METHODOLOGY FOR THE DESIGN AND ENHANCEMENT OF GENETIC IMPROVEMENT PROGRAMS ILLUSTRATED IN THE CONTEXT OF THE NEW ZEALAND DAIRY INDUSTRY

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SUMMARY

This paper describes methodology that can be used for the design and enhancement of breeding programs of any livestock enterprise. It uses the New Zealand dairy industry as an example. The steps are arranged in a logical sequence starting with the definition of a breeding goal (what to improve), followed by the definition of a breeding objective (what traits should be improved and their relative emphasis) and the definition of the selection criteria (traits measured on the animals in order to evaluate them for the breeding objective traits). The breeding program requires the design of a breeding scheme to select the animals with highest estimated genetic merit for the breeding objective. There needs to be a system for the transfer of genes from high genetic merit animals into the commercial population. A mating system allocates cows to bulls under various plans including crossbreeding or assortative mating. The final step is economic analysis of the breeding program. These steps should be repeated iteratively to evaluate various scenarios including changes in the definition of the breeding objective, alternative selection criteria, different breeding schemes, dissemination systems and mating plans along with changes in the production system and adoption of new technologies at the farm level. In the presence of genotype by environment interactions there is a need to align the genetic and environmental resources. In the New Zealand dairy industry this has been achieved by modifying genotypes to match the pastoral production system. Current trends in the dairy industry are leading to more diverse farming systems that will demand specific genotypes (breed groups or specific bulls). The challenge for the dairy industry is to keep in harmony the collective actions of dairy farmers in concert with the management, economic and production circumstances.

KEY WORDS: breeding program, breeding objective, genetic resources, genotype by environment interaction.

RESUMEN

METODOLOGÍA PARA DISEÑAR Y PERFECCIONAR PROGRAMAS DE MEJORAMIENTO GENÉTICO ILUSTRADA DENTRO DEL CONTEXTO DE LA INDUSTRIA LECHERA DE NUEVA ZELANDA

Este escrito describe la metodología que puede ser usada para diseñar y perfeccionar un programa de mejoramiento genético de una organización de producción animal. Esta metodología es ilustrada en el contexto de la industria lechera de Nueva Zelanda. Los pasos son arreglados en una secuencia lógica iniciando con la definición de una meta de selección (que mejorar), seguido por la definición de un objetivo de selección (características de los animales que deben ser mejoradas y cual es la importancia relativa de cada una de estas características) y la definición de un criterio de selección (características que pueden ser medidas en los animales y que permitan la evaluación genética de las características incluidas en el objetivo de selección). El programa de mejoramiento requiere de un esquema de selección para seleccionar los animales con los valores genéticos más altos de acuerdo al objetivo de selección. Después se requiere de un sistema de diseminación para transferir los genes de los animales de alto valor genético a las vacas de la población comercial. Luego a nivel de granja se requiere de un

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plan de apareamiento para asignar a cada vaca el toro con que va a ser apareada bajo diferentes planes incluyendo cruzamiento y apareamientos ordenados. El paso final es la evaluación económica del programa de mejoramiento.
Estos pasos deben ser repetidos en forma iterativa para evaluar diferentes escenarios incluyendo cambios en la definición del objetivo de selección, diferentes criterios de selección, esquemas de selección, sistemas de diseminación, y planes de apareamiento, en paralelo con cambios en el sistema de producción y la adopción de nuevas tecnologías a nivel de granja. La presencia de una interacción entre el genotipo y el medio ambiente requiere de la sincronización entre el uso de los recursos genéticos y el uso de los recursos ambientales. En el caso de la industria lechera de Nueva Zelanda esta sincronización ha sido lograda por medio de la modificación de los genotipos existentes adaptándoles al sistema pastoril de producción de leche. Las tendencias actuales en la industria lechera están creando sistemas de producción de leche más diversos los cuales demandaran genotipos más específicos tales como grupos raciales o toros. El reto para la industria lechera de Nueva Zelanda es mantener en armonía las decisiones colectivas de los productores con los cambios en las circunstancias de manejo, económicas y productivas.

PALABRAS CLAVE: programa de mejoramiento genético, objetivo de selección, recursos genéticos, interacción genotipo por medio ambiente

INTRODUCTION

Genetic resources are defined as “the heritable characteristics of a plant or animal of real or potential benefit to people”. The term includes modern cultivars and breeds; traditional cultivars and breeds; special genetic stocks (breeding lines, mutants, etc.); wild relatives of domesticated species; and genetic variants of wild resource species. The reasons for conserving such a resource include the provision of direct and indirect economic benefits. However, the conserved genetic material must be made available to the people who require it to improve the productivity, quality, or pest resistance of utilized plants or animals”(Dunster & Dunster, 1996). The exploitation of genetic resources is therefore an important element in the development of livestock enterprises that provide economic benefit for commercial farmers. The rational use of genetic resources and their improvement for commercial livestock enterprises requires the design of a breeding program. Harris *et al*. (1984) presented a procedure for arranging choices, decisions and other relevant information to develop a breeding program in a procedure of eight steps. Garrick (2005) schematically summarised these steps and discussed their use in the design and enhancement of breeding programs of any livestock enterprise (Figure 1). The objective of this paper is to describe these steps, in relation to the rational use and the improvement of genetic resources. This will be done in the context of the New Zealand dairy industry.

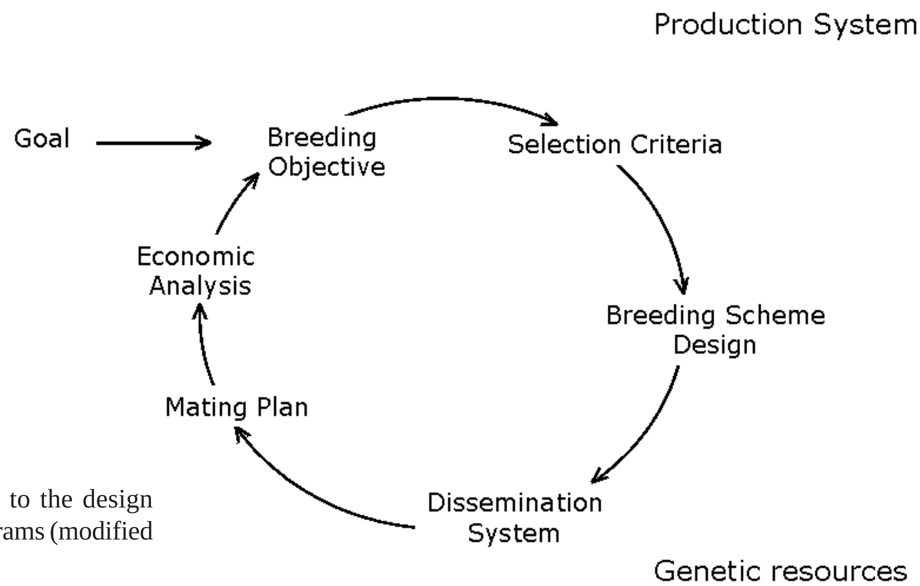

Figure 1. A systematic approach to the design and enhancement of breeding programs (modified from Garrick, 2005).

DESCRIPTION OF THE NEW ZEALAND DAIRY INDUSTRY AND PRODUCTION SYSTEMS

New Zealand is located at latitudes from 34 to 47° South of the equator. The country is mostly hilly and mountainous with relatively little easily-cultivable land. Rainfall distribution is strongly influenced by the mountains. The west coast of the South Island and mountain regions of the North Island receive over 2400 mm rainfall/annum. The northern and western regions of the North Island receives 1000-2000 mm, which together with mild winters are favourable for pasture growth, and it is here that dairy farming predominates. The east costs of both islands have a rainfall of 500-1000 mm, which is also good for pasture production, but the rainfall is less reliable and the winters are colder. Mean temperature during January rises to 19°C and the mean temperature in July, in some regions, lowers to 9°C. Total sunshine per year ranges from 1600 to 2100 hours.

The New Zealand dairy industry is vertically integrated from milk production, through manufacturing, to the marketing and foreign investment operations of Cooperative Dairy Companies. Fonterra Co-operative Group Ltd is the leading company controlling 95% of total milk production. For the production season 2003-04, the New Zealand dairy industry comprised 3.85 million cows distributed in 12,751 herds (Livestock Improvement, 2004). Dairy companies processed 14.599 billion litres of milk and 1.254 billion kilograms of milk solids. Only 5% of the milk produced is consumed within the country, the remaining 95% exported as butter, cheese, dried milk powders, and more than 800 dairy products. New Zealand currently produces less than 2% of the world's milk, but contributes about 30% of the traded produce. The dairy industry is New Zealand's largest business, making up about 7% of the country's gross domestic product and providing about 20% of its export receipts.

The milk payment system used to reward the producers reflects the international market situation for dairy products. The system incorporates protein, fat and volume: over the season 2003-04 the average payments were $2.80/kg fat, $5.70/kg protein and -4.0 cents/litre. The messages from the payment system are that higher concentrations of fat and protein result in higher milk value and that protein is more valuable than fat.

Milk production is based almost entirely on grazed high quality fresh pasture. There is a seasonal pattern of milk production dictated by the pasture growth curve. Management practices are directed to synchronise feed requirements of the herd with rates of pasture growth. Successful dairy businesses must achieve concentrated calvings (starting in late July) and this requires high submission and high conception rates in a typically eight-week period of artificial breeding. Variations in calving dates with latitude results in most artificial breeding occurring during October, November and December. Cows must calve every 365 days and reproductive management is therefore critical.

Indoor housing is not required at any time although supplementary feeding may be beneficial in certain management circumstances. Soil temperatures and sunshine hours limit yields of cereal and forage crops, which along with high fuel and machinery costs result in most concentrate feeds being more expensive than pasture. The average dairy farm is 111 hectares with 302 lactating cows grazing on mainly ryegrass-clover pastures, at 2.75 cows/ha. Some 10-16 t dry matter (DM) is grown annually per hectare with 60-85% of this being consumed by cows which can produce 70-90 kg milksolids (fat plus protein) per tonne DM consumed, or 500-1200 kg milksolids per ha. Summer pasture growth rates are often limited by moisture deficits, eroding daily milk yields and necessitating the early drying off of some cows. Accordingly, average lactation lengths are short by international standards.

Farming systems used on the majority of New Zealand dairy farms are very different from systems used in the rest of the world, and there are now wider differences between farming systems within New Zealand e.g. all-grass versus grass plus intensive supplementation. Farming systems in New Zealand can be classified (Table 1) according to the level of supplements (including hay, pasture silage, maize silage, concentrates and other feeds) used for milk production (Silva-Villacorta *et al*., 2005). High feed input farms have higher stocking rates than low feed input farms. High feed input farms achieve higher production of milksolids per cow per hectare than low feed input farms. The use of nitrogen fertiliser is also higher in the high feed input farms than in low input feed farms. There are also significant differences in farm size, reproductive characteristics of the herds and estimated pasture consumed per hectare. On average, extra feed was significantly associated with extra cows (0.17 cows/ha for 1 t extra DM) and extra milk solids (50 g/cow for 1 kg extra DM/cow and 96 g/ha for 1 kg extra DM/ha). The high feed input farms produced higher gross farm incomes per hectare but had higher farm working expenses per hectare, so that farm profit (economic farm surplus) per hectare was similar for these farms. Economic farm surplus is a measure of farm income less farm expenses and includes adjustments for changes in stock numbers, labour inputs and depreciation.

Table 1. Physical and financial characteristics of owner operated dairy farms in New Zealand classified by level of extra feed used for milk production during the season 2001-02 (Silva-Villacorta *et al*., 2005).

	Level of Extra Feed [1]		
	Low	**Intermediate**	**High**
Number of farms surveyed	46	76	73
Herd breeding worth ($/4.5 t DM)	77 [a]	79 [a]	74 [a]
Stocking rate (cows/ha)	2.5 [a]	2.6 [a]	2.7 [a]
Comparative stocking rate (kg live weight/t DM)	83 [a]	83 [a]	83 [a]
Extra feed input (kg DM/cow)	20	250	943
Extra feed input (kg DM/ha)	50	650	2546
Milk solids (kg/cow)	295 [a]	310 [a]	341 [b]
Milk solids (kg/ha)	744 [a]	808 [a]	921 [b]
Nitrogen (kg/ha/year)	67 [a]	84 [a]	116 [b]
Milk income ($/ha)	3941 [a]	4251 [a]	4888 [b]
Stock income ($/ha) [2]	471 [a]	540 [ab]	594 [b]
Gross farm income ($/ha)	4362 [a]	4679 [a]	5377 [b]
Labour costs ($/cow) [3]	307 [a]	314 [a]	316 [a]
Other animal costs ($/ha) [4]	348 [a]	380 [a]	462 [b]
Fertiliser costs ($/ha)	330 [a]	378 [b]	428 [c]
Total feed costs ($/ha) [5]	263 [a]	398 [b]	716 [c]
Overhead costs ($/ha) [6]	893 [a]	898 [b]	1202 [c]
Farm working expenses ($/ha) [7]	1735 [a]	2063 [a]	2675 [b]
Economic farm surplus ($/ha)	1849 [a]	1926 [a]	1902 [a]

[1] Values with different superscript letters are statistically different (within row) ($P < 0.05$).
[2] Stock income = net stock income + stock adjustment used for the estimation of economic farm surplus/ha.
[3] Labour costs = wages + labour adjustment used for the estimation of economic farm surplus/ha.
[4] Animal health, herd improvement, farm dairy and electricity.
[5] Total feed costs ($/ha) = costs of supplements made on farm (crop and re-grassing), supplements purchased, winter grazing-off and young stock grazing.
[6] Overhead costs = freight, weed and pest control, administration, standing charges, run-off lease and other expenses.
[7] Farm working expenses include wages but not the labour adjustment.

DESCRIPTION OF GENETIC RESOURCES

The breed composition of the New Zealand dairy herd is very dynamic. In the period of early settlement over 130-160 years ago, the cattle were mostly Shorthorns. Jersey cattle gradually became the dominant breed accounting for 79% of the cow population by 1960. Holstein-Friesian cattle accounted for 12% of the cow population at that time and represented a closed population used for fluid milk production. Those Holstein-Friesian cows were originally developed from animals imported from the West coast of the United States before 1925 (Harris and Kolver, 2001). From 1960 to 1985 the national herd was gradually upgraded to Holstein-Friesian using semen from New Zealand Holstein-Friesian bulls. Continued crossbreeding (rather than upgrading) between Holstein-Friesian and Jersey breeds has been actively practised since 1985. Crossbreeding with Ayrshire bull semen also takes place, but at a low level compared to the other two breeds (Montgomerie, 2002). The current national herd comprises 51% Holstein-Friesian, 15% Jersey, 26% crossbred Holstein-Friesian/Jersey, 1% Ayrshire and 7% other dairy breeds and their crosses (Livestock Improvement, 2004).

Productive performance, live weights and some measures of efficiency for the representative breeds of New Zealand dairy cattle are shown in Table 2. Holstein-Friesian cows produce on average 1193 litres milk and 24 kg protein more than Jersey cows but are on average 112 kg heavier than Jersey cows. Jersey cows have the highest concentrations of fat and protein. Ayrshire cows and Holstein- Friesian/Jersey crosses have intermediate productive performances and live weights in comparison to straight bred Holstein-Friesian and Jersey cows.

Three measures of efficiency can be calculated for each of the breed groups. Jersey cows have the highest feed conversion (kilograms of fat plus protein/kg pasture DM eaten) and the highest biological efficiency (kilograms of fat plus protein/kg metabolic live weight) than the other breed groups. In contrast under New Zealand conditions crossbred cows have the greatest economic efficiency or ability to convert feed into farm profit.

GOAL AND BREEDING OBJECTIVE

Definition of a breeding goal is the first step in designing an animal breeding program for the exploitation and enhancement of genetic resources in any livestock enterprise. Improvement of genetic resources focuses on directional change in the genetics of animals in coming generations such that they will produce the desired products more efficiently under expected future economic, social and ecological production environments (Groen, 2000). This direction of the improvement is formalised in

Table 2. Productive performance of major breed groups of dairy cattle in New Zealand (production season 2003-04; Livestock Improvement, 2004).

	Holstein-Friesian (F)	Jersey (J)	Crossbred FxJ	Ayrshire
Number of lactating cows	1,956,461	562,290	1,009,041	42,364
Lactation length, days	219	223	222	225
Milk yield, litres	4167	2974	3729	3739
Fat yield, kg	183	173	187	164
Protein yield, kg	146	122	141	134
Fat concentration, %	4.4	5.7	5.0	4.4
Protein concentration, %	3.5	4.1	3.7	3.6
Live weight, kg	490	378	444	442
Pasture dry matter required, kg[1]	4454	3732	4234	4064
Feed conversion efficiency[2]	73.9	79.1	77.5	73.3
Biological efficiency[3]	3.16	3.44	3.39	3.09
Economic efficiency[4]	126	132	146	86

[1] Pasture dry matter required for production, maintenance and pregnancy calculated according to AFRC (1991).
[2] Feed conversion efficiency calculated as (kg fat + kg protein)/t pasture dry matter.
[3] Biological efficiency calculated as (kg fat + kg protein)/(live weight$^{0.75}$).
[4] Economic efficiency calculated as the genetic superiority, with respect to a base cow born in 1985, to convert feed into farm profit per 4.5 t dry matter.

the breeding objective that identifies those animal traits that influence the goal and that farmers would therefore like to be improved.

The New Zealand dairy industry is one of few dairy industries of the world that has defined and communicated a clear goal for the rational use and improvement of genetic resources. The New Zealand Animal Evaluation Limited (www.aeu.org.nz) is a wholly owned subsidiary of Dairy InSight and has been set up to manage the national breeding objective. The logo of this organisation is the following "Animal Evaluation is designed for the New Zealand dairy industry, with the objective of identifying animals whose progeny will be the most efficient converters of feed into farmer profit".

Given a goal, the breeding objective can then be formally developed. This involves two somewhat discrete steps. First, the list of traits that influence the goal can be identified. Second, the relative emphasis of each of the traits in the list can be quantified. The resulting function of economic weights and breeding values defines the breeding objective. Some authors refer to this as the breeding goal. We prefer to use breeding goal to refer to a higher level description of what being sought after by genetic improvement. In the New Zealand case, this is farm profit per unit of feed. The traits in the breeding objective reflect milk revenue, beef revenue, reproduction costs, health costs, and feed costs. The breeding objective has the following form (AEU, 2005):

$$\begin{aligned} BW = {} & BV_{MILK} \times EV_{MILK} \\ & + BV_{FAT} \times EV_{FAT} \\ & + BV_{PROTEIN} \times EV_{PROTEIN} \\ & + BV_{LIVEWEIGHT} \times EV_{LIVEWEIGHT} \\ & + BV_{FERTILITY} \times EV_{FERTILITY} \\ & + BV_{SOMATIC\ CELL\ SCORE} \times EV_{SOMATIC\ CELL\ SCORE} \\ & + BV_{LONGEVITY} \times EV_{LONGEVITY} \end{aligned}$$

where BW is the aggregate genotype or index value defined as Breeding Worth and measures the genetic superiority or inferiority of an animal to convert 4.5 t pasture dry matter into farm profit. The amount of pasture dry matter required to satisfy the requirements of metabolisable energy for maintenance, pregnancy, production and proportional requirements of the average New Zealand dairy cow born in 1985 is considered the unit of feed and 4.5 t of dry matter. BV_i is the breeding value of animal for trait *i*, and EV_i is its corresponding economic value. The economic value expresses the extent to which the breeding goal is improved by one unit of genetic superiority for that trait, i.e., the economic value for each trait is the additional profit per 4.5 t of dry matter (average quality pasture) for a unit change in breeding value for trait *i*, all other traits in the objective held constant.

The economic values for each of the traits considered in the breeding objective are derived from a farm model that includes incomes from milk, cull cows and surplus calf sales; costs associated with farm operations, and feed required for production, growth and maintenance of cows and replacements (Harris, 1998a). These economic values are updated each year considering current farm costs and future values of milk components (Animal Evaluation Unit, 2005). Economic values calculated at February 2005 are shown in Table 3.

Table 3. Economic values of traits included in the breeding objective of New Zealand dairy cattle breeding program (values at February 2005; Animal Evaluation Unit, 2005).

Trait	Economic value
Lactation yield of milk, $/litre	-0.069
Lactation yield of fat, $/kg	0.840
Lactation yield of protein, $/kg	6.041
Cow live weight, $/kg	-0.822
Cow fertility, $/1%	1.509
Somatic cell score, $/unit	-21.456
Longevity, $/day	0.028

The negative value per litre of milk reflects that farm profit per 4.5 t pasture dry matter (the breeding objective) is reduced by $0.069 if the genetic superiority of the average cows is increased by 1 litre milk. Part of this is accounted for by the $0.04 penalty for milk volume to account for collection of milk and processing costs of dairy products. The remainder reflects the feed costs for lactose production that are not associated with increases in milk value. The economic value for live weight estimates a $0.822 reduction in farm profit/4.5 t pasture dry matter if a cow is genetically 1 kg heavier than the average cow. The economic value of protein yield is more than six times the economic value of fat yield; this is a direct function of the values of these components in the milk payment formula for the current and future years, and the feed costs for each of the components. The value of protein in the current milk payment system is about two times the value of fat but according to Fonterra predictions (Animal

Evaluation Unit, 2005) the future value of fat is declining with respect to the value of protein. Furthermore the feed cost for fat synthesis is higher than for protein synthesis; metabolisable energy requirements are 56 MJ/kg fat, 32 MJ/kg protein and 2 MJ/litre milk. Increases in the genetic superiority for cow fertility and longevity are associated with increases of $1.509/1% and $0.028/day, respectively, in farm profit/4.5 t dry matter. Increases in the genetic superiority for somatic cell score are associated with -$21.456 of farm profit/4.5 t pasture dry matter per score unit.

SELECTION CRITERIA

The second step in designing a breeding program for the rational exploitation of genetic resources of a livestock enterprise is determination of the selection criteria. In this step, the breeding program has to create a system to identify the animals with the highest genetic merit for the breeding objective. Hazel (1943) defined the selection criteria as those traits that can be measured on the animals and can be used as predictors of the traits included in the breeding objective. Traits included in the selection criteria may be the same or different from the traits in the breeding objective. If the traits are different, the selection criterion is known as an indicator trait and in this case it must be strongly linked to traits in the breeding objective. Indicators traits are commonly used as they are often easier or cheaper to measure than the objective trait itself.

The formulation of a selection index introduced by Hazel (1943) provided the means of combining phenotypic traits with relative weights in such a way that the correlations between true and estimated index values are maximized. The selection index apportions selection emphasis in the most appropriate way, based on the relative economic importance of the traits in the breeding objective, and the strength of genetic associations between selection criteria traits and breeding objective traits.

The New Zealand dairy industry, through the Animal Evaluation Unit (2005), has a well advanced system for the genetic evaluation of dairy cattle. There is a centralised data base in which herd-testing results are stored from about 74% of the lactating cows in each production season (Livestock Improvement, 2004). Since 1996 the national genetic evaluation system has been conducted across breed using single trait animal models with best linear unbiased procedures (Harris *et al.*, 1996). This system allows the simultaneous evaluation of cows and sires using all known relationships and is conducted with a common base for all breeds and crosses. The genetic base is that group of 1985-born cows of all breeds which had all traits recorded in 1987. The purpose of the evaluation system is the identification of the most efficient dairy animals to convert feed into farm profit, regardless of breed.

Estimated breeding values are obtained for the following traits:

Production: lactation yields of milk, fat and protein.

Cow liveweight.

Cow fertility.

Longevity.

Somatic cell score.

Traits other than production: adaptability to milking, shed temperament, milking speed, farmer's overall opinion, stature, capacity, rump angle, rump width, legs, udder support, front udder, rear udder, front teat placement, rear teat placement, udder overall and dairy conformation.

Calving difficulty.

Livestock Improvement Corporation additionally calculates breeding values for gestation length and feed intake.

The industry has created recording systems that links farm information to the national database for genetic evaluation. Reproductive and health events are being recorded in addition to the traditional herd-testing records. Advances in computer capacity and new methods of genetic evaluation and more comprehensive farm individual cow details are leading toward the estimation of breeding values with higher accuracy and the estimation of breeding values for new traits, especially health traits such as mastitis and lameness.

A crossbreeding experiment with crossbred Friesian-Jersey has been established in New Zealand for the identification of loci and chromosomal regions that contain loci that affect traits of importance in dairy cattle (Spelman *et al*., 2004). Results from this experiment are expected to enhance genetic gain by enabling direct selection on genes or genomic regions that affect economic traits through marker-assisted selection (Spelman & Garrick, 1997). Theoretically the use of genetic markers in conjunction with phenotypic observations provides more information on the genetic merit of the animal than phenotypic information alone, but the practical widespread application of marker assisted selection in the commercial cow population is still problematic due to costs of genotyping and technical feasibility of conducting genetic evaluation at the national scale. The use of marker assisted selection has been used in New Zealand in the pre-selection of bull mothers and young bulls entering progeny test (Spelman, 2002).

BREEDING SCHEME

A third step in the design of a breeding program involves a structure for the selection of animals with highest estimated genetic merit for the breeding objective. Reproductive rate of breeding animals and uncertainty about true genetic merit of breeding animals make up the most important limiting factors in the design of the breeding scheme; the task in designing a breeding scheme is to determine how many and which animals should be selected as parents of the next generation (Simm, 1998; Van der Werf, 2000). The breeding scheme dictates the potential rate of genetic progress that can be achieved in the breeding objective and has considerable influence on the cost-effectiveness of the breeding program (Garrick, 1993).

In New Zealand, progeny testing of young bulls continues to be the main strategy used by artificial insemination (AI) organisations (Livestock Improvement Corporation and Ambreed New Zealand Ltd) to provide farmers with semen from bulls of high genetic merit for farm profit. There are about 500 commercial herds totally dedicated to progeny testing about 440 bulls per year based on the performance of about 70 daughters per bull. Each year the AI organisations identify elite cows to be bull mothers and negotiate with the cow owners for the contract matings. About 6 bull mothers are contract-mated in order to produce each progeny tested bull. Once the results of the progeny test are available, about 10% of the best 5-year old bulls are selected to breed future replacements. Within such a breeding scheme, several factors can be varied, such as number of bull fathers (bulls to breed bulls), the age of bull mothers (cows to breed bulls), use of embryo transfer on bull mothers, number of young bulls to test, and number of test daughters per bull tested (size of progeny group).

Foundation publication regarding the selection of breeding animals through four selection pathways was outlined by Roberston and Rendel (1950). The four pathways were cows to breed cows (*cc*), cows to breed bulls (*cb*), bulls to breed cows (*bc*) and bulls to breed bulls (*bb*). Each path differs in the age at which animals are selected, the amount of information available for the selection decision, the number of animals available for selection and the number of animals selected. Table 4 shows approximate numbers for these pathways although in reality each artificial insemination company runs a separate breeding scheme for each breed. Livestock Improvement Corporation is also progeny testing crossbred Holstein-Friesian/Jersey bulls within the breeding scheme, taking advantage of the across-breed genetic evaluation system. Information provided in Table 4 can be used to calculate the rate of genetic gain (ΔG) for the breeding goal using Rendel and Robertson (1950) formula:

$$\Delta G = \frac{(í_{cc} \times r_{cc}) + (í_{cb} \times r_{cb}) + (í_{bc} \times r_{bc}) + (í_{bb} \times r_{bb})}{L_{cc} + L_{cb} + L_{bc} + L_{bb}}$$

where σ_g is the genetic standard deviation of aggregate genotype of all the animals of the population (estimated at $40.8), í is the intensity of selection, *r* is the accuracy with which the genetic merit (or aggregate genotype) of the animals can be estimated using the available selection criteria, *L* is the generation interval defined as the age of the parents when their progeny is born. Subscripts *cc*, *cb*, *bc* and *bb* denotes each selection pathway. Using relevant genetic parameters, current economic values and information provided in Table 4, the theoretical annual rate of genetic gain is calculated to be $9.94/4.5 t dry matter. Actual genetic gain for the whole population during the last 10 years is $9.23/4.5 t dry matter, very similar to the theoretical value.

Many possible alternative breeding schemes can be imagined. These involve various combinations of sizes of the active cow population (cows to breed cows), number of half-sib offspring in each progeny group, number of young bulls to be progeny tested each year, number of bulls selected to breed cows and bulls, age at which parents are selected, etc. each leading to a different rate of genetic gain and different overall costs of the breeding program. Research has reported many techniques to help develop optimum breeding schemes for maximum rates of genetic gains (Searle, 1962; Skjervold, 1963; Hunt *et al.*, 1974) and maximum rates of genetic gains at minimum costs of the breeding program (Oltenacu and Young, 1974; Dekkers *et al.*, 1996).

DISSEMINATION SYSTEM

This involves considers the design of a system for the transfer of genes from high genetic merit animals, already identified in the breeding scheme, into the commercial population. The choice of the transfer strategy is largely determined by the size of the commercial population and by the cost and efficiency of biotechnologies available such as artificial insemination, multiple ovulation and embryo transfer (MOET), trans vaginal recovery and in vitro production of oocytes (TVR / IVP), cloning, and sexed semen.

Table 4. Cow and bull populations, number of animals selected, their accuracy, and generation intervals for the four selection pathways in the selection scheme considering all breeds.

Selection Pathway	Population size	Number Selected	Accuracy of selection[1]	Generation interval
Cow to cow	3,850,000	3,850,000	0.61	5.3
Cow to bull	600,000	2,500	0.61	4.0
Bull to cow	440	44	0.88	6.5
Bull to bull	440	12	0.88	6.0

[1]Accuracy of selection is the correlation between the true and estimated aggregate merit. The square of this number is known as reliability and is published on sire summaries and herd reports.

Artificial insemination has remained the main breeding technology in New Zealand for dispersal of favourable genes from high genetic merit bulls into the cow commercial population. The speed with which these genes are established in the commercial population depends on the number of cows inseminated to the bulls carrying the favourable genes and the proportion of cows calving to the inseminations. About 75% of lactating cows and less than 10% of heifers are artificially inseminated; the rest of the animals are naturally mated (Livestock Improvement, 2004). These percentages combined with high pregnancies rates at the end of the mating season (about 90%) and low culling rate (22%) ensure that virtually every cow replacement entering the herd is the progeny of a high genetic merit bull.

One unique feature of the dissemination system in New Zealand is the widespread use of fresh semen for artificial insemination. Using fresh semen has allowed the semen concentration in each straw to be reduced, so the top bulls can be used more intensively. Using a sperm concentration of 1 million per straw, over 300,000 inseminations per bull per year have been achieved (Vishwanath, 2004). Breeding companies provide fresh semen to farmers from a team of selected bulls under a rostering system rather than individual bulls. Bulls of the higher genetic merit within the team receive the greatest possible use, while bulls further down the list are used only if required to meet demand. Semen will probably come from 8-10 bulls for any one herd during the spring mating period. The leading group of bulls provides 65-80% of inseminations. Animal Evaluation continually updates the bulls' proofs using herd tests and breeding companies continuously revise the composition of the bull team; this process may result in the team being rostered in a different ranking than originally planned.

Artificial insemination as a breeding technology used for the dissemination of genetic improvement into the commercial dairy cow population has proven to be simple, economical and successful (Vishwanath, 2004). The use of MOET and TVR / IVP as dissemination systems, has been restricted to production of progeny from elite cows carrying specific set of genes or genetic markers. Cloning is still commercially infeasible and will be probably integrated into specialised sectors of the breeding scheme rather than used as a widespread dissemination strategy. Vishwanath (2004) indicated that there is a reliable and practical technique to sex semen based on measurement of the DNA content of individual sperm. However, there are currently significant impediments that limit the national use of this technology as a dissemination system: the slow speed of the sexing process and high costs to use this technology.

The effectiveness of a dissemination system is partly reflected by the genetic lag, which is defined as the time needed to transfer genes from the high genetic merit animals (the bull team in the case of the dairy cattle) to the commercial cow population. In the New Zealand dairy industry the actual rate of genetic gain is about $9.2 per year, the genetic merit of the bull team (top 50 bulls of all breeds in September 2005) was $198 and the genetic merit of all lactating cows in the commercial population was $85. Based on these numbers the actual genetic lag between the bull team and the commercial population represents 12.3 years of genetic progress (($198-$85)/$9.2/year).

MATING PLANS

Designing a mating plan includes deciding among inbreeding, crossbreeding, assortative mating, or random mating strategies (Harris *et al*., 1984). Inherent in these decisions are the specification of the mating ratio of female to male and the number of breeding seasons to be used for the selected individuals.

Decisions on the breeding program are more under the control of artificial insemination companies than individual dairy farmers. They decide the number of young bulls entering the progeny testing scheme and number of proven bulls available for the dairy farmers. Therefore, individual farmers have little control over the direction and the rate of genetic change achieved by the whole industry. Farmers, however, can choose the breed of the bulls used to breed the cows of the herd. These decisions are facilitated by the system of genetic evaluation across breed and adjusted to a common genetic base.

Farmers are using crossbreeding as a mating plan to exploit heterosis effects. Montgomerie (2005) reported estimates of heterosis for traits considered in the breeding objective of the New Zealand dairy industry for the first crosses between Holstein-Friesian, Jersey and Ayrshire (Table 5). Farmers are practicing crossbreeding with systematic mating plans such as a two-breed rotational system. Other farmers are using the bulls with the highest genetic merit regardless of breed. Effects of crossbreeding and breed complementarity can increase profitability for commercial farmers (Lopez-Villalobos and Garrick, 2002).

Breeding companies have included in the progeny testing scheme crossbred bulls and now they are commercially available for dairy farmers. In the latest runs of genetic evaluation, 3 crossbred bulls have appeared in the top 30 bulls ranked by BW; the top sire of the list at September 2005 was a crossbred bull. Availability of crossbred bulls for mating commercial cows allows farmers many complex mating plans that should consider breed and crossbreeding effects, preferences for individual bulls and traits and some control of inbreeding at the herd level (Lopez-Villalobos I 2004). Artificial insemination companies have developed computer programs for the design of mating plans considering these factors. Livestock Improvement Corporation has developed Customate Plus and Ambreed New Zealand Ltd have made available TGRM™ to commercial farmers.

Level of inbreeding of dairy cattle populations is increasing and becoming a concern in many countries. Inbreeding in dairy cows reduces their viability and their productive, reproductive and economic performance (Smith *et al*., 1998). In the United States, the current inbreeding coefficients of Holstein, Jersey and Ayrshire cow replacements born in 2005 are 5.1, 7.0 and 6.0%, respectively (AIPL, 2005). Kearney *et al*. (2004) reported average inbreeding coefficients of 2.6 and 3.1% for female and male animals born in 2002 in the British Holstein-Friesian population. The authors of this paper are not aware of some publications reporting the level of inbreeding in the New Zealand cow population.

The increase in inbreeding in the cow population can be attributed to a number of factors including, the tendency to select and mate related animals as a result of using breeding values estimated using best linear unbiased procedures, which use all known relationships between the individuals with records and without records, and 2) the use of few sires in the commercial population facilitated by artificial insemination. In the case of the New Zealand breeding program, the effects of these two factors are reduced by the fact that a large proportion of cow replacements are produced by crossbreeding. Some significant inbreeding levels may appear in straight bred animals if few sires are used in the breeding scheme (bull fathers) and commercial population (cow fathers).

Table 5. Estimates of first-cross heterosis effects in New Zealand dairy cattle (adapted from Montgomerie, 2005).

	Holstein-Friesian x Jersey	Holstein-Friesian x Ayrshire	Jersey x Ayrshire
Milk, litres	139	88	146
Fat, kg	7.7	3.6	8.1
Protein, kg	5.5	3.0	5.6
Cow live weight, kg	9.4	0.1	13.5
Cow fertility, %	3.4	3.4	2.2
Somatic cell score	-0.06	-0.16	-0.05
Longevity, days	227	137	131

ECONOMIC ANALYSIS

The last but perhaps the most important step in the design of a breeding program is the economic analysis of the breeding program, which is a very complex exercise only achieved through modeling of the whole system (Harris *et al*., 1984). The simulation must assume that the breeding program is not under the control of the industry, but a result of the collective actions of dairy farmers in concert with economic and genetic aspects of the available genetic material (Garrick & Lopez-Villalobos, 1998).

A difficulty in the simulation work is the definition of the variable measuring the overall effectiveness of the breeding program. Some variables may be: 1) rate of genetic gain in the breeding goal achieved in the commercial population, 2) industry economic benefit considering an integrated industry accounting for all factors affecting farm productivity, factors affecting the processing of milk into dairy products and its commercialisation in the form of dairy products, 3) profit for artificial breeding companies which basically is determined by semen revenue minus the costs of the breeding scheme, and 4) profit for commercial dairy farmers. Figure 1 shows that design of the breeding involve the definition of a number of steps in a sequential way. Each step is linked to the other steps and each single factor considered in one step affect previous and later steps of the design. The simulation work should consider these relationships to find optimum values of variables considered in the breeding program under given economic and environmental circumstances. For example, Figure 2 shows the optimum size of the progeny group, in which the Breeding Worths of dairy sires are estimated, to maximise the annual genetic gain in the breeding objective ($ farm profit/4.5 t DM) or industry benefit (industry revenue minus cost of the breeding scheme) of the New Zealand dairy industry. Annual genetic gain is maximised with 40 recorded daughters per bull whereas industry benefit is maximised with 65 recorded daughters per bull.

Artificial insemination companies continuously review their breeding programs to evaluate current and futures changes at the farm or industry level. For example, Rendel et al. (1996) outlined a methodology used (at that time) by Livestock Improvement Corporation to evaluate different breeding schemes that maximised sustainable net income of New Zealand dairy farmers. This methodology was described in five steps: 1) calculate the change in genetic merit expected in each selection pathway of the breeding scheme, 2) calculate the change in on-farm product flows expected from the changes in genetic merit, 3) calculate the change in on-farm revenues and costs associated with the product flows, excluding semen and/or technology costs, and discount to a present value, 4) calculate the change in costs associated with semen production and/or technology costs and discount to a present value, and 5) calculate the net present value of the change - this being (3) - (4).

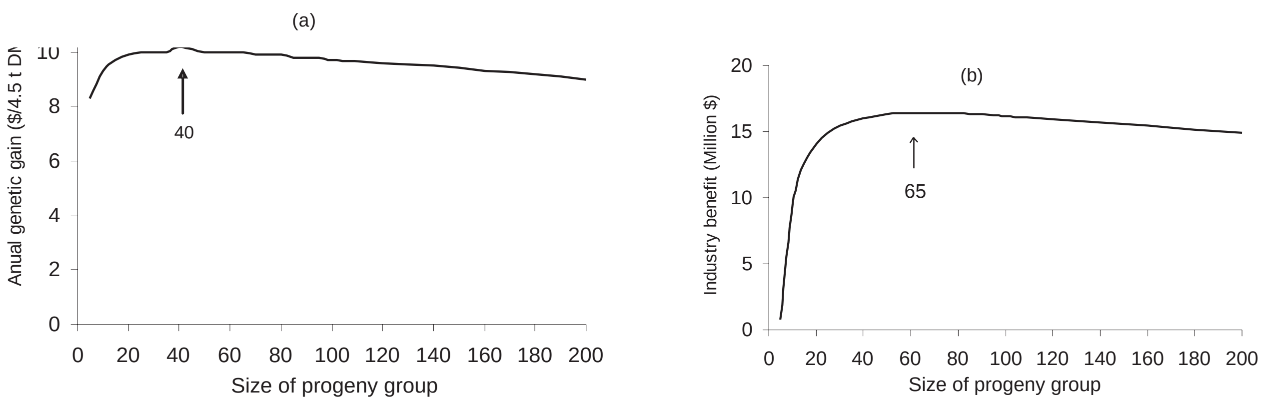

Figure 2. Optimum sizes of progeny groups to maximise (a) annual genetic or (b) industry benefit.

SYNCHRONISING GENETIC IMPROVEMENT WITH DIFFERENCES IN MANAGEMENT AND ENVIRONMENT

The general equation to represent the phenotypic performance (*P*) of an animal is given by the equation (Falconer and Mackay, 1996): $P = G + E$, where G = genotype of the individual and E = environmental influences. Traditional population genetics shows that the phenotypic variation (V_P) observed between individuals is caused by three components (Falconer and Mackay 1996): $V_P = V_G + V_E + 2COV_{GE}$, where V_G is the genetic variation, V_E is the environmental variation and COV_{GE} is the covariance between genotype and environment. Generally COV_{GE} is assumed to be zero assuming that phenotypic variation measured in a population is only the result of the genotypic and environmental variations. In many situations, however, the COV_{GE} term is significant and arises as an interaction between the genotype and the environment (Falconer and Mackay, 1996). Genotype by environment interaction (*GE*) is defined as the differential phenotypic expression of different genotypes subjected to a range of environments. Studies in dairy cattle show that significant *GE* can be caused by level of production (or feeding level), herd size, lactation persistency, days in milk to peak yield, calving pattern, age at first calving, rate of maturity, percentage of North American Holstein genes, temperature, radiation and annual rainfall (Fikse *et al*., 2003; Kolmodin, 2003; Zwald *et al.*, 2003; Bryant *et al.*, 2005).

Evidence of *GE* in New Zealand has been shown in a number of studies (Kolver, 2001; Bryant *et al*., 2003; Kolver *et al.*, 2005; Bryant *et al*., 2005). For example Kolver (2001) reported results from an experiment comparing two strains of Holstein Friesian cows under two feeding systems; grazed pasture (all-pasture) or total mixed ration (TMR). Strains were New Zealand Holstein-Friesian (NZHF) and overseas Holstein-Friesian (OSHF) cows with similar Breeding Worth. Results from three consecutive years (Table 6) indicate that the feeding system influences the relative performance of the two strains. On the all-pasture diet, OSHF cows were significantly less likely to get in calf, lost more body condition during spring, gained less live weight during lactation, and were less efficient at producing a kilogram of milksolids per kilogram of live weight compared to NZHF. When fed TMR, OSHF had similar reproduction, gained live weight at similar rates during mid and late lactation, and had a similar efficiency of milksolids production as NZHF.

The presence of *GE* requires that genetic and environmental resources should be in synchrony, which can be achieved in two ways (Harris, 1998b): 1) the producers modifying the production system to match that required by the genetic material generated by the breeding program, or 2) the breeding organisation modifying the genetic material to match the production system. Harris (1998b) indicated that the poultry industry has achieved a high degree of synchronisation between genotypic and environmental resources through to modification of the environment (housing, feeding system, health management, etc). The second option has been taken by extensively managed cattle and sheep because of the limited ability of producers to modify their environment when reliance is on grazed pasture feed sources.

The New Zealand industry has followed the second option to exploit genetic resources in synchrony with prevalent economic and environmental conditions. The current breeding program has been designed to improve the genotype of the cows for future market conditions but still under grazing conditions. However, the New Zealand dairy industry is continuously changing the production system. Main trends at the farm level are: strategic use of supplementary feed paralleling the genetic improvement of dairy cows, use of crossbreeding, increases in herd size, and once a day milking. These factors can create important *GE's* and breeding companies are considering modifications in the breeding program to match these environmental changes. There is good reason for concern if the ranking of bulls which are progeny tested on the average farm production system (grazing herd, 302 cows, and twice a day milking) do not rank the same when progeny of those bulls are exploited under high feeding systems, bigger herds or once a day milking. There is evidence of significant re-ranking of bulls when they are tested in low and high feed input systems (Bryant *et al*., 2005). Whether we like it or not the environment will change and the breeding program has to be continuously revised and adjusted to produce genetic material that will match the future production, management and environmental circumstances.

CONCLUSIONS

There is a logical and systematic procedure to design new breeding programs and enhance current breeding programs for the genetic improvement of animals in livestock enterprises. The breeding program for the genetic improvement of New Zealand dairy cattle can be used to illustrate the application of this methodology. The breeding goal of the New Zealand dairy industry is clearly defined

Table 6. Production and reproduction of New Zealand Holstein-Friesian (NZHF) and Overseas Holstein Friesian (OSHF) cows with similar genetic merit for farm profit, grazing grass at approximately 80 kg LW/t DM (all-pasture) or fed a total mixed ration (TMR) (Kolver, 2001).

	Feeding system			
	All-pasture		TMR	
	NZHF	OSHF	NZHF	OSHF
Days in milk				
1998/1999	261	242	268	261
1999/2000	277	243	272	256
2000/2001	300	298	300	298
Milksolids, kg/cow				
1998/1999	281	271	380	401
1999/2000	356	329	497	509
2000/2001	465	459	602	720
2000/2001 (3rd lactation cows)	508	494	696	773
LW gain during lactation, kg/cow				
1998/1999	55	22	123	139
1999/2000	57	21	125	110
2000/2001	44	-20	92	77
Drying-off condition				
1998/1999	4.6	3.9	6.2	5.5
1999/2000	4.4	3.6	6.8	5.4
2000/2001	5.0	4.6	7.6	6.1
Efficiency, kg MS/kg metabolic LW				
1998/1999	3.11	2.74	4.0	3.82
1999/2000	3.64	3.14	4.68	4.34
2000/2001	4.42	3.97	5.26	5.72
Intake, %LW (2000/2001)				
Spring	3.57	3.26	4.01	4.07
Summer	3.24	3.26	3.32	3.44
Autumn	2.96	2.92	3.04	3.32
Empty rate, % (No. of cows) brackets)				
1998/1999 season	0	22(2)	7(1)	10(1)
1999/2000 season	7(1)	38(5)	14(2)	21(3)
2000/2001 (to 28th February)	7(1)	62(8)	14(2)	29(4)*
Time to walk to paddock, min				
1998/1999	5.39	6.15	-	-

as farm profit per unit of feed, as feed is the most limiting resource. This breeding goal is expanded in terms of a breeding objective considering the economically relevant animal traits affecting the breeding goal and their relative emphasis. Many traits are considered in the selection criteria and current statistical procedures allow the estimation of breeding values for these traits. The breeding scheme is still based on a sire progeny testing scheme exploiting four selection pathways but advances in molecular genetics and genetic evaluation can be integrated to enhance this scheme not only on the sire selection pathway. Genes from few high genetic merit bulls are rapidly disseminated into the commercial cow population through the use of artificial insemination principally from fresh semen. Other reproductive technologies are currently used in the breeding scheme but limited to the generation of young bulls entering the progeny test scheme. New Zealand dairy farmers use few high genetic bulls because semen technology (fresh semen) and artificial insemination allow the heavy used of few bulls for the whole cow population. Systematic crossbreeding schemes are used by dairy farmers as mating plans to exploit crossbreeding effects; computer programs to assist farmers with complex decisions are available. There are complex relationships between the components of the breeding program and the economic analysis of the breeding program can be achieved only through system modeling. The presence of genotype by environment interaction requires that genetic and environmental resources should be in synchrony. This has been achieved in the New Zealand dairy industry by modifying the genotype of the animals to fit the production system. However, many genotypes will be required because tomorrow's farming systems are becoming more diverse.

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