude. Only three character states were considered for altitude as a large proportion of herds were at low altitudes.

### Estimation of genetic parameters

The univariate multi-breed sire model, in matrix notation, applied to all first lactation (2 year-old) records (184,288) across all or within each environmental character state was:

$$y = Xb + Zs + e$$

where

- y** is the vector of first lactation records for milk, fat or protein total yield deviations
- b** is the vector of fixed effects of HYS, second order polynomial regressions on age at parturition (in months), linear regressions on parturition date deviation from the mean HYS parturition date, breed proportions (OHF, NZJ and Other), heterosis and recombination coefficients
- s** is the vector of random additive genetic effects of sire
- X and Z** are incidence matrices associating records with the elements of **b** and **s**, respectively
- e** is the vector of random residuals

Residual effects were assumed to have mean of zero and to be independently normally distributed with variance ( $\sigma_e^2$ ). Accordingly,  $E[y]=Xb$ ,  $\text{var}(s_i) = \mathbf{A}\sigma_{s_i}^2$  and  $\text{var}(e) = \mathbf{I}\sigma_e^2$  where **A** is the numerator relationship matrix for sires and ancestral sires,  $\sigma_{s_i}^2$  is the sire variance and **I** is an identity matrix. Variance components, and solutions for random effects were calculated in each character state environment using an average information restricted maximum likelihood algorithm (Johnson and Thompson, 1995). Random sire solutions ( $\hat{s}$ ) were transformed to EBV using:  $\hat{u} = \mathbf{Q}\hat{b} + 2\hat{s}$ , where **Q** is a matrix relating fractions of breed group effects to the sire,  $\hat{b}$  is a vector of fixed additive breed group effects or breed group means,  $\hat{s}$  is a vector of random additive genetic effects for sire (Arnold et al., 1992).

**Tests for re-ranking between the top and bottom character states for each environmental descriptor**

**1. Genetic correlations**

Genetic correlations were estimated by applying a bivariate version of the univariate model to lactation yield deviations where performances in extreme character states were treated as distinct traits. Animals were included in the analysis if 1) their sire had at least two daughters in each of the two corresponding environments and 2) there were a minimum of 4 animals in their HYS group.

**2. Observed versus expected rank correlations between sire estimated breeding values**

Testing the significance of genetic correlation estimates is not straightforward, as the distribution of the estimates is not known. Therefore, as an alternative to genetic correlation estimates, rank correlations between estimated breeding values from the independent datasets were calculated and compared to the simulated distribution of the rank correlation according to the null hypothesis of a unity genetic correlation between environments. The simulation of the expected distribution of correlations requires knowledge of the reliability of the EBV from each character state. The test statistic for the expected correlation ( $r_e$ ) corresponding to the fifth percentile ( $\alpha=0.05$ ) were compared to the observed rank correlation (Garrick, 2005). Sire reliabilities in each character state were estimated as:

$$1 - \left( \frac{4 \times SEP^2}{\sigma_g^2} \right)$$

where  $SEP^2$  is the squared standard error of prediction derived from the inverse of the coefficient matrix and  $\sigma_g^2$  is the genetic variance calculated as:  $4 \times \sigma_s^2$  where the average information restricted maximum likelihood estimate of the sire variance was assumed to be the true parameter. Spearman's rank correlations ( $r_s$ ) of EBV of commonly used sires (reliability in excess of 0.40 or approximately >15 daughters in each character state) between the top and bottom character states for each environmental descriptor were calculated, and these were then compared with 0.05 percentile of  $r_e$ . A value where  $r_s$  is lower than  $r_e$  indicates the true genetic correlation between character states is significantly less than unity.

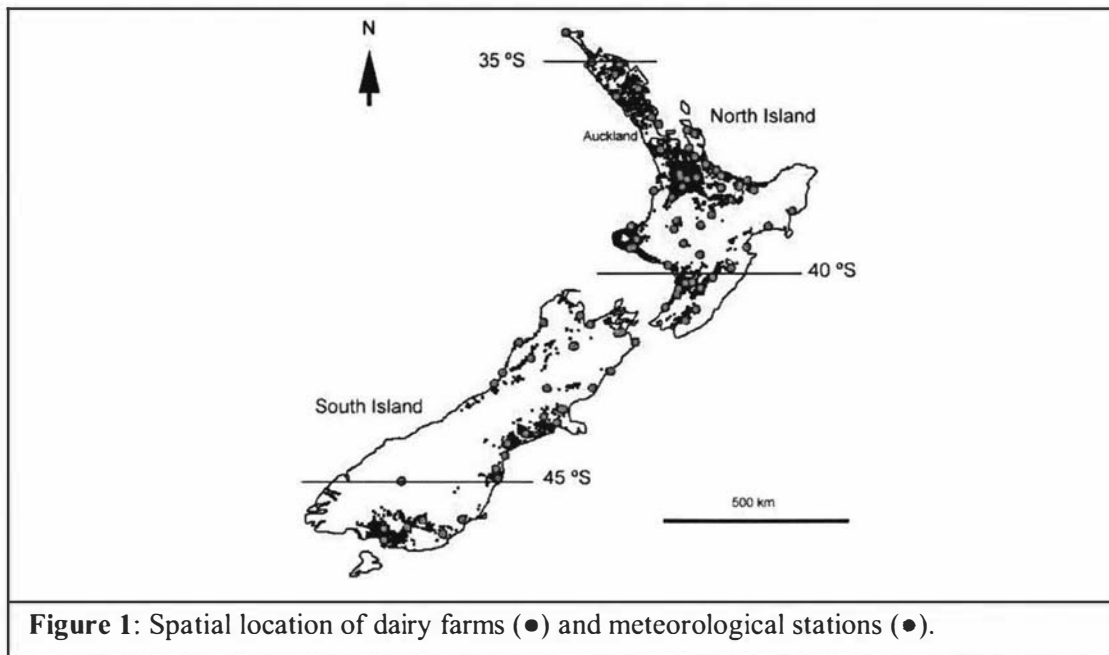
### 3. Environment-specific selection differential

The economic impact of selecting sires nationally as compared to selecting sires within character states was quantified by computing selection differentials for the top 20 sires. The selection criterion was an economic index (EI) of lactation value calculated as:  $(EBV_{Fat} \times EV_{Fat}) + (EBV_{Pro} \times EV_{Pro}) + (EBV_{Milk} \times EV_{Milk})$  where  $EBV_{Fat}, EBV_{Pro}, EBV_{Milk}$  are EBV for fat, protein and milk, respectively, and  $EV_{Fat}, EV_{Pro}, EV_{Milk}$  are NZ Dairy Industry 2006 economic values reported at 1.251/kg fat, 6.328/kg protein and -0.07/L milk (2006). The top 20 national sires were first identified from an analysis that included data from all character states. Within each separate analysis for a particular character state, EI were recalculated using the environment state-specific EBV. The average EI for the best 20 sires in that state, selected after calculating the EI of all sires in a character state, was then compared to the average EI for the nationally best 20 sires. The resulting difference in average merit would be zero if the nationally best 20 sires were also the best in that particular state, otherwise the selection differential would be positive. Denoting the average EI of the best 20 environment state-specific sires in character state k as  $\bar{X}_{EI_k}^{ESS_{sires}}$  and the EI of the nationally-best 20 sires in character state k as  $\bar{X}_{EI_k}^{SS_{sires}}$ , the environment state-specific selection differential is:  $\bar{X}_{EI_k}^{ESS_{sires}} - \bar{X}_{EI_k}^{SS_{sires}}$

## RESULTS

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The majority of sire proving scheme dairy herds were located in Northland (midpoint of 35.5 °S, 174.2 °E) or Waikato (37.5 °S, 175.2 °E) (Figure 1). Other regions, which were heavily represented, were Taranaki (39.2 °S, 174.2 °E), Manawatu (40.2 °S, 175.2 °E), Canterbury (43.5 °S, 171.2 °E) and Southland (46.1 °S, 168.2 °E). Each farm generally had at least one weather station within a 50 km radius, however not all had sufficient measurements to estimate HLI.



Average character state yields for MS ranged from 227 to 376 kg MS/cow (Table 1). The two extreme MS yield states were the smallest incorporating 884 (12.5 % of total data) and 475 HYS (10.7 % of total data), respectively (Table 2). High MS yield herds tended to be located at more southern latitudes (Table 1). For example, for every 1 ° change in latitude in a southern direction, MS yield increased by 6.45 kg after fitting a simple linear regression ( $r^2 = 0.16$ ). Average character state HLI ranged

**Table 1:** Means (standard deviation) of environmental descriptors for each character state across all age groups.

	MS yield (kg)	HLI	Herd Size	Altitude (m asl <sup>1</sup> )	Latitude (° S)
MS yield					
1	227 (18.5)	67.3	204	97	37.7
2	263 (11.8)	66.6	226	104	38.4
3	305 (12.7)	65.7	241	110	39.4
4	376 (25.8)	64.4	291	102	41.9
HLI					
1	307	61.4 (1.46)	219	121	42.2
2	290	64.7 (0.73)	223	161	39.2
3	283	67.2 (0.65)	239	74	37.9
4	268	69.6 (1.01)	230	46	37.6
Herd Size					
1	258	65.8	154 (30.0)	105	38.6
2	269	66.2	263 (36.8)	103	39.1
3	285	65.9	414 (79.9)	129	39.9
Altitude					
1	289	66.5	231	50 (31.0)	39.1
2	284	65.1	234	178 (43.6)	39.4
3	287	64.8	260	367 (77.4)	39.2

<sup>1</sup>metres above sea level



**Table 2:** Character state means of environmental descriptors and corresponding numbers of herd-year-seasons (HYS), animals, sires, average breed proportions and percentage of total two-year old data for each character state.

	Mean environment	HYS (n)	Sires (n)	Animals (n)	Breed proportions				% of data <sup>1</sup>
					NZF	OHF	NZJ	Other	
MS yield (kg MS/cow /year)									
1	227	884	2,486	23,030	0.48	0.18	0.28	0.05	12.5
2	263	2,224	3,048	70,887	0.43	0.20	0.34	0.03	38.5
3	305	1,971	3,023	70,705	0.41	0.22	0.35	0.02	38.4
4	376	475	2,097	19,666	0.43	0.26	0.30	0.01	10.7
HLI									
1	61.4	647	2,088	20,622	0.39	0.18	0.40	0.03	11.2
2	64.7	1,279	2,745	40,729	0.39	0.20	0.38	0.03	22.1
3	67.2	1,337	2,755	45,137	0.44	0.24	0.30	0.03	24.5
4	69.6	703	1,794	22,146	0.45	0.22	0.31	0.03	12.0
Herd size (cows/herd)									
1	154	1,298	2,745	33,757	0.42	0.19	0.36	0.03	18.3
2	263	380	2,212	16,804	0.41	0.24	0.34	0.01	9.1
3	414	377	2,388	22,641	0.43	0.26	0.29	0.02	12.3
Altitude (m above sea level)									
1	50	3,446	3,231	111,327	0.43	0.21	0.34	0.03	60.4
2	178	1,264	2,850	41,594	0.41	0.22	0.34	0.03	22.6
3	367	531	2,551	19,577	0.42	0.24	0.31	0.03	10.6

<sup>1</sup>The percentage of total data represented in each character state

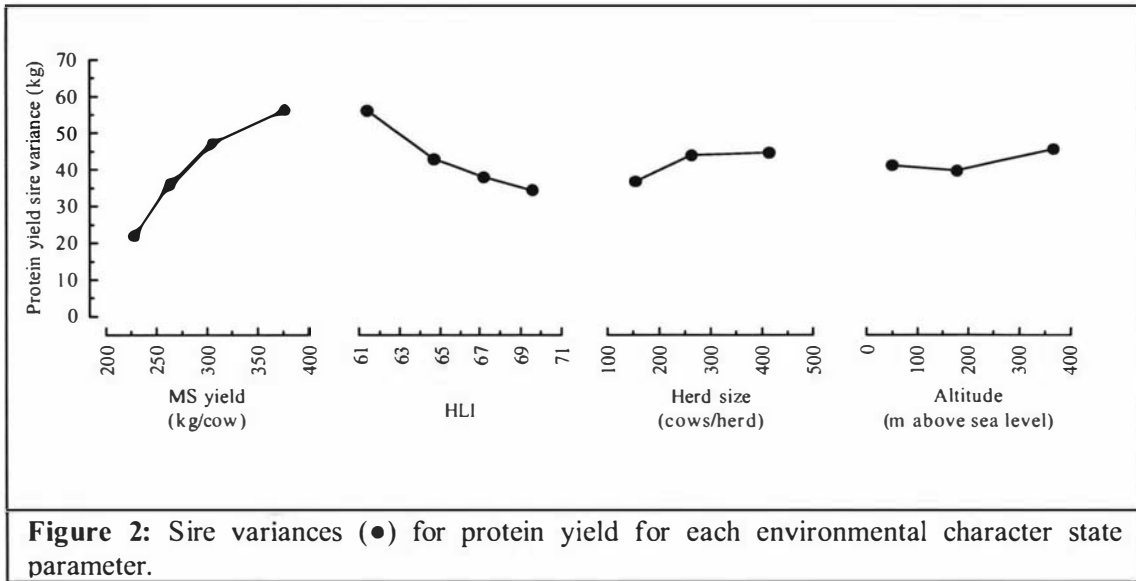
from 61.4 to 69.6 (Table 1). The HLI of 61.4 and 69.6 represented the extreme character states in this study and are approximately equivalent to average summer maximum temperatures of 19 and 25 °C at 80 % humidity.

Lower HLI herds tended to be located at southern latitudes (Table 1). For example, for every 1 ° change in latitude in a southern direction, HLI decreased by 0.73 kg after fitting a simple linear regression ( $r^2 = 0.40$ ). The least number of HYS were represented in the coldest (61.4 HLI) character state.

**Table 3:** Estimates of heritability for milk, fat and protein yields within the bottom and top character states for environmental descriptors.

	Bottom character state				Top character state			
	n <sup>1</sup>	Heritability			N	Heritability		
		Milk	Fat	Protein		Milk	Fat	Protein
MS yield	23,030	0.28	0.20	0.23	19,666	0.34	0.27	0.25
HLI	20,602	0.37	0.30	0.31	22,146	0.36	0.25	0.28
Herd size	33,757	0.38	0.27	0.28	22,641	0.34	0.32	0.29
Altitude	111,327	0.35	0.28	0.28	19,557	0.34	0.32	0.29

<sup>1</sup>Number of records (animals) in the character state



Average character state herd size ranged from 154 to 414 lactating animals per herd (Table 1). Larger herds achieved significantly higher MS yields. Herd size ranged from 70 to 830 cows per herd. Average character state farm altitude ranged from 50 to 367 m above sea level. HLI was reduced at high altitudes, and farm altitude did not affect MS yields. A high proportion (63 %) of herds in the analysis were located at altitudes of less than 100 m above sea level.

Heritability estimates were highest for milk ( $0.35 \pm 0.011$ ), followed by protein ( $0.28 \pm 0.010$ ) and fat yield ( $0.28 \pm 0.010$ ). Sire variance increased with MS yield (Figure 2), as did residual variance but at a lesser rate such that heritability increased with MS yield (Table 3). For the remaining environmental parameters, differences in character state environment had little effect on heritability estimates.

The only genetic correlation estimate less than 0.9 was for protein yield (Table 4) when comparing the most extreme herd MS yield (227 versus 376 kg MS/cow) states. All other genetic correlations between extreme character states were above 0.90. Nevertheless, the genetic correlations between states tended to be lower for MS and HLI than for herdsize or altitude. Rank correlations were only below their expected value for fat yield in the extreme HLI character states (Table 5).

**Table 4:** Genetic correlations (standard errors) for milk, fat and protein yields for the bottom and top character states for environmental descriptors.

	Milk	Fat	Protein
MS yield	0.92 (0.047)	0.93 (0.055)	0.87 (0.063)
HLI	0.93 (0.038)	0.94 (0.044)	0.90 (0.047)
Herd size	0.95 (0.026)	0.98 (0.029)	0.97 (0.030)
Altitude	1.00 (0.006)	0.94 (0.023)	0.98 (0.022)

**Table 5:** Spearman’s rank ( $r_s$ ) and expected ( $r_e$ ) correlations between estimated breeding values for milk, fat and protein yields for the bottom and top character states for environmental descriptors.

	Milk		Fat		Protein	
	$r_s$	$r_e$	$r_s$	$r_e$	$r_s$	$r_e$
MS yield	0.76	0.53	0.50	0.43	0.83	0.43
HLI	0.91	0.53	0.41*	0.47	0.83	0.50
Herd size	0.86	0.59	0.53	0.52	0.81	0.51
Altitude	0.88	0.67	0.65	0.65	0.79	0.63

\*Rank correlation is significantly different to the 0.05 percentile of expected correlations

Environment-specific selection differentials were greatest in the MS yield environment that averaged 376 kg MS per cow and was NZ\$10.5. This is about equivalent to the value of one year’s genetic gain. Environment-specific selection differentials averaging greater than NZ\$5 were observed in the environments that achieved low MS yields, experienced low HLI, comprised large herds, and were located at high altitudes. Negligible advantages were observed by selecting sires based solely on daughter performance in low altitude herds. Selection on EI within character state resulted in higher average sire EBV for milk, fat and protein yield in  $ESS_{sires}$  over  $SS_{sires}$  (Table 6).

## DISCUSSION

There was little evidence of sire re-ranking for milk, fat or protein yield within NZ. Genetic correlations were above 0.80, a threshold level suggested by Robertson (1959), and well in excess of 0.60, suggested by Mulder et al. (2005) as a break-even point that warrants separate breeding schemes for environments of equal importance. Genetic correlations estimates between nutrition or production environment, as measured by herd MS yield, are similar to the range of 0.74 to 0.98 within a country presented by Konig et al. (2005) when summarising international studies. The rank correlation estimates obtained in this study fluctuated around the values reported by Calus et al. (2002), Cromie (1999), Kearney et al. (2004) and Kolmodin et al. (2002).

**TABLE 6:** Environment-specific selection differentials for milk, fat and protein yield and economic index (EI; \$NZ) in the lowest and highest character state for each environmental descriptor.

Environment <sup>1</sup>	Milk (kg)		Fat (kg)		Protein (kg)		EI (\$NZ)		
	ESS <sub>sires</sub> <sup>2</sup>	SS <sub>sires</sub> <sup>3</sup>	ESS <sub>sires</sub>	SS <sub>sires</sub>	ESS <sub>sires</sub>	SS <sub>sires</sub>	ESS <sub>sires</sub>	SS <sub>sires</sub>	Advantage
MS									
227 kg MS	316	270	7.5	6.1	10.1	8.2	50.9	40.4	+10.5
376 kg MS	495	408	7.5	5.7	12.9	10.9	56.1	47.4	+8.7
HLI									
61.4	394	349	9.0	6.4	13.5	12.0	68.9	59.3	+9.6
69.6	405	368	9.5	8.8	11.3	10.0	55.2	48.5	+6.7
Herd size									
154 cows/herd	485	456	9.7	8.6	13.6	13.0	64.1	61.0	+3.1
414 cows/herd	378	340	3.4	1.3	10.0	8.7	41.3	32.9	+8.3
Altitude									
50 m asl	450	405	9.3	9.3	13.6	12.8	66.0	64.1	+1.9
367 m asl	544	402	5.8	4.5	14.0	11.2	57.8	48.5	+9.3

<sup>1</sup>Abbreviations: MS = Milk solid, HLI = Heat Load Index, asl = above sea level.

<sup>2</sup>Average EI of the top 20 sires selected based on performance within an environment

<sup>3</sup>Average EI of the top 20 sires within an environment, which were selected based on performance in a standard general evaluation.

Rank correlations for fat yield were generally less than previously reported by Kearney et al. (2004) and this may be a reflection of the multibreed dataset used in the present study. For example, the difference between NZJ, NZF and OHF cattle for fat yield is not as marked as for milk and protein yields, which would increase the likelihood of re-ranking for fat yield.

Selection differentials indicated small benefits of environment-specific selection would occur in an environment that achieves low MS yields (Table 6). The EI and corresponding yield traits of some of the  $SS_{\text{sires}}$  dropped based solely on the performance of their daughters in low MS yield environments and this was most common for Friesian (OHF or NZF) sires. Conversely, the EI of sires that were predominantly of NZJ origin improved or maintained their ranking in low MS yield environments. Out of the twenty sires selected on EI in a general genetic evaluation, eleven and thirteen were still in the top twenty sires when selecting solely based on performance in low and high MS yield herds, respectively. By contrast, seventeen out of the twenty sires selected on EI in a general genetic evaluation were still in the top twenty sires based on performance in herds located at low altitudes. There was also some benefit in the environment-specific selection of sires in herds, which experienced low HLI, were large, or located at high altitudes. Further investigation is needed to determine the level at which environmental-specific differentials become economically important, warranting the publication of environment-specific estimated breeding values or environmental sensitivity information. Calus and Veerkamp (2003) estimated sire economic merit across a range of environments in The Netherlands but found little evidence for re-ranking. However, the range of production systems in The Netherlands is expected to be significantly less than those encountered in NZ. It is unclear which measure of sire re-ranking is more important. However, high genetic correlations between environments do not guarantee environmental sensitivity of sires is not important, especially when comparing the performance of sire breeds in different environments (see chapters 4 and 5).

The specific causes for re-ranking of animals is still largely unknown. A potential reason for re-ranking may be a reduced consumption ability or genetic-drive of one genotype compared to another genotype when each is subjected to a specific

environment (Bryant et al., 2005). For example Illius et al. (2002), Kyriazakis et al. (1999) and Yearsley et al. (2001) proposed that animals adapt or evolve to the environment in which they were selected. The evolutionary adaptations that allow specific genotypes to function better in one environment include the ability to dissipate heat easily (Bianca, 1965) and consume and process concentrates faster than other genotypes. At the genomic level, genes responsible for production traits may show different expression (degree of penetrance) in different environments (Lin and Togashi, 2002). For example, they may be “switched” on or off depending on the environmental conditions in which the animal is managed (de Jong, 1990; Via et al., 1995). The first evidence of this switching mechanism were provided by Rutherford and Lindquist (1998), who found a deformed-eye trait in *Drosophila* was expressed more frequently at high temperatures. Possibly, environmental-switch mechanisms also occur in dairy cattle.

On average, MS yields were greater at lower latitudes (Table 1). This may have been due to supplementation being greater at lower latitudes although this cannot be confirmed, or an effect of summer HLI on animal performance and feed availability. The summer HLI encountered in the warmest character state environment would not be normally associated with heat stress conditions (Castaneda et al., 2004; Ravagnolo and Misztal, 2000; Zwald et al., 2003b). However, NZ dairy cows generally walk long distances, are exposed to wind and very high solar radiation levels which can all modify HLI value when heat stress occurs (Bianca, 1965; Kadzere et al., 2002; McKenzie et al., 2003). Alternatively, greater performance at more southern latitudes may be related to cows being exposed to shorter photoperiods prior to parturition. Cows exposed to short compared to long photoperiods prior to parturition are reported to have greater mammary development, resulting in increased milk yields in the former cows (Miller et al., 2000; Wall et al., 2005).

There was limited evidence for significant re-ranking amongst different herd sizes. In comparison to our study, Zwald et al. (2003b) estimated a genetic correlation of 0.78 when comparing herds with an average of 30 and 2.5 first lactation animals per year, respectively. Konig et al. (2005), estimated genetic correlations for protein yield of 0.79 and 0.92 when comparing large herds ( $\geq 150$  cows) in Eastern states of Germany with small herds ( $\leq 50$  cows) in Western states of Germany and small and

large herds in Eastern states, respectively. Fikse et al. (2003a) using data from Guernsey cows in four countries (Australia, Canada, USA and Republic of South Africa) observed a genetic correlation of 0.94 between small and large herds. Kondo et al. (1989) found under conditions of excessively large group sizes, individual animals find it difficult to memorise their social rank within the herd and consequently aggressive interactions increase. Under predominantly grazing conditions any genotype-based advantage in large or small group sizes might not be expressed to the extent of intensive environments.

In conclusion, this study has provided valuable insight into the environmental heterogeneity experienced by the NZ dairy cattle population. The results confirm there is insufficient sire re-ranking in NZ to warrant formation of separate breeding schemes for different environments.

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## CHAPTER 4

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### **Effect of environment on the expression of breed and heterosis effects for production traits**

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## **ABSTRACT**

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In this NZ study, character states of herds were formed within the environmental ranges of herd average total lactation yield of MS, which is a proxy for feeding level, summer HLI, herd size and altitude. A univariate multi-breed sire model was applied to first lactation (2 year-old) records of milk, fat and protein within each environmental character state to estimate breed and heterosis effects. A scaling effect was observed for MS yield between OHF and NZJ animals as the differences for milk, fat and protein yield between these breeds were 561, 1.3 and 9.3 kg, respectively at 227 kg MS/cow, much smaller than the differences of 1151, 3.1 and 23.0, at 376 kg MS/cow. Heterosis levels for milk, fat and protein yields were highest for OHF x NZJ, followed by NZF x NZJ and OHF x NZF with average heterosis for all traits of 7.3, 5.7 and 2.7 %, respectively. Heterosis levels for OHF x NZF were suppressed in very low MS yield environments and in many cases were not significantly different to zero. Heterosis was suppressed in crosses with OHF in the high HLI environment.

## **INTRODUCTION**

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The performance of dairy breeds in different environments has been evaluated in a number of recent studies (Demeke et al., 2004; Dillon et al., 2003; Nielsen et al., 2003). These studies have shown that not all breeds perform equally in each environment, however, crosses among breeds can result in significant improvements in production and survival traits over the average of the parental breeds (heterosis) incurring economic benefits (Lopez-Villalobos et al., 2000; McAllister, 2002; Swan and Kinghorn, 1992; VanRaden and Sanders, 2003). Environment has also been shown to influence the expression of heterosis, further complicating the estimation of crossbred performance (Barlow, 1981). Genetic evaluation of New Zealand dairy cattle is undertaken using a multi-breed animal model, analysing all breeds and breed crosses simultaneously. Breeding value estimates are on one scale allowing direct comparison of individual animals regardless of breed (Harris et al., 1996). The objective of the current report was to quantify if environment within New Zealand influences the expression of breed and heterosis effects.

## MATERIALS AND METHODS

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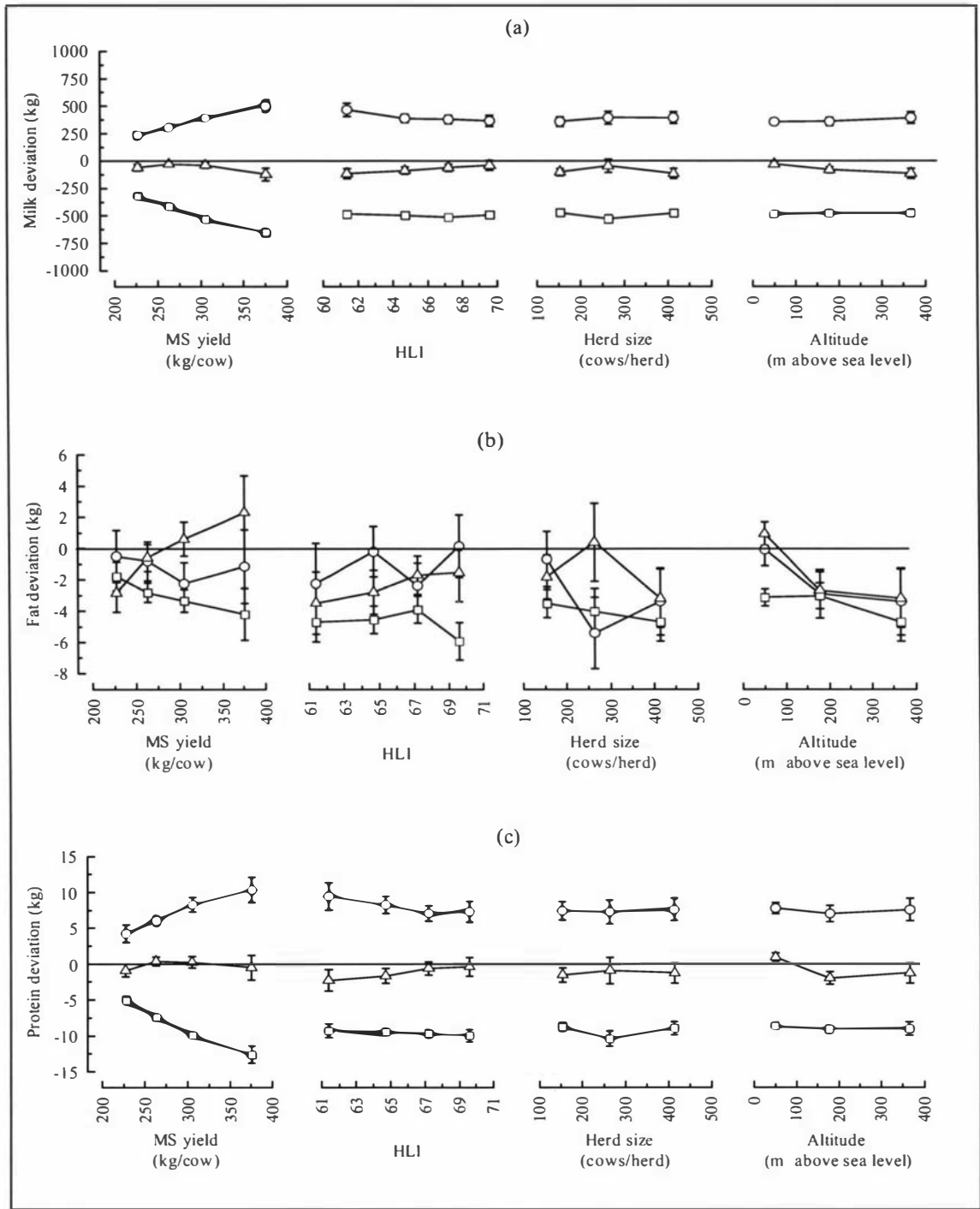
For a full description of data and statistical analyses refer to Chapter 3. In this report, confidence intervals at the 95 % level ( $\mu \pm 1.96$  standard error) were used to test if heterosis effects differed between character states or were significantly different from zero.

## RESULTS AND DISCUSSION

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Overall, OHF cattle achieved the highest milk and protein yields in all environments, with NZJ cattle producing the least milk and protein. The highest fat yields of all breeds were in NZF cattle, with NZJ cattle producing the lowest yields of fat (Figure 1). A scaling effect for milk, fat and protein yield was observed in relation to MS yield (or nutritional environment) for the OHF and NZJ breeds. The differences for milk, fat and protein yield between these breeds was 561, 1.3 and 9.3 kg, respectively at 227 kg MS/cow, much smaller than the differences of 1151, 3.1 and 23.0, at 376 kg MS/cow. These results suggest OHF, traditionally managed and selected in an intensive feeding system, are better suited to a high MS yield environment than NZJ, which were traditionally selected for performance on a pasture-based diet. Oldenbroek (1988) also observed that the difference in milk, fat and protein yields and feed intake between Jersey and Friesian cattle was greater on a concentrate than on a roughage diet. Smaller Jersey dairy cattle have lower requirements for maintenance than larger Friesian cattle (Oldenbroek, 1988). Consequently, it is expected that at low feeding levels i.e. a roughage diet, Jersey cattle are able to partition a greater proportion of available nutrients towards milk production than larger Friesian cattle.

Heterosis levels for milk, fat and protein yield (calculated as a percentage relative to the phenotypic average of the parental breeds) were highest for crosses between OHF and NZJ, followed by NZF x NZJ and OHF x NZF (Figure 2). Heterosis levels for OHF x NZJ were greater in intermediate (263 and 305 kg MS per cow) than low

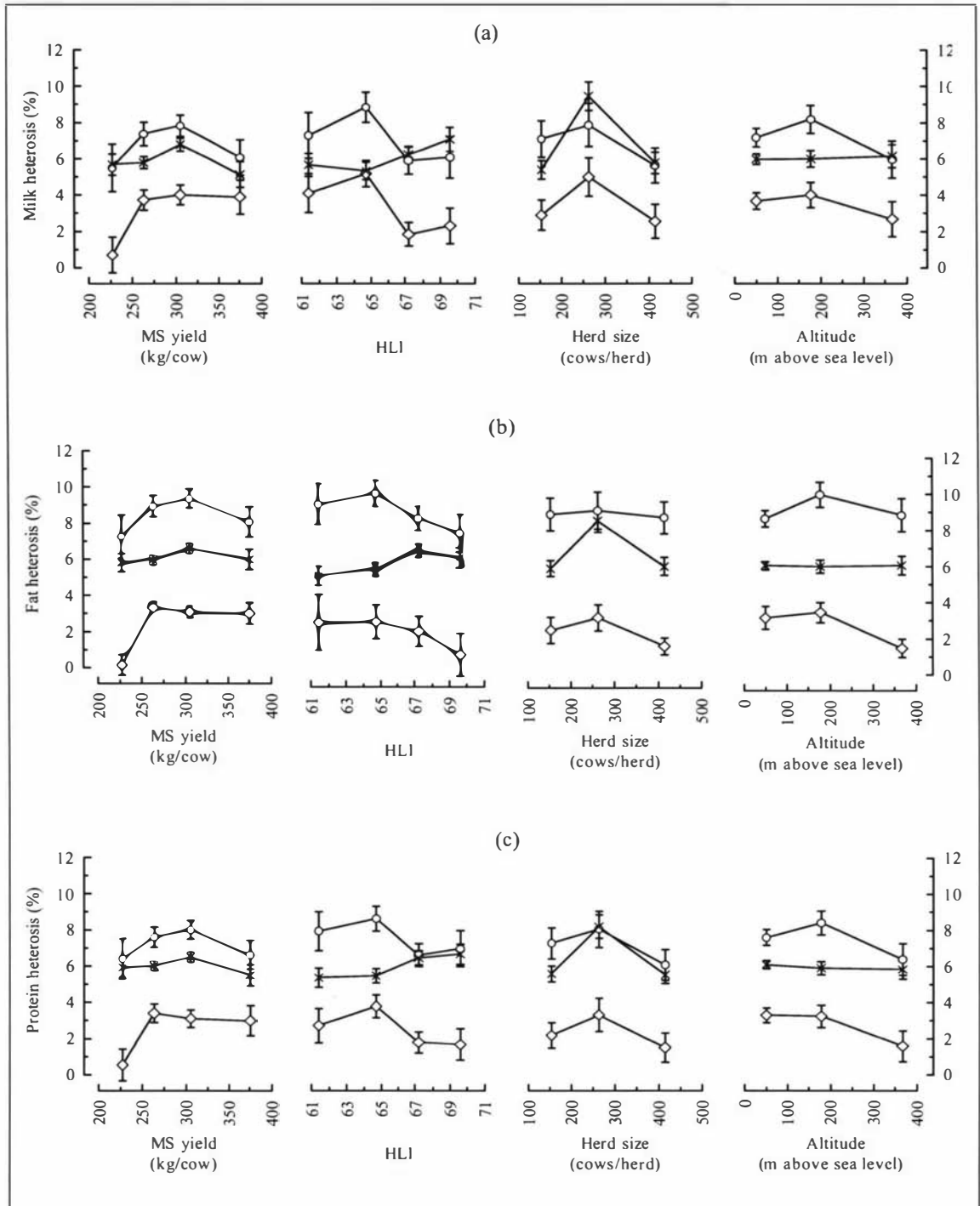


**Figure 1:** Observed breed deviations (bars represent standard errors) from a New Zealand Friesian base for overseas Holstein Friesian (○), New Zealand Jersey (□) and Other (△) for (a) milk yield (b) fat yield and (c) protein yield in relation to character state milk solids (MS) yield, heat load index (HLI), herd size and altitude.



(227 kg MS per cow) and high (376 kg MS per cow) MS yield environments, and similar results were observed in intermediate HLI environments for protein yields. Heterosis levels for OHF x NZF were suppressed in very low MS yield environments and in many cases were not significantly different to zero. Heterosis was suppressed in crosses with OHF in the high HLI (69.6 HLI) environment. A HLI of 69.6 is approximately equivalent to average summer maximum temperatures of 25 °C, humidity of 75 %, wind speeds of 2 m/sec and a black globe temperature of 27.5 °C or a temperature-humidity index of 74. Heterosis for fat yield for the crosses between OHF and NZF was not significantly different from zero in the high HLI and low MS yield environments, whereas in the other HLI and MS environments the level of heterosis expressed were significant and ranged from 2.0 to 3.2 %. Limited heterosis for fat yield in crosses between OHF and NZF was observed at high altitudes. Estimates of recombination loss were mostly positive; however few were significantly different from zero (results not shown).

Heterosis estimates of milk and fat yield for OHF x NZF were similar to the estimates of 2.0 to 2.5 % reported by Boichard et al. (1993) for crosses between OHF and French Black and White cattle, and similar values of 5.0 to 7.0 % were obtained for crosses between NZF x NZJ by Harris et al. (1996) and Ahlborn-Breier and Hohenboken (1991). The largest heterosis estimates were obtained for crosses between OHF x NZJ cattle (5.0 to 9.5 %), suggesting significant genetic differences between these breeds. Crosses between these two breeds results in individuals which have a high proportion of heterozygous loci with complementary attributes leading to significant increases in performance over the average of the parental breeds (Lopez-Villalobos, 1998). The positive heterosis estimates for OHF x NZF, suggests these are also distinct breeds. Recombination estimates for milk, fat and protein yields for back-crosses between the major milk producing dairy breeds are generally negative (Lopez-Villalobos, 1998), as opposed to the non significant positive estimates obtained in this study. However, VanRaden and Sanders (2003) in the United States also estimated positive recombination effects for back-crosses between Holstein Friesian cattle and other breeds such as Ayrshire, Jersey, and Guernsey.



**Figure 2:** Observed heterosis (bars represent standard errors) for crosses between overseas Holstein Friesian and New Zealand Jersey (o), New Zealand Friesian and New Zealand Jersey (x) and overseas Holstein Friesian and New Zealand Friesian (o) for (a) milk yield (b) fat yield and (c) protein yield in relation to character state MS yield, summer HLI, herd size and altitude.

Barlow (1981) in a comprehensive review of different species, found expression of heterosis is dependent on the environment in which breed crosses are managed (i.e. heterosis x environment interaction), and is generally greater in a stressful environment than in a supportive environment. However, as with this study, the nature of heterosis x environment interactions vary and definite conclusions on environment-dependent expression cannot be made. Heterosis for crosses with OHF cattle may have been suppressed in high HLI and low MS environments due to an elevated metabolic rate of the hybrid animals, thereby, initiating the earlier onset of heat stress effects on performance. Alternatively, nutrient supply in low MS yield herds may have been insufficient to allow expression of heterosis in the crossbred cows, which were genetically capable of high yields.

In conclusion, an observed scaling effect between OHF and NZJ cattle in relation to MS yield environment, would suggest these breeds are better suited to environments of high and low MS yields, respectively. Significant gains in performance over the averages of parental breeds can be utilized by crossing OHF and NZF with NZJ cattle, with evidence that the environment can affect the size of the heterosis effect.

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## CHAPTER 5

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### **Reaction norms used to quantify the responses of New Zealand dairy cattle of mixed breeds to nutritional environment**

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## ABSTRACT

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A reaction norm, where phenotype or genotype is expressed as a function of environment, can be used to measure environmental sensitivity. This study investigates the environmental sensitivity of dairy cattle genotypes (or breeds), in relation to the range of herd MS yield (a proxy for feeding level) in NZ. Genetic variation in environmental sensitivity was observed with OHF genotypes, originating largely from North America, exhibiting higher environmental sensitivity levels and environmental optimums than NZF and NZJ genotypes in a range of feeding level environments. OHF genotypes were more likely to be considered specialists (i.e. perform to high levels in superior feeding level environments), whereas NZF and NZJ genotypes were largely generalists (i.e. tolerant to changes in environment), or specialists in a grassland-type environment. This confirmed the theory that generalist genotypes evolve in heterogeneous environments, whereas specialist genotypes evolve in homogeneous environments. However, variations in environmental sensitivity within genotypes did exist. Generalist genotypes appear to be indirectly selected in NZ as environmental sensitivity levels are decreasing. Potential ways in which environmental sensitivity information can be used in dairy cattle systems and evaluation are suggested.

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## INTRODUCTION

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The reaction norm, a mathematical function relating an environmental variable to the phenotype expressed by a genotype, has become a valuable tool to investigate the responses of organisms to their environment (de Jong and Bijma, 2002; Pigliucci, 2005). Reaction norms have traditionally been used to describe nutritional and thermal responses in smaller organisms such as *Drosophila* (David et al., 1997) and *Arabidopsis* (Pigliucci and Byrd, 1998). However, it has recently been applied for use in studies of larger organisms such as dairy cattle managed in commercial farm environments (Calus and Veerkamp, 2003; Kolmodin, 2003). In dairy cattle, reaction norms have the potential to be used to predict responses to changes in environment and to ensure the correct selection of dairy sires for particular environments. This is



especially important where genetic estimates obtained in one environment are not reliable for use in another environment (Kearney et al., 2004; Zwald et al., 2003).

There are two mathematical representations of a reaction norm (Via et al., 1995). Firstly, the character state model where traits means or breeding values are estimated in a defined number of discrete environments. The environmental sensitivity of an animal is described by changes in the mean phenotype or breeding value expressed in each environment. Secondly, the polynomial model where trait means or breeding values are estimated in all environments in a continuous manner. In the polynomial approach, environmental sensitivity is described by changes in the coefficients of the polynomial. In discrete environments, the character state and polynomial approaches are mathematically equivalent descriptions of the same biological pattern (Via et al., 1995). In continuous environments, the two models are probably not interchangeable, but they can each provide valuable information into the responses of an animal to its environment. Jaffrezic and Pletcher (2000) found the character state model compared favourably to random regression models when analysing empirical data on age-specific mortality and reproduction in *Drosophila* and growth in beef cattle. The character state model generally provided a better fit to the covariance structure (genetic and non-genetic) with a reduction in the number of estimated parameters, leading to easier interpretation of results.

Recent studies in dairy cattle using both the character state and polynomial approach have identified that genotypes differ in environmental sensitivity. For example, Berry et al. (2003) found a difference in the environmental sensitivity of sires for body condition score as a polynomial function of herd mean milk yield. Kearney et al. (2004) found the best sires for milk yields of their daughters in a pastoral environment were not necessarily the best sires in an intensive feeding environment. In the presence of genetic variation in environmental sensitivity such information would be valuable to make informed decisions about the suitability of a given genotype for a particular environment.

Genetic variation in environmental sensitivity, measured by the slope components of the reaction norm, have also been used to determine the tolerance of a genotype to changes in environment (Simms, 2000) and to define specialist and generalist

genotypes (Kassen, 2002). Specialist genotypes have an optimal environment where their performance (e.g. milk yield, growth) is significantly higher than in alternative environments. The performance of generalist genotypes are largely unaffected by environmental changes and they are less likely to perform differently when exposed to novel environments which can often be the case with specialist genotypes. Specialists are more likely to evolve in environments that are homogeneous as selection in one environment may lead to fixation of genes that are beneficial in that environment (Kassen, 2002; Price et al., 2003). Generalist genotypes on the other hand are more common in heterogeneous environments due to the existence of multiple types of loci with different additive effects (Scheiner, 1998). The types of environmental sensitivity genotypes which evolve (i.e. generalists versus specialists) are dependent on the degree of additive genetic variation, costs associated with specialisation, the predictability of environmental changes or the frequency of minority environments, migration and genetic drift (van Tienderen, 1997).

The NZ dairy cattle population consists of two major breeds, Holstein Friesian and Jersey, and crosses between these breeds. In the 2004/2005 season, 48.6% of dairy cows were Holstein Friesian, 14.8% Jersey, and 28.3% Holstein Friesian/Jersey cross (Livestock Improvement, 2005). The Holstein Friesian population is a mixture of two Holstein Friesian strains (Harris and Kolver, 2001). Firstly, a NZF strain, originally developed from animals imported from the West Coast of USA prior to 1925, and remained as a closed population until the 1960s. From the 1960s onwards, NZF were bred from a Jersey background by upgrading Jersey with NZF semen. Secondly, an OHF strain imported from Canada in the 1960s and 1970s, USA in the 1980s, and Europe, but derived from North American strains, from the 1990s onwards. In 2001, it was estimated that the average percentage of North American ancestry were 70 % for sires and 24 % for cows in the current population (Harris and Kolver, 2001). The OHF strain has been traditionally selected under an intensive concentrate feeding system, whereas the NZF strain has been selected under a predominantly pasture-based system where efficient foraging is essential. NZJ cattle originate from the Channel Islands, with the first bull and two cows imported in 1862 (Meadows, 1996). The NZJ was the dominant breed in NZ until the 1960s when NZF became more common. As with the NZF, NZJ selection has been under a predominantly pasture-based system, with NZJ largely a closed breed. The objectives of this study

were to test if these different selection pressures and genetic origins have resulted in genotypes, or breeds, specialising in a particular environment, or breed(s) that can adapt to a range of environmental conditions. We also wanted to determine if environmental sensitivity has changed over time.

## MATERIALS AND METHODS

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### Production data

Data comprised 184,288 total milk, fat and protein yield deviations (Johnson, 1996) and actual yields from 2 year old animals which were in sire-proving scheme herds of the Livestock Improvement Corporation from 1989 to 2003. For full details of the calculation of breed composition, and coefficients for heterosis and recombination for each animal refer to Chapter 3. Only the four MS yield character states were considered in this analysis, with the statistical model applied to each character state described in Chapter 3.

### Reaction norm analyses

Reaction norm intercepts and coefficients for each sire relating to milk, fat and protein yields were estimated by fitting a regression of the four character state sire EBV against the mean of the four MS character state environments. The SAS package, version 8 (SAS, 1999) was used in this analysis. Each regression equation was weighted using the calculated reliability of the sire in each character state. The reaction norm regression equations (1 - 3) are equivalent to intercept, linear and 2<sup>nd</sup> degree polynomial reaction norms, respectively:

$$y = \beta_0 + e \tag{1}$$

$$y = \beta_0 + \beta_1 x + e \tag{2}$$

$$y = \beta_0 + \beta_1 x + \beta_2 x^2 + e \tag{3}$$

where  $y$  = EBV,  $\beta_0$ , = intercept,  $\beta_1$  and  $\beta_2$  = linear and quadratic regression coefficients, respectively,  $x$  = environmental level and  $e$  = residual error.

In each case, a stepwise procedure was used to determine the most appropriate reaction norm function for each trait related to each sire. Parameters commonly used

to select the most appropriate model to describe a system, or in our case a reaction norm, include minimisation of Akaike's Information Criteria (AIC) which is defined as:  $-2 \log(\text{ML}_k) + 2p_k$  where  $\log(\text{ML}_k)$  is the natural logarithm of the maximum likelihood function for model  $k$  and  $p_k$  is the number of parameters in the model (Lancelot et al., 2002). In our analysis, if the linear and quadratic regression coefficients of model (3) were significant ( $P < 0.10$ ), model (3) was initially selected. However, if model (3) did not provide a significant reduction in AIC (i.e. greater than 7 as suggested by Burnham and Anderson, 2002) over model (2), then the latter model was selected. In the instances where the linear regression coefficient of model (2), or the linear and quadratic regression coefficients of model (3) were not significant ( $P > 0.10$ ), model (1) was assumed and the sire was deemed unaffected by the environment, classified as a generalist sire. The procedure ensured the chosen model provided a balance between predictive accuracy while minimising the number of estimable parameters.

Once the most appropriate reaction function for each trait related to each sire was determined, estimates of the intercept, linear, quadratic regression coefficients, where appropriate, were obtained. The 2<sup>nd</sup> degree polynomial regression functions were also used to derive the global maxima ( $G_{\text{max}}$ ) environment by obtaining the environmental value where the first derivative of the function was equal to zero. The  $G_{\text{max}}$  represents the environmental value (herd MS yield) where reaction norm estimates of sire breeding values were at their maximum point. This procedure was only carried out for sires whose second derivative at the inflection point was positive, as negative values result in the global optimum being the environmental value where reaction norm estimates of sire breeding values are at their minimum point.

The reaction norm parameters were also used to determine if a sire could be classified as a specialist or generalist for production environment. The imposed levels to be classified as a specialist are equivalent to a sires' EBV changing by greater than 200, 10.0, and 8.0 kg for milk, fat and protein yield, respectively from the minimum and maximum MS character states. For example, if the linear regression coefficient for MS was between +1.34 and -1.34, +0.067 and -0.067, and +0.054 and -0.054 for milk, fat, and protein yield, respectively i.e. minimal response to environment, the sire was considered a generalist. If the linear regression

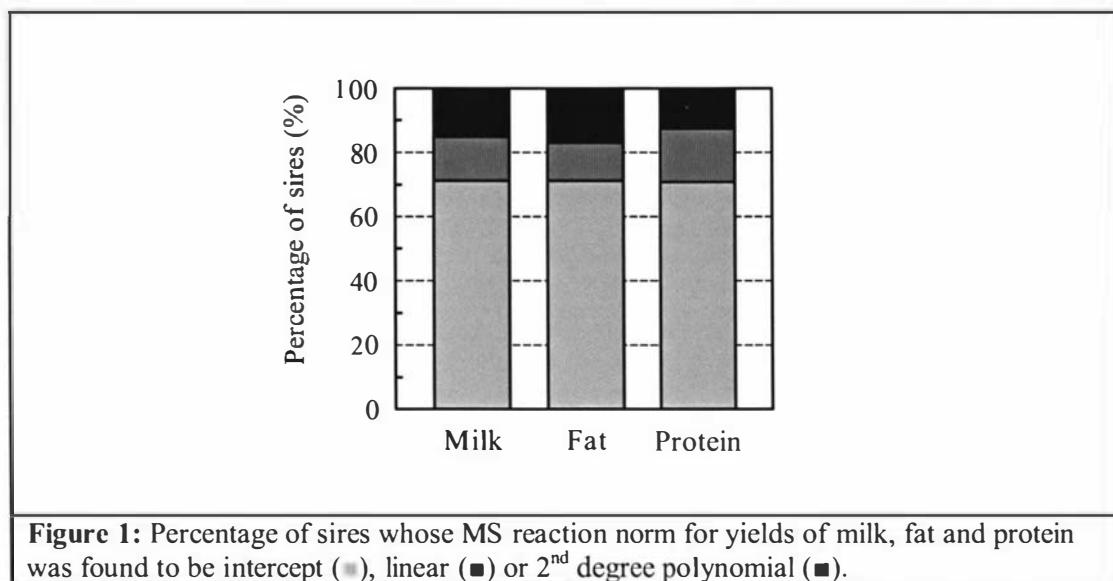
coefficient for a sire exceeded these limits, the sire was considered a specialist. In addition, for sires whose reaction norms were found to be 2<sup>nd</sup> degree polynomial, the  $G_{max}$  parameter was used to define if the sire could be considered a specialist or generalist for a particular environmental parameter. If the  $G_{max}$  exceeded the average of the highest character state (376 kg MS), the sire was considered a specialist on concentrate-type diets. Likewise, if the  $G_{max}$  was lower than the average of the lowest character state (227 kg MS), the sire was considered a specialist on grassland-type diets. Otherwise, the sire was considered a generalist. These values are arbitrary, as no previous attempts have been made to classify dairy cattle into environmental sensitivity genotypes. Specialist sires are most likely to re-rank when managed in the different environments, thereby requiring careful consideration of the environment in which their daughters are to be managed.

Breed was determined using a pedigree file traced back to the original parents of a sire, and was used to compute the degree of OHF ancestry in each sire. A sire was classified as being OHF if their breed composition was greater than or equal to 66 % OHF. Sires with less than 66 % OHF were considered NZF. Sires of NZJ origin were the only other major breed represented in the analysis. NZJ sires were bred largely using NZ genotypes; hence, no differentiation based on country of origin was needed. To determine if sire reaction norms have changed in the past 20 years, the year of birth of the sire was considered. Sires born prior to 1990 were classified as generation “pre90” and sires born after this time were classified as generation “post90”. The regression equation estimates for each sire were analysed using the GLM procedure in SAS (SAS, 1999). The fixed effects were breed and generation. Linear and polynomial reaction norm sires were analysed separately.

## **RESULTS AND DISCUSSION**

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Sire reaction norms for milk, fat and protein yield were predominantly intercept models i.e. unaffected by environment (Figure 1). Kolmodin et al. (2002) and Hayes et al. (2003) used linear reaction norms to describe sire responses to environment in Nordic and Australian data sets, respectively. In our study, for 12 – 17% of sires the



linear reaction norm was the best description for its response to environment in relation to milk, fat or protein yield and significant improvements were not obtained by extending the reaction norm model to a 2<sup>nd</sup> degree polynomial. Calus and Veerkamp (2003) in The Netherlands, found a 2<sup>nd</sup> degree polynomial in relation to herd average protein yield, was the most suitable reaction norm function. However, the random regression approach they adopted prevented the selection between reaction norm models for each sire. In our study, for 13 – 17% of sires the 2<sup>nd</sup> degree polynomial reaction norm was the best description for its response to environment in relation to milk, fat or protein yield.

**Table 1:** Average of estimated breeding values (EBV) for milk, fat, and protein yield for the most widely-used overseas Holstein Friesian (OHF), New Zealand Friesian (NZF) and New Zealand Jersey (NZJ) sires in each character state.

Average character state MS yield (kg)	227	263	305	376
<b>Across breeds (n = 271)</b>				
Milk EBV	143	147	238	186
Fat EBV	5.0	5.1	5.2	4.9
Protein EBV	5.5	5.6	7.5	5.9
<b>Within breeds</b>				
<b>OHF sires (n = 77)</b>				
Milk EBV	316	391	534	488
Fat EBV	3.0	0.6	2.8	0.4
Protein EBV	6.4	7.3	11.3	8.0
<b>NZF sires (n = 158)</b>				
Milk EBV	173	253	329	209
Fat EBV	5.0	6.3	7.3	3.1
Protein EBV	5.2	7.2	9.4	4.8
<b>NZJ sires (n = 36)</b>				
Milk EBV	-358	-412	-527	-807
Fat EBV	4.3	6.4	4.5	-1.3
Protein EBV	-3.4	-4.4	-6.3	-15.3

The average EBV for milk, fat and protein yields of OHF and NZF sires were at their highest values in the character state that averaged 305 kg MS/cow/year (Table 1). For NZJ sires, average EBV for milk, fat and protein yields were at their highest values in the character state that averaged 227 kg MS/cow/year. For every ten-kg increase in herd MS yield environment, milk, fat and protein yield EBVs of linear reaction norm OHF sires increased by 21.3, 1.0 and 0.68 kg, respectively. The corresponding values for NZF were 9.4, -0.1 and 0.0 kg, respectively. The corresponding increase in herd MS yield environment resulted in reductions in EBVs of -10.9, -0.98 and -0.50 kg, respectively in NZJ sires. The differences in the linear regression coefficient between breeds for all yield traits were significant (Table 2;  $P < 0.05$ ). Similar results were observed in the 2<sup>nd</sup> degree polynomial reaction norm OHF sires, as their global maxima were numerically higher than the other breeds for fat and protein yield (Table 3). However, the relationship was only significant for the comparison of  $G_{max}$  for OHF and NZJ sires for protein yield. OHF were also more likely to be classified as a specialist in a high production level or intensive-type environment than either, NZF or NZJ, whereas, NZF and NZJ were more likely to be classified as a specialist in a low production level or grassland-type environment than OHF (Table 4). As expected, the linear regression coefficients, or environmental sensitivity, of milk, fat and protein traits for each sire were correlated with Pearson correlation coefficients ranging from 0.68 to 0.89.

**Table 2:** Least square means (standard errors) for linear MS reaction norm parameters for the comparison of overseas Holstein Friesian (OHF), New Zealand Friesian (NZF) and New Zealand Jersey (NZJ) sires, and sires born prior to 1990 (Pre90), and post 1990 (Post90).

Trait	Milk		Fat		Protein	
	$\beta_0$	$\beta_1$	$\beta_0$	$\beta_1$	$\beta_0$	$\beta_1$
Breed						
OHF	-222 <sup>a</sup> (140.0)	+2.13 <sup>a</sup> (0.415)	-28.4 <sup>a</sup> (10.46)	+0.100 <sup>a</sup> (0.0328)	-12.0 <sup>a</sup> (4.65)	+0.068 <sup>a</sup> (0.0138)
NZF	74 <sup>a</sup> (111.5)	+0.94 <sup>b</sup> (0.331)	10.4 <sup>b</sup> (4.90)	-0.011 <sup>b</sup> (0.0154)	7.9 <sup>b</sup> (3.17)	-0.001 <sup>b</sup> (0.0094)
NZJ	-315 <sup>a</sup> (168.3)	-1.09 <sup>c</sup> (0.499)	32.3 <sup>b</sup> (24.92)	-0.098 <sup>b</sup> (0.0781)	5.6 <sup>b</sup> (5.76)	-0.050 <sup>c</sup> (0.0171)
Significance <sup>1</sup>	NS	***	**	**	**	***
Generation						
Pre90	-373 (129.6)	+1.12 (0.384)	-4.6 (9.83)	+0.034 (0.0308)	-8.56 (3.987)	+0.030 (0.0118)
Post90	-33.7 (104.4)	+0.20 (0.310)	14.1 (10.36)	-0.040 (0.0324)	9.56 (3.401)	-0.019 (0.0101)
Significance <sup>2</sup>	P=0.06	P=0.08	*	*	**	**

<sup>abc</sup>Least square means within columns with different superscripts are significantly different ( $P < 0.05$ )

<sup>1</sup>To test differences between breeds

<sup>2</sup>To test differences between generations

**Table 3:** Least square means (standard errors) for polynomial MS reaction norm parameters for the comparison of overseas Holstein Friesian (OHF), New Zealand Friesian (NZF) and New Zealand Jersey (NZJ) sires, and sires born prior to 1990 (Pre90), and post 1990 (Post90).

Trait	Milk				Fat				Protein			
	$\beta_0$	$\beta_1$	$\beta_2 (x 10^{-2})$	$G_{max}$	$\beta_0$	$\beta_1$	$\beta_2 (x 10^{-4})$	$G_{max}$	$\beta_0$	$\beta_1$	$\beta_2 (x 10^{-4})$	$G_{max}$
Breed												
OHF	-1643 <sup>a</sup> (706.7)	+12.6 <sup>ab</sup> (4.68)	-1.87 <sup>ab</sup> (0.765)	325 <sup>a</sup> (22.1)	121.6 <sup>a</sup> (39.38)	-0.86 <sup>a</sup> (0.271)	+14.9 <sup>a</sup> (4.41)	373 <sup>a</sup> (46.8)	-47.9 <sup>a</sup> (25.42)	+0.34 <sup>a</sup> (0.168)	-4.8 <sup>a</sup> (2.67)	335 <sup>a</sup> (13.3)
NZF	-2106 <sup>a</sup> (464.1)	+16.2 <sup>a</sup> (3.07)	-2.62 <sup>a</sup> (0.502)	327 <sup>a</sup> (13.2)	-5.7 <sup>b</sup> (18.10)	+0.02 <sup>b</sup> (0.124)	-0.5 <sup>b</sup> (2.03)	295 <sup>a</sup> (11.8)	-67.6 <sup>a</sup> (19.40)	+0.50 <sup>a</sup> (0.128)	-8.0 <sup>a</sup> (2.04)	318 <sup>a</sup> (8.8)
Jersey	-64.5 <sup>a</sup> (961.8)	-3.2 <sup>b</sup> (6.37)	-0.27 <sup>b</sup> (1.04)	264 <sup>a</sup> (37.6)	-124.7 <sup>c</sup> (30.79)	+0.90 <sup>c</sup> (0.212)	-15.1 <sup>c</sup> (3.45)	292 <sup>a</sup> (15.0)	-8.0 <sup>a</sup> (33.38)	+0.02 <sup>a</sup> (0.221)	-1.0 <sup>a</sup> (3.51)	274 <sup>b</sup> (18.7)
Significance <sup>1</sup>	NS	*	*	NS	***	***	***	NS	NS	NS	NS	*
Generation												
Pre90	-1857 (543.7)	+11.98 (3.603)	-1.90 (0.588)	322 (17.0)	-7.1 (26.39)	+0.06 (0.181)	-0.5 (2.96)	317 (5.6)	-60.7 (20.05)	+0.40 (0.133)	-6.1 (2.11)	321 (9.4)
Post90	-686 (579.8)	+5.10 (3.842)	-0.91 (0.627)	289 (20.5)	8.8 (20.28)	+0.01 (0.139)	-0.0 (2.27)	300 (5.0)	-21.6 (22.47)	+0.18 (0.149)	-3.0 (2.36)	300 (12.3)
Significance <sup>2</sup>	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS

<sup>abc</sup> least square means within columns with different superscripts are significantly different ( $P < 0.05$ )

<sup>1</sup>To test differences between breeds

<sup>2</sup>To test differences between generations



**Table 4:** Frequency distribution of overseas Holstein Friesian (OHF), New Zealand Friesian (NZF) and New Zealand Jersey (NZJ) sires classified as a specialist concentrates, generalist or specialist grasslands genotype for milk, fat and protein and all yield traits.

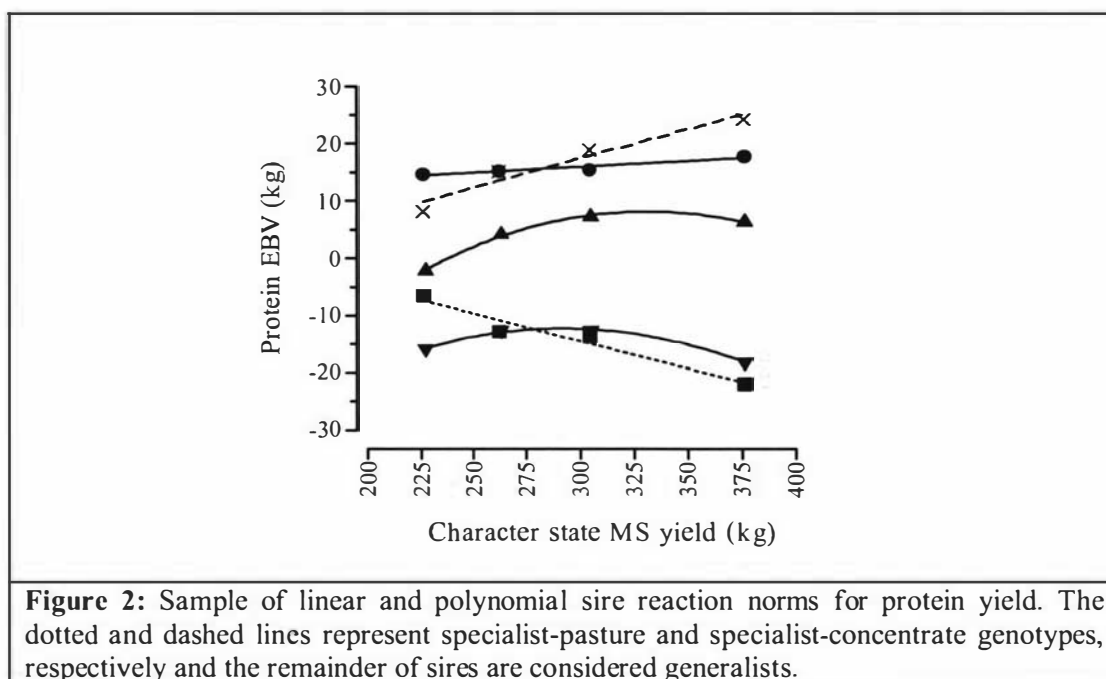
Genotype	Specialist Concentrates		Generalist		Specialist Grasslands		
	n	%	n	%	n	%	
Across breeds							
Milk	22	8.1	244	90.0	5	1.9	
Fat	12	4.4	249	92.2	9	3.3	
Protein	17	6.3	250	92.3	4	1.5	
All traits	4	1.5	223	97.8	1	0.4	
Within breeds							
OHF	Milk	11	16.4	55	82.1	1	1.5
	Fat	3	4.5	64	95.5	0	0.0
	Protein	9	13.4	58	86.6	0	0.0
	All traits	1	1.9	51	98.1	0	0.0
NZF	Milk	10	6.0	156	92.9	2	1.2
	Fat	9	5.4	149	89.2	9	5.4
	Protein	7	4.2	159	94.6	2	1.2
	All traits	3	2.1	140	97.2	1	0.7
NZJ	Milk	1	2.8	33	91.7	2	5.6
	Fat	0	0.0	36	100.0	0	0.0
	Protein	1	2.8	33	91.7	2	5.6
	All traits	0	0.0	32	100.0	0	0.0

Sires of OHF origin have traditionally been selected in a homogeneous environment where high levels of concentrate are offered and high levels of production are achieved, whereas, NZF or NZJ sires are selected in pasture-based, low production level environment with high levels of environmental heterogeneity. Consequently, each genotype has adapted to enable it to perform to highest possible level within the constraints of its normal environment. When exposed to the novel environment, phenotypic performance deviates from genetic expectations due to the need to adapt to the new environment. This would explain why OHF, on average, improve their ranking in a high production level environment, and why NZJ sires improve their ranking in a low production level, grassland-type environment. The result are also consistent with the results from farmlet experiments carried out by Kolver et al. (2002), Linnane et al. (2004) and Horan et al. (2005) which compare the performance of different strains of Holstein Friesian and Friesian in different feeding system. Differences in performance of each genotype in each environment may be the result of genotype differences in feed intake drives, or feed processing ability (Chapter 2, Friggens *et al.*, 2004; Linnane *et al.*, 2004).

Our results illustrate that each genotype appears to have genetic differences in reaction norm trajectories and an optimal environment state. Gabriel and Lynch (1992) and Wright (1931) believe the optimal environmental state (or  $G_{max}$ ) is expected to evolve to the long-term average value of the environment; for detailed reviews see Scheiner (1993) and Via et al. (1995). Price et al. (2003) proposed that animals, which are exposed to limited levels of environmental variation such as OHF sires, may lose the ability to adapt to a new environment and evolve into specialised individuals. Conversely, generalist genotypes are more likely to evolve in environments which are unstable over a long period of time i.e. the NZ pastoral production system, (Kassen, 2002). Generalist genotypes have a compromise genotype that allows them to meet the demands of different environments (van Tienderen, 1997). Calus et al. (2002) and Kolmodin et al. (2002) who found significant genetic variances for reaction norm slope indicate environmental sensitivity is a heritable trait in dairy cattle. Therefore, there is potential to select for generalist and specialist dairy cattle genotypes.

The mechanisms, which have resulted in generalist versus specialist genotypes, include the concepts of genetic assimilation and resource allocation. Genetic assimilation is the phenomenon where beneficial genes or alleles become canalised or fixed in a particular environment (Waddington, 1961), thereby affecting adaptation to another environment (Kassen, 2002). Canalisation may constrain phenotypic evolution, alternatively it could increase phenotypic diversity after a decanalising event such a sharp shift in environment (Flatt, 2005). Our results suggest both could have occurred, for example, in some instances OHF genotypes have not been able to adapt to their new environment and their daughters have largely remained specialist individuals (Table 4). While, other OHF genotypes have adapted to their new environment and their daughters have adopted generalist or grassland specializing strategies.

The environment where an animal or species has been selected influences the types of genotypes that are favoured in a population. An environment, which is abundant in resources with limited emphasis placed on fertility, may favour genotypes that place



a higher priority on milk production than on survival or fertility traits (van der Waaij, 2004). In this environment, directing more energy to milk production would have limited effects on the likelihood of an animal surviving to the next lactation or producing offspring (i.e. getting in calf). In a limited resource environment, such as the traditional dairy production environment in NZ, fertility traits may have been allocated a higher priority due to the necessity of getting in calf at 365-day intervals. This may explain the greater reductions in fertility of overseas compared to NZ genotypes (Horan et al., 2004), and is a result of the antagonistic tradeoff that occurs between fertility and milk production (Pryce et al., 2001; Pryce et al., 2004).

Variations in genotype classification (Specialist Concentrates, Specialist Grasslands or Generalist) existed within sire breeds (Table 4). Of OHF sires, one for milk yield could be classified as specialists in a low production level or grassland-type environment and a high proportion of OHF sires were considered generalists. The complete range of generalist and specialist genotypes were exhibited in NZF sires, and one of the NZJ sires for milk and protein yield could be classified as a specialist in a high production level or intensive-type environment (for examples of specialist and generalist genotypes see Figure 2). Variations also existed within breeds for global maxima. There is then potential to select these adaptable genotypes within sire breeds, if the advantages of such genotypes are warranted.

Sires born after 1990, exhibited significantly reduced levels of environmental sensitivity, as measured by the linear regression coefficient for fat and protein yield, towards differences in herd MS yield compared to sires born prior to 1990 (Table 2). These results suggest a generalist genotype is now preferred, albeit unknowingly, in the NZ dairy system. Alternatively, the selection of international genotypes for use in the NZ production environment has improved. This may be a result of advances in the methodology to convert international sire proofs. For example, the use of multiple-trait across, country-evaluation, which considers production data from siblings and relatives in the country where the proof is to be estimated (Schaeffer, 1994; Weigel and Powell, 2000). Our results also illustrate the need for progeny testing programs to implement strategies to ensure an even distribution of sire daughters amongst different environments. For example, if one particular environment, region or niche dominates the selection environment, it is likely the genotype which is better adapted to such an environment could start to dominate the population (Kassen, 2002).

The optimal degree of environmental sensitivity in dairy cattle is not known. Kolmodin et al. (2003) suggested in intensive farming systems, high environmental sensitivity may be preferred due to the ability of an animal to respond significantly to any improvement in environment. In highly variable environments, low sensitivity may be preferred as animal performance is less likely to be compromised. However, any environmental disturbance to an intensive system, such as the need to use more pasture, may pose physical issues such as reduced fertility and survival. For example, Calus et al. (2005) found the survival EBV of some sires declined at higher fat to protein ratios. Higher fat to protein ratios are an indicator that the diet contains a higher proportion of roughage (i.e. fibre) and less concentrates (Bargo et al., 2003) and such a diet is open to environmental disturbances. Selection for low sensitivity, which appears to be possible i.e. results from *Drosophila* (Hillesheim and Stearns, 1991), may result in a genotype which cannot respond to environmental change. Therefore, unless the future environment can be predicted with complete certainty, the range of environmental sensitivity genotypes needs to be maintained. This should maintain sufficient genetic diversity to ensure animals are able to adapt and evolve to any environment, especially in a heterogeneous environment such as in NZ.

The results of Chapter 3, in conjunction of the results of Mulder et al. (2005), suggest the formation of two separate breeding schemes for different environments within NZ is not warranted as a large proportion of sires are generalists, or unaffected by environment (Table 4). However, investigating the phenotypic, or plastic, responses of animals to heterogeneous environments is vital to gain a better understanding of the environment where dairy cattle genotypes are best suited. Indeed, different plastic responses to heterogeneous environments is one of the most common phenomena characterising the living world (Pigliucci, 2005). In this context, environmental sensitivity information still has vast potential to be used in a number of ways. Kolmodin et al. (2002) suggested unique rankings could be presented for each environmental level. Producers could then consult the appropriate ranking list to find the best sires for their particular environment. Alternatively, an EBV could be presented which represented the average environment; essentially the current situation. However, this EBV would now effectively be the intercept of a reaction norm i.e. zero environment. The environmental deviation of the herd from the average environment and the slope components of the reaction norm could then be used to predict environment-specific EBV of particular sires to calculate customised selection indices.

## **CONCLUSION**

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Sires of OHF origin are likely to perform better in an improved system with higher levels of feed as concentrates (specialists), whereas a higher proportion of NZJ and NZF will perform across the range of environments (generalists). There are, however, genetic variations in the environmental sensitivity of the different breeds. Environmental sensitivity levels appear to have reduced over time, indicating indirect selection for generalist genotypes.

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## CHAPTER 6

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### **Quantifying the effect of thermal environment on production traits in three breeds of dairy cattle in New Zealand**

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## ABSTRACT

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In this study, the effects of hot and cold conditions throughout NZ were assessed from 1989 to 2002 using 65,945 first lactation records of daily milk yield, fat and protein concentration from three breeds of dairy cattle, HF, NZJ and first cross HFxNZJ. Hot conditions were assessed using a 3-day average of THI and cold conditions were assessed using a 3-day average cold stress index (CSI), which includes the effects of temperature, rain and wind. Hot conditions were associated with reductions in milk yields in all breeds, with reductions of greater than 0.05 kg of daily milk yield per unit of THI occurring at THI of 67, 69 and 77 in HF, HFxNZJ and NZJ, respectively. THI of 67 and 77 are equivalent to temperatures of 20 and 26.5°C, respectively at 80% humidity. Fat and protein concentrations also exhibited significant reductions at high THI. There was also some evidence that HF cows of high genetic merit, as determined by their estimated breeding value for milk, exhibited greater milk yield reductions due to hot conditions than their low genetic merit counterparts. Cold conditions significantly reduced milk yields in HF and HFxNZJ cattle. However, the frequency of cold conditions where performance is likely to be compromised is low (1 to 3% of days). The results illustrate that heat and cold stress can significantly affect dairy cattle performance in NZ.

## INTRODUCTION

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Cattle are susceptible to the effects of thermal stress outside the thermoneutral range (Holmes and Sykes, 1984; Kadzere et al., 2002). There are two key points relating to the thermoneutral range: 1) the lower critical temperature defined as the “lowest temperature to which an animal can be exposed without being forced to increase its heat production by thermoregulatory means” and 2) the upper critical temperature defined as “highest temperature to which the animal can be exposed without showing a large increase in deep body temperature, and an associated increase in metabolic rate (Holmes and Sykes, 1984)”.

In a hot environment, cattle are susceptible to heat stress due to the combined accumulation of heat gained from the environment and heat produced by the

metabolic processes that are necessary to produce large quantities of milk (West, 2003). Environmental factors contributing to an animal's heat load include high temperature, humidity and solar radiation, and low wind speeds (Bianca, 1965; Blackshaw and Blackshaw, 1994). A number of authors have observed milk yield reductions in intensive environments when THI exceeds an average of 72 for the three days prior to the herd test (Aharoni et al., 2002; Ravagnolo et al., 2000; West et al., 2003). In these heat stress conditions, heat gained exceeds heat lost by radiation, convection, evaporation and conduction (Kadzere et al., 2002). To decrease its heat load, the cow reduces its feed intake and consequently milk production.

A number of studies demonstrate that lactating dairy cattle are more tolerant to cold than heat (Blaxter, 1958; Broucek et al., 1991; Young, 1981). For example, the lower critical temperature for a dairy cow in peak lactation is around  $-30^{\circ}\text{C}$  in dry-still conditions (Blaxter, 1958; Gregory, 1995; Young, 1981). These lower critical temperatures may be more relevant for Northern hemisphere environments where housing is very common, thereby limiting exposure to wind or rain. For example, it is important in outdoor year-round grazing systems that a cold stress index includes the effects of wind and rain, as dairy cattle seek shelter or modify their posture to reduce their exposure (Gregory, 1995; Olson and Wallander, 2002). An improved cold stress measure for year-round grazing systems may be the chill, or CSI as applied to sheep by Donnelly et al. (1984), and includes adjustments for ambient temperature, wind speed and rain.

The acceptable thermo neutral range varies with species, breed and production level. For example, *Bos indicus* cattle are better equipped than *Bos taurus* cattle to cope with heat stress, due to *Bos indicus* cattle having more sweat glands per unit area, and a slower metabolic rate (Bianca, 1965). There is also variation in tolerance to heat among and within *Bos taurus* breeds. For example, Jersey cattle are often favoured over HF cattle in southern parts of the United States, as they exhibit a superior ability to maintain feed intake, milk production and reproduction at THI above 78 (Keister et al., 2002). High-producing dairy cows are more susceptible to the effects of heat stress in summer than their low-producing counterparts, as they have to dissipate more heat produced as a result of their increased metabolic rate (Kadzere et al., 2002).

As stated by Holmes and Sykes (1984), the environmental conditions causing heat or cold stress in dairy cattle in NZ are poorly defined, with few relevant studies and this is still the case. Therefore, the first objective of this study was to use two environmental indices, temperature-humidity and cold stress, to quantify the phenotypic responses to extremes in thermal environment of three breeds of cattle managed in a grazing system in NZ. The second objective was to test if a cow's genetic merit for milk yield influenced her susceptibility to become heat stressed.

## **MATERIALS AND METHODS**

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### **Data**

Herd test day records were obtained for spring calving, first lactation animals from sire proving scheme herds of the Livestock Improvement Corporation from 1990 to 2002. Each animal record included NZ meteorological service map co-ordinates for the herd, date of birth, date of calving, date of test, breed composition, milk yield, and fat and protein concentrations in the milk. From this information, days in milk (DIM) at test, and age at calving (in months) were calculated. In addition, animals were classified based on breed with HF ( $> \frac{15}{16}$  NZF or OHF origin), NZJ ( $> \frac{15}{16}$  NZJ) and first cross HFxNZJ (HFxNZJ;  $\frac{1}{2}$  HF and  $\frac{1}{2}$  NZJ). Data was subsequently discarded for DIM of less than 5 days and greater than 270 days, for animals that were not HF, NZJ or HFxNZJ, and for animals with less than three records in a herd-year.

Meteorological data was obtained for 65 stations throughout NZ from the National Institute of Water and Atmospheric Research (NIWA) from 1990 to 2002. Meteorological station data included a map reference, daily measures of maximum and minimum temperature, rainfall, average relative humidity, solar radiation, and wind speed. These data was then used to calculate 3-day averages for temperature humidity index (THI) of Davis et al. (2003), and CSI (units of  $\text{kJ m}^{-2} \text{h}^{-1}$ ) as shown below:

$$\text{THI} = 0.8T + [\text{RH} \times (\text{T}-14.4)] + 46.4$$

where T is temperature (°C) at 1200 h and RH is mean daily relative humidity divided by 100 (Davis et al., 2003). The function of Davis et al. (2003) was used because it adopts the same units for temperature and humidity that are measured in NZ meteorological stations.

$$CSI = [11.7 + (3.1 \times WS^{0.5})] \times (40 - T) + 481 + R$$

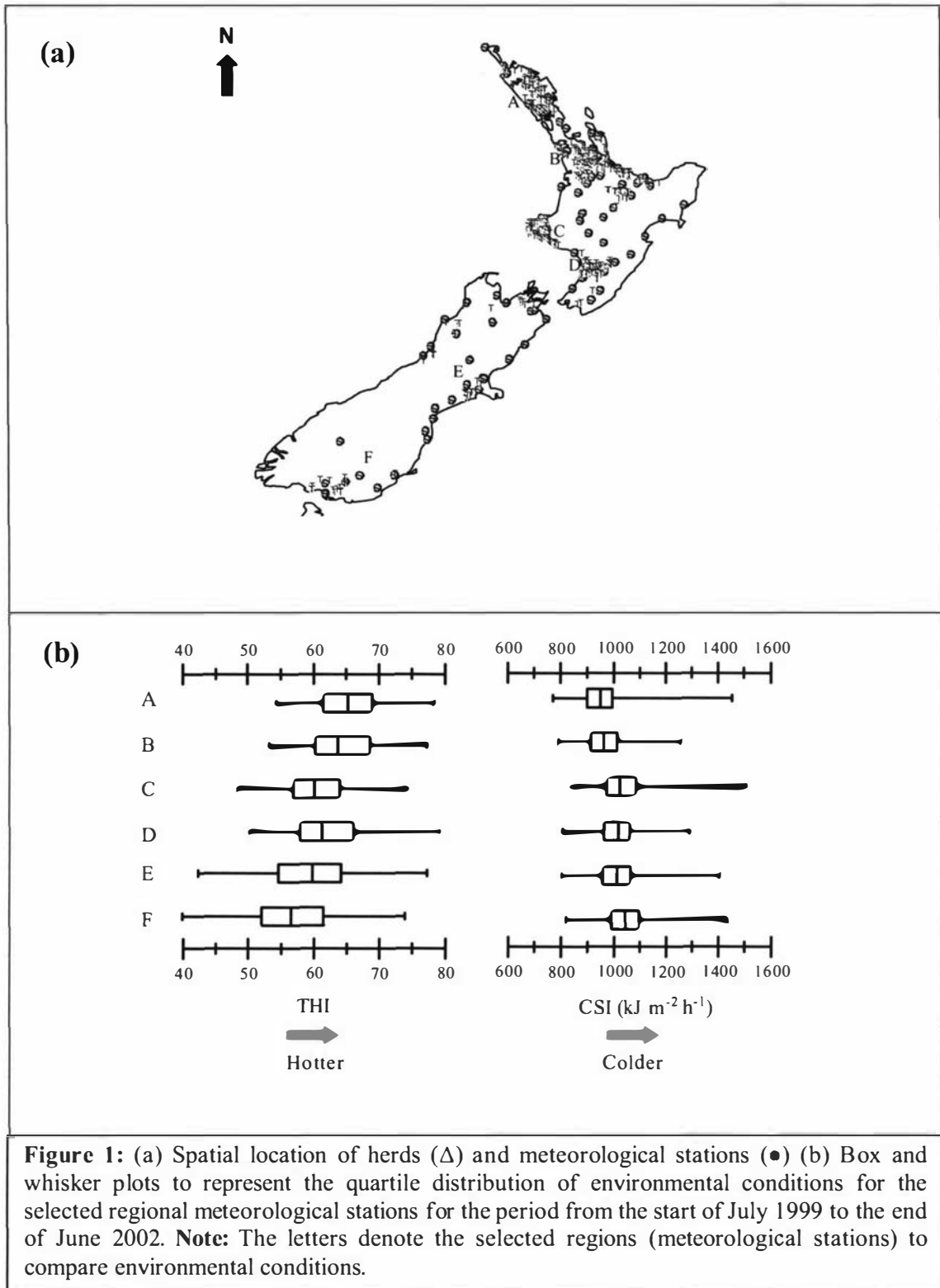
where WS is mean daily wind speed (m/s), T is the mean daily temperature (°C) calculated as the average of the maximum and minimum temperature, and  $R = 418 \times (1 - e^{-0.04 \times \text{rain}})$  where rain is the total daily rainfall in millimetres (Donnelly, 1984).

Herds and meteorological stations were then spatially located on a map using ArcView GIS version 3.2 (ESRI, 1999). The nearest meteorological station with climate data (within a 50 km radius) to each herd test day, found using the Nearest Neighbor Script 3.4 (Weigel, 2004), was then used as the measure of environment for that particular herd test day. The THI and CSI matched to each herd test day included the day of the test and two days prior to the test day. In cases where a herd had multiple meteorological stations with THI and CSI data within a 50 km radius, data from the nearest meteorological station was used. After editing and matching of environmental data, the full dataset consisted of 65,945 records, 19,315 animals, 1,063 herd-years, and 496 herds.

### **Representative meteorological stations to assess environmental conditions**

To quantify environmental conditions within NZ, the range of 3-day average THI and CSI of seven meteorological stations (Figure 1), which were representative of the major dairy regions, were assessed from the start of July 1999 to the end of June 2002. The meteorological stations represented (town/city, region and assigned letter in brackets) were located in Whangarei, Northland (A); Ruakura, Waikato (B); Normanby, Taranaki (C); Palmerston North, Manawatu (D); Rangiora, North Canterbury (E); and Gore, Southland (F). The time period was chosen as complete environmental data were available for it, but it was still recent enough to be relevant. Box and Whisker plots were created to represent the quartile ranges of environmental data at each meteorological station. Pearson correlation coefficients between daily

and 3-day average THI and CSI were also calculated for the subset of data using the correlation procedure (SAS, 1999).





**Data analyses**

The statistical analyses were performed using the AIREML program of Johnson and Thompson (1995), applying an average information restricted maximum likelihood algorithm. The full model was as follows:

$$y_{ijkl} = \mu + H_i + Y_j + B_k + b_1 a_{ijk} + b_2 d_{ijk} + \sum_{n=0}^4 \alpha_n t_{ijkl} + \sum_{o=0}^2 \gamma_o x_{ijl} \times B_k + c_{ijk} + e_{ijkl}$$

where  $y_{ijkl}$  is daily yield of milk, or concentrations of fat or protein in the milk,  $\mu$  is the general mean,  $H_i$  is the fixed class effect of herd  $i$ ,  $Y_j$  is the fixed class effect of year  $j$ ,  $B_k$  is the fixed class effect of breed  $k$ ,  $b_1$  is the fixed linear regression coefficient of age ( $a$ ) at calving in months,  $b_2$  is the fixed linear regression coefficient of parturition date deviation from the mean herd-year parturition date ( $d$ ),  $\alpha_n$  are Legendre polynomial coefficients, as described by Kirkpatrick et al. (1990), of days in milk ( $t$ ) for test day  $l$ ,  $\gamma_o$  is the fixed linear and quadratic regression coefficients for the environmental index ( $x$ ), THI or CSI, of breed  $k$ ,  $c_{ijk}$  is the random permanent effect of cow in herd  $i$ , calving in year  $j$  of breed  $k$  and  $e_{ijkl}$  is the residual effect for each observation. Residual and random permanent cow effects were assumed to have mean of zero and to be independently and identically normally distributed with variance,  $\sigma_e^2$  and  $\sigma_c^2$ , respectively.

The environmental value (THI or CSI) when performance declines for each breed group were calculated by deriving the  $G_{\max}$  of the 2<sup>nd</sup> degree polynomial regression functions. The  $G_{\max}$  is the environmental value where the first derivative of the 2<sup>nd</sup> degree polynomial regression function is equal to zero i.e. the environment turning point. To test for significant differences ( $P < 0.05$ ) between breed groups for linear and quadratic regression coefficients and global maxima, the standard errors of the linear and quadratic estimates were used to obtain an estimate of the lower (LCI) and upper (UCI) confidence intervals for the linear and quadratic estimates calculated as:  $\mu - (\text{standard error} \times 1.96)$  and  $\mu + (\text{standard error} \times 1.96)$ , respectively. The LCI and UCI for the linear and quadratic estimates were then used to derive LCI and UCI for global maxima.

**Testing the effect of cow genetic merit on the sensitivity to hot conditions**

To test if high genetic merit animals were more susceptible to declines in performance in hot conditions than their low genetic merit counterparts, estimated breeding values for milk for the individuals in the dataset were extracted from the NZ Dairy Core database and the Livestock Improvement national database. Animals were then assigned to a low or high genetic merit breed group based on the individuals estimated breeding value for milk relative to the breed average. The means, standard deviation and ranges of estimated breeding values for milk in each genetic merit breed group are presented in Table 1, along with the corresponding numbers of animals and records. Data were analysed with the same statistical model described earlier, but the fixed effect of breed was replaced with a fixed effect of genetic merit by breed, and the linear and quadratic breed group x THI interactions were replaced by linear and quadratic genetic merit by breed x THI interactions.

**Table 1:** Mean, standard deviation (SD) and range of estimated breeding values for milk yield of the high and low genetic merit HF, NZJ and HFxNZJ groups.

	<i>n</i> animals <sup>1</sup>	<i>n</i> records <sup>2</sup>	Mean	SD	Range
HF					
High genetic merit	6,686	22,955	863	173.6	641 to 1746
Low genetic merit	6,710	22,894	429	157.3	-238 to 640
HFxNZJ					
High genetic merit	874	3,053	382	166.8	158 to 1162
Low genetic merit	882	3,021	-38	142.3	-585 to 157
NZJ					
High genetic merit	2,019	6,996	-141	134.9	-308 to 718
Low genetic merit	2,030	6,986	-458	111.4	-949 to -309

<sup>1</sup>Number of animals

<sup>2</sup>Number of records

**RESULTS**

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**Effect of each environmental parameter on THI and CSI**

The effects of each environmental parameter on CSI and THI are shown in Table 2 and Table 3, respectively. Wind speed and rainfall has significant effects on CSI. In contrast, in dry conditions with no wind, any change in temperature has a minimal effect on CSI. Unit change in temperature has a larger effect on THI than humidity.

**Regional averages for THI and CSI**

For the subset of regional environmental data, Pearson correlation coefficients of 0.91 between daily and the 3-day average THI (as used in this study), 0.80 between daily and the 3-day average CSI (as used in this study) and -0.68 between 3-day average THI and the 3-day average CSI were observed. Presented in Figure 1 are the distribution of CSI and THI conditions for the representative meteorological stations. As expected, herds located in Northland, denoted by an A, were exposed to the warmest environment with mean THI of 65.4 (SD = 4.8) and mean CSI of 960 kJ m<sup>-2</sup> h<sup>-1</sup> (SD = 97 kJ m<sup>-2</sup> h<sup>-1</sup>) and herds located in Southland, denoted by an F, were exposed to the coldest environment with mean THI of 56.7 (SD = 6.4) and mean CSI of 1047 kJ m<sup>-2</sup> h<sup>-1</sup> (SD = 89 kJ m<sup>-2</sup> h<sup>-1</sup>) (Figure1a-b). However, the cooler regions in the South Island did occasionally experience conditions well in excess of THI of 70. Taranaki, denoted by a C, experienced the highest value for CSI. For the period from the start of July 1999 to the end of June 2002, the percentage of days throughout the year where THI exceeded 70 were 20, 17, 10, 4, 6 and 2 % in regions A-F respectively (see Figure1a-b).

**Table 2:** Illustration of the effect of incremental changes in rain, wind and temperature on cold stress index (CSI)

<b>Base CSI of 832 kJ m<sup>-2</sup> h<sup>-1</sup>: 10 °C temperature, 0 mm of rain, 0 m/s wind speed</b>							
Rain	5 mm	10 mm	15 mm	20 mm	25 mm	30 mm	35 mm
CSI	908	970	1021	1062	1096	1124	1147
Wind	1 m/s	2 m/s	3 m/s	4 m/s	5 m/s	6 m/s	7 m/s
CSI	925	1018	1111	1204	1297	1390	1483
Temperature	9 °C	8 °C	7 °C	6 °C	5 °C	4 °C	3 °C
CSI	844	855	867	879	891	902	914
Cumulative CSI <sup>1</sup>	1016	1133	1233	1320	1397	1468	1532

<sup>1</sup>The effect on CSI of all the incremental changes to rain, wind and temperature within a column.

**Table 3:** Illustration of the effect of incremental changes in temperature and humidity on temperature-humidity index (THI).

<b>Base THI of 65.8: 20 °C temperature, 60 % humidity</b>							
Temperature	21 °C	22 °C	23 °C	24 °C	25 °C	26 °C	27 °C
THI	67.2	68.9	70.4	71.8	73.3	74.7	76.2
Humidity	65 %	70 %	75 %	80 %	85 %	90 %	95 %
THI	66.0	66.3	66.6	66.9	67.2	67.4	67.7
Cumulative THI <sup>1</sup>	67.5	69.3	71.3	73.3	75.4	77.6	80.0

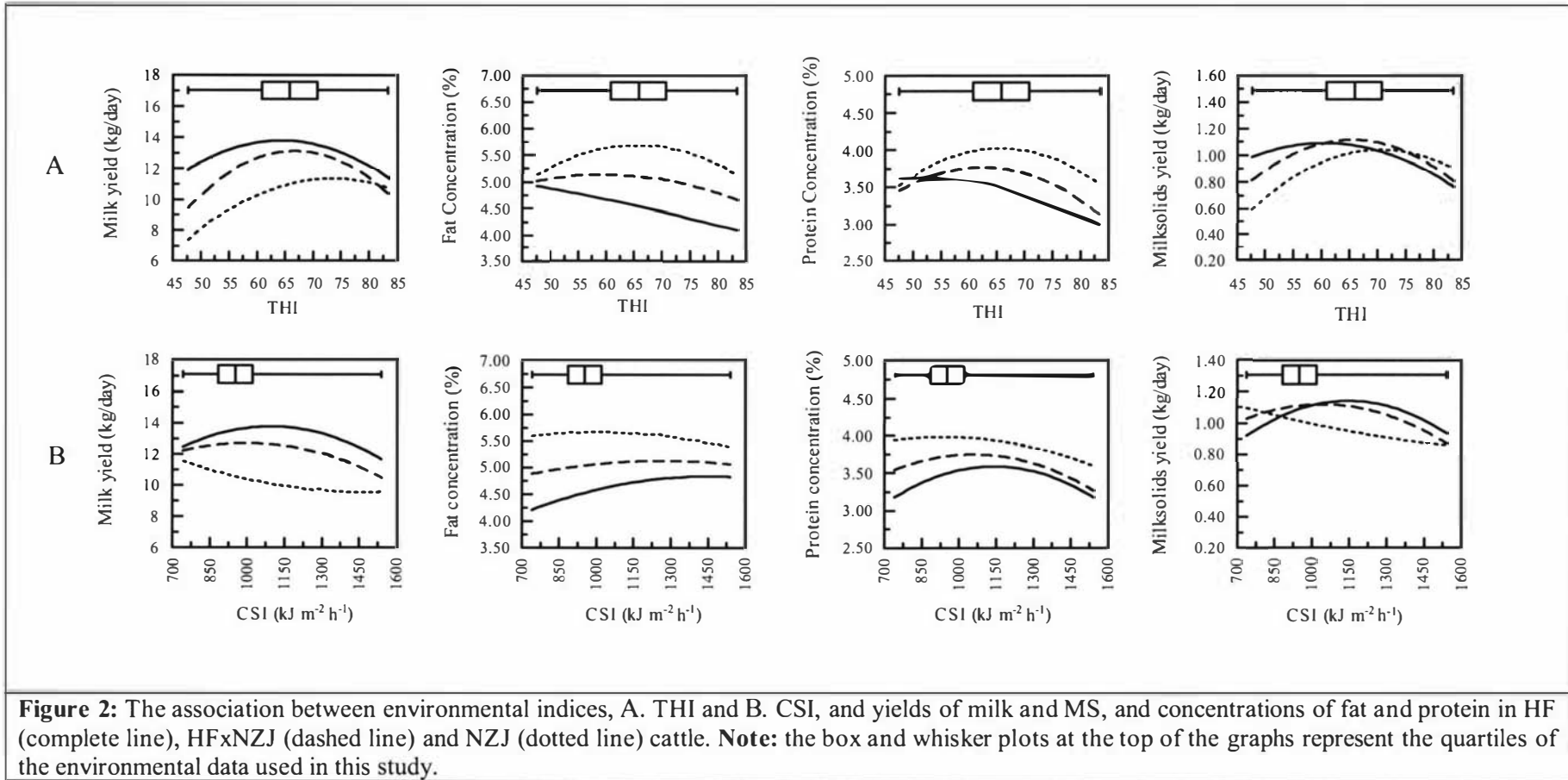
<sup>1</sup>The effect on THI of all the incremental changes to temperature and humidity within a column.

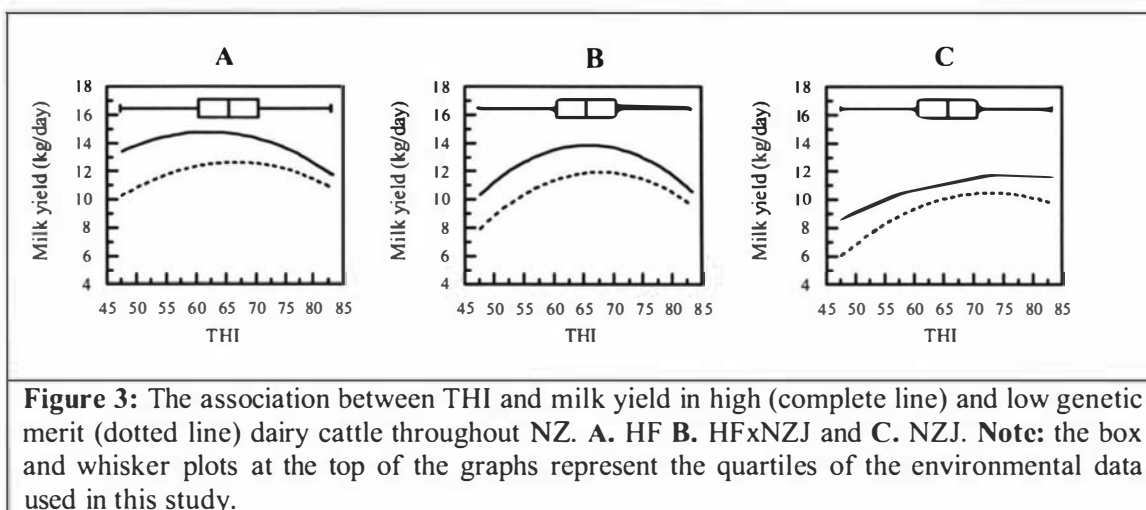
**Effect of THI conditions on yields of milk and MS, and concentrations of fat and protein in the different breeds**

In general, milk yield, and fat and protein concentration declined to a greater extent with lower THI in HF than in HFxNZJ or NZJ cattle (Figure 2). The  $G_{\max}$  THI for milk yield, and fat and protein concentration occurred at a lower THI value for HF than NZJ cattle, with the HFxNZJ being intermediate between the two straight-breeds (Table 4). The difference in  $G_{\max}$  THI was significant ( $P < 0.05$ ) only for milk yield for the comparison of HF and NZJ, and for protein concentration for the comparison of HF with HFxNZJ and NZJ. Fat and protein concentration generally started to decline at lower values of THI than was the case for milk yield. Fat concentration exhibited a linear decline as THI increased in HF cattle. At low THI values, MS yields were greater for HF than NZJ or HFxNZJ cattle. At high THI values, there were minimal differences in MS yields between the three breeds.

**Effect of CSI conditions on yields of milk and milk solids, and concentrations of fat and protein in the different breeds**

Significant curvilinear relationships were observed in relation to CSI for milk yield, and fat and protein concentration in HF and HFxNZJ cattle, and for fat and protein concentration in NZJ cattle, with yields and concentrations being lower in cold conditions (Figure 2). Cold conditions had no effect on milk yield in NZJ cattle. As with THI, the difference in milk yield between breeds was reduced in warmer conditions (i.e. higher THI and lower CSI). A significant difference ( $P < 0.05$ ) between breeds for  $G_{\max}$  CSI was only observed for the comparison of HF and NZJ cattle for protein concentration (Table 4).





**Table 4:** Values of global maximum THI and CSI for yields of milk, and concentrations of fat and protein of HF, HFxNZJ and NZJ cattle throughout NZ.

		<b>Breed</b>		
		<b>HF</b>	<b>HFxNZJ</b>	<b>NZJ</b>
<b>THI</b>				
Milk	Mean <sup>1,2</sup>	64.3 <sup>a</sup>	66.7 <sup>ab</sup>	73.3 <sup>b</sup>
	CI <sup>3</sup>	[61.8, 67.2]	[62.6, 71.9]	[67.9, 80.4]
Fat	Mean	NS <sup>a</sup>	59.4 <sup>a</sup>	65.5 <sup>a</sup>
	CI	-	[52.3, 72.5]	[62.3, 69.5]
Protein	Mean	52.4 <sup>a</sup>	62.5 <sup>b</sup>	65.6 <sup>b</sup>
	CI	[50.5, 54.5]	[59.7, 65.9]	[63.6, 67.9]
<b>CSI</b>				
Milk	Mean	1094 <sup>a</sup>	998 <sup>a</sup>	NS <sup>a</sup>
	CI	[1022, 1187]	[839, 1391]	-
Fat	Mean	1444 <sup>a</sup>	1261 <sup>a</sup>	1009 <sup>a</sup>
	CI	[1265, 1724]	[928, 3329]	[853, 1362]
Protein	Mean	1140 <sup>a</sup>	1056 <sup>ab</sup>	930 <sup>b</sup>
	CI	[1102, 1183]	[968, 1183]	[848, 1056]

<sup>1</sup>Means within rows with different superscripts are significantly different ( $P < 0.05$ )

<sup>2</sup>Means denoted with NS indicate the quadratic term related to the environmental variable was not significant ( $P > 0.05$ )

<sup>3</sup>Confidence interval [LCI, UCI]

### Interaction between genetic merit and THI

Daily milk yields were greater in high than in low genetic merit animals for the three breeds studied (Figure 3). The  $G_{max}$  THI of milk yield was at a lower THI value in the high than low genetic merit animals for HF and HFxNZJ animals, with the difference between genetic merit groups being 4.6 THI units for HF cattle and 2.0 units for HFxNZJ cattle. In contrast, the  $G_{max}$  THI of milk yield was at a higher THI value in the high than low genetic merit NZJ animals. However, differences in  $G_{max}$  THI between genetic merit groups within a breed were not significant ( $P > 0.05$ ). No

significant differences between genetic merit groups within breeds were observed for the rate of decline in milk yield after reaching the  $G_{max}$  THI.

## DISCUSSION

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The present study found a significant association between THI and daily milk yield. Declines in milk yield start to occur at THI of 64.3, 66.7 and 73.3 in HF, HFxNZJ and NZJ, respectively. Major reductions, deemed to be -0.05 kg of milk per day per unit of THI, started to occur at THI of 67 in HF, 69 in HFxNZJ, and 78 in NZJ cattle. The regional averages indicate expected milk yield performance reductions due to heat conditions could be marked in HF and HFxNZJ cattle in the northernmost regions of NZ. An economic analysis such as the one carried out by St-Pierre et al. (2003) in The United States, would be useful to assess the effect of heat stress conditions on dairy cattle performance in northern regions.

The breed comparisons of  $G_{max}$  THI found milk yield and protein concentration started to decline at a significantly lower THI value in HF than in NZJ cattle, similar to the findings of West et al. (2003), Keister et al. (2002) and Sharma et al. (1983). At high THI values, any difference in milk solids yield between breeds is minimal (Figure 2), whereas at lower values for THI, the HF cattle achieve higher yields than NZJ cattle. Consequently, as milk payment in NZ is primarily based on MS yield, the present results would suggest NZJ cattle are better suited than HF cattle for farms located in a hot environment such as Northland, region A, where THI exceeds 70 for 20% of days (Figure 1). The difference in heat tolerance between breeds may be due to the higher metabolic rate in HF than in NZJ cattle associated with the higher milk yields achieved by HF cattle (West et al., 1990). For example, it has been estimated that increasing milk production from 35 to 45 kg/day decreases threshold heat stress temperatures by 5°C (Berman, 2005).

In a prior study (Chapter 3), average summer heat was measured through a HLI which included adjustments for solar radiation and wind speed. However, a limited number of meteorological stations measure solar radiation or wind speed. In addition, topography and the availability of shelter for a particular herd may result in the meteorological station values for solar radiation and wind speed being markedly

## ..... **Effect of thermal environment on daily performance**

different to those experienced by the herd on a daily basis. For these reasons the THI value was used as a measure of heat conditions in the present study. The effect of solar radiation on THI thresholds is noted in a later section.

The present results provide some evidence, within HF and HFxNZJ, that cows of high genetic merit were more susceptible to the effects of environmental heat than their low genetic merit counterparts. This is in accordance with general expectations, as milk yield and heat production are mutually antagonistic (Bianca, 1965; Ravagnolo and Misztal, 2000; Ravagnolo et al., 2000). Continued genetic improvement for milk yield will reduce heat tolerance, unless heat tolerant genotypes are identified. With improvements in genetic merit for milk yield, HF genotypes will become more susceptible to increased heat from the environment as their performance is already compromised at a lower THI value than NZJ cattle.

The present study has identified a significant association between CSI and yields of milk, concentrations of fat and protein in most breeds of dairy cattle (Figure 2). CSI has been used to measure cold stress in sheep, but to our knowledge CSI has not been applied to quantify the effect of cold in cattle. It is proposed that a dairy cow exposed to a high value for CSI may adopt two different responses 1) invoke thermoregulatory mechanisms, including increased heat production e.g. by shivering, to maintain an adequate body temperature when exposed to cold conditions or 2) cease grazing and seek shelter. For the first option, the environmental conditions encountered in this study were never below accepted lower critical temperatures for lactating cattle. Therefore, it is unlikely thermoregulatory mechanisms such as elevation in resting heat production were invoked (Holmes and Sykes, 1984; Young, 1981). Instead, grazing time was probably reduced in response to high wind and rain.

Milk yield started to decline at CSI exceeding 1100 and 1000  $\text{kJ m}^{-2} \text{h}^{-1}$  in HF and HFxNZJ cattle respectively, with major reductions deemed to be -0.05 kg of milk per day per unit 10 unit increase in CSI, starting to occur at 1300  $\text{kJ m}^{-2} \text{h}^{-1}$  in both breeds. A CSI value of 1300  $\text{kJ m}^{-2} \text{h}^{-1}$  is approximately equivalent to a 3-day average temperature of 10 °C, wind speed of 7 m/s (25 kilometers/hour), and 20 millimeters of rain/day. For the period from the start of July 1999 to the end of June 2002, the percentage of days throughout the year when CSI exceeded 1300  $\text{kJ m}^{-2} \text{h}^{-1}$



were 1.4, 0.0, 2.9, 0.0, 1.1 and 1.3% in regions A-F respectively (see Figure 1). These low frequency values of cold conditions highlight the fact that milk yield performance is rarely compromised due to cold. Cold conditions may, however, significantly affect performance in high rainfall areas for herds milking throughout the winter. Strategies to limit the effect of a combination of low temperatures, strong wind and heavy rain on dairy cattle performance include providing additional feed in the form of supplements, utilising shelterbelts or housing. However, purpose-built housing is unlikely to be economically viable in NZ.

A possible confounding effect of this study is that under grazing conditions, prolonged hot or cold (wet and windy) periods are expected to decrease pasture availability and quality. Reductions in pasture availability and quality, depress daily metabolisable energy intake per cow. Consequently, while the 3-day average THI or CSI may be specific to a short-term period, it is also possible the THI or CSI conditions are indicative of a weather trend, for instance, drought conditions that can affect the supply and quality of feed. Ideally, weather trends prior to the test day or some measure of pasture availability and quality on the test day could be accounted for in the statistical model. However, nutritional data were not available and fitting a specific within year, seasonal weather effect proved difficult in the present analysis and was itself confounded with days in milk.

The effects of hot conditions in NZ appear to occur at lower level of THI than in other countries. Often, a THI of 72 (equivalent to a THI of 70 based on the equation used in this study) is seen as a level when animal performance is compromised in HF cattle (Aharoni et al., 2002; Ravagnolo et al., 2000; West et al., 2003). However, we observed that milk yields in HF cattle declined from THI of 64, with significant declines from THI of 67. This may be related to the effects of solar radiation, physical activity associated with walking to and from the dairy shed or to the diet of grazed pasture. Dairy cattle in NZ are exposed to solar radiation levels that are higher than many parts of the world (McKenzie et al., 2001), potentially lowering the THI at which heat stress starts to occur.

Eigenberg et al. (2005) found solar radiation contributed 51.4% to overall respiration rate dynamics in beef crossbred steers. Similarly, Bianca (1965) presented results

that showed high solar radiation levels contributed significantly to increasing respiration rate and rectal temperature, two reliable indicators of heat stress. Grazing compounds the problem of heat stress, due the physical nature of grazing and travelling to and from the dairy. For example, Coulon et al. (1998) observed significant increases in body temperatures of 0.7 to 1.5°C in cows walking up to 10 km per day compared to cows kept in stalls with minimal walking. A survey of large herds in NZ by Tucker et al. (2005), found NZ dairy cows often walk distances to and from the dairy shed of up to 5 km (average of 1.9 km). However it should be noted that cows in the study by Coulon et al. (1998) were not accustomed to the physical exertion of walking such long distances, with regular exercise likely to reduce the effect of walking on body temperature changes. It has also been proposed, although not proven, that diets consisting of a high proportion of forage such as a typical dairy cow diet in NZ, elevate heat production over concentrate diets (West, 2003).

In the present study, fat and protein concentration in milk declined at high THI (Figure 2). Lower concentrations of fat (Bandaranayaka and Holmes, 1976) and protein (Bandaranayaka and Holmes, 1976; Knapp and Grummer, 1991) have been reported at high temperatures. The exact mechanisms by which heat stress depresses fat and protein concentrations in dairy cattle are not clear (West, 2003). It is known, however, that in heat stressed cows, blood flow to the peripheral tissues is increased. This acts to aid cooling, but at the expense of blood flow to the mammary gland, potentially affecting substrate supply for milk fat and protein synthesis in the mammary gland (Lough et al., 1990; West, 2003). In addition, a reduction in the proportion of acetic acid in the rumen due to heat stress conditions would depress the availability of fat precursors (Bandaranayaka and Holmes, 1976).

Provision of shade, use of sprinklers in the milking shed, reducing walking distances or dietary manipulation may act to mitigate the effects of heat stress. However, these are more practical and affordable in intensive systems where cattle are housed, and where concentrates are a more cost-effective feed source than under the grazing environment in NZ. The most feasible option for heat stress minimisation in NZ would appear to be the use of sprinklers in the milk shed, a practice which up to 40% of large NZ farms already adopt during summer or for other reasons (Tucker et al.,

2005). Unfortunately in the present study, we did not have information on which farms, if any, used sprinklers in the milk shed. Valtorta and Gallardo (2004) tested the usefulness of sprinklers and fans by using them for at least 20 minutes before the morning milking and 30 minutes before the afternoon milking. They found at THI values exceeding 72, cooled cows produced 7% more milk per day than cows, which did not receive the sprinkler treatment (22.9 versus 21.4 kg milk per day, respectively;  $P < 0.10$ ). They also observed significant ( $P < 0.05$ ) increases in fat and protein yield and concentrations in the cooled versus non-cooled cattle. Kendall et al. (2006) in NZ, found grazing dairy cows with access to shade achieved significantly higher milk yields than un-shaded cows, even at moderate THI. Practical dietary manipulation to increase milk yields and dry matter intakes in heat stressed cattle may include the addition of chelated chromium to the diet (Al-Saiady et al., 2004), and increasing the dietary cation-anion balance (West et al., 1992). Further studies are needed to determine the feasibility of using chelated chromium or altering dietary cation-anion balance in heat stressed grazing cattle. High yielding cows that are susceptible to heat stress may benefit from preferential treatment such as more prolonged use of sprinklers, to limit reductions in performance due to heat stress conditions.

## **CONCLUSION**

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In comparison to NZJ cattle, HF cattle are more sensitive to the effects of heat or cold. The milk yield performance of HF or HFxNZJ cattle is significantly reduced at THI exceeding 67 and 69, and at THI exceeding 77 in Jersey cattle. Heat conditions that are likely to affect HF cattle are common (17 to 20% of all the days in a year) in the northernmost regions of NZ. Cold stress significantly affected performance at CSI exceeding  $1300 \text{ kJ m}^{-2} \text{ h}^{-1}$  for HF or HFxNZJ, although these environmental conditions are rarely (<1% of all days) encountered in spring calving herds.

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**Chapter 6**.....

Young, B. A. 1981: Cold stress as it affects animal production. *Journal of Animal Science* 52: 154-163.

# CHAPTER 7

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## **The effect of level of feeding, genetic merit, body condition score and age on biological parameters of a mammary gland model**

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Submitted to *Animal*



## ABSTRACT

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A genetic algorithm was applied to a mechanistic model of the mammary gland to estimate parameter values, which minimised the difference between predicted and actual lactation curves of milk yields in NZJ cattle managed at different feeding levels. The effect of feeding level, genetic merit, BCS at parturition and age on total lactation yields of milk, fat and protein, days in milk, liveweight and each mammary gland parameter was then determined using a multiple regression model. The mechanistic model of the mammary gland was able to fit lactation curves which corresponded to actual lactation curves with a high degree of accuracy. The senescence rate of quiescent (inactive) alveoli was highest at the very low feeding level. The active alveoli population at peak lactation was highest at very low feeding levels, but lower nutritional status at this feeding level prevented high milk yields from being achieved. Genetic merit had a significant linear effect on the active alveoli population at peak and mid-late lactation, with higher values in animals, which had higher breeding values for milk yields. A type of genetic merit x feeding level scaling effect was observed for total yields of milk and fat, and total number of alveoli produced from conception until the end of lactation with the benefits of increases in genetic merit being greater at high feeding levels. Initial rates of differentiation of progenitor cells declined with age. Animals that were 5 to 8 years of age achieved the highest total lactation yields of fat. Similarly, total lactation yields of milk and protein were higher in older animals, with a genetic merit x age scaling effect being observed for total lactation protein yields. Production levels of alveoli from conception to the end of lactation were lowest in 5 to 8 year-old animals; however, in these older animals, quiescent alveoli were reactivated more frequently. Higher BCS at parturition had a negative linear effect on milk and protein yields. The active alveoli population at peak lactation and rates of active alveoli proceeding to quiescence were highest in animals of intermediate BCS of 4.0 to 5.0. The results illustrate the potential uses of a mechanistic model of the mammary gland to fit a lactation curve and to quantify the effects of feeding level, genetic merit, BCS, and age on mammary gland dynamics throughout lactation.

## INTRODUCTION

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Biological processes of milk synthesis in the mammary gland have been studied extensively and modeled (Dijkstra et al., 1997; Neal and Thornley, 1983; Vetharanim et al., 2003b). Yields of milk in dairy cattle and other species are largely a function of the number of mammary secretory cells and the secretory activity per cell (Capuco et al., 2001; Dijkstra et al., 1997; Knight, 1989, 2000). The numbers of active secretory mammary cells at different stages of the lactation are determined by the balance between the rates of proliferation and quiescence into non-secretory cells (Knight, 2000; Molenaar et al., 1992). Proliferation, the process where undifferentiated mammary cells progress to an active secretory state, occurs at an exponential rate from the start of gestation and reaches a maximum soon after parturition when mammary cell numbers are at their peak (Pollott, 2000). Shortly after parturition, a proportion of mammary cells progress to a quiescent or resting pool of non-secretory mammary cells. These quiescent cells can either be reactivated to milk-secreting mammary cells, or they can proceed to senescence which is often termed apoptosis (Molenaar et al., 1992; Wilde et al., 1997).

The effects of nutrition, or feeding level, genetic merit, levels of body fat or age on each process of the mammary gland are not clear. Nutritional changes affect circulating levels in blood of glucose, a major precursor of milk, to the mammary gland (Pollott, 2004). Knight (2000) showed the amount of mammary tissue was directly proportional to milk yield in cows of low or high genetic merit. Similar results were obtained in a study of Jersey cattle by Davis et al. (1985). Broster and Broster (1998) reported that higher BCS, in the range of thin to moderate levels, generally resulted in elevated milk yields in early lactation, but they concluded the benefits of higher BCS are unclear for later lactation. Age affects milk yields, with lower potential milk yield in younger animals (Nielsen et al., 2003), which may be partially due to the lower live weight of younger animals. For example, Linzell (1972) presented results within and amongst species which illustrated that both milk yield and mammary gland weight were positively correlated with live weight. Although these results illustrate the effects of nutrition, genetic merit, body fatness

and age on total or daily yields, they do not provide a quantitative framework with which the effect of each factor can be simulated in a model of the mammary gland.

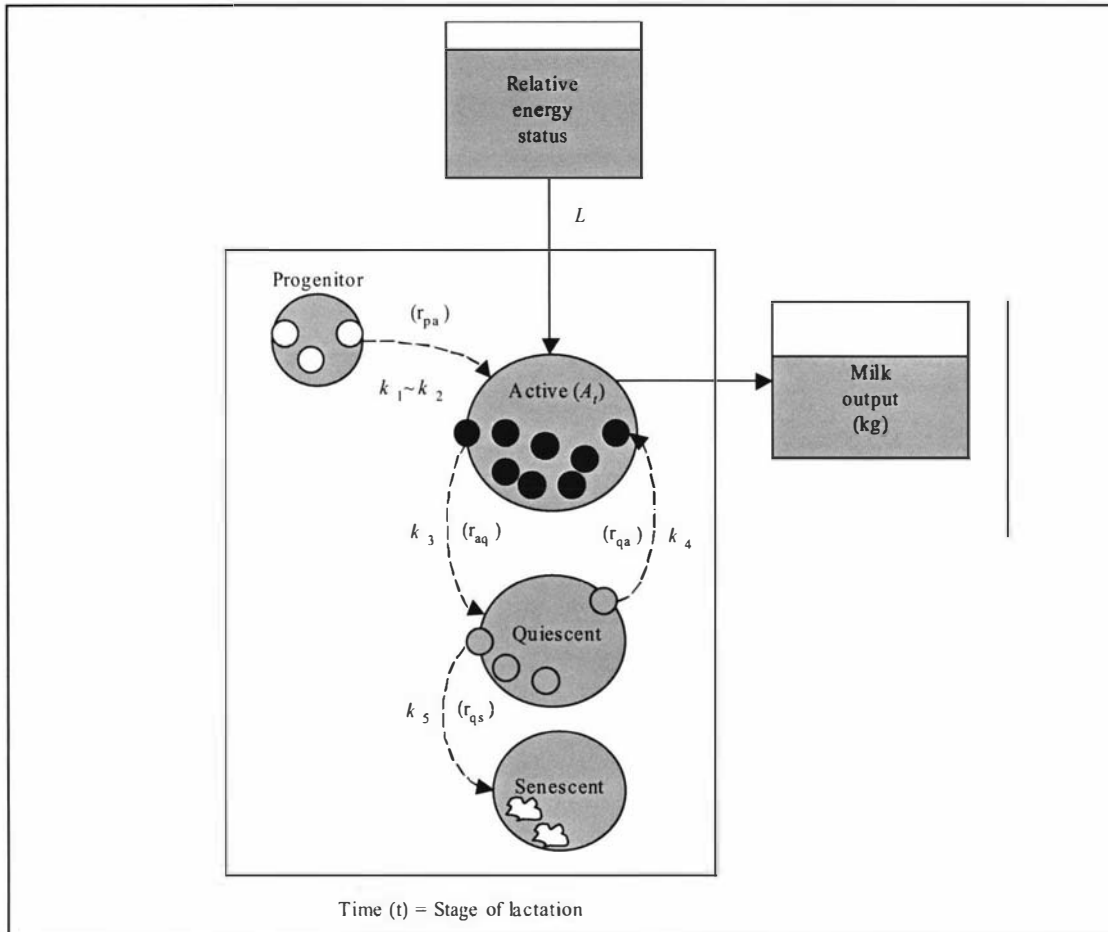
Vetharaniam et al. (2003b) constructed a model that simulated milk synthesis in the mammary gland by linking the effects of nutrition and genotype. Using a small data set of two Holstein Friesian genotypes managed on diets of pasture or total mixed ration, they found the estimated active population of alveoli, or milk-secreting mammary cells, throughout lactation was related to actual yields. In addition, the quiescence rate of active alveoli exhibited a significant genotype x diet interaction, which was related to actual MS yields of each genotype in each environment. The objectives of the present study were to utilise data from a New Zealand trial to further quantify the effects of nutrition, genetic merit, BCS and age on the parameters in the model of the mammary gland constructed previously by Vetharaniam et al. (2003a; 2003b).

## **MATERIALS AND METHODS**

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### **Mammary gland model**

The mammary gland model of Vetharaniam et al. (2003a; 2003b) consists of alveoli (groups of secretory cells) in various states of activation or inactivation (Figure 1). At the start of lactation each animal has an initial pool of active alveoli,  $A_0$ . The number of active alveoli,  $A_t$ , at time  $t$ , is dependent on a series of equations, with each active alveolus assigned a theoretical maximum secretion rate,  $S$ , of  $3 \times 10^{-9}$  MJ/d based on previous data. The rate of production of active alveoli by progenitor (undifferentiated) cells,  $r_{pa}$ , decays exponentially throughout the lactation with an initial constant,  $k_1$ , and decay constant,  $k_2$ . Throughout lactation, active alveoli can proceed to a state of quiescence (non-secretory cells). The rate of quiescence of active alveoli,  $r_{aq}$ , is proportional to  $A_t$  and  $k_3$ . The quiescent alveoli then become either, reactivated to secretory alveoli (secretory cells) or proceed to senescence. The



**Figure 1:** Schematic diagram of the mammary gland model (adapted with permission based on Vetharaniam et al., 2003a). **Abbreviations:**  $A_t$  = active secretory alveoli at time  $t$ ,  $r_{pa}$  = rate of differentiation from progenitor to active secretory alveoli,  $r_{aq}$  = rate at which active secretory alveoli proceed to quiescence,  $r_{qa}$  = rate at which quiescent alveoli are reactivated to become active secretory alveoli, and  $r_{qs}$  = rate at which quiescent alveoli proceed to senescence.

rate of reactivation of quiescent alveoli,  $r_{qa}$ , is proportional to the quiescent alveoli population and a constant  $k_4$ . The rate of senescence of quiescent alveoli,  $r_{qs}$ , is proportional to the number of quiescent alveoli and  $k_5$ . The total production of alveoli from conception until the end of lactation,  $A_{produced}$ , is:  $A_0 + k_1/k_2$ . At any stage of the lactation, milk output is influenced by the relative energy status of the animal, which is a ratio of actual intake versus theoretical maximum intake and a nutritional response factor,  $L$ , which is invoked when the relative energy status is less than 1.00.

### **Animal data**

To quantify the effect of level of feeding, genetic merit, BCS, and age on the biological parameters of the described mammary gland model, a data set was obtained from a New Zealand trial with Jersey cattle in the 1999/2000 season. Data consisted of an initial estimate of BCS around parturition and then up to fifteen (herd tests carried out at 14 day intervals) measurements of daily yields of milk, fat and protein per cow per lactation, and corresponding days in milk at each test. Total lactation yields of milk, fat and protein, liveweight at peak lactation (22<sup>nd</sup> of October), days in milk and EBV for milk for each individual animal were also obtained. Estimates of intakes of pasture and supplements at each test were calculated from the area grazed per cow daily, pre and post grazing masses of pasture and supplements offered.

The Jersey cows were managed at different feeding levels: high, medium, low and very low. The corresponding estimates of average feed intakes for each feeding level group over the lactation period were 13.47, 13.02, 12.40 and 11.74 kg DM/cow/day, respectively. Initially, forty cows were assigned to each feeding level group. Little supplement was fed, and was generally high-quality pasture silage conserved on the farmlets. The relative energy status,  $E$ , at each herd test was determined based on estimated intakes of pasture and supplements of each feeding level group divided by theoretical maximum intakes of 16 kg DM per cow per day (approximately 4 % of live weight). The energy value per kilogram of milk was calculated from milk yields, and fat, protein and lactose component concentrations based on the equations of Dado et al. (1993).

### **Genetic algorithm analyses**

To determine estimates of model parameters,  $A_0$ ,  $k_1$ ,  $k_2$ ,  $k_3$ ,  $k_4$ ,  $k_5$ ,  $L$  and  $A_{\text{produced}}$ , for the milk yield lactation curve of each individual animal, a genetic algorithm add-in for Microsoft Excel<sup>®</sup> (YearStretch, 2005) was applied to the system of equations outlined by Vetharanim et al. (2003b). Genetic algorithms have proved efficient at finding the global optima in a number of agricultural models (Hart et al., 1998; Mayer et al., 1996). Genetic algorithms are based on the biological concepts of reproduction where two selected individuals, with different genetic codes, are ‘mated’ or crossed to produce the next generation. Over generations, or iterations, the

process combines successful traits, which improve the fitness of the population. While crossover is the dominant genetic operation, mutation is also introduced at each mating to rediscover any potential beneficial genes. Through successive mating of selected individuals, the population structure tends to find a near-optimal solution (Mayer et al., 1999).

In the context of the present study, each individual of a population is an array of estimates of mammary gland model parameters. The parameter bounds specified in Table 1 were based on the estimates obtained by Vetharaniem et al. (2003b). Fitness was maximised by finding mammary gland model parameters, which resulted in the lowest values for mean prediction error (MPE) of actual compared to predicted milk yields, as outlined by Fuentes-Pila et al. (1996). Mayer et al. (2001) recommends a population size of approximately twice the dimensionality of the problem, but not too small to ensure genetic diversity. Based on the present seven-dimensional problem, an initial population size of 50 with the 25 best individuals surviving per generation seemed reasonable. However, MPE was reduced further when using a population size of 100 with the best 50 selected and was therefore adopted for genetic algorithm analyses. Mutation, which was at an automated rate in the genetic algorithm add-in, was used to rediscover any potential beneficial parameters values in subsequent generations. The genetic algorithm ran for 50 generations, and the parameter values that minimised MPE were then kept for each individual cow. Based on these individual parameter values, an estimate of the number of active alveoli was also obtained at peak ( $A_{peak}$ ) and mid-late ( $A_{mid-late}$ ) lactation. Peak and mid-late lactation corresponded to the test nearest to day 35 and day 150 after a cow's parturition, respectively.

**Table 1:** Summary of parameter bounds for the mammary gland model

Mammary gland parameters	Bounds
$A_0 (\times 10^{10})$	1.0-3.0
$k_1 (\times 10^9 \text{ d}^{-1})$	0.5-2.5
$k_2 (\times 10^{-1} \text{ d}^{-1})$	0.5-4.0
$k_3 (\times 10^{-1} \text{ d}^{-1})$	2.0-6.0
$k_4 (\times \text{d}^{-1})$	3.0-7.0
$k_5 (\times 10^{-2} \text{ d}^{-1})$	0.01-5.0
$L (\times 10^{-1})$	3.0-7.0

### Multiple regression analyses

To determine the effect of feeding level, genetic merit, BCS at parturition and age on total lactation yields of milk, fat and protein, liveweight around the time of peak milk yield, days in milk,  $A_0$ ,  $k_1$ ,  $k_2$ ,  $k_3$ ,  $k_4$ ,  $k_5$ ,  $L$ ,  $A_{produced}$ ,  $A_{peak}$  and  $A_{mid-late}$ , the REG procedure in the SAS package, version 8 (SAS, 1999) was used. The multiple regression models included linear and quadratic effects of feeding level, genetic merit, BCS and age, and linear interactions between feeding level and genetic merit, and genetic merit and age. Genetic merit was defined as the deviation in milk EBV relative to the animal in the dataset with the lowest milk EBV. For each trait, a stepwise regression procedure was used where the non-significant ( $P>0.10$ ) effects were removed from the model. If the intercept was deemed non-significant ( $P>0.10$ ) it was also removed from the model.

Multicollinearity among predictor variables of the multiple regression models, which can inflate standard errors and parameter estimates, was investigated by obtaining the variance inflation factor calculated as  $1/(1 - r^2)$ , where  $r^2$  is the coefficient of determination from ordinary least-squares regression of a predictor variable in relation to all other predictors in the model (Phillipi, 1994). Variance inflation factors of 10 or greater were considered to indicate a problem with multicollinearity (Phillipi, 1994). In the instances where multicollinearity was detected, the ORTHOREG procedure (SAS, 1999), which accounts for multicollinearity by orthogonalising the data using a Gentleman-Givens transformation, was applied to the selected regression model to find unbiased standard errors and parameter estimates (Yu, 2000).

## RESULTS

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The parameter  $k_5$ , which influences persistency of milk yield, showed the greatest variability (Table 2). The degree of variability of  $L$ , which determines the animal response at times of nutritional stress, was low even though the pre-defined parameter space was  $3.0$  to  $7.0 \times 10^{-1}$ . The model was able to match predicted and actual milk yield values with a high degree of accuracy (Figures 2 and 3). Accuracy was greatest at the intermediate feeding levels. The threshold of 0.10 error as

suggested by Fuentes-Pila et al. (1996) where there is a poor fit between actual and predicted values was not exceeded for any animals in the dataset.

As expected, greater total lactation yields of milk, fat and protein were observed at higher feeding levels (Table 3). Contributing to these differences in yields were an increase in lactation lengths at higher feeding levels. The initial rate of differentiation of progenitor cells into active alveoli,  $k_1$ , was highest at very low feeding levels (Table 4). Level of feeding significantly affected the senescence rate of quiescent alveoli,  $k_5$  (higher senescence rate = reduced persistency), with the highest value at a very low feeding level.  $A_{produced}$  and  $A_{peak}$  were at their maximum value in the lowest feeding level environment.

Greater gains in milk and fat yields per 1-kg increase in milk EBV were observed at high then at low feeding levels; a type of genetic merit x feeding level scaling effect (Table 3). The total production of alveoli from conception until the end of lactation,  $A_{produced}$ , also exhibited a genetic merit x feeding level scaling effect. A significant genetic merit x age scaling effect was observed for protein yield and  $A_0$ , the initial population of active alveoli at the start of lactation. The senescence of quiescent

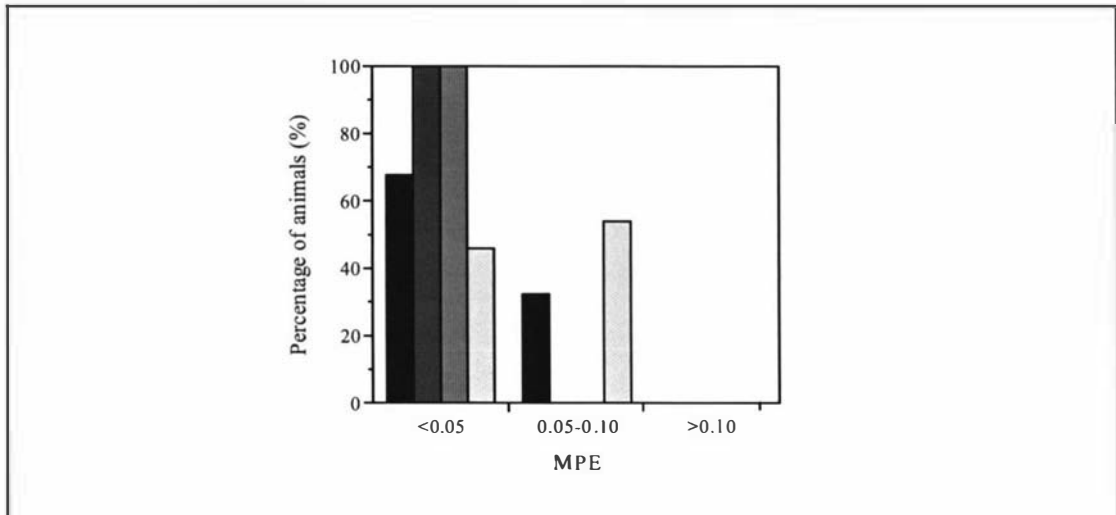
**Table 2:** Descriptive statistics for the mammary gland parameters

Mammary gland parameters	Number of observations	Mean	SD <sup>†</sup>	CV <sup>‡</sup>	Min	Max
$A_0$ ( $\times 10^{10}$ )	150	2.06	0.19	8.98	1.33	2.46
$k_1$ ( $\times 10^9$ d <sup>-1</sup> )	150	1.27	0.48	37.87	0.56	2.49
$k_2$ ( $\times 10^{-1}$ d <sup>-1</sup> )	150	2.98	0.57	19.18	0.93	3.89
$k_3$ ( $\times 10^{-1}$ d <sup>-1</sup> )	150	3.07	1.05	34.01	2.01	5.98
$k_4$ ( $\times$ d <sup>-1</sup> )	150	5.79	1.07	18.48	3.56	6.99
$k_5$ ( $\times 10^{-2}$ d <sup>-1</sup> )	150	0.80	0.57	72.13	0.08	4.48
$L$ ( $\times 10^{-1}$ )	150	3.23	0.10	3.17	3.02	3.51
$A_{peak}$ ( $\times 10^{10}$ )	146	2.34	0.08	3.25	2.22	2.61
$A_{mid-late}$ ( $\times 10^{10}$ )	149	2.25	0.06	2.71	2.12	2.44
$A_{produced}$ ( $\times 10^{10}$ )	150	2.51	0.10	4.15	2.32	2.94

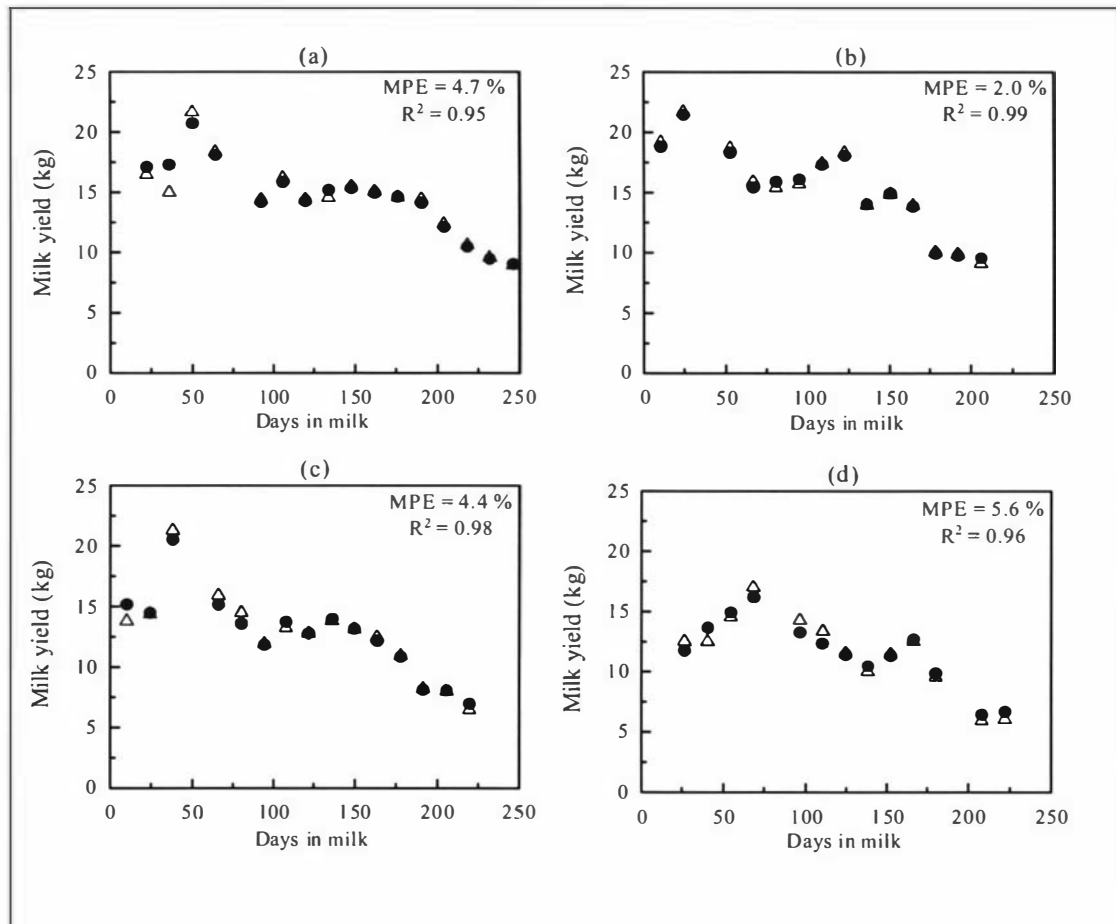
<sup>†</sup>standard deviation

<sup>‡</sup>Coefficient of variation  $\times 100$





**Figure 2:** The percentage of animals with mean prediction error (MPE) of predicted versus actual values of <0.05, 0.05-0.10 and >0.10 at high (■), medium (■), low (■) and very low (■) feeding levels.



**Figure 3:** Example lactation curves of predicted (Δ) and actual (●) milk yields (a) High feeding level (b) Moderate feeding level (c) Low feeding level (d) Very low feeding level. Abbreviations: MPE = Mean prediction error, R<sup>2</sup> = coefficient of determination

**Table 3:** Significant regression coefficients for feeding level (FL), genetic merit (GM), BCS at parturition and age for milk, fat and protein yield, days in milk and liveweight around the time of peak lactation.

Dependent variable	Intercept	FL		Genetic merit		BCS		Age		Interaction		R <sup>2</sup>
		L <sup>†</sup>	Q <sup>‡</sup>	L	Q	L	Q	L	Q	FL*GM	GM*Age	
Milk yield (kg)	-	223.63***	-	-	-	-171.89***	-	88.03***	-	0.139***	-	0.99
Fat yield (kg)	-305.6***	31.18***	-	-	-	-	-	32.49***	-2.26***	0.004***	-	0.61
Protein yield (kg)	-97.6**	19.89***	-	-	-	-6.64*	-	-	-	-	0.008	0.52
Days in milk	-158.8***	37.23***	-	-	-	-12.60***	-	-	-	-	-	0.59
Liveweight (kg)	175.4***	-	-	0.023 <sup>†</sup>	-	15.79***	-	34.95***	-2.13***	-	-	0.50

<sup>†</sup>L = Linear, <sup>‡</sup>Q = Quadratic, <sup>†</sup>P < 0.10, \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001

**Table 4:** Significant regression coefficients for feeding level (FL), genetic merit, BCS at parturition and age for parameters of the mammary gland model.

Dependent variable	Intercept	FL		Genetic merit		BCS		Age		Interaction		R <sup>2</sup>
		L <sup>†</sup>	Q <sup>‡</sup>	L	Q	L	Q	L	Q	FL*GM	GM*Age	
$A_0$ ( $\times 10^{10}$ )	2.03***	-	-	-	-	-	-	-	-	-	0.00002 <sup>†</sup>	0.02
$k_1$ ( $\times 10^9$ d <sup>-1</sup> )	4.32***	-0.23***	-	-	-	-	-	-0.035*	-	-	-	0.11
$k_2$ ( $\times 10^{-1}$ d <sup>-1</sup> )	2.99***	-	-	-	-	-	-	-	-	-	-	0.00
$k_3$ ( $\times 10^{-1}$ d <sup>-1</sup> )	-	-	-	-	-	1.48***	-0.174***	-	-	-	-	0.89
$k_4$ ( $\times$ d <sup>-1</sup> )	5.02***	-	-	-	-	-	-	0.317*	-0.026*	-	-	0.03
$k_5$ ( $\times 10^{-2}$ d <sup>-1</sup> )	96.74***	-15.10***	0.594***	-0.0006**	-	-	-	-	-	-	-	0.16
$L$ ( $\times 10^{-1}$ )	2.79***	0.04*	-	-	-	-	-	-	-	-	-	0.04
$A_{peak}$ ( $\times 10^{10}$ )	9.05***	-1.03**	0.037**	0.0001***	-	0.16 <sup>†</sup>	-0.020*	-	-	-	-	0.71
$A_{mid-late}$ ( $\times 10^{10}$ )	-	0.42***	-0.020***	0.0001***	-	-	-	-	-	-	-	1.00
$A_{produced}$ ( $\times 10^{10}$ )	3.18***	-0.12***	-	-	-	0.39*	-0.044**	-0.025*	0.002*	0.00001***	-	0.52

<sup>†</sup>L = Linear, <sup>‡</sup>Q = Quadratic, <sup>†</sup>P < 0.10, \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001

alveoli,  $k_5$ , displayed a significant linear effect for genetic merit with lower senescence rates in animals of superior genetic merit. Genetic merit had a significant linear effect on  $A_{peak}$  and  $A_{mid-late}$  with more active alveoli in animals of superior genetic merit (Table 4).

BCS at parturition had a negative linear effect on total lactation yields of milk and protein (Table 3). As expected, BCS at parturition had a significant positive linear effect on liveweight around the time of peak milk yield.  $A_{produced}$ ,  $A_{peak}$  and  $k_3$  were highest at intermediate BCS of 4.0 to 4.5 (Table 4). Age had a significant positive linear effect on total lactation yields of milk, and a linear and quadratic effect on total lactation yields of fat with fat yields increasing initially up to approximately 8 years of age and declining thereafter (Table 3). Age also had a significant linear effect on  $k_1$ , which influences the rates at which new alveoli are produced, with higher rates in younger animals (Table 4). The reactivation of quiescent alveoli,  $k_4$ , increased initially up to about 6 years of age but declining thereafter. The total number of alveoli produced from conception until the end of lactation,  $A_{produced}$ , declined initially as animals aged reaching its lower asymptote at 5 years of age but rose thereafter.

## DISCUSSION

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The model was able to fit individual lactation curves that corresponded to actual curves with a high degree of accuracy. This was achieved using information related to the nutritional status of the group of cows at each feeding level rather than for individual animals. While it would have been preferable to have an individual estimate of feed intake for each cow, measured by the n-alkane method or calculated from measurements of milk yield, liveweight and live weight changes, this was not possible from available data.

The amount of active alveoli around the time of peak milk yield,  $A_{peak}$ , was highest at very low feeding levels. However, this did not result in high milk yield in the very low feeding level environment because milk energy output ( $I$ ) is a function of the number of active alveoli ( $A_t$ ), secretion rate per active alveoli ( $S$ ), energy status ( $E$ ) and the nutritional response factor ( $L$ ) i.e.  $I = SE^L A_t$  (Vetharanim et al., 2003b).

Therefore, as  $E$  is often below unity in a very low feeding level than in a high feeding level environment, milk yields are suppressed in the former compared to latter environment. In addition, low feeding levels are expected to have a negative effect on BCS and based on the results presented in Table 4, this would result in a reduction in  $A_{peak}$ .

The senescence rate of quiescent alveoli,  $k_5$ , was highest at the very low feeding level. This is consistent with results presented by Knight (2001) for supplemented and un-supplemented cows. However, high  $k_5$  values were observed at the highest feeding level. This result may have been due to animals at the high feeding level being dried off considerably later than animals at the very low feeding level. Consequently, a decrease in production in late lactation may have been arrested earlier in the very low feeding level group than in the high feeding level group, because of the earlier dry off of the former group. No effect of diet or level of feeding on  $k_4$  was found in contrast to the results of Vetharaniam et al. (2003b). This suggests a diet effect on  $k_4$  may be expressed only when two widely different diets are compared e.g. pasture versus total mixed ration, or wide ranges of feeding levels are imposed.

In the present study, we observed a scaling effect for total lactation yields of milk and fat in relation to genetic merit and feeding level and this is consistent with numerous other studies (Kennedy et al., 2002; O'Connell et al., 2000; Veerkamp et al., 1994). Based on the values presented in Table 4, at feed intakes of 12 and 13 kg DM/cow that correspond to an approximate average of the present study, we would expect for every 1-kg increase in milk EBV that total lactation yields of milk would increase by 1.67 and 1.81 kg, respectively. This is significantly greater than the theoretical expectation of 1 kg milk/1 kg increase in milk EBV. The scaling effect is possibly due to the overall study environment being superior to the environment which Jersey cows experience in the national herd (Livestock Improvement, 2000). The observed genetic merit x feeding level scaling effect for  $A_{produced}$ , provides a potential mechanism by which scaling effects are expressed at a mammary cell level.

In the present study, the total number of active alveoli at peak and mid-late lactation ( $A_{peak}$  and  $A_{mid-late}$ , respectively) increased linearly with genetic merit. Similarly,

Vetharaniam et al. (2003b) reported that a North American Holstein Friesian genotype had lower values for  $A_b$  than a New Zealand Holstein Friesian genotype when they were managed on pasture. Whereas, on a diet of total mixed ration,  $A_t$  was higher in the North American than New Zealand Holstein Friesian genotype, indicating a re-ranking type of genotype x environment interaction. The re-ranking for the parameters were consistent with the significant re-ranking for milk solid yields exhibited by the two genotypes when managed on diets of either pasture or total mixed ration (Kolver et al., 2002). Davis et al. (1985) found udder volume, theoretically correlated to the population of active alveoli (i.e.  $A_t$ ; see Figure 1), was significantly greater in high than low genetic merit Jersey cattle. In Friesian cattle, udder volume did not differ between low and high genetic merit groups, but secretory output per active alveoli was significantly greater in the high genetic merit group. We also observed lower rates of senescence of quiescent alveoli, largely determined by  $k_3$ , in superior genetic merit animals. In addition, the initial population of active alveoli at the start of lactation,  $A_0$ , exhibited a genetic merit x age scaling effect. In practical terms, the expected increase in  $A_0$  per 1-kg increase in milk EBV is expected to be greater in older than younger animals. Based on the results of this study and previous studies, high genetic merit animals in a particular environment achieve higher yields through greater pools of active alveoli throughout lactation ( $A_t$ ), or increased secretory output per active alveolus, elevated levels of persistency (i.e. flatter lactation curve), and higher levels of total alveoli produced from conception until the end of lactation than low genetic merit animals.

In the present study, increased BCS at parturition resulted in reduced total yields of milk and protein. We also observed that animals at intermediate BCS of 4.0 to 4.5 at parturition had the highest values for  $A_{produced}$  and  $A_{peak}$ . However, the rates of active alveoli proceeding to quiescence ( $k_3$ ) were highest at intermediate BCS at parturition. Waltner et al. (1993) found total lactation yields were reduced at very high and low BCS compared to intermediate BCS. Heuer et al. (1999) and Domecq et al. (1997) found higher BCS at parturition did not increase total lactation yields or yields to 120 days of lactation, respectively. While, the benefits of higher BCS at parturition on milk yield appear to be minimal, there may be a confounding effect of genetic merit (Waltner et al., 1993). For example, there is a negative genetic correlation between BCS and milk yield, meaning animals which are genetically fatter, achieve lower

milk yield than genetically thin animals (Coffey et al., 2004; Pryce et al., 2001; Veerkamp et al., 2001). Due to the confounding effects of genetic merit we cannot make any definite conclusions on a BCS at parturition, which will optimise milk yields or the number of active alveoli throughout lactation.

We observed increased yields of fat up to eight years of age but decreases thereafter. Initial rates of differentiation of progenitor cells,  $k_1$ , declined with age. The reactivation of quiescent alveoli,  $k_4$ , was greatest in animals of five to eight years of age. The exact mechanisms by which quiescent alveoli are reactivated into secretory alveoli is not certain (Molenaar et al., 1992). Reactivation of quiescent alveoli may be lower in two-year-old animals than five to eight year-old animals because the former are often still partitioning energy towards growth i.e. a trade-off mechanism between milk production and growth. The trade-off mechanism, combined with the expected reduction in mammary tissue for animals at lower live weights (Linzell, 1972), could also explain the significantly reduced total lactation yields in two year-old animals. Our results, do not provide compelling evidence to explain the findings of previous empirical studies (Tozer and Huffaker, 1999; Varona et al., 1998), where lactation persistency is reduced in older animals than in two and three year old animals.

Knight (2000) and Wilde et al. (1997) stated that manipulating mammary cell proliferation and senescence holds potential to modify persistency of milk yield. In the present model, genetics of lactation persistency are expressed in a number of the mammary gland parameters, namely  $k_2 - k_5$  which control the flow of alveoli from states of active secretory to senescence. We observed from our analyses that cows of superior genetic merit exhibited reduced rates of quiescent alveoli proceeding to senescence ( $k_5$ ). Vetharanim et al. (2003b) observed  $k_5$  was lower on a diet of total mixed ration compared to pasture. Therefore, lactation persistency could be enhanced through the use of energy dense diets (i.e. total mixed ration) and superior genotypes. The potential to select genotypes for lactation persistency was illustrated by Muir et al. (2004), who reported a moderate heritability (0.18) for lactation persistency in first lactation Canadian Holstein Friesians.

## CONCLUSION

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Overall, the results illustrate the model's potential as a tool to fit a lactation curve and to help in understanding the effects of level of feeding or diet, genetic merit, BCS and age on the dynamics of milk yield during lactation. The next logical progression is to use the derived mathematical functions to assess their ability to accurately predict milk yield for any cow, at any stage of lactation, based on information related to her nutritional status, genetic merit, BCS and age. Further studies could also investigate the effect of specific genes on milk yield and milk composition throughout lactation.

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# CHAPTER 8

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## **Development of a simulation model that predicts dairy cattle performance based on genotype and environment, and includes genotype by environment interactions**

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## ABSTRACT

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In this paper, a dairy cattle simulation model for pastoral systems that considers how dairy cow genotypes respond to different environments is described. Five modules relating to maintenance, pregnancy, growth, body energy stores and lactation represent the dairy cow, with various environmental factors influencing processes within each module. An initial estimate of feed intake is used to define cow genetic potential based on EBV for total yields milk, fat and protein, and breed-specific environmental sensitivity information. A mammary gland module then predicts daily yields of milk, fat and protein based on the cow's genetic potential after considering her age, stage of lactation, BCS, nutritional status and the thermal environment. Live weight change is also predicted via a body energy stores module, which considers the effect of age, stage of lactation, current BCS, nutritional status, and an estimated breeding value for BCS. Feed intake is then predicted from the requirements for maintenance, growth and pregnancy, and the genetic drive for yields of milk, fat and protein and body fat change. A preliminary evaluation of the model illustrated the model was able to predict cow performance in line with previous experimental findings.

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## INTRODUCTION

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There are a number of dairy cattle system simulation models, which can be used to predict the effect on performance of different climatic and feeding environments (for a review see Chapter 2). However, these models do not succeed in integrating the quantitative components of cow genotype (i.e. EBV and reaction norms) to accurately predict how a cow will respond to a particular environment (Chapter 2). In most simulation models, milk yield or responses to additional feed are predicted after specifying peak milk yield potential (Chapter 2). However, peak milk yield potential is difficult to estimate, especially if the quantity and the quality of feed offered differs greatly from the normal environment.

Oldham and Emmans (1989) stated “responses to additional feed are a consequence of the animals interaction with an offered feed and other aspects of its environment”. It has subsequently been shown that not all genotypes increase milk yield, or increase intake, to the same degree when given extra feeds due to the existence of GxE interactions (Horan et al., 2005; Kennedy et al., 2003a; Veerkamp et al., 1994). Reaction norms are useful in these circumstances, because they define an animal’s expected response to changes in environment. Reaction norms have been used recently to quantify changes in sire EBV across the environmental range of feeding levels and climate for yields of milk, fat and protein, and BCS (Chapter 5, Berry et al., 2003; Calus and Veerkamp, 2003; Kolmodin et al., 2004). Information from these reaction norms can then be used to more accurately predict expected responses to changes in environment.

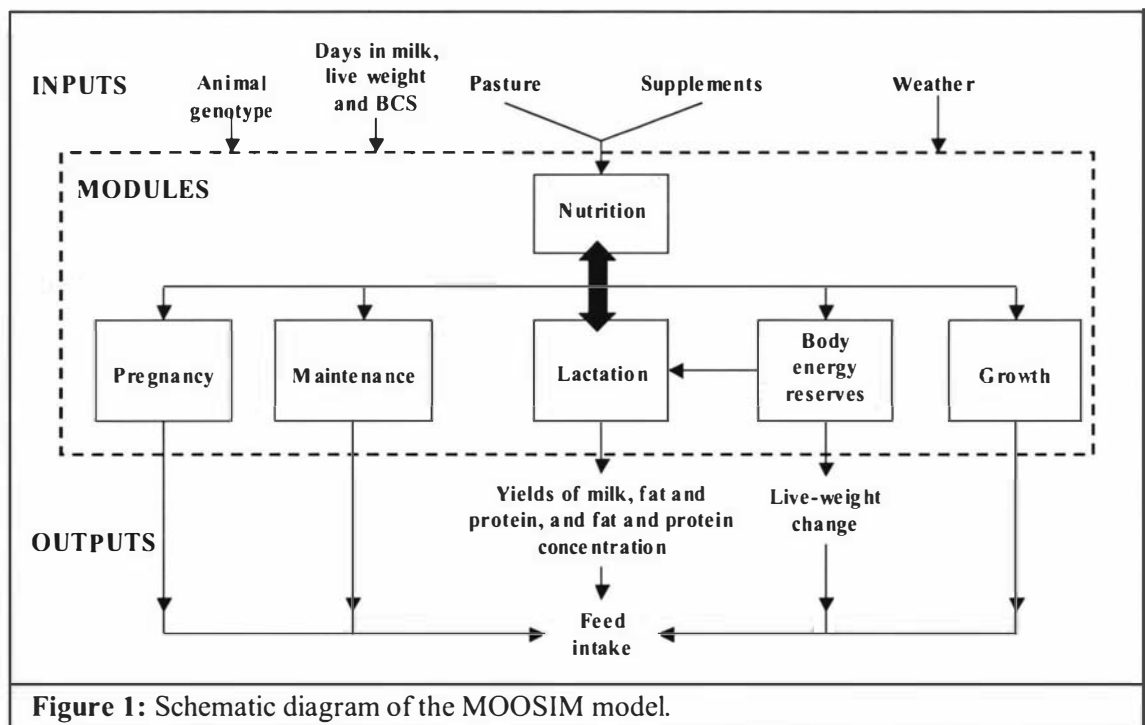
It has been proposed that once an animal’s potential, or genetic drive to consume feed in a given environment is defined (i.e. using EBV and reaction norm information), nutrients are allocated to particular functions or modules in a priority order (Glazier, 2002; Oldham and Emmans, 1989). Oldham and Emmans (1989), suggest the priority order in cattle is 1) maintenance of essential metabolic processes 2) pregnancy 3) lactation (i.e. genetically driven milk yields) 4) growth to ensure target live weights at maturity are achieved, and 5) fat deposition or depletion to achieve a desired fat mass. When feed is scarce, body maintenance (homeostasis and survival), will take precedence over traits related to production, reproduction or growth (Glazier, 2002).

This paper describes a dairy cattle simulation model for pastoral systems that applies a modular approach to predict milk yield and live weight change in dairy cattle, with feed intake being determined by the cumulative effect of each animal module. The essential modules of maintenance and pregnancy are satisfied before all other modules. Feed intake can then be predicted from the animal’s genetic potential for milk yield and live weight change in the specified environment. Various temporary environmental factors such as cow BCS, climate, feed quality and the stage of pregnancy are also considered when predicting yields of milk, fat and protein and DM intake.

## MATERIALS AND METHODS

### Model Overview

The dairy cattle simulation model for pastoral systems, referred to as MOOSIM, was written using the VisualBasic.net programming language. The schematic diagram presented in Figure 1, gives a broad overview of the MOOSIM model. The required inputs of the model are outlined in Table 1. Figure 2 is an illustration of the input and output screens of MOOSIM. The first set of inputs describes the cow with the novel components being the use of EBV for total lactation yield traits and BCS. Various pasture parameters are entered and range from pasture allowance (PA) per cow to pasture quality (mega joules [MJ] of Metabolisable Energy [ME], digestibility, neutral detergent fibre [NDF]) and pre-grazing sward mass. The typical terrain of the farm is needed to calculate the animal's energy requirements for maintenance with greater maintenance requirements as grazing land becomes steeper. Expected weather conditions are entered to ensure accurate prediction of milk yield for the effects of heat stress. Days in milk,  $t$ , is entered as the simulation model predicts values on a daily basis.



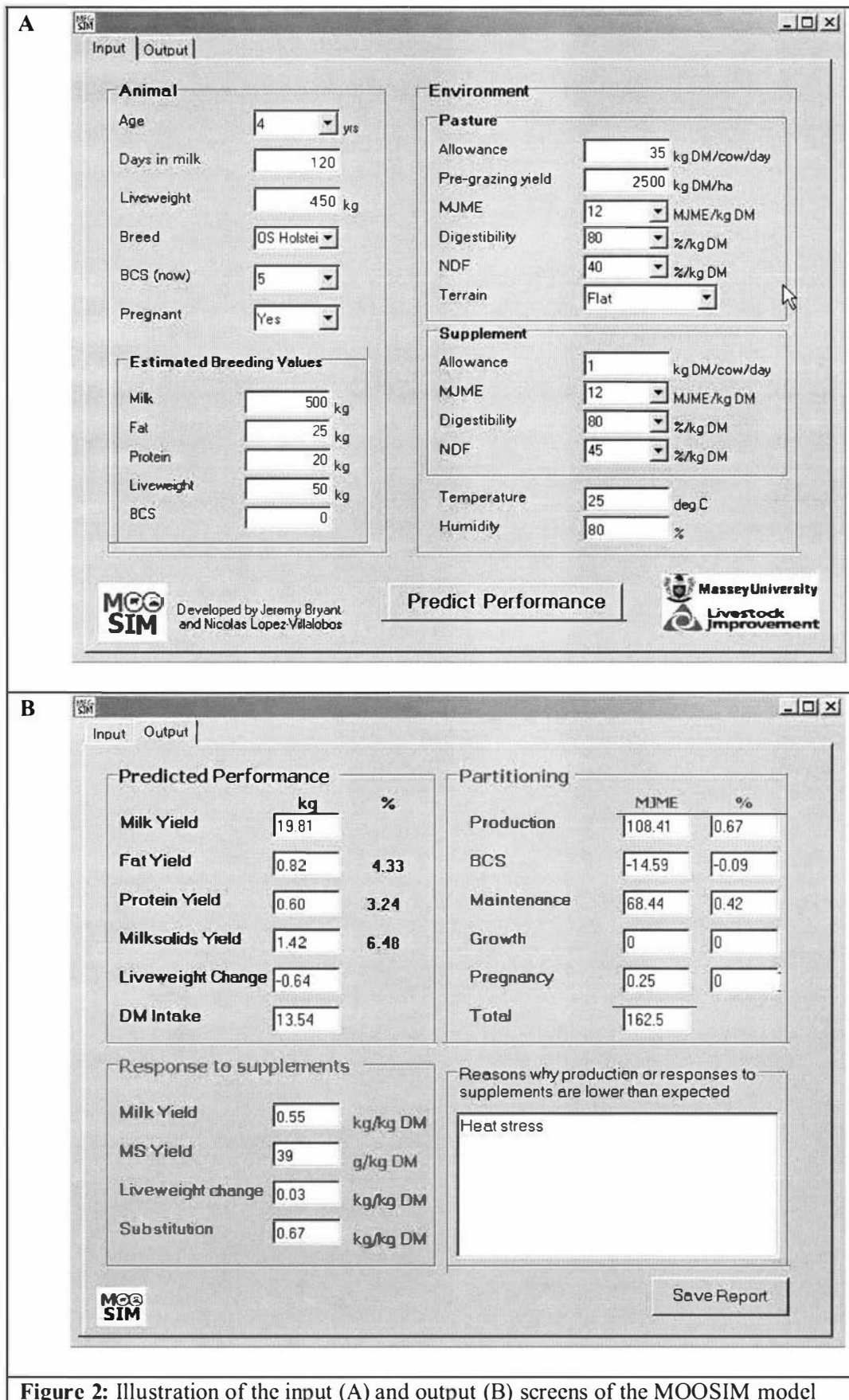


Figure 2: Illustration of the input (A) and output (B) screens of the MOOSIM model

**Table 1:** Abbreviation, units and description of parameters required as inputs in the MOOSIM model

Abbreviation	Units	Description
<b>Animal</b>		
AGE	years	Age
W	kg	Live weight of the herd
BRD	-	Animal breed (5 Classes: OHF, NZF, NZJ, FxJ and Other)
PREG	-	Pregnant (Yes or No)
BCS <sub>curr</sub>	-	Current BCS
t	days	Days in milk or stage of lactation
EBV <sub>Milk</sub>	kg	EBV for total lactation milk yield
EBV <sub>Fat</sub>	kg	EBV for total lactation fat yield
EBV <sub>Pro</sub>	kg	EBV for total lactation protein yield
EBV <sub>W</sub>	kg	EBV for live weight
EBV <sub>BCS</sub>	kg	EBV for BCS
<b>Pasture</b>		
PA	kg/cow/d	Daily allowance of pasture per cow
ME <sub>past</sub>	MJ/kgDM	Metabolisable energy concentration of pasture offered
NDF <sub>past</sub>	%/kgDM	Neutral detergent fibre content of pasture offered
DIG <sub>past</sub>	%/kgDM	Digestibility of pasture offered
HM <sub>pre</sub>	kgDM/ha	Pre-grazing mass of the pasture offered
TER	-	Terrain of land grazed (4 classes: flat, flat-rolling, rolling, steep)
<b>Supplement</b>		
SA	kg/cow/d	Daily allowance of supplements per cow
ME <sub>supp</sub>	MJ/kgDM	Metabolisable energy concentration of supplements offered
NDF <sub>supp</sub>	%/kgDM	Neutral detergent fibre content of supplements offered
DIG <sub>supp</sub>	%/kgDM	Digestibility of supplements offered
<b>Weather</b>		
TEMP	°C	Temperature on day of simulation
HUM	%	Humidity on day of simulation

After the required inputs are entered, up to five modules (maintenance, lactation, body energy reserves, pregnancy and growth) are implemented, depending on the age of the animal, stage of lactation and pregnancy. The equations in each of these modules then determine outputs for yields of milk and components, feed intakes, live weight and BCS changes, and nutrient partitioning. Presented in Appendix 1 is a description of each parameter. The full list of model equations are outlined in Appendix 2, with each function classified on its primary area of action, divided into sections describing nutritional environment (N), live weight and growth (W), body energy reserves (R), lactation (L), maintenance (M), pregnancy (P) and total (T) measures of intake and energy partitioning. Each component of the MOOSIM model is now described in more detail.

### Nutrition

To drive the mammary gland model (described in a subsequent section) and to determine an animal's genetic potential, an initial estimate of feed intake is



calculated based on PA and daily allowance of supplementary feed (SA). The initial estimate of feed intake is for an “average” cow, and therefore may be different to the final intake estimate because of differences between animals in their mammary gland feeding drive. The mammary gland feeding drive is proportional to the active population of alveoli that is quantified, based on EBV for yields of milk, fat and protein, reaction norm information and the stage of lactation.

Daily PA to ground level follows the definition and equation described by Sollenberger et al. (2005), and is typically in the range of 20 to 70 kg DM/cow/day. The relationship of feed intake with PA and SA was quantified by performing a meta-analysis based on the results of studies carried out in grazing conditions in NZ (Suksombat et al., 1994), Australia (Dalley et al., 1999; Robaina et al., 1998; Stockdale, 2000a; Wales et al., 1999), and Ireland (Horan et al., 2005) (Appendix 3). Data were analysed using the mixed procedure in the SAS package, version 8 (SAS, 1999) considering three different models. As suggested by St-Pierre (2001), study was fitted as a random effect. If two or more different genotypes were compared within a study, then each genotype was considered a separate study. Based on Akaike’s Information criteria, the model that fitted the data best was:  $\text{Feed intake} = -0.0107(\text{SA} \times \text{PA}) + 3.94\text{LOG}(\text{PA})$  where LOG is the natural logarithm.

The relationship to predict feed intake, however, does not account for quality of feed. More specifically the NDF content of feed, which can have a significant effect on DM intake potential through its effect on rumen fill and the rate of passage of digesta (Allen, 2000). In an analysis of 27 studies, Vazquez and Smith (2000) quantified that DM intake potential decreases by 0.13 kg per 1% increase NDF in pasture, and this has been incorporated to provide an initial estimate of pasture intake ( $\text{PI}_0$ , Equation N1 of Appendix 2). A general mean during the lactating period for NDF content in pasture of 40% was assumed, based on information presented in Holmes et al. (2002).

The pre-grazing mass of pasture also influences intakes, with each additional tonne DM of pre-grazing mass increasing DM intakes by 2.29 kg/cow/day at day 36 of lactation, and 1.29 kg/cow/day at day 126 of lactation (Stockdale, 1985; Wales et al., 1999) and these results have been incorporated into the model (HM, Equation N2 of

Appendix 2). The substitution rate of pasture for supplements, defined as the amount of pasture not eaten because it was substituted for supplements, has been shown to be greater in autumn/late lactation than in spring/early lactation (Stockdale, 2000b). Effectively, the first terms of model estimated from the meta-analysis i.e.  $-0.0107 \times (SA \times PA)$ , represent substitution rates in mid lactation. To incorporate the findings of Stockdale (2000b), a linear regression was developed where substitution rate was calculated by assuming early, mid and late lactation as day 45, 135 and 225 of lactation, respectively ( $SUB_1$ , Equation N3 of Appendix 2). Also, note  $SUB_1$  is an initial substitution rate with the actual substitution rate influenced by cow genotype.

A second iteration to predict pasture intake was then performed incorporating these results and also accounting for energy concentration of pasture and terrain ( $PI_1$ , Equation N4 of Appendix 2). Additional feeds, assuming 90 % utilisation, were then incorporated to predict the supplementary feed intake accounting for feed quality ( $SI_1$ , Equation N5 of Appendix 2). An initial total feed intake was then calculated ( $FI_1$ , Equation N6 of Appendix 2), after adjusting for the animal's EBV for BCS (discussed in more detail in a later section) that is used as an initial measure of feed intake drive.

The relative energy status ( $ES$ , Equation N7 of Appendix 2) of the animal is the ratio of the initial total feed intake and a theoretical maximum intake of 4% of BCS adjusted live weight ( $aW$ , Equation W4 of Appendix 2). However, it should be noted that relative energy status could exceed 1 or 4% of BCS adjusted live weight. Therefore, a physical limit on intake is not imposed and can alter due to improvements in genetic merit or animal capacity. The relative intake is used in later sections, assuming the average NZ environment is 75% of the theoretical maximum intake ( $RI$ , Equations N8 of Appendix 2). Information related to the proportion of the diet as pasture or supplement, MJME concentration of the feed supplied, and the net energy content of the feed are calculated in Equations N9-12 of Appendix 2.

### **Live weight and growth**

Mature live weight potential is most accurately described by an animal's EBV for live weight ( $EBV_w$ ). In a previous study (Bryant et al., 2004), individual  $EBV_w$  were used to calculate live weight targets throughout an animal's lifetime by applying an

adapted Von Bertalanffy growth curve function. The live weight of an animal at birth ( $W_B$ , Equation W1 of Appendix 2) was calculated using the equation of Roy (1980), and the mature live weight of animal was estimated from individual EBV<sub>w</sub> ( $W_M$ , Equation W2 of Appendix 2) based on Bryant et al. (2004). An increase of one-unit of BCS was assumed to be equivalent to an increase in live weight of 26, 34 and 42 kg in Jersey, Friesian x Jersey and Friesian cows, respectively, which were on average 4 years of age (Grainger et al., 1982). The live weight of each of these breeds was not reported, but average live weights at 4 years of each breed were assumed to be 413, 488 and 528 kg, respectively (Livestock Improvement, 2005). Using these data, the relationship between the live weight equivalent of one-unit BCS and  $W_m$  was estimated (BCS<sub>w</sub>, Equation W3 of Appendix 2). Subsequently, live weight was adjusted for body condition to truly represent the maintenance live weight of the cow ( $aW$ , Equation W4 of Appendix 2).

A live weight target for each animal was then used in order to determine the energy requirements for growth when an individual is 2 or 3 years old. To estimate the energy requirements for growth, the animal's target live weight at a date 365 days later was estimated (Equations W5-8 of Appendix 2). For simplicity, the average growth rate was calculated assuming linear growth for the next year. The energy requirements for growth were calculated (Equations W9-11 of Appendix 2) using the equations of AFRC (1993).

### **Body energy reserves**

Lactation in dairy cattle is characterised by marked post-partum reductions in lipogenesis and increases in lipolysis resulting in significant losses in body fat from parturition until around the time of normal conception (McNamara and Hillers, 1986). These lipogenic and lipolytic responses are necessary as the cow is not immediately able to increase feed intake according to mammary requirements for glucose, amino acids and fatty acids, which can exceed three times the requirements of the foetus and foetal components (Bell, 1995; Knight, 2001). Once the post-parturition adjustments have been made, and with sufficient nutrient supply to the lactating animal, lipogenesis increases and levels of body fat are restored. Following these principles, Friggens et al. (2004) developed a model in which mobilisation and gain of body reserves was driven to achieve two set levels of body fatness, one at or

around conception and another at the next parturition. If an animal was thin at parturition it would compensate by altering mechanisms of intake, nutrient partitioning and lipogenesis in order to achieve a certain level of fatness at each of these two time points. Likewise, if a cow were in good condition at parturition it would direct a large amount of its energy intake and energy reserves towards milk production, again to achieve certain levels of fatness. The model of Friggens et al. (2004) forms the framework for our body energy reserves module, with adaptations described below.

### **Adaptations to the body lipid trajectory**

The model of Friggens et al. (2004) matched well with experimental data, but as they noted, the effects of genotype or diet on body lipid trajectories across lactation were not modeled. The effect of increasing feeding level or supplement intake (SI) on BCS change and milk composition in primarily grazing systems was evaluated with a meta-analysis of studies carried out in NZ (Kolver et al., 2005), Australia (Robaina et al., 1998; Stockdale, 2000a; Wales and Doyle, 2003; Wales et al., 1999; Wales et al., 2001), Northern Ireland (Ferris et al., 1999; Gordon et al., 2000), Ireland (Kennedy et al., 2003b) and the United States (Bargo et al., 2002) (Appendix 3). Reported BCS changes over the course of each study were converted to NZ BCS using the conversion equations proposed by Roche et al. (2004). Data was analysed using the mixed procedure in the SAS package, version 8 (SAS, 1999) with a linear model that considered the fixed effect of lactation stage (early: study complete by 100 days after parturition, and mid-late: study completed from 100-305 days after parturition), linear and quadratic covariate effect of SI and random effect of study. If two or more different genotypes were compared within a study, then each genotype was considered a separate study. Intercepts, class and covariate effects that were not significant ( $P > 0.05$ ) were removed from the model. The significant prediction equation for NZ BCS change was:  $0.00117SI$ . Using the conversion equations proposed by Gregory et al. (1998), for every 1-kg increase in concentrate intake or relative intake, total body fat increases by 0.2% ( $L_{dietadj}$ , Equation R4 of Appendix 2). The effect of feeding level on milk composition is incorporated into Equations L36 and L37 of Appendix 2.

Studies by Berry et al. (2003) and Pryce et al. (2005) have also found BCS has a genetic component, meaning some cows are genetically fatter than others. In light of these studies, an estimated breeding value for BCS ( $EBV_{BCS}$ ) (Pryce et al., 2005) has been used to scale the body lipid curve with lower  $EBV_{BCS}$  values resulting in a lower BCS target at the lower asymptote of BCS ( $L'$ , Equation R9 of Appendix 2). In the model, it has been assumed a first parity base cow ( $EBV_{BCS}$  of 0) has a BCS of 4.5 at the lower BCS asymptote at time  $T'$  ( $L'_{base}$ , Equation R2 of Appendix 2) and 5.0 at the time of the next calving ( $L'_{nextbase}$ , Equation R3 of Appendix 2).

Heat stress also influences BCS with feed intakes depressed in very hot conditions, resulting in lower live weights in heat stressed cows (West et al., 1999). In previous studies (Chapter 6; West et al. 2003), milk yield and DM intake were depressed at lower THI values in HF than Jersey cattle. Therefore to account for the effect of heat stress and breed differences in heat susceptibility, adjustments have been added to body lipid change to account for the depression in intakes at THI values exceeding 68 (NZF and OHF), 72 (FxJ) and 76 (NZJ) ( $L_{heat}$ , Equation R5a-c of Appendix 2).

Age or parity has also been shown to influence the rates of body lipid loss in early lactation with first parity animals exhibiting negative energy balances smaller than in older animals (Coffey et al., 2004; Domecq et al., 1997; Gallo et al., 1996; Lopez-Villalobos et al., 2001). Based on these results, we have assumed the nadir of BCS are 0.2 and 0.4 NZ BCS units lower in 2<sup>nd</sup> parity and 3+ parities compared to 1<sup>st</sup> parity animals, respectively ( $BCS'_{agcadj}$ , Equation R6 of Appendix 2). In subsequent steps (Equations R7-R12 of Appendix 2), the daily rate of change of lipid is calculated (Equation R14a-b) and estimated body lipid at time  $t+1$  can be converted to BCS ( $BCS^{+1}$ , Equation R15 of Appendix 2) based on the results of Gregory et al. (1998). The energetic cost of live weight gain was calculated assuming an average value of 19 MJ/kg live weight gain divided by the efficiency of energy use for gain,  $k_g$ , in lactating ruminants based on the equations proposed by AFRC (1993).

### **Lactation**

Vetharaniam et al. (2003) developed a model of the mammary gland which provides the framework for the present lactation module. In addition, the functions derived in Chapter 7 that quantify the effects of genetic merit, feeding level, age and body

condition on mammary gland dynamics are used. For a full description of the results, functions and methodology behind the lactation module readers should consult Vetharanim et al. (2003) and Chapter 7. Only adaptations to the model are presented below.

Initially, EBV for milk, fat and protein were used to define total lactation yield potentials (Equations L1-3 of Appendix 2; see Bryant, 2003 for more details), with the effect of age incorporated by multiplying potential mature yield by the ratio of  $aW$  to  $W_M$  ( $avMY$ , Equation L4 of Appendix 2). Average concentrations in milk of fat, protein and MS are then estimated (Equations L5-6 of Appendix 2). Thereafter, daily concentrations in milk of fat and protein are estimated by applying a Legendre polynomial function of days in milk (Equations L8-14 of Appendix 2) calculated in the analysis of Chapter 6.

The key component of the mammary gland model is the estimation of the genetic potential of the cow for milk production in a given environment. Cow genotype and genotype by environment interactions influence phenotypic responses to changes in nutritional environment. For example, OHF achieve greater milk yield responses to supplements than NZF genotypes (Horan et al., 2005; Kolver et al., 2005). In addition, differences in milk yield between high and low genetic merit cows (measured through EBV for milk) are greater in a high than low feeding level environments (Veerkamp et al., 1994). Taking the linear reaction norm sires as a representative sample, it has been quantified that, on average, for every 1 kg increase in herd MS yield as the measure of environment, the estimated breeding value for milk yield of OHF cattle increase by 2.13 kg (Chapter 5). The corresponding values for NZF and NZJ are + 0.94 kg and – 1.09 kg. Every additional kg of MS produced requires approximately an additional 65 MJME (Holmes et al., 2002), which at an average of 11 MJME/kg DM is equivalent to 0.025 kg DM/cow/day over a 240-day lactation. Therefore, it can be estimated that for every 1 kg DM increase in daily relative intakes, EBV would increase by 85.2 (i.e.  $2.13 \times 1/0.025$ ) and 37.6 kg for OHF and NZF, respectively and decrease by 43.6 kg for NZJ (RN, Equation L15 of Appendix 2). The scaling and reaction norm effects are then incorporated to provide an estimate of the cow's genetic potential for milk production in the specified

environment ( $GP_{\text{milk}}$ , Equations L16a-c of Appendix 2). Breed-specific intercepts are used, as otherwise excessive scaling effects between breeds would have occurred.

Applying the equations derived from Vetharanim et al. (2003) and those presented in Chapter 7 resulted in the ratio of milk yields of two-year-old cows to milk yields in mature cows (six years) being much higher than the ratio, 0.80, seen in the national dairy cow population (Livestock Improvement, 2005). In addition, the ratio of two-year old and mature (six years) live weight in NZJ cows in NZ (0.80), is the same as the ratio of two-year old milk yield and mature milk yield (0.80). A very similar relationship is observed in HF (0.78 versus 0.74, respectively) and HFxNZJ (0.79 and 0.77, respectively) cows (Livestock Improvement, 2005). Consequently to incorporate these findings, the ratio of  $aW$  and  $W_m$  has been used to scale  $A_0$  in Equation L17a of Appendix 2. An adjustment has also been made to  $k_5$  for each breed (Equation L23a-d of Appendix 2) based on subsequent analysis of the dataset used in Chapter 7.

An initial estimate of the amount of milk energy expressed by the mammary gland,  $I$ , is calculated using Equation L30 of Appendix 2. The major adaptation to the equation for  $I$  is the addition of a mammary gland drive factor, estimated from the ratio of the active population of alveoli at the time of the simulation versus the active population of alveoli at day 100 ( $D$ , Equation L29 of Appendix 2). The mammary gland drive factor was included as the initial estimate of feed intake calculated earlier ( $FI_1$ , Equation N6 of Appendix 2) represents an average cow in the middle of lactation. The adjustment accounts for differences in feeding drive as the lactation progresses, with the peak feeding drive expected to be around days 30-60 of lactation. In early lactation (i.e. day 1 to 30), it is likely the drive for feed intake and production is suppressed until the animal's digestive tract adapts to the vast increase in feed volume compared to its pregnant, non-lactating feed consumption. Consequently, we have assumed the animal's drive for feed intake lags behind mammary cell numbers until day 30 of lactation (Equations L24-28a of Appendix 2). Thereafter, feeding drive is proportional to mammary cell numbers ( $A_i$ , Equation L28b of Appendix 2).

### **Adjustment factors**

Pregnancy has a significant negative effect on milk yields from the 5<sup>th</sup>–6<sup>th</sup> month after conception onwards, and the negative effect is greater in animals which achieve high milk yields (Coulon et al., 1995). To account for this we have used a linear logistic function related to days in milk and the initial estimate of milk yield potential ( $P_{adj}$ , Equation L31 of Appendix 2), as outlined by Grossman and Koops (2003), the function used being most appropriate for a NZ system.

Lactating dairy cows generate a large quantity of metabolic heat and can also accumulate additional heat from the thermal environment (West, 2003). In hot conditions, when this heat cannot be dispersed readily, body temperature rises and intake declines leading to a reduction in milk production levels. Previous studies have found milk yields start to decline at temperature humidity indices (THI, Equation L32 of Appendix 2) of greater than 72 (Aharoni et al., 2002; Ravagnolo et al., 2000; West et al., 2003). In NZ, the adverse effect of heat stress on milk yield and composition appears to occur at a lower THI value than overseas (Chapter 6). In addition, heat tolerance also differs between breeds with HF being more susceptible to heat stress than NZJ. These results have been incorporated into Equations L33-35 of Appendix 2 to adjust for the effects of heat stress on daily milk yield, and daily fat and protein concentration.

Cows in early and late lactation are generally in states of negative and positive energy balance, respectively. When estimating milk yields using the present model, we have assumed a cow in negative energy balance, and in thermo neutral conditions, can use the energy derived from energy stores. The energy requirements for growth in 2 and 3 year old animals are also subtracted to estimate milk yield. The consequence of this adjustment is that animals that are significantly below their genetic target weights, preferentially direct energy to growth over milk production.

### **Predicting milk, fat and protein yield and lactation feed requirements**

Daily fat, protein and MS yield concentrations were then calculated, adjusting for feeding level effects on milk composition ( $DFY_{conc}$  and  $DPY_{conc}$ , Equations L36-37 of Appendix 2). Daily milk yield was predicted after incorporating the adjustments



for pregnancy, climate and energy provided by body energy stores ( $MY_{pred}$ , Equation L41a-b of Appendix 2). Daily fat and protein yield were calculated from predicted daily milk yield, and daily fat and protein concentration ( $FY_{pred}$  and  $PY_{pred}$ , Equation L42-43 of Appendix 2).

### **Maintenance**

The ME requirements for maintenance were calculated from the equations of SCA (1990). However, maintenance requirements have been scaled based on genetic merit for milk yield instead of current milk yield, which ensures ME requirements for maintenance and production are independent ( $MER_m$ , Equation M4 of Appendix 2). Use of these equations, allows the scaling of  $MER_m$  to account for the increases in metabolic rate of modern genotypes associated with increased milk yields. For example, analyses of energy balance data by Kebreab et al. (2003) found maintenance requirements of modern genotypes were equivalent to 0.65 MJ ME/ kg of  $Lwt^{0.75}$  compared to an estimate of 0.49 MJ ME/ kg of  $Lwt^{0.75}$  for genotypes from the 1960-1970. The energetic costs of grazing were accounted for in EGRAZE (Equation M1 of Appendix 2) which considers the effect of pasture availability, quality and terrain on energy expenditure (Corbett and Freer, 2003; NRC, 2001).

### **Pregnancy**

Significant energy costs are incurred to support the growth and development of the foetus and foetal components. The energy cost of pregnancy was calculated using standard equations (Equations P1-5 of Appendix 2) proposed by AFRC (1993), with the expected birthweight of the calf calculated from the dams expected mature live weight (Equations W1 and W2 of Appendix 2).

### **Model outputs**

The model produces a number of outputs. Values predicted include daily milk, fat and protein yields, fat and protein concentrations, live weight change, DM intake and ME intake. Relative ME partitioning to the modules of milk, maintenance, growth, pregnancy, body fat is calculated by dividing each module's requirements by total ME. The amount partitioned to each module is then displayed as a ratio of ME total. If supplements are added to the system the response to supplements is calculated by performing an initial iteration with supplements added and then a second iteration

with no supplements added. Responses to supplements are quantified in terms of kg of milk/kg DM supplement, kg MS/kg DM supplement, kg live weight/kg DM supplement, and pasture substitution.

### **Model evaluation**

The model was initially tested and demonstrated by changing parameters of an initial base cow in a base environment with the simulation running from day 1 to day 270 of lactation. The initial BASE (Cow 1) animal was a 4 year old NZ Friesian, 450 kg live weight and BCS 5.0 at parturition, EBV for milk, fat, protein, live weight, and BCS of +500 kg, +25 kg, +20 kg, +50 kg and +0.0, respectively, grazing flat terrain with a solely pasture diet (35 kg/cow/day PA, 12 MJ ME/kgDM, 40% NDF, 80% digestibility, 2500 kg DM pre-grazing herbage mass). Thereafter, the following cows were simulated: THIN (Cow 2): BASE with a BCS of 4.0 at parturition, SUPP (Cow 3): BASE with a 2.0 kg DM allowance of supplements (12 MJ ME/kg DM, 35% NDF) and HGM (Cow 4): BASE with +1000, +35 and +30 kg EBV for milk, fat and protein yield, respectively.

To illustrate the effect of changes to environmental parameters on milk yield, MS and live weight change, three different environmental scenarios were imposed from day 50 to 60 of lactation in Cows 1 to 4 described above. The predicted values, including the effect of each environmental scenario, were averaged over the 10-day period and compared with the original predicted values. The environmental scenarios were 1) hot conditions of 25°C and 90% humidity, equivalent to a THI of 76, 2) poor pasture quality of 50% NDF, 10.5 MJ ME/kg DM and rolling terrain, and 3) an additional 1 kg DM allowance of supplement (12 MJME/kg DM, 35% NDF). A more detailed validation of the model is carried out using data from 1990's Holstein Friesian dairy cattle of North American or European or NZ origin managed in a pasture-based system in early to peak lactation (Chapter 9).

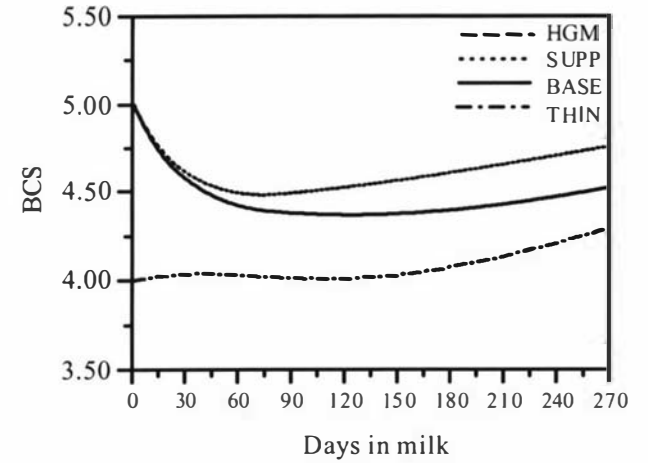
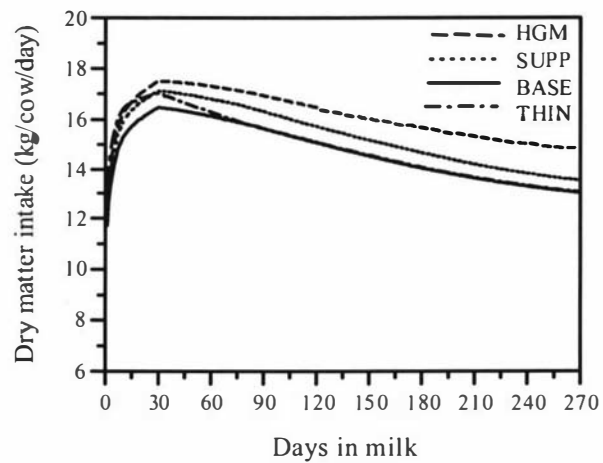
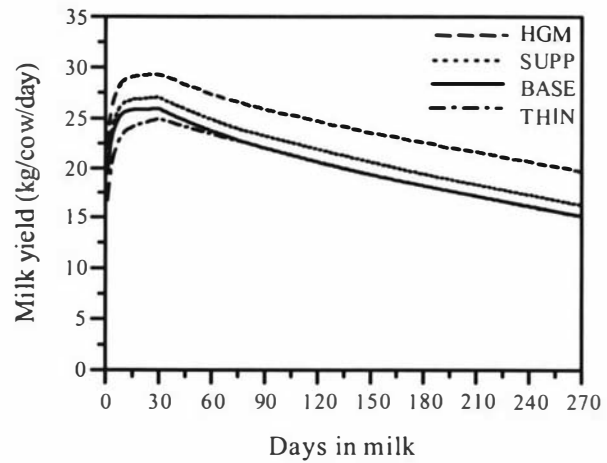
## **RESULTS AND DISCUSSION**

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Results of the dynamic simulation for a range of cows in different environments are demonstrated in Figure 3, and the accumulated values of the 270-day lactation are

presented in Table 3. The THIN cow simulated was BCS of 4.0 at parturition. Milk production in early lactation was depressed compared to the other simulation cows, as the THIN cow did not have the fat reserves to support high levels of milk production. Broster and Broster (1998) found cows of low BCS at parturition were associated in early lactation with increased feed intakes, generally reduced milk yield, and a reduction in BCS loss, or at very low BCS, gains in BCS compared to cows of medium to high BCS at parturition which is consistent with the simulated results of the THIN cow. The model recognises a cow will not reduce its body condition or fatness below a certain amount, but this level can vary depending on genotype (i.e. estimated breeding value for BCS). The amount of body fat mobilisation by a cow in early lactation also depends on the amount of body fat present at parturition.

Offering supplements at the rate of 2 kg DM per day throughout lactation (SUPP cow) resulted in an increase in total milk yield of 316 kg compared to the BASE cow, equivalent to 0.59 kg milk/kg DM supplement. The nutritional effect is simulated through the calculation of relative intake, which increases with the addition of more supplements. The simulated response to supplements is between the values of 0.55 and 0.67 kg milk/kg DM concentrate for NZ Holstein Friesian genotypes in pastoral based systems reported by Horan et al (2005) in Ireland, and Kolver et al. (2005) in NZ. The SUPP cow also ended the lactation at a higher BCS than the other simulation cows, and was equivalent to 0.00045 BCS units/kg DM concentrate. The simulated value is at the low end of the scale presented by Kolver et al. (2005), who quantified the values at 0.0010 and 0.0006 BCS units/kg DM concentrate for NZF and OHF genotypes, respectively. The simulated value is, however, similar to the value of 0.00033 BCS units/kg DM concentrate which was calculated for the NZF genotype based on results presented by Horan et al. (2005), adopting the Irish to NZ BCS conversion equation of Roche et al. (2004). The substitution rate of pasture was equivalent to 0.59 kg DM/kg DM supplement offered, which is similar to values of 0.55 to 0.68 kg DM/kg DM supplement offered that were obtained when applying the equations of previous studies presented by Stockdale (2000b).



**Figure 3:** Dynamic demonstration of the simulation model in terms of milk yield, DM intake and BCS throughout lactation for BASE, THIN, SUPP and HGM simulation cows.

**Table 2:** Accumulated 270-day yields of milk, fat and protein, average fat and protein concentration, season end BCS and DM intake for the simulation cows BASE, THIN, SUPP and HGM.

	270-day yield (kg)			Concentration (%)		Season end BCS	270-day DM intake (kg)
	Milk	Fat	Protein	Fat	Protein		
<b>BASE</b>	5,474	256	191	4.68	3.49	4.52	3,969
<b>THIN</b>	5,400	253	189	4.69	3.49	4.29	4,015
<b>SUPP</b>	5,790	270	203	4.66	3.51	4.76	4,137
<b>HGM</b>	6,554	287	217	4.37	3.32	4.52	4,353

Simulated milk yield for the HGM cow was 1,080 kg milk higher than the BASE cow; effectively a 2.16 kg increase in milk per kg increase in milk EBV which is greater than the theoretical expectation of a 1 kg increase in milk per kg increase in milk EBV. To compare the present result with a previous NZ result, Bryant et al. (2003) quantified the phenotypic benefit of genetic gain at 0.89 to 1.78 kg milk per kg increase in milk EBV at a low feeding level (equivalent to a typical NZ environment). Whereas at a high feeding level, but probably still below the feeding level simulated in the present study, the corresponding value was 1.86 to 2.01 kg milk per kg increase in milk EBV. Hence, the result is not unrealistic and demonstrates a scaling effect where the phenotypic difference between low and high genetic merit animals are greater at high than low feeding levels (Veerkamp et al. 1994).

The BASE and HGM cows were offered the same amount of feed, yet a greater feeding drive, equivalent to an increase in 270-day and daily DM intake of 384 and 1.42 kg DM, respectively, was simulated in the HGM compared to the BASE cow. In the present model, feed intake is driven by mammary cell numbers with mammary cell numbers greatest in cows of high genetic merit. The higher daily DM intake in the HGM compared to BASE cow is equivalent to 0.0028 kg DM/kg milk EBV, and is similar to values estimated from Kennedy et al. (2003a) in Ireland where daily intakes of pasture and concentrates were increased by 0.0020, 0.0021 and 0.0030 kg DM/kg milk EBV in low, medium and high concentrate feeding level systems in early lactation. There was no difference in BCS throughout lactation between the BASE and HGM cows, as both cows had the same EBV for BCS, feeding levels, and BCS at parturition (Figure 3).

Results of the simulations from days 50 to 60 of lactation, where different environmental scenarios were imposed, are presented in Table 3. Hot conditions suppressed DM intake and MS yield and resulted in more marked live weight reductions in all cows. Hot conditions had a marked effect on MS yield in the HGM cow, in agreement with the simulation results presented by Berman (2005). The reduced DM intake, and hence greater live weight loss, in heat stressed cows is consistent with the findings of West et al. (2003). Poor pasture quality and rolling terrains resulted in a marked reduction in MS yields, greater live weight losses, similar DM intakes, but marked reductions in ME intake and reduced the efficiency of converting feed into milk (Equation L40 of Appendix 2).

Additional supplements increased MS yield and DM intake, reduced the degree of live weight loss or resulted in the cow being in positive energy balance (Table 3). The HGM (0.78 kg milk/kg DM supplement or 54 g MS/kg DM supplement) and

**Table 3:** The effect of hot conditions, poor pasture quality and additional supplements on milk yield, MS yield and live weight change for the BASE, THIN, SUPP and HGM simulation cows from days 50 to 60 of lactation.

	DM intake		MS yield		Live weight change	
	Predicted (kg/day)	Change (%)	Predicted (kg/day)	Change (%)	Predicted (kg/day)	Change (kg/day)
<i>Original Predicted Values</i>						
BASE	16.34	-	1.83	-	-0.06	-
THIN	16.55	-	1.84	-	+0.05	-
SUPP	17.01	-	1.92	-	-0.03	-
HGM	17.52	-	1.97	-	-0.06	-
<i>Hot conditions: 25°C and 90% humidity</i>						
BASE	14.82	-9.3	1.57	-14.5	-0.78	-0.72
THIN	15.14	-8.5	1.59	-13.6	-0.63	-0.68
SUPP	15.48	-9.0	1.65	-14.0	-0.75	-0.72
HGM	15.90	-9.2	1.49	-24.1	-0.78	-0.72
<i>Poor pasture quality (55% NDF, 10.5 MJ ME/kg DM) and rolling terrain</i>						
BASE	16.58	+1.4	1.40	-23.9	-0.29	-0.23
THIN	16.84	+1.8	1.38	-24.8	-0.17	-0.22
SUPP	16.65	-2.1	1.51	-21.2	-0.26	-0.23
HGM	17.24	-1.6	1.43	-27.1	-0.29	-0.23
<i>Additional supplements: 1 kg DM supplement (35% NDF, 12 MJ ME/kg DM)</i>						
BASE	16.70	+2.4	1.88	+2.7	-0.04	+0.02
THIN	16.88	+2.2	1.89	+3.1	+0.08	+0.03
SUPP	17.36	+2.2	1.96	+2.5	0.00	+0.03
HGM	17.95	+2.7	2.02	+3.6	-0.04	+0.02

SUPP (0.55 kg milk/kg DM supplement or 41 g MS/kg DM supplement) cows achieved the highest and lowest response to supplements, respectively. Diminishing response to supplements at higher supplement allowances are consistent with the findings of Reis and Combs (2000). The finding that the HGM cow achieved a greater response to supplements than the medium genetic merit cows (BASE, THIN and SUPP) is also consistent with the findings of Kennedy et al. (2002) who estimated responses to concentrates of 0.89 and 0.66 kg of milk/kg of concentrate in high and medium genetic merit animals at medium concentrate allowances.

After considering the results of the simulations, and their general agreement with experimental studies, a more in depth explanation of the model is warranted. Firstly, the MOOSIM model recognises the cow has certain requirements to maintain life and functional processes such as maintenance and pregnancy (Oldham and Emmans, 1989). Maintenance and then fetal growth have the highest priority for energy use. Once the maintenance and fetal growth functions have been satisfied, the mammary gland acts as a pull mechanism driving feed intake, which has been a long held view (Bauman and Currie, 1980; Knight et al., 1994).

In the present model, however, the extent of the feeding drive is not controlled entirely by the mammary gland. An animal's feeding drive is predicted through the use of total lactation EBV and reaction norm information, which provide an estimate of an animal's genetic potential to consume feed and then to convert this feed into milk. Use of reaction norm information accounts for inherent or evolutionary drives of specific genotypes in particular environments (Emmans and Kyriazakis, 2001; Yearsley et al., 2001). The methodology applied in the present model provides a more robust genetic basis for milk yield potential than prior expressions such as peak milk yield potential. Future inclusion of individual differences in reaction norms, might improve the accuracy of the model. For instance, genetic variation ensures some OHF genotypes perform well in low input, pasture-based environments (Chapter 5).

A key advance of the model is it predicts what will happen rather than to account for what has already happened (Emmans and Kyriazakis, 2001). For example, feed intake is not needed to predict milk yield, and milk yield is not needed to predict feed

intake. Instead, animal genotype and feed allowance are specified and then feed intake and milk yield are predicted from these two components. This approach may then lead to differences between predicted and actual values. But, it is unrealistic to know the feed intake of a cow before it is even offered the feed. Likewise, it is highly unlikely that the potential milk yield of animal offered a specific feed is known.

The MOOSIM model has been developed for NZ production systems and cows. However, the aim is for the concepts and functions to be applied and transferred to all production systems and cows. Conversion of EBV to the scales and genetic bases used in each country, reaction norm information and adaptation of feed allowance and BCS measures are needed for the international application of MOOSIM. The present study has provided reaction norm functions for overseas Holstein Friesian genotypes. However, these functions are relative to other NZ breeds of cattle. The validity of these functions compared to other breeds of cattle in different systems must be verified. Local scales of BCS can be converted to a NZ basis using the equations of Roche et al. (2004), or functions adapted to be relevant for localised scales. Similar procedures can be used for the conversion of feed allowance measures.

The nutritional components of feed have been described by the three key quality measures of ME concentration, NDF content and digestibility, each used for a specific purpose. For instance, the estimated average ME concentration of the diet is used to define efficiencies of feed use for maintenance, lactation, and growth. NDF content is used to account for physical limitations to intake (i.e. rumen fill and distension) through the initial estimate of feed intake. Digestibility is used to adjust the energy cost of grazing with higher grazing costs associated with low digestibility feeds. No additional feed quality measures were used such as protein content or macro and micro-mineral densities. The model assumes an animal's requirements for these components are met through a balanced diet. The balance should be assessed through the use of models such as CamDairy (Hulme et al., 1986) and the Cornell Net Carbohydrate and Protein System model (Fox et al., 1992), which use feed databases describing the exact nutrient compositions of each feed.



## CONCLUSION

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The MOOSIM model represents the first attempt to include reaction norm information when predicting dairy cattle performance in a wide range of environments. Reaction norm information, in conjunction with total lactation EBV for milk, fat and protein, are used to calculate a cow's genetic potential in the specified environment. An estimated breeding value for BCS is also used to define the body fat trajectory of cow, which is also modified by climatic and nutritional environment. The features of the model enable it to estimate feed intake independently of milk yield, and milk yield independently of feed intake.

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# CHAPTER 9

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## **Predicting the performance of two modern strains of Holstein-Friesian dairy cattle using a simulation model that incorporates genetic and environmental sensitivity information**

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## **ABSTRACT**

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A dairy cattle simulation model for pastoral systems, MOOSIM, has been developed that uses genetic (EBV and reaction norms) and environment information to predict yields of milk, fat and protein, concentrations of fat and protein, DM intake and liveweight change in dairy cattle. In this study, the predictive ability of the MOOSIM model was tested using information from a prior study with 1990's Holstein-Friesian dairy cattle of North American or European (OS90) or NZ (NZ90) origin managed in a pasture-based system in early to peak lactation. The model simulated to a high degree of accuracy, mean values for yields of milk, fat and protein, and concentrations of fat and protein. Model simulated DM intakes were significantly higher than actual DM intakes that were based on the n-alkane technique, which itself is an estimate only. Various tests identified the major source of error between simulated and actual values were due to a lack of simulated variation, rather than any systematic bias. The model was able to correctly predict higher yields of milk, fat and protein in NZ90 than OS90 cows, even though there were minimal genetic differences between the two strains. A lower feed intake in first compared to second parity animals was also correctly simulated. These results indicate the model is able to simulate phenotypic performance of dairy cows based on concepts of animal genotype, environment and genotype by environment interactions.

## **INTRODUCTION**

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Most simulation models that are currently available do not fully succeed at integrating the effect of genotype by environment interactions in dairy cattle systems (Chapter 2). Yet, recent studies have identified that not all genotypes or breeds respond similarly, in terms of feed intakes or yields of milk, fat or protein, when exposed to different nutritional or climatic environment (Chapters 5 and 6, Dillon et al., 2003; Horan et al., 2005; Kolver et al., 2005; Kolver et al., 2002).

Farmlet studies reported by Horan et al. (2005) and Kolver et al. (2002) have shown OHF cows have a stronger genetic drive for feed intake and milk, fat and protein yield when offered a diet with high levels of concentrates than NZF cows. When

offered a pasture-based diet, the NZF cow exhibits a greater genetic drive than OHF cows. In relation to climate, milk yield, and fat and protein concentration is compromised at a lower value for temperature-humidity index in HF than in NZJ cattle (Chapter 5). It could, therefore, be assumed that genetic merit for milk production acts to drive intake to achieve a preferred level of production in the environment to which the animal is exposed (Emmans and Kyriazakis, 2001; Knight et al., 1994; Oldham and Emmans, 1989; Yearsley et al., 2001).

Most simulation models quantify a cow's genetic potential for milk yields through peak milk yield potential (Chapter 2). A few simulation models, however, stochastically simulate breeding values to represent cow genetic potential for milk yield when predicting phenotypic performance (Congleton, 1984; Dijkhuizen et al., 1986). A breeding value is the genetic estimate of an animal's potential, relative to contemporaries, when exposed to an average environment. However, an estimated breeding value does not infer the expected outcomes when an animal is exposed to environments deviating from the average. This information is provided through reaction norms, which quantify genetic or phenotypic responses of an individual, breed or genotype as a function of environment (West-Eberhard, 2003).

A dairy cattle simulation model for pastoral systems, MOOSIM, has been developed to simulate dairy cattle performance in a wide range of environments based on genetic and environment information (Chapter 8). The model represents the cow as a series of modules. Firstly, a mammary gland module predicts yields of milk, fat and protein and concentrations of fat and protein. The mammary gland module considers the effects of nutrition, climate and genotype (including EBV and reaction norm information) to predict phenotypic performance, thereby accounting for genotype x environment interactions. Operating concurrently is a body energy deposition module that predicts liveweight loss or gain, depending on animal genotype and the environment in which the animal is managed. Three other modules, defining the requirements for maintenance, growth and pregnancy, are used to predict a variety of outputs in conjunction with the mammary gland and body energy deposition modules.

The objective of this study was to test if the MOOSIM model is able to predict yields of milk, fat and protein, concentrations of fat and protein, feed intake and liveweight change for two different strains of Holstein-Friesian dairy cattle after considering the effects of genotype, environment and genotype by environment interactions.

## MATERIALS AND METHODS

### Animal Data

Data were obtained from the Dexcel Holstein-Friesian Strain Trial, and in particular from a study carried out at Hamilton, NZ as described by Rossi et al. (2004). The objective of the study by Rossi et al. (2004), was to compare intake and grazing behaviour of individual cows of three different Holstein-Friesian strains on a solely pasture-diet in early lactation. Only the two modern strains of 1990's Holstein-Friesians of overseas (OS90) and NZ (NZ90) origin were used in the present study. The 1970's Holstein-Friesians of NZ origin were excluded from the present study because they do not represent dairy cows in the current NZ dairy cattle population and reaction norm information was not available for this genotype.

Necessary inputs for the MOOSIM model were known, such as pre-grazing pasture mass, measures of pasture quality per kilogram of DM (i.e. NDF, MJ ME and digestibility), EBV of each cow for total yields of milk, fat and protein, liveweight, and BCS, along with corresponding days in milk, yields of milk, fat and protein, liveweight and pasture intakes estimated by the n-alkane method (Dove, 1992). Breeding values for BCS are an estimate of BCS at day 60 of lactation compared to the NZ genetic base (Pryce et al., 2005).

**Table 1:** Description of the number of animals of each strain, and the pre grazing mass and daily herbage allowances offered to each treatment group.

Treatment	Strain	Number of animals <sup>1</sup>	PGM <sup>2</sup> (kg DM/ha)	DHA <sup>3</sup> (kg DM/cow/day)
1	NZ90	18 (5, 13)	2097	41.9
	OS90	17 (5, 12)	2116	42.3
2	NZ90	18 (5, 11)	2585	34.1
	OS90	17 (6, 11)	2547	33.6

<sup>1</sup>Numbers in brackets are the number of animals in first and second parity, respectively.

<sup>2</sup>Pre grazing mass

<sup>3</sup>Daily herbage allowance

**Table 2:** Summary of actual data for the 68 cows of NZ 1990's and overseas 1990's Holstein-Friesian origins used in the simulations.

	<b>Mean</b>	<b>SD</b>	<b>Range</b>
Days in milk	56	19.5	9 to 81
Milk yield (kg/day)	27.0	4.6	15.0 to 36.9
Fat yield (kg/day)	1.08	0.23	0.50 to 1.58
Fat concentration (%)	4.00	0.53	2.94 to 5.39
Protein yield (kg/day)	0.94	0.17	0.45 to 1.29
Protein concentration (%)	3.49	0.23	3.00 to 4.09
n-alkane DM intake (kg/day)	15.0	2.30	9.3 to 20.6
Liveweight (kg)	443	43.3	365 to 536
BCS (BCS units; scale 1-9)	4.34	0.47	3.5 to 5.5

Cows were offered only high quality pasture with an average digestibility of 0.82 (range of 0.77 to 0.88), ME concentration of 12.59 MJ/kg DM (range of 12.2 to 12.7), NDF content of 32.3 % (range of 30 to 35 %). Details of the number of animals in each strain and the pre grazing mass and pasture allowances offered are presented in Table 1. A summary of means, standard deviations and ranges of data from a total of 68 cows of either strain is presented in Table 2. Means, standard deviations and ranges of EBV for the OS90 and NZ90 origin cows are presented in Table 3.

Individual intakes were measured using the n-alkane technique, as described by Rossi et al. (2004). Live weight was measured at weekly intervals coinciding with the day when yields of milk, fat and protein, concentrations of fat and protein, and DM intake were measured. However, data from day 0 to day 100 of lactation was

**Table 3:** Means, standard deviations (SD) and range of EBV for total yields of milk, fat and protein, live weight and body condition score (BCS) relating to the NZ 1990's (NZ90) and Overseas 1990's (OS90) Holstein-Friesian strains of cattle.

	<b>Mean</b>	<b>SD</b>	<b>Range</b>
<b>NZ90</b>			
Milk	915	197	488 to 1495
Fat	32.1	6.9	18.4 to 44.6
Protein	33.3	5.0	24.6 to 47.7
Live weight	50.1	14.5	19.5 to 86.2
BCS	0.03	0.08	-0.13 to 0.21
<b>OS90</b>			
Milk	1211	235	772 to 1699
Fat	29.9	9.3	12.9 to 52.1
Protein	39.2	5.7	30.7 to 51.4
Live weight	84.6	14.2	53.8 to 113.9
BCS	-0.11	0.10	-0.26 to 0.18

obtained to allow a piecewise polynomial smoothing spline function to be fitted to data in an attempt to reduce live weight errors associated with changes in gut fill and water content of tissues. The TRANSREG procedure of Statistical Analysis System (SAS) package was used (SAS, 1999) with knots at day 5, 20, 35, 50, 70 and 90, fitting second-degree polynomials between knots. The distance between knots was shorter in early lactation as this is the period of greatest energy mobilisation. The predicted values at each time point were then used to estimate the daily rate of live weight change over the seven-day experimental period, and are the live weight change values reported in subsequent sections.

### **Testing model adequacy**

Data relating to each cow, and her corresponding nutritional environment were run through MOOSIM after creating an interface between the model and model inputs. Reaction norm functions described in Chapter 8 relating to NZF for the NZ90 genotype and OHF for the OS90 genotype were applied when defining cow genotype. Initially, simulated values were compared with actual values by calculating linear regressions of simulated and actual values using the general linear model procedure of SAS (SAS, 1999). A paired t-test comparing actual and simulated means was also performed. Plots displaying limits of agreement, defined as the mean difference  $\pm$  2 SD of the difference, were produced using the procedure described by Bland and Altman (1986). Based on the review of Tedeschi (2006), a range of model test parameters were calculated. Mean bias (MB) calculated as:

$$MB = \bar{y}^a - \bar{y}^s$$

where  $\bar{y}^a$  and  $\bar{y}^s$  are mean actual and simulated values with an ideal MB value of 0.

Coefficient of determination ( $r^2$ ) calculated as:

$$r^2 = \frac{\sum_{i=1}^n (y_i^a - \bar{y}^a)(y_i^s - \bar{y}^s)}{\sum_{i=1}^n (y_i^a - \bar{y}^a)^2}$$

where  $y_i^a$  and  $y_i^s$  are the actual and simulated values.

The MPE, as a proportion of the actual mean, was calculated as described by Rook et al. (1990) to measure general model efficiency:

$$MPE = \frac{\sqrt{\frac{1}{n} \sum_{i=1}^n (y_i^s - y_i^a)^2}}{\bar{y}^a}$$

Values for MPE less than 0.10, 0.10 to 0.20 and >0.20 indicate good, moderate and poor simulation adequacy, respectively.

Variance ratio (v) calculated as:

$$v = \frac{\sigma_a^2}{\sigma_s^2}$$

where  $\sigma_s^2$  and  $\sigma_a^2$  are the variances of the simulated and actual values with a value of 1 indicating the degree of variation in the simulated and actual values is equal.

Bias correction factor ( $C_b$ ) calculated as:

$$C_b = \frac{2}{v + \frac{1}{v} + \mu^2}$$

where  $\mu^2 = \left[ (\bar{y}^a - \bar{y}^s) / \sqrt{\sigma_s \sigma_a} \right]^2$ , as defined above with a  $C_b$  value of 1 indicating no bias of the data from the  $y=x$  line.

Concordance correlation coefficient (CCC) calculated as:

$$CCC = r \times C_b$$

The CCC value is a combined measure of precision and the degree of bias of the data from the  $y=x$  line (Lin, 1989).

## RESULTS

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### Estimated breeding values

The NZ90 strain had lower EBV for total yields of milk and protein than the OS90 strain, but similar EBV for total fat yield (Table 3). The OS90 strain was genetically heavier than the NZ90 strain, as indicated by significantly higher EBV for live

weight. Estimated breeding values for BCS were lower for the OS90 strain, indicating the OS90 strain is genetically thinner in a pasture-based system.

**Simulation model ability**

The means of simulated values were not significantly different ( $P>0.05$ ) to the mean of actual values for daily yields of milk, fat and protein, and concentrations of fat and protein (Table 4). Simulated DM intake was significantly ( $P<0.05$ ) higher than intake predicted from n-alkanes. The simulation predicted slight live weight gains, in contrast to actual live weight losses. However, the difference between simulated and actual means for live weight change was not significant ( $P>0.05$ ).

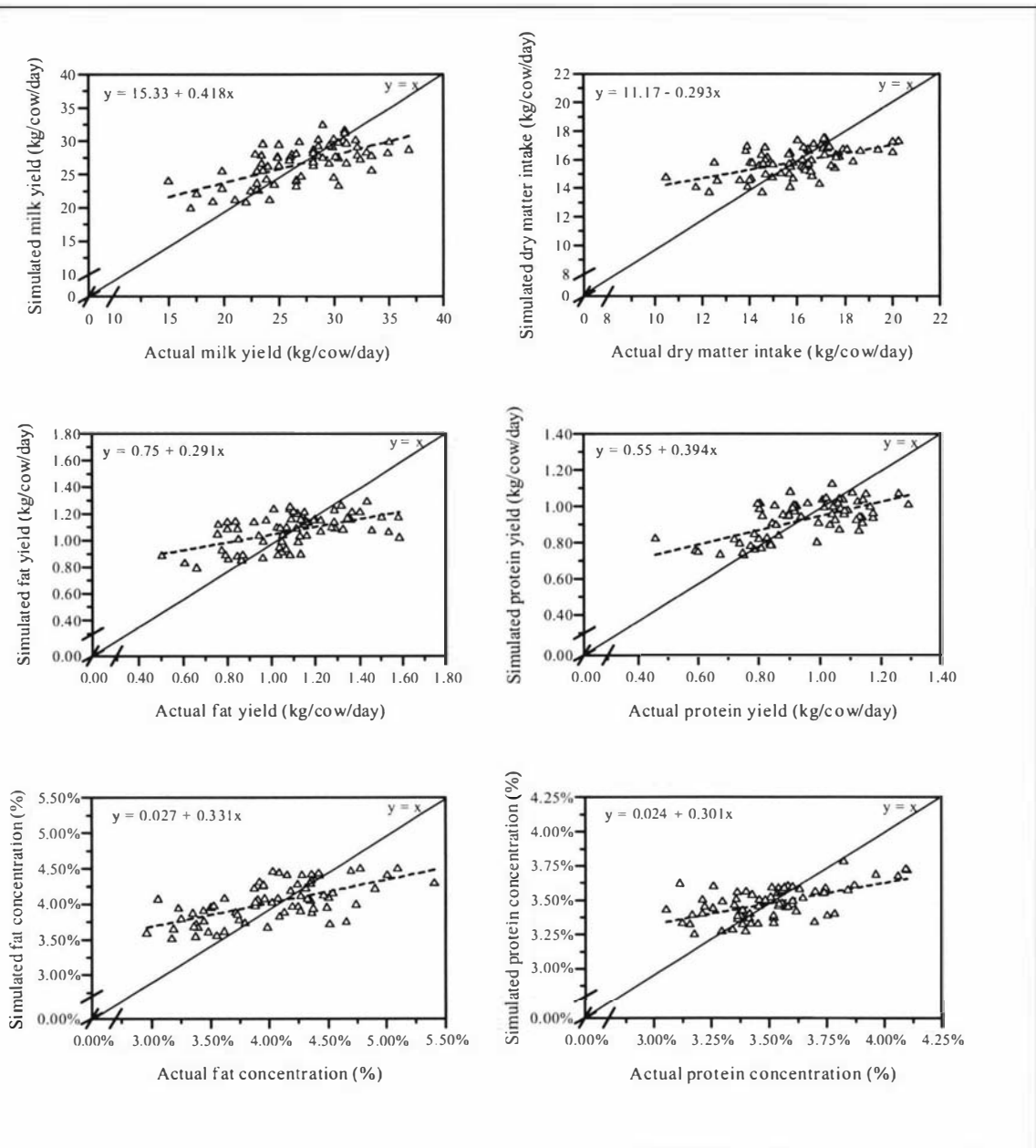
Values for MPE ranged from 5 % for protein percentage to 18 % for fat yield (Table 4), indicating satisfactory to moderate model efficiency. Values for CCC ranged from 0.16 (worst) for live weight change to 0.59 (best) for milk yield. Simulated values varied from the  $y=x$  line for all traits (Figure 1) and regression coefficients and intercepts were less than 1.0 and greater than zero, respectively. Values for  $C_b$  were less than 1 for all measures. The greatest bias from the  $y=x$  line occurred for live weight change, as indicated by the low value for  $C_b$ . Some systematic bias was observed for DM intake and live weight change, with Bland Altman plots confirming systematic bias for DM intake occurred at high and low values of actual intake i.e. the model did not accurately predict the extremes of intake (Figure 2).

**Table 4:** Comparison of actual and simulated data for daily yields (kg/day) of milk (MY), fat (FY) and protein (PY), fat (F%) and protein (P%) concentration, DM intake (DMI) and liveweight change (LWC) relating to the combined dataset of NZ 1990’s (NZ90) and overseas 1990’s (OS90) Holstein-Friesian strains of cattle.

	MY	FY	PY	F%	P%	DMI	LWC
Actual	27.0	1.09	0.95	4.02	3.50	15.0	-0.15
Simulated	26.6	1.07	0.92	4.02	3.48	15.9	0.02
Mean bias <sup>1</sup>	0.40 <sup>NS</sup>	0.02 <sup>NS</sup>	0.02 <sup>NS</sup>	0.00 <sup>NS</sup>	0.02 <sup>NS</sup>	-0.92 <sup>***</sup>	-0.17 <sup>NS</sup>
$r^2$	0.42	0.30	0.41	0.40	0.35	0.19	0.17
MPE	0.13	0.18	0.14	0.10	0.05	0.15	NA
$v$	1.55	1.88	1.63	1.91	1.95	2.51	4.84
$C_b$	0.91	0.82	0.88	0.82	0.80	0.60	0.38
CCC	0.59	0.45	0.57	0.52	0.47	0.27	0.16

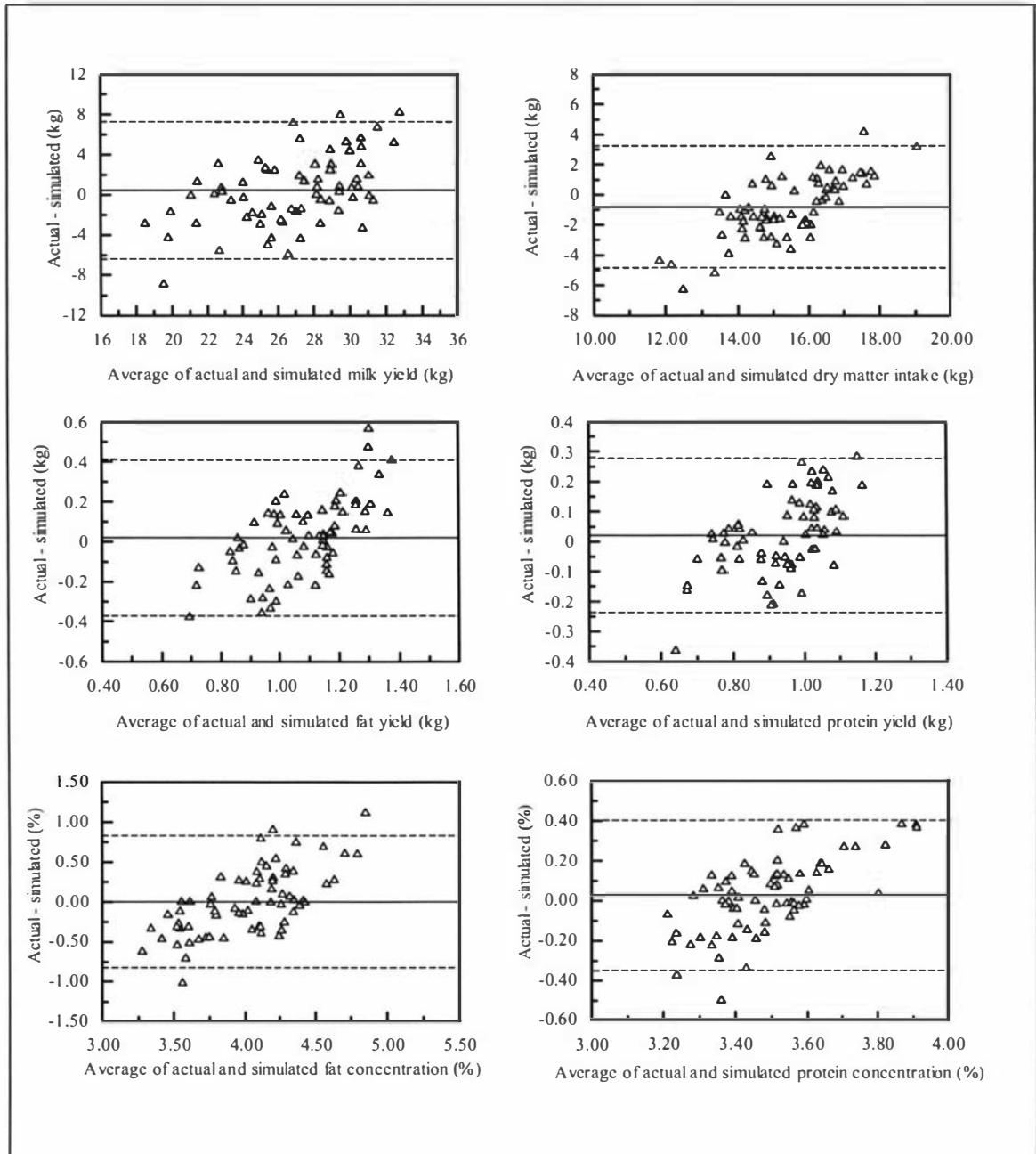
<sup>1</sup>superscripts indicate the significance of difference between simulated and actual means.

**Abbreviations:**  $r^2$  = coefficient of determination,  $v$  = variance ratio, and  $C_b$  = bias correction factor, CCC = concordance correlation coefficient, MPE = mean prediction error.

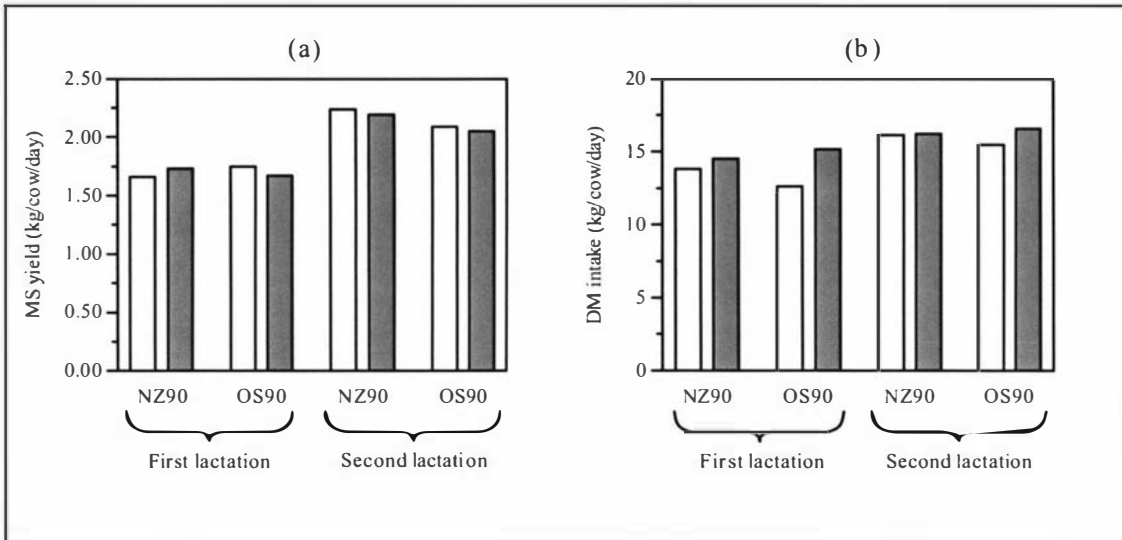


**Figure 1:** The relationship between simulated values and actual values for daily yields of milk, DM intake, daily yields fat and protein, and concentrations of fat and protein relating to the combined dataset of NZ 1990's (NZ90) and Overseas 1990's (OS90) Holstein-Friesian strains of cattle.



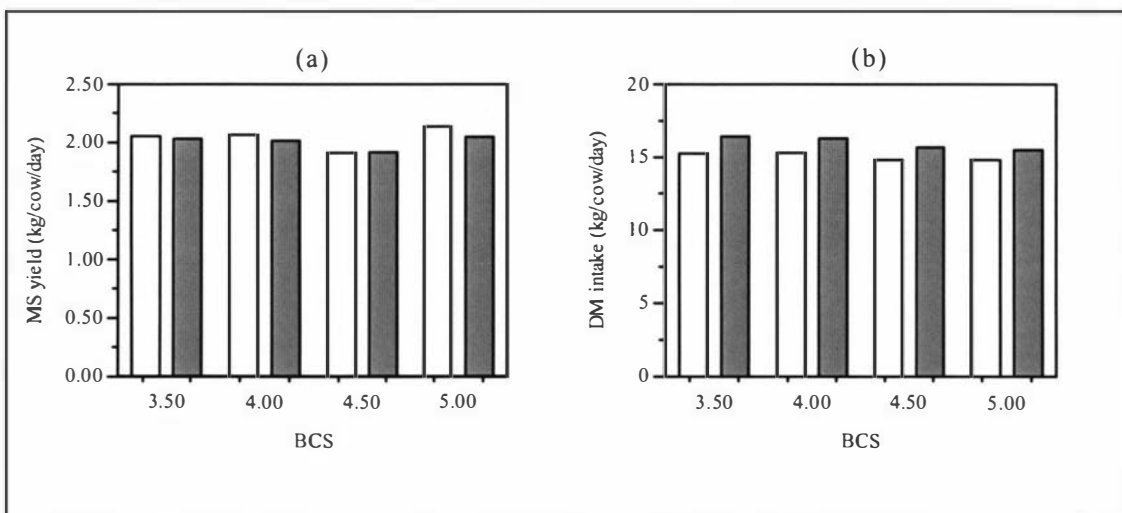


**Figure 2:** Bland-Altman plots displaying the 95% upper and lower confidence limits (dashed lines) of agreement of simulated values for daily yields of milk, DM intake, daily yields fat and protein, and fat and protein concentration. **Note:** the solid line represents the mean bias value in each case.



**Figure 3:** Average of actual (□) and simulated (■) values for (a) daily MS yields and (b) Dry matter intakes of NZ 1990's (NZ90) and Overseas 1990's (OS90) Holstein-Friesian strains of cattle in their first or second lactation.

The degree of variation of simulated values was less than that observed in the actual values in all simulated versus actual comparisons, as shown by variance ratios,  $v$ , greater than 1 (Table 4). The difference in variation between simulated and actual values is also illustrated in the Bland-Altman plots (Figure 2), as simulated values for cows with low and high actual values are most likely to be outside of the 95% lower and upper limits of agreement. The most marked discrepancy for variation occurred for live weight change and DM intake, with significantly less variation in simulated values than in actual values as indicated by high values for  $v$  for DM intake and live weight change, respectively.



**Figure 4:** Average of actual (□) and simulated (■) values for (a) daily MS yields and (b) DM intakes of cows at a range of BCS.

### **Simulation of age, genotype and BCS effects**

The model simulated accurately the different MS yields when grouping by age and genotype as indicated by mean values (Figure 3a). The model did, however, significantly over-predict feed intake in first lactation OS90 animals (Figure 3b). The model simulated accurately the pattern of MS yield and DM intake across the trajectory of average BCS (Figure 4). Simulated DM intake were greater in thin animals, which were also found in the actual data (Figure 4). However, as mentioned earlier, simulated DM intake were higher than actual n-alkane estimated values.

## **DISCUSSION**

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The model simulated, to a high degree of accuracy, mean values for daily yields of milk, fat and protein, and concentrations of fat and protein in two modern Holstein-Friesian genotypes based on genetic and environmental information. These yield results were achieved even though feed intake was not entered as an input, which is the approach generally adopted by dairy cattle simulation models (Chapter 2).

The model was most efficient at predicting fat and protein concentrations with MPE values of 0.05 and 0.10, respectively, indicating a very good predictive ability for these two traits (Fuentes-Pila et al., 1996). Concentrations of fat and protein are often not predicted or not reported in studies using simulation models, with their primary output being yields of milk (Chapter 2). This is a major limitation for applying the models to practical situations where payment is based on multiple components. However, Hanigan et al. (2006) reported the “Molly” model of Baldwin et al. (1987), under predicted concentrations of fat and protein in early and late lactation and over predicted them at peak and mid lactation. In the present model, errors were mainly associated with a lack of agreement of variation.

Feed intake and liveweight change were simulated less reliably. However, actual values for feed intake and liveweight change are only estimates themselves. The n-alkane method to predict feed intake can be inaccurate due to diurnal variation in n-alkane excretion, and to the possibility that the herbage consumed includes plant species different from the herbage sample taken from the pasture (Dove et al., 1996;

Smit et al., 2005). Similarly, variations in water content of the body, gut fill and organ weights all influence liveweight (Schroder and Staufienbiel, 2006). In addition, further error can be associated with electronic measurements and data recording. The present analyses attempted to remove these sources of error by fitting a smoothing spline function to the liveweight data, however, the success of this procedure is uncertain.

The model correctly simulated MS yield of NZ90 genotype cows (2.07 and 2.06 kg MS/day for actual and simulated values, respectively) to be slightly greater than the OS90 genotype cows (1.99 and 1.93 kg MS/day for actual and simulated values, respectively). These results were achieved even though the combined EBV for fat and protein yields of the NZ90 genotype was lower than for the OS90 genotype (65.4 and 69.1 kg for NZ90 and OS90, respectively). The greater MS yield achieved by the NZ90 genotype was a result of them having more feed available to direct to milk production due to their lower maintenance requirements than the larger OS90 genotype and the influence of the reaction norm functions applied. The higher relative intake of the NZ90 compared to OS90 strain, allowed the NZ90 strain to achieve MS yield in excess of the OS90 strain. Incorporated reaction norm functions also predict the OS90 strain would exhibit greater responses to supplements than the NZ90 strain, which is consistent with the results of previous studies (Horan et al., 2005; Kolver et al., 2005).

A MPE value of 0.15 for DM intake indicates relatively high error of prediction, and is larger than previous reported results using empirical equations (Roseler et al., 1997). However, it should be noted that yields of milk, fat or protein are often used in empirical feed intake prediction equations (Fuentes-Pila et al., 1996; Roseler et al., 1997; Vadiveloo and Holmes, 1979). This is not the case in the present model, which is preferable as feed intake can then be predicted independently of yields of milk, fat or protein. The approach adopted by the model predicts what will happen rather than accounting for, or explaining, what has already happened.

Simulated feed intake and yields of milk, fat and protein were lower in first compared to second parity animals (Figure 3), in agreement with results for milk, fat and protein yields on commercial farms (Livestock Improvement, 2004), and for

comparisons of feed intakes in animals of different parities (Kennedy et al., 2003; Oldenbroek, 1989). The model was not, however, able to predict the extent of the depression in feed intake in the OS90 first parity cows. Potentially, the OS90 strain requires a longer period to adapt to the demands of lactation and foraging for pasture than NZ90 animals with differences in feed intake between the two strains not as evident in their second lactation (Figure 3). For liveweight change of each strain and parity, the model was able to correctly predict that NZ90 cows in their second parity would, on average, lose weight. However, the simulated liveweight loss ( $-0.05$  kg liveweight/day) was less than actual values ( $-0.51$  kg liveweight/day). For the other strain by parity averages, simulated liveweight changes were within  $0.11$  kg liveweight/day of actual values. The model was able to simulate correctly that thin cows would have higher feed intakes than fat animals (Figure 4). This is consistent with the findings of a meta-analysis carried out by Broster and Broster (1998).

The lack of agreement between simulated and actual values on an individual basis and smaller variation in simulated than in actual data could arise from a number of sources. Firstly, the EBV for milk, fat and protein become more reliable, in terms of predictive ability, as the animal ages. For instance, estimated breeding values of first calving heifers are based on the expected combination of genes inherited from the animal's parents. As is the case with a number of other models (Chapter 2), the present model does not consider some temporary environmental effects that are known to affect performance due to incomplete information. Clinical mastitis or elevated somatic cell counts (De Vliegher et al., 2005; Rajala-Schultz et al., 1999), oestrous behaviour (Van Vliet and Van Eerdenburg, 1996) and calving difficulty (Deluyker et al., 1991), are all expected to significantly reduce milk yield at the time of their instance. Clinical mastitis and calving difficulty can also impair subsequent milk yield. Likewise, the model does not consider the permanent environmental effect of feeding regime at and around puberty, which is known to affect mammary development and subsequent milk yield (Sejrsen and Purup, 1997). Incorporation into the simulation model of many possible permanent and temporary environment effects may result in more realistic variation within simulated data. For example to introduce variation, Dijkhuizen et al. (1986) simulated temporary and permanent effects stochastically from a normal distribution, and this approach may be incorporated in the present model.

In conclusion, the initial results indicate the model is able to simulate the intended concepts of animal genotype, environment and genotype x environment interactions and how they affect phenotypic performance. However as with all models, testing and validation is an ongoing process, with each study acting to improve the model (Sargent, 2004). Further testing requires a wider range of breeds and genotypes, age groups, supplementary feeding levels, systems, lactation stages and environmental compromises such as heat stress conditions. The intention is to apply and adapt the model to represent different production systems and genotypes.

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# CHAPTER 10

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## General Discussion

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To reiterate, the objectives of this research were firstly, to investigate if dairy cattle genotypes in NZ exhibit genetic variation in environmental sensitivity and to determine if this genetic variation is statistically significant from a genetic evaluation perspective, and secondly, to use genetic information including environmental sensitivity data to simulate dairy cattle responses to changes in nutritional regime.

## **REVIEW OF DAIRY CATTLE SIMULATION MODELS**

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Initially, a comprehensive review of literature relating to currently available simulation models and their ability to model the effects of genotype, environment and GxE interactions was carried out (Chapter 2). The study identified that simulation models either, overlook or do not represent GxE interactions. Numerous studies have investigated GxE interactions in dairy cattle sires or genotypes, examples of which are distributed throughout this thesis. However, the findings of these studies have not been applied for use in dairy cattle simulation models.

## **ENVIRONMENTAL SENSITIVITY**

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In Chapter 3, 4 and 5, differences in environmental sensitivity between sires and breeds was investigated using total lactation yields of milk, fat and protein from a large dataset of progeny test records in NZ. The environmental factors studied were feeding level with herd average milk solids yield used as a proxy due to the absence of feeding level information; HLI, which included the effects of temperature, humidity, solar radiation and wind speed; an estimate of herd size and altitude. In Chapter 3, a range of tests and indicators were applied to determine if the level of sire re-ranking across environmental character states warranted the formation of separate breeding schemes for different environment. The estimated genetic correlation values between extreme character states were in some cases less than unity, but never less than 0.8, a threshold level suggested by Robertson (1959). Likewise, rank correlations between extreme character states were only below genetic expectations in one case. Selection differentials identified the greatest gains in economic index could be achieved by selecting sires based on progeny performance in her's with low MS yield (low feeding levels), and relatively hot environmental conditions, rather than selection based on an economic index

representing all environments. Based on the results of Chapter 3, however, sire re-ranking was not sufficient to warrant major revision of the genetic evaluation scheme in NZ.

Some environmental differences in the expression of breed and heterosis effects for yields of milk, fat and protein were outlined in Chapter 4. Differences in yields of milk, fat and protein between NZJ and OHF were greater in an environment where herds achieve high milk solid yields, presumably with greater feeding levels of pasture and supplements, than environments where herds achieve low milk solid yields with minimal supplementary feed inputs or limited pasture supply. These results suggest NZJ are best suited to a grassland-type environment, and OHF are more suited to an intensive-type environment. Performance differences between NZJ and other breeds of cattle were smaller in hot compared to cold environments, a phenomenon investigated on a daily basis in Chapter 6. Heterosis effects between OHF and NZF cattle were suppressed in herds either, very low MS yields or high HLI.

Specialist or generalist-type strategies in different dairy cattle breeds were assessed in Chapter 5. A specialist is an animal that achieves high performance levels in specific environments such as hot conditions or high feeding levels, but performs to average or poor levels in an environment not optimal for the specialist. The performance of a generalist is relatively unaffected by environmental change with minimal fluctuations in performance. Based on the findings presented in Chapter 5, most sires were generalists. However, OHF sires were more likely to be considered specialist in intensive-type environments, which included large proportions of homegrown or imported feeds in the cow's diet than NZJ or NZF. NZJ sires were most likely to be specialists in a grassland-type environment, expected to use limited supplementary feeds with low pasture allowances.

The findings of Chapters 4 and 5 have significant practical implications for farmers, who may unknowingly use sires or breeds better suited to a particular environment. The performance of daughters of an intensive specialist sire may be significantly compromised in farming systems using low levels of supplements or where pasture supply is limited. Whereas, daughters of a grassland specialist sire are unable to fully

exploit an environment where feed is abundant. Both situations would impact on farm profitability. Therefore it may be wise in each progeny test run to determine whether a sire is a specialist in a particular environment or can be considered a generalist. Should a sire be classified as a specialist in particular environment it could be marketed to target this environment, or warnings about the potential unsuitability of the sire in particular environment provided to purchasers of semen. The accuracy of sire classification (generalist, specialist-intensive or specialist-grassland) would also benefit from the collection of nutritional information from each progeny test herd, as in the present study, a proxy for feeding level (herd MS yield) was used.

The present animal breeding approach adopted in NZ and overseas is where traits are considered the same in each environment with overall performance and EBV estimated across environments. The majority environment where most records are collected has the greatest influence on EBV, with performance in minority environments diluted (de Jong and Bijma, 2002). The results of studies presented in this thesis suggest the current animal breeding approach is acceptable, as low levels of re-ranking occur when comparing sire performance in the extremes of environment (Chapter 3), and the fact that most sires were classified as generalists (Chapter 5).

The animal breeding approach may need adjustment, however, if the commercial environment is expected to change considerably such as marked future increases in concentrate use, or if specific farm environments are outside the extreme environments presented in this study. In these instances, a wide and even distribution of herds in different production and climatic environments is needed. This would be beneficial for two reasons: firstly, EBV generated from the progeny test scheme would not rely as heavily on performance in low to moderate production level herds that comprise a large proportion of progeny test herds; and secondly, reliable estimates of sire ability could be generated in high production environments. Information on sire ability in high production environment could then be passed onto farmers to allow them to make more informed selection decisions.

Another alternative to create niche genotypes that perform best in specific environments may be achieved by modifying the external environment of the parent during foetal development (Gabriel and Lynch, 1992; Piersma and Drent, 2003). The Barker or ‘thrifty phenotype’ hypothesis is where a poorly nourished mother may give her offspring a forecast of the nutritional environment it is likely to encounter when it is born (Hales and Barker, 2001). Evidence of this hypothesis has been shown for humans and rats, where poor foetal nutrition modifies insulin metabolism in the unborn infant (Hales and Barker, 2001; Wells, 2003). In adult life at high levels of nutrition, the offspring are unable to cope with high levels of glucose, resulting in an increased risk of developing Type-2 diabetes. Such forecasts, or epigenetic alterations in gene expression (Jaenisch and Bird, 2003), may lead to differences in metabolic mechanisms that allow dairy cows to perform to high levels in a nutritionally challenging environment or an environment abundant in nutrition.

It is also important to consider the effect of evolutionary environment at a gene level. Genetic canalisation is proposed to be the primary mechanisms controlling plasticity (Flatt, 2005). Genetic canalisation is where genes controlling a phenotypic character, which was initially only produced in response to a specific environment, become fixed due to direct or indirect selection (Waddington, 1961). Exposure of the genotype to a different environment can then produce unexpected or undesirable responses, as there is insufficient genetic variation at important loci to adapt to a “new” environment. Therefore, even if the uterine environment is altered to “target” a specific environment, the individual may not have the genes to exploit such an environment due to gene fixation in previous generations.

Chapters 4 and 5 identified NZJ cattle were better suited to low feeding level or high summer HLI environments than OHF or NZF. Consequently, a daily analysis was performed determining the effects of hot or cold conditions on yields of milk, fat and protein (Chapter 6). This study identified that NZJ cattle were more tolerant to the effects of heat than HF (NZF or OHF) cattle with straight crosses between the breeds intermediate. Performance was significantly affected at THI values exceeding 67, 69 and 77 in HF, HFxJ and NZJ. Differences in susceptibility to heat stress between breeds may explain the findings of Chapters 4 and 5, where trait differences of NZJ compared to other breeds of cattle were less in low MS yield and high HLI

environments than in high MS yield and low HLI environments. For example, the effect may have been mediated through heat stress with NZJ cattle more tolerant to hot conditions than other breeds of cattle.

Results relating to heat stress are most important for northerly regions of NZ such as Northland, Waikato and Bay of Plenty. In these regions, selection of heat tolerant genotypes may be needed, or heat mitigation strategies such as those suggested in Chapter 6 be implemented. Before heat tolerant genotypes are developed or heat abatement strategies implemented, an economic analysis investigating regional losses due to heat stress is warranted. For example, St-Pierre et al. (2003) estimated that 43 out of 48 United States dairying states would benefit from fans and sprinklers in the dairy shed with the remaining 5 states needing high pressure evaporative cooling systems in the dairy shed. It was estimated that use of the recommended cooling systems would reduce economic losses due to heat stress by US\$610 million in the United States. Elevated heritability for production traits in hot compared to moderate or cold conditions would provide a strong basis for the selection of heat tolerant genotypes (Hayes et al., 2003; Ravagnolo and Misztal, 2000). Use of microarrays to identify large-scale changes in gene expression during acute and chronic heat stress holds potential for identifying these heat tolerant genotypes. However, the number of genes involved in response to acute heat stress is ~100, with each requiring further characterisation (Collier et al., 2006; Sonna et al., 2002).

## **SIMULATION MODEL**

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In Chapter 7, an analysis was carried out to determine the effect of genetic merit, level of feeding, age and BCS on the parameters of a mechanistic model described by Vetharaniam et al. (2003). The mechanistic model represented the mammary gland, its growth and involution, via mammary alveoli which head to quiescence, were reactivated or died off, depending on energy supply and other factors of the environment. The necessary data was obtained from an earlier farmlet study using NZJ cattle managed at various stocking rates (Bryant et al., 2003). Using these data, the best parameter values were chosen by applying a genetic algorithm to the system of equations to find lactation curves that matched actual data. Mathematical



functions were then estimated to quantify the significant linear and quadratic effects of genetic merit, level of feeding, age and BCS on mammary gland dynamics.

A simulation model, MOOSIM, was then constructed to simulate the effect of genotype, environment and genotype and environment interactions on dairy cattle performance (Chapter 8). The model incorporated a large proportion of the results generated from studies presented in Chapters 4, 5, 6 and 7. The lactation module was the most complex, and was based around the general framework of a mechanistic model provided by Vetharanim et al. (2003) with adaptations estimated in Chapters 4, 5, 7 and 8. In addition, a meta-analysis of studies relating to the effect of feeding levels on fat and protein concentrations (summarised within Chapter 8) were included when developing the simulation model. The body energy store module adopted the general framework of Friggens et al. (2004), again with some key adaptations. These adaptations, which included the effect of age, feeding level and genotype on body lipid trajectories, were identified from results of prior studies or newly available genetic information such as estimated breeding values for BCS.

The effect of heat stress on milk yield and concentrations of fat and protein in the different breeds (identified in Chapter 6) were also incorporated into the model using different breed THI thresholds. An advanced biological representation of the effect of heat stress on animal performance could be based on the findings of a study by Collier et al. (2006). They found hot conditions appeared to increase expression of genes regulating the progression of mammary cells to a state of senescence. Including an adjustment to the  $k_5$  parameter of MOOSIM, which controls the rate at which quiescent mammary cells proceed to senescence, may best simulate the negative effect of hot conditions on milk yields.

Using environment and genotype information obtained for two modern strains of HF cattle, the MOOSIM model showed a reasonable degree of agreement between predicted and observed values for yields of milk, fat and protein, and concentrations of fat and protein based on a number of measures used to test model accuracy (Chapter 9). The model was able to predict mean values well, but it was unable to simulate the amount of variation present in the observed values. It was hypothesised that this was due to some temporary environmental effects not simulated by the

model. A solution may be to incorporate a stochastic component representing temporary environmental effects.

The model could be enhanced in a number of ways, such as including a feed database where the nutritional composition of each feed is known. An economic module that considers the cost of different feeds and expected yield responses could assess profitability of different feeds. The effect of different milking frequencies on predicted yields of milk, fat and protein could be modelled using the methodology described by Shorten et al. (2002). Incorporation of heterosis effects on mammary gland dynamics and live weight is another area that needs inclusion. Likewise, including average daily wind speed and rainfall, as inputs would allow the effects of cold stress on performance to be modelled. Including the effect of specific genes on milk yields, milk composition and lactation persistency would add to the genetic applicability of the model. Incomplete information (such as for heterosis effects), precluded the inclusion into the model or investigation of these important areas.

The greatest use of the model could be in the area of optimisation, such as optimising profit through identifying the best feeds and feeding levels for each genotype. Evolutionary algorithms such as those described and implemented by Mayer et al. (2001) hold significant potential in this area. Using a differential evolution algorithm applied to a beef production systems model, Mayer et al. (2001) was able to efficiently find the management options such as stocking rates, mating and weaning policies that maximised accumulated 10-year gross margin. Likewise, Lopez-Villalobos et al. (2004) was able to allocate sires and dams using a differential evolution algorithm to maximise farm profit from future progeny while minimising inbreeding. The differential evolution algorithm is an extension of the genetic algorithm applied in Chapter 7.

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## CONCLUSIONS

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The key findings from the research presented in this thesis are:

- The extent of GxE interactions for yields of milk, fat and protein within the range of NZ environments are not sufficient to warrant the formation of separate breeding schemes for distinct environments. However, observed breed x environment interactions suggest NZJ cattle are better suited to low production level, grassland-type environments than OHF cattle, which are better suited to high production, intensive-type environments.
- Environmental extremes of cold (characterised by low temperatures, high wind speeds and heavy rainfall) or heat (characterised by high temperatures, humidity, solar radiation and low wind speeds) can have significant effects on milk and MS yields, and concentrations of fat and protein. Cattle of HF origin are more susceptible to hot conditions than HFxNZJ or NZJ cattle with reductions of greater than 0.05 kg of milk per unit of THI occurring at THI of 67, 69 and 77 in HF, HFxNZJ and NZJ, respectively.
- Previous simulation models were unable to simulate known GxE interactions when predicting dairy cattle performance. A dairy cattle simulation model for pastoral systems was subsequently developed in an attempt to simulate GxE interactions. Findings from studies presented in this thesis, and adapted modules from the literature used to simulate the mammary gland and body fat deposition were incorporated into the model. Initial investigations were promising, with the developed model able to accurately predict mean values for daily yields of milk, fat and protein and concentrations of fat and protein for two modern Holstein-Friesian genotypes managed in a pasture-based system. The model can predict milk yield independent of feed intake, and feed intake independent of milk yield.

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# **Appendix 1**

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## **Abbreviations, units and description of parameters used in the MOOSIM model**

Abbreviation	Unit	Description
<b>Nutritional environment</b>		
PI <sub>0</sub>	kg DM/cow/d	Initial estimate of pasture intake
SI <sub>1</sub>	kg DM/cow/d	Initial estimate of supplementary feed intake (iteration 1)
HM	-	Adjustment of initial pasture intake for pre-grazing herbage mass
SUB <sub>1</sub>	-	Initial pasture substitution adjusted for stage of lactation
PI <sub>1</sub>	kg DM/cow/d	Pasture intake adjusted for herbage mass, quality, terrain and substitution
FI <sub>1</sub>	kg DM/cow/d	Initial estimate of feed intake
ES	-	Energy status
Prop <sub>past</sub>	-	Proportion of the diet as pasture
Prop <sub>supp</sub>	-	Proportion of the diet as supplement
ME <sub>feed</sub>	MJ ME/kg DM	Metabolisable energy concentration of total feed offered
RI	-	Relative intake
Prop <sub>past</sub>	-	Proportion of the diet as pasture
Prop <sub>supp</sub>	-	Proportion of the diet as supplements
ME <sub>feed</sub>	MJ ME/kg DM	Metabolisable energy concentration of total feed offered
NE <sub>feed</sub>	MJ NE/kg DM	Net energy concentration of total feed offered
<b>Live weight</b>		
W <sub>B</sub>	kg	Estimated birth live weight
W <sub>M</sub>	kg	Estimated mature live weight
aW	kg	Current live weight adjusted for BCS
k <sub>w</sub>	-	Rate of maturity
T <sub>w</sub>	d	Age at next calving
W <sub>T</sub>	kg	Target live weight at next calving
GR <sub>T</sub>	kg/d	Growth rate from now to next calving
EV <sub>g</sub>	MJ/kg	Energy value of live weight gain
k <sub>g</sub>	-	Efficiency of energy use for growth
MER <sub>g</sub>	MJ ME/d	Metabolisable energy requirements for growth
<b>Body energy reserves</b>		
T'	d	Stage of lactation when the lower asymptote of the body lipid trajectory is reached
L' <sub>base</sub>	kg lipid/kg W	Proportion of total body lipid for a base cow at the lower asymptote of the body lipid trajectory
L' <sub>Nextbase</sub>	kg lipid/kg W	Proportion of total body lipid for a base cow at the time of next calving
L' <sub>dietadj</sub>	kg lipid/kg W	Lipid adjustment to account for the effects of diet and level of feeding
L' <sub>heat</sub>	kg lipid/kg W	Lipid adjustment to account for the effects of heat stress
BCS <sub>ageadj</sub>	-	BCS adjustment for the effect of age
TN'	days	The number of days from T' until the next calving
L' <sub>curr</sub>	kg lipid/kg W	Current proportion of total body lipid for the simulation cow
L'	kg lipid/kg W	Proportion of total body lipid for the simulation cow at the lower asymptote of the body lipid trajectory
L' <sub>next</sub>	kg lipid/kg W	Proportion of total body lipid for the simulation cow at the time of next calving
DF <sub>T'</sub>	d	Days from T'
d <sub>L<sub>curr</sub></sub>	kg/d	Initial rate of lipid mobilisation (or deposition) from calving until T'
dL <sub>next</sub>	kg/d	Rate of lipid mobilisation (or deposition) from T' until next calving

dL/dT	kg/d	Rate of change of body lipid
BCS <sup>+1</sup>	-	Estimated BCS on the next day of simulation
BCS <sub>GL</sub>	-	Estimated loss (or gain) of BCS
W <sub>GL</sub>	kg d	Estimated loss (or gain) of live weight
MER <sub>GL</sub>	MJ ME/cow/d	Metabolisable energy requirements for live weight gain or loss
<b>Lactation</b>		
MYTP	kg	Initial prediction for total lactation yield of milk
FYTP	kg	Initial prediction for total lactation yield of fat
PYTP	kg	Initial prediction for total lactation yield of protein
avMY	kg	Initial prediction for daily lactation yield of milk
FY <sub>conc</sub>	-	Initial fat yield concentration
PY <sub>conc</sub>	-	Initial protein yield concentration
t <sub>ip</sub>		Stage of lactation on the Legendre polynomial scale
LP <sub>1</sub>		1 <sup>st</sup> degree Legendre polynomial term related to t <sub>ip</sub>
LP <sub>2</sub>		2 <sup>nd</sup> degree Legendre polynomial term related to t <sub>ip</sub>
LP <sub>3</sub>		3 <sup>rd</sup> degree Legendre polynomial term related to t <sub>ip</sub>
LP <sub>4</sub>		4 <sup>th</sup> degree Legendre polynomial term related to t <sub>ip</sub>
GP <sub>milk</sub>	kg	Genetic potential for milk
IDFY <sub>conc</sub>	%	Initial daily fat yield concentration
IDPY <sub>conc</sub>	%	Initial daily protein yield concentration
RN	-	Reaction norm adjustment factor
S	MJ/d	Secretion rate per active alveolus
A <sub>0</sub>		The initial number of active alveoli at t = 0
A <sub>1</sub>		The number of active alveoli at t = 1
A <sub>30</sub>		The number of active alveoli at t = 30
A <sub>100</sub>		The number of active alveoli at t = 100
Q <sub>t</sub>		The number of quiescent alveoli
dA <sub>30</sub>	n/d	Average rate of active alveoli change from day 1 to day 30
dAdT	n/d	Rate of change of active alveoli
dAdT <sub>mid</sub>	n/d	Rate of change of active alveoli at day 15
A <sub>t</sub>		The number of active alveoli at t
k <sub>1</sub>	per d	Controls the initial rate of production of active alveoli by progenitor cells
k <sub>2</sub>	per d	Controls the decay rate of production of active alveoli by progenitor cells
k <sub>3</sub>	per d	Controls the rate of quiescence of active alveoli
k <sub>4</sub>	per d	Controls the rate of reactivation of quiescent alveoli to the active alveoli population
k <sub>5</sub>	per d	Controls the rate of senescence of quiescent alveoli
L	-	Elasticity of production
D	-	Mammary gland feeding drive
I	MJ/d	Initial estimate of daily milk production in terms of energy
THI	-	Temperature humidity index
P <sub>adj</sub>	kg/d	Milk yield adjustment for the effects of pregnancy
C <sub>MYadj</sub>	kg/d	Milk yield adjustment for the effects of climate
C <sub>FPadj</sub>	kg/d	Fat concentration adjustment for the effects of climate
C <sub>PPadj</sub>	kg/d	Protein concentration adjustment for the effects of climate
DFY <sub>conc</sub>	-	Daily fat yield concentration adjusted for the effects of climate and diet
DPY <sub>conc</sub>	-	Daily protein yield concentration adjusted for the effects of climate and diet



$DMSY_{conc}$	-	Daily milk solids (fat + protein) yield concentration adjusted for the effects of climate and diet
$NE_{kgmilk}$	MJ/kg milk	Net energy concentration per kilogram of milk
$ME_{kgmilk}$	MJ/kg milk	Metabolisable energy concentration per kilogram of milk
$MY_{pred}$	kg/d	Final predicted daily milk yield
$FY_{pred}$	kg/d	Final predicted daily fat yield
$PY_{pred}$	kg/d	Final predicted daily protein yield
$MER_l$	MJ ME/cow/d	Metabolisable energy requirements for lactation
<b>Maintenance</b>		
EGRAZE		Additional energy requirements associated with grazing
$q_m$	-	The metabolisability of the gross energy of a feed at maintenance
$k_m$	-	Efficiency of utilisation of energy for maintenance
$MER_m$	MJ ME/cow/d	Metabolisable energy requirements for maintenance
<b>Pregnancy</b>		
$T_p$	d	Stage of pregnancy
$E_t$	MJ	Total energy retention in the gravid foetus
$E_c$	MJ/d	Daily energy retention in the gravid foetus
$k_c$	-	Efficiency of utilisation of energy for pregnancy
$MER_p$	MJ ME/cow/d	Metabolisable energy requirements for pregnancy
<b>Total</b>		
$MER_{total}$	MJ ME/cow/d	Total metabolisable energy consumption
$P_l$	-	Ratio of total metabolisable energy partitioned to lactation
$P_m$	-	Ratio of total metabolisable energy partitioned to maintenance
$P_{gl}$	-	Ratio of total metabolisable energy partitioned to gain/loss
$P_g$	-	Ratio of total metabolisable energy partitioned to gain
$P_p$	-	Ratio of total metabolisable energy partitioned to pregnancy



## Appendix 2

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### Description of equations used in the MOOSIM model

Variable	Equation	Eqn No.
<b>Nutritional environment</b>		
PI <sub>0</sub>	$\{(-0.0107 \times SA \times PA) + [3.94 \times \text{LOG}(PA)] - [0.13 \times (\text{NDF}_{\text{past}} - 40)]\}$	N1
HM	$2.69 + (-0.011 \times t)$ ; if HM $\leq 0$ then HM = 0	N2
SUB <sub>1</sub>	$0.165 + (-0.0012 \times t)$	N3
PI <sub>1</sub>	$PI_1 + \{[(\text{HM}_{\text{pre}} - 2600) / 1000] \times \text{HM}\} + (\text{SA} \times \text{iSUB}) + (2 \times [\text{ME}_{\text{past}} - 12]) + (2 - [2 \times \text{TER}_Q])$ ; if $\text{HM}_{\text{pre}} > 3200$ then $\text{HM}_{\text{pre}} = 3200$	N4
SI <sub>1</sub>	$[(0.9 \times \text{SA}) \times (\text{ME}_{\text{supp}} / 11)]$	N5
FI <sub>1</sub>	$(PI_1 + SI_1) \times [(\text{EBV}_{\text{BCS}} + 4.5) / 4.5]$	N6
ES	$FI_1 / (aW \times 0.04)$	N7
RI	$FI_1 - (0.75 \times aW \times 0.04)$	N8
Prop <sub>past</sub>	$PI_1 / FI_1$	N9
Prop <sub>supp</sub>	$SI_1 / FI_1$	N10
ME <sub>feed</sub>	$(\text{Prop}_{\text{past}} \times \text{ME}_{\text{past}}) + (\text{Prop}_{\text{supp}} \times \text{ME}_{\text{supp}})$	N11
NE <sub>feed</sub>	$[\text{Prop}_{\text{past}} \times (18.4 / \text{ME}_{\text{past}})] + [\text{Prop}_{\text{supp}} \times (18.4 / \text{ME}_{\text{supp}})]$	N12
<b>Live weight</b>		
W <sub>B</sub>	$(W_M^{0.73} - 28.89) / 2.064$	W1
W <sub>M</sub>	$529.3 + (\text{EBV}_W - 50.6)$	W2
BCS <sub>W</sub>	$(0.1286 \times W_m) - 22.95$	W3
aW	$W - [(BCS_{\text{curr}} - 5) \times \text{BCS}_W]$	W4
k <sub>W</sub>	$\text{LOG}([1 - (W_B / W_M)^{0.33}] / \{1 - [(W_M \times 0.814) / W_M]^{0.33}\}) / 24$	W5
T <sub>W</sub>	$[(\text{AGE} + 1) \times 365 / 30.42]$	W6
W <sub>T</sub>	$W_m \{1 - [1 - (W_B / W_m)^{1/3}] \times e^{-k_W T_W}\}^3$ ; if AGE < 4 years else $W_T = aW$	W7
GR <sub>T</sub>	$(W_T - aW) / 365$	W8

$EV_g$	$1.15 \times [4.1 + (0.033 \times aW) - (0.000009 \times aW^2)] / [1 - (0.1475 \times GR_T)]$	W9
$k_g$	$0.043 \times ME_{fcd}$	W10
$MER_g$	$(EV_g \times GR_T) / k_g$	W11
<b>Body energy reserves</b>		
$T'$	80	R1
$L'_{base}$	$[-1.1043 + (1.7541 \times 4.5)] / 100$	R2
$L'_{Nextbase}$	$[-1.1043 + (1.7541 \times 5.0)] / 100$	R3
$L'_{dietadj}$	$0.00002 \times RI$	R4
$L'_{heat}$	$(THI-68) \times -0.00005$ ; where BRD = HF or NZF and THI >68 $(THI-72) \times -0.00005$ ; where BRD = FxJ and THI >72 $(THI-76) \times -0.00005$ ; where BRD = NZJ and THI >76	R5a R5b R5c
$BCS'_{ageadj}$	2yr = 0, 3yr = -0.2 and 4yr+ = -0.4	R6
$TN'$	$365 - T'$	R7
$L'_{curr}$	$[-1.1043 + (1.7541 \times BCS_{curr})] / 100$	R8
$L'$	$\{-1.1043 + [1.7541 \times (4.5 + EBV_{BCS} + BCS'_{ageadj})]\} / 100$	R9
$L'_{next}$	$\{-1.1043 + [1.7541 \times (5.0 + EBV_{BCS})]\} / 100$	R10
$DF_{T'}$	$t - T'$	R11
$dL_{curr}$	$[2 \times (L' - L'_{curr})] / T'$	R12
$dL_{next}$	$[2 \times (L'_{next} - L')] / TN'$	R13
$dL/dt$	$\{dL_{calv} \times [1 - (t/T')]\} + L'_{dietadj} + L'_{heat}$ ; where $DF_{T'} > 0$ $(dL_{next}/TN') \times (t - T') + L'_{dietadj} + L'_{heat}$ ; where $DF_{T'} < 0$	R14a R14a
$BCS$	$[(L'_{curr} \times 100) + 1.1043] / 1.7541$	R15
$BCS^{+1}$	$\{[(L'_{curr} + dL/dt) \times 100] + 1.1043\} / 1.7541$	R16
$BCS_{GL}$	$BCS^{+1} - BCS$	R17
$W_{GL}$	$BCS_{GL} \times BCS_w$	R18
$MER_{gl}$	$W_{GL} \times 32$ ; if $W_{GL} > 0$	R19a

$W_{GL} \times 25$ ; if  $W_{GL} < 0$ 

R19b

**Lactation**

MYTP	$3527 + EBV_{milk}$	L1
FYTP	$173.5 + EBV_{fat}$	L2
PYTP	$126.2 + EBV_{prv}$	L3
avMY	$(MYTP/240) \times (aW/W_m)$	L4
FY <sub>conc</sub>	FYTP/MYTP	L5
PY <sub>conc</sub>	PYTP/MYTP	L6
MSY <sub>conc</sub>	FY <sub>conc</sub> + PY <sub>conc</sub>	L7
t <sub>lp</sub>	$[2t - (270 + 5)] / (270 - 5)$	L8
LP <sub>1</sub>	$\sqrt{3/2} \times t_{lp}$	L9
LP <sub>2</sub>	$(\sqrt{45/8} \times t_{lp}^2) - \sqrt{5/8}$	L10
LP <sub>3</sub>	$\frac{1}{2}[(5 \times t_{lp}^3) - (3 \times t_{lp})]$	L11
LP <sub>4</sub>	$\frac{1}{8}[(35 \times t_{lp}^4) - (30 \times t_{lp}^2) + 3]$	L12
IDFY <sub>conc</sub>	$-0.2 + (FY_{conc} \times 100) + (0.509 \times LP_1) + (0.177 \times LP_2) + (0.027 \times LP_3) + (0.112 \times LP_4)$	L13
IDPY <sub>conc</sub>	$-0.1 + (PY_{conc} \times 100) + (0.3 \times LP_1) + (0.182 \times LP_2) + (0.094 \times LP_3) + (0.216 \times LP_4)$	L14
RN	HF = 85.2, NZF = 37.6 and NZJ -43.6	L15
GP <sub>milk</sub>	$(RI \times RN) + [(EBV_{milk} - 500) \times 0.139 \times FI_1]$ ; BRD = OHF or NZF	L16a
	$(RI \times RN) + [(EBV_{milk} + 200) \times 0.139 \times FI_1]$ ; BRD = NZJ	L16b
	$(RI \times RN) + [(EBV_{milk} - 150) \times 0.139 \times FI_1]$ ; BRD = FxJ	L16c
c, d, w <sub>6</sub> , w <sub>7</sub> , l <sub>6</sub> , l <sub>7</sub> , k, q <sub>6</sub> , and q <sub>7</sub>	as described by Vetharanim et al. (2003)	
S	$3 \times 10^{-9}$	
A <sub>0</sub>	$(aW/W_M) \times \{(2.05 \times 10^{-10}) + [(5 \times 10^5 \times GP_{milk}) \times AGE]\}$ ; AGE = 2	L17a
	$\{(2.05 \times 10^{-10}) + [(5 \times 10^5 \times GP_{milk}) \times AGE]\}$ ; AGE = 3-8	L17b

	$\{(2.05 \times 10^{10}) + [(5 \times 10^5 \times GP_{milk}) \times AGE]\}$ ; AGE >9	L17c
$A_t$	$de^{-k_2 t} + l_6 e^{w_6 t} + l_7 e^{w_7 t}$ ; Initial condition (t = 0) $A_t = A_0$	L18
$Q_t$	$ce^{-k_2 t} + q_6 e^{w_6 t} + q_7 e^{w_7 t}$ ; Initial condition (t = 0) $Q_t = 0$	L19
$k_1 (\times 10^9)$	$1.67 + (-0.035 \times AGE)$	L20
$k_2 (\times 10^9)$	0.3	
$k_3$	$(0.148 \times BCS_{curr}) + (-0.0174 \times BCS_{curr}^2) + [-0.00005 \times (GP_{milk} - 1000)]$ ; BRD = OHF	L21a
	$(0.148 \times BCS_{curr}) + (-0.0174 \times BCS_{curr}^2) + [-0.00005 \times (GP_{milk} - 500)]$ ; BRD = NZF	L21b
	$(0.148 \times BCS_{curr}) + (-0.0174 \times BCS_{curr}^2) + [-0.00005 \times (GP_{milk} + 200)]$ ; BRD = NZJ	L21c
	$(0.148 \times BCS_{curr}) + (-0.0174 \times BCS_{curr}^2) + [-0.00005 \times (GP_{milk} - 400)]$ ; BRD = FxJ	L21d
$k_4$	$5.02 + (0.317 \times Age) + (-0.026 \times Age^2)$	L22
$k_5 (\times 10^{-2})$	$3.41 + [-0.0005 \times (GP_{milk} - 1000)] - [0.19 \times (adjFS_{total} - 14)]$ ; BRD = OHF	L23a
	$3.41 + [-0.0005 \times (GP_{milk} - 500)] - [0.19 \times (adjFS_{total} - 14)]$ ; BRD = NZF	L23b
	$3.41 + [-0.0005 \times (GP_{milk} + 200)] - [0.19 \times (adjFS_{total} - 14)]$ ; BRD = NZJ	L23c
	$3.41 + [-0.0005 \times (GP_{milk} - 400)] - [0.19 \times (adjFS_{total} - 14)]$ ; BRD = FxJ	L23d
L	0.4	
$A_1$	$de^{-k_2 \times 1} + l_6 e^{w_6 \times 1} + l_7 e^{w_7 \times 1}$	L24a
$A_{30}$	$de^{-k_2 \times 30} + l_6 e^{w_6 \times 30} + l_7 e^{w_7 \times 30}$	L24b
$A_{100}$	$de^{-k_2 \times 100} + l_6 e^{w_6 \times 100} + l_7 e^{w_7 \times 100}$	L24c
$dA_{30}$	$[2 \times (A_{30} - A_1)] / 30$	L25
$dAdT$	$dA_{30} \times [1 - (t/30)]$	L26
$dAdT_{mid}$	$dA_{30} \times 0.5$	L27
$A_i$	$A_1 + (t \times dAdT_{mid}) + dAdT$ ; $t \leq 30$	L28a

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	Else $A_i = A_t$	L28b
D	$A_i / A_{i00}$	L29
I	$S \times (ES \times D)^L \times A_i$	L30
$P_{adj}$	$(-0.07 \times avMY) / \{1 + e^{[-(t-178)/10.4]}\}$	L31
THI	$0.8TEMP + [HUM \times (TEMP-14.4)] + 46.4$	L32
$C_{MYadj}$	$[(THI - 68) \times -0.05] \times (IMY / 20)$ ; BRD = OHF or NZF and THI>68	L33a
	$[(THI - 72) \times -0.05] \times (IMY / 20)$ ; BRD = FxJ and THI>72	L33b
	$[(THI - 76) \times -0.05] \times (IMY / 20)$ ; BRD = NZJ and THI>76	L33c
$C_{FCadj}$	$[(THI - 68) \times -0.03]$ ; BRD = OHF or NZF and THI>68	L34a
	$[(THI - 72) \times -0.03]$ ; BRD = FxJ and THI>72	L34b
	$[(THI - 76) \times -0.03]$ ; BRD = NZJ and THI>76	L34c
$C_{PCadj}$	$[(THI - 68) \times -0.03]$ ; BRD = OHF or NZF and THI>68	L35a
	$[(THI - 72) \times -0.03]$ ; BRD = FxJ and THI>72	L35b
	$[(THI - 76) \times -0.03]$ ; BRD = NZJ and THI>76	L35c
$DFY_{conc}$	$(IDFY_{conc} + C_{FCadj}) + (-0.020 \times RI)$	L36
$DPY_{conc}$	$(IDPY_{conc} + C_{PCadj}) + (0.017 \times RI)$	L37
$DMS_{conc}$	$(DFY_{conc} + DPY_{conc})/100$	L38
$NE_{kgmilk}$	$0.782 + [0.3255 \times (MSY_{conc} \times 100)]$	L39
$ME_{kgmilk}$	$NE_{kgmilk} \times \{[Prop_{past} \times (18.4/ME_{past})] + [Prop_{supp} \times (18.4/ME_{supp})]\}$	L40
$MY_{pred}$	$(I/NE_{kgmilk}) + P_{MYadj} + C_{MYadj} + \{(-1 \times MER_{GL} \times 0.84)/ME_{kgmilk}\}$ ; $MER_{GL} < 0$	L41a
	$(I/NE_{kgmilk}) + P_{MYadj} + C_{MYadj}$ ; $MER_{GL} \geq 0$	L41b
$FY_{pred}$	$(DFY_{conc}/100) \times MY_{pred}$	L42
$PY_{pred}$	$(DPY_{conc}/100) \times MY_{pred}$	L43
$MER_l$	$ME_{kgmilk} \times [(I/NE_{kgmilk}) + P_{MYadj} + C_{MYadj}]$	L44

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<b>Maintenance</b>		
TER <sub>Q</sub>	TER converted to a quantitative scale: Flat = 1, Flat-Rolling = 1.33, Rolling = 1.66 and Steep = 2.00	
EGRAZE	$0.0025 \times \{FI_1 \times [0.9 - (DIG_{past}/100)]\} + \{0.05 \times TER_Q / [(GRAZE_{pre}/1000) + 3]\}$	M1
q <sub>m</sub>	ME <sub>feed</sub> /18.4	M2
k <sub>m</sub>	0.35q <sub>m</sub> + 0.503	M3
MER <sub>m</sub>	$[(1.5 \times 0.28 \times aW^{0.75} \times e^{-0.03 \times Age}) / k_m] + (0.62 \times avMY) + [(EGRAZE/k_m) \times aW]$ ; if Age >5 then Age = 6	M4
<b>Pregnancy</b>		
T <sub>p</sub>	t - 84	P1
E <sub>t</sub>	$10^{151.665 - (151.64 \times e^{-0.0000576T_p})}$ ; if T <sub>p</sub> > 0	P2
E <sub>c</sub>	$0.025 \times W(E_t \times 0.0201 \times e^{-0.0000576T_p})$	P3
k <sub>c</sub>	0.133	P4
MER <sub>p</sub>	$(E_c / k_c) \times (W_B / 40)$	P5
<b>Total ME and DMI and partitioning</b>		
MER <sub>total</sub>	MER <sub>m</sub> + MER <sub>p</sub> + MER <sub>g</sub> + MER <sub>l</sub> + MER <sub>gl</sub>	T1
DMI	MER <sub>total</sub> /ME <sub>feed</sub>	T2
P <sub>L</sub>	MER <sub>l</sub> /MER <sub>total</sub>	T3
P <sub>M</sub>	MER <sub>m</sub> /MER <sub>total</sub>	T4
P <sub>GL</sub>	MER <sub>gl</sub> /MER <sub>total</sub>	T5
P <sub>G</sub>	MER <sub>g</sub> /MER <sub>total</sub>	T6
P <sub>P</sub>	MER <sub>p</sub> /MER <sub>total</sub>	T7

## **Appendix 3**

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**Effect of concentrate use on body condition score (BCS) change,  
milk yield, and fat and protein composition for cows consuming  
pasture or forages**



Reference	Treatment	Dry matter intake (kg/cow/day)				BCS change <sup>2</sup> per 10 days	Milk kg	Fat %	Protein %
		DIM	Forage	Concentrate <sup>1</sup>	Total				
Bargo et al., 2002	30 kg PA + 1 kg C/4 kg milk yield	109-256	12.9	8.7	21.6	-0.043	28.5	3.13	2.82
Ferris et al., 1999 <sup>3</sup>	15 kg PA + 17 kg TMR + 2 - 3 kg C	109-256	7.5	17.7	25.2	0.002	32.0	3.35	2.95
	37 % C HGM	1-80	12.4	7.2	19.6	-0.016	35.4	4.20	3.23
	48 % C HGM	1-80	11.3	10.2	21.5	-0.016	35.6	4.10	3.30
	59 % C HGM	1-80	9.3	13.1	22.3	-0.016	37.9	4.02	3.38
	70 % C HGM	1-80	6.8	15.4	22.2	0.016	39.2	3.94	3.35
	37 % C MGM	1-90	11.4	6.6	18.0	0.036	31.5	4.10	3.10
	48 % C MGM	1-90	10.1	9.2	19.3	0.036	31.0	3.90	3.28
	59 % C MGM	1-90	8.8	12.5	21.3	0.064	34.1	3.84	3.34
	70 % C MGM	1-90	6.7	15.5	22.2	0.119	35.2	3.59	3.30
Gordon et al., 2000	PS + 5.5 kg C	1-132	14.7	4.6	19.4	-0.038	29.7	4.19	3.15
	PS + 15.4 kg C	1-132	9.4	11.7	21.1	0.019	33.9	4.22	3.43
	PS + P + 5.5 kg C	132-167	7.6	4.7	22.6	0.071	29.7	4.10	3.29
	PS + P + 15.4 kg C	132-167	8.5	10.9	22.0	0.000	30.9	4.27	3.54
	P + 5.5 kg C	167-305	19.2	0.4	19.7	0.018	21.1	4.23	3.49
	P + 15.4 kg C	167-305	14.4	3.8	18.1	0.036	22.1	4.41	3.63
Horan et al., 2005 <sup>4</sup>	MPFS HP	1-100	-	0.0	-	-0.213 <sup>5</sup>	-	-	-
	HSFS HP	1-100	-	0.0	-	-0.183	-	-	-
	HCFS HP	1-100	-	3.7	-	-0.150	-	-	-
	MPFS HD	1-100	-	0.0	-	-0.173	-	-	-
	HSFS HD	1-100	-	0.0	-	-0.158	-	-	-
	HCFS HD	1-100	-	3.7	-	-0.115	-	-	-
	MPFS NZ	1-100	-	0.0	-	-0.153	-	-	-
	HSFS NZ	1-100	-	0.0	-	-0.143	-	-	-
	HCFS NZ	1-100	-	3.7	-	-0.118	-	-	-
	MPFS HP	100-305	-	0.0	-	0.026	-	-	-
	HSFS HP	100-305	-	0.0	-	0.023	-	-	-
	HCFS HP	100-305	-	3.7	-	0.033	-	-	-
	MPFS HD	100-305	-	0.0	-	0.027	-	-	-
	HSFS HD	100-305	-	0.0	-	0.034	-	-	-

Reference	Treatment	Dry matter intake (kg/cow/day)				BCS change <sup>2</sup> per 10 days	Milk kg	Fat %	Protein %
		DIM	Forage	Concentrate <sup>1</sup>	Total				
Table continued									
Horan et al., 2005 <sup>4</sup>	HCFS HD	100-305	-	3.7	-	0.023	-	-	-
	MPFS NZ	100-305	-	0.0	-	0.029	-	-	-
	HSFS NZ	100-305	-	0.0	-	0.034	-	-	-
	HCFS NZ	100-305	-	3.7	-	0.034	-	-	-
Kennedy et al., 2003 <sup>6</sup>	PS or P + 3 - 5 kg C HGM	1-74	15.6	3.6	19.2	-0.152	34.4	-	3.23
	PS or P + 4 - 7.5 kg C HGM	1-74	14.9	5.4	20.3	-0.125	36.1	-	3.31
	PS or P + 6 - 10 kg C HGM	1-72	15.6	7.2	22.8	-0.135	39.6	-	3.23
	PS or P + 3 - 5 kg C MGM	1-73	15.2	3.6	18.8	-0.110	30.1	-	3.28
	PS or P + 4 - 7.5 kg C MGM	1-75	14.1	5.4	19.5	-0.140	32.3	-	3.30
	PS or P + 6 - 10 kg C MGM	1-70	15.0	7.2	22.4	-0.089	34.9	-	3.31
Kolver et al., 2005 <sup>7</sup>	50 kg PA NZ	1-296	-	0.0	-	-0.009	18.8	4.77	3.56
	50 kg PA + 3 kg C NZ	1-290	-	3.0	-	0.001	21.9	4.48	3.64
	50 kg PA + 6 kg C NZ	1-297	-	5.6	-	0.054	22.3	4.28	3.69
	50 kg PA US	1-288	-	0.0	-	-0.068	21.2	4.17	3.48
	50 kg PA + 3 kg C US	1-283	-	2.9	-	-0.058	25.1	3.95	3.43
	50 kg PA + 6 kg C US	1-289	-	5.7	-	0.008	27.1	3.74	3.57
Robaina et al., 1998	20 kg PA	180-240	12.1	0.0	12.1	-0.185	10.6	4.33	3.16
	20 kg PA + 5 kg C	180-240	10.7	4.3	15.0	-0.018	14.8	4.48	3.16
	40 kg PA	180-240	14.9	0.0	14.9	0.035	14.0	4.23	3.13
	40 kg PA + 5 kg C	180-240	12.3	4.4	16.7	0.071	16.4	4.37	3.21
	26 kg PA	180-210	14.3	0.0	14.3	0.265	12.9	4.33	3.10
	26 kg PA + 2 kg C	180-210	13.5	3.4	15.3	0.265	15.7	4.33	3.19
	26 kg PA + 4 kg C	180-210	12.1	6.7	15.5	0.265	16.1	4.36	3.17
	26 kg PA + 8 kg C	180-210	10.4	4.4	17.1	0.441	18.4	4.36	3.29
Stockdale, 2000	40 kg PA + Thin <sup>8</sup>	40-85	16.7	2.4	19.1	0.085	29.4	3.57	3.02
	40 kg PA + Fat <sup>9</sup>	40-85	16.7	2.3	19.0	-0.270	30.5	3.90	3.09
	25 kg PA	40-85	14.1	2.4	16.5	-0.148	28.7	3.81	3.04
	50 kg PA	40-85	19.3	2.3	21.6	-0.032	31.2	3.67	3.07
	40 kg PA	40-85	17.9	0.0	17.9	-0.196	29.0	3.79	3.00
	40 kg PA + 5 kg C	40-85	15.5	4.7	20.2	0.016	30.9	3.69	3.11

Reference	Treatment	Dry matter intake (kg/cow/day)				BCS change <sup>2</sup> per 10 days	Milk kg	Fat %	Protein %
		DIM	Forage	Concentrate <sup>1</sup>	Total				
Table continued									
Stockdale, 2000	40 kg PA + Light <sup>10</sup>	40-85	11.6	2.0	13.6	-0.085	24.0	3.68	2.90
	40 kg PA + Heavy <sup>11</sup>	40-85	13.1	2.1	15.2	-0.116	27.0	3.61	2.81
	25 kg PA <sup>11</sup>	40-85	11.3	2.0	13.3	-0.175	24.3	3.61	2.79
	50 kg PA <sup>11</sup>	40-85	13.4	2.1	15.5	-0.032	26.7	3.68	2.92
	40 kg PA <sup>11</sup>	40-85	13.6	0.0	13.6	-0.116	25.0	3.62	2.78
	40 kg PA + 5 kg C <sup>12</sup>	40-85	11.1	4.1	15.2	-0.090	26.1	3.66	2.94
Wales et al., 1999	25 kg PA	126-164	11.6	0.0	11.6	-0.253	16.1	3.89	2.90
	25 kg PA + 5 kg C	126-164	10.3	5.0	15.3	0.019	22.2	3.80	2.99
	45 kg PA	126-164	14.4	0.0	14.4	-0.083	19.8	3.89	2.90
	45 kg PA + 5 kg C	126-164	12.3	5.0	17.3	0.044	24.6	3.69	2.90
Wales et al., 2001	20 kg PA	49-89	11.2	0.0	11.2	-0.046	20.7	3.80	2.80
	40 kg PA	49-89	15.6	0.0	15.6	0.000	24.2	3.68	3.00
	20 kg PA + 2.5 kg hay pellets	49-89	10.9	2.4	13.3	0.046	22.1	3.75	2.81
	20 kg PA + 2.5 kg Hay Cubes	49-89	10.6	2.1	12.7	-0.046	20.1	3.75	2.84
Wales and Doyle, 2003	19 kg PA <sup>8</sup>	43-70	13.0	0.8	13.8	-0.480	23.8	4.14	2.84
	19 kg PA + 5 kg C	43-70	12.5	5.7	18.2	-0.226	27.9	3.86	2.98
	20 kg PA + 2.5 kg C	49-89	10.3	4.5	14.8	-0.093	26.2	3.57	3.03
	20 kg PA + 2.5 kg C + hay pellets	49-89	10.1	7.2	17.3	0.093	25.6	3.73	3.08
	20 kg PA + 2.5 kg C + hay cubes	49-89	10.0	7.4	17.4	0.046	25.7	3.43	2.88

**Abbreviations:** DIM = days in milk, PA = pasture allowance (units: DM/cow/day), P = pasture, C = concentrates, BCS = BCS

<sup>1</sup>Includes all feeds other than pasture, pasture silage or offered forage

<sup>2</sup>BCS change divided by the treatment period. BCS change converted from national scales to the NZ BCS scale using the equations proposed by (Roche et al., 2004)

<sup>3</sup>High (HGM) and Medium (HGM) genetic merit Holstein Friesian cows were offered diets with differing proportions (on a dry matter basis) as concentrates.

<sup>4</sup>High production North American (HP), high durability North American (HD) and New Zealand (NZ) Holstein Friesian genotypes were managed on pasture diets with a: moderate stocking rate of 2.47 cows/ha + 368 kg of concentrate per cow (MPFS), a High Stocking rate of 2.74 cows/ha + 364 kg of concentrate per cow (HSFS) and a moderate stocking rate of 2.47 cows/ha + 1452 kg of concentrate per cow (HCFS). Forage intake, milk yield or fat and protein concentration data not available.

<sup>5</sup>Data relates to Table 9 of Horan et al., 2005. We have assumed nadir of BCS occurs at 100 days after parturition (see text).

<sup>6</sup>High (HGM) and Medium (HGM) genetic merit Holstein Friesian cows.

<sup>7</sup> Holstein Friesian genotypes of New Zealand (NZ) and United States (US) origins were used

<sup>8</sup> Treatment using thin cows (NZCS = 2.2)

<sup>9</sup> Treatment using fat cows (NZCS = 5.4)

<sup>10</sup> Treatment using cows of light Body Size (pre-experimental liveweight of 486 kg)

<sup>11</sup> Treatment using cows of heavy Body Size (pre-experimental liveweight of 618 kg)

<sup>12</sup> Replicates of Year 1, but cows selected based primarily on differences in liveweight