ADVANCES IN DAIRY CATTLE BREEDING

Johan A.M. *Van Arendonk*, Piter *Bijma*, Ab F. *Groen*, Henk *Bovenhuis*, E.W. *Brascamp*

Animal Breeding and Genetics group
Wageningen University, PO Box 338, 6700 AH Wageningen
The Netherlands
E-mail: Johan.vanArendonk@alg.vf.wau.nl

SUMMARY

One of the conditions for sustainable dairy cattle breeding is the long term availability of breeding stock which meets sustainable breeding goals. Sustainable breeding goals pay proper attention to all traits relevant from an economic, societal and environmental point of view. In practice this implies broadening of formal breeding goals by including both yield traits and functional traits. It is discussed how long term genetic change can be achieved maintaining genetic variation on an acceptable level. It is shown that in Holstein Friesian, which is the currently predominant dairy cattle population, the effective population size is too low, which deserves attention from a long term perspective. It is argued that embryo cloning for commercial use of crossbreds may enhance sustainable genetic improvement. Also the opportunities offered by incorporating molecular genetic information are discussed.

Key words: Dairy cattle, breeding goals, genetic change, inbreeding, cloning, genetic markers

INTRODUCTION

Long term availability of breeding stock which meets sustainable breeding goals can be seen as one of the factors leading to sustainable animal production. This implies that genetic changes achieved should aim at breeding goals which are relevant from a economic, societal and environmental point of view. Long term availability of stock probably predominantly concerns economic and political factors, but we will focus on genetic ones and will discuss ways to maintain long term genetic variability and population fitness. We will limit our paper to dairy cattle breeding.

World wide there currently are about 1.3 x 10^9 head of cattle of which some 225 million (17%) are dairy. Although these harbour large genetic variability maintained in a large number of breeds, in developed countries dairy production is highly dominated by a small number. Of these, Holstein Friesians (some 75% of all milk recorded dairy cattle) is the most important one, with a strong degree of exchange of genetic material world wide. We will, therefore, discuss aspects affecting genetic variability in this population. Doing this we will particularly focus on ways to genetically improve the population maintaining genetic variation and on the effects of new technologies like molecular biology and cloning.

BREEDING GOAL

Genetic improvement of cattle has a long history. Hengeveld (1865), for example, refers to Dutch "melkerijën en kaasmakerijën", which have been famous since older times, and cattle from Holland and Friesland which were preferred above other cattle. This suggests that selection for dairy traits has a long history and it is probably fair to say that selection primarily has been for a combination of dairy production traits and conformation traits. Particularly in Europe, with a large herdbook influence, conformation received considerable attention. In the second part of the 20th century attention gradually shifted to milk production traits receiving most attention in selective breeding, particularly stimulated by the availability of well predicted breeding values for bulls for these traits. Currently, in national evaluations of bulls and in international comparisons, increasingly the ranking of bulls is on total merit, combining milk or solids and functional traits. In Germany, for example RZG combines milk production, conformation, somatic cell count, longevity, fertility and calving difficulty. In the table below some examples of these total merit indices are given.

Table 1: Examples of total merit indices (index) in various countries.

Land	Index	Groups of traits in addition to milk, fat and protein
Canada	LPI	Udder score, leg score, total conformation score and capacity
Denmark	S-index	feed intake, fertility, calving ease, mastitis, frame, feet & legs, udder, milkability, temperament
Germany	RZG	Conformation, Somatic cell count, longevity, fertility and calving ease
France	ISU	conformation, milkability
The Netherlands	DPS	Sustainability: longevity, udder, somatic cell count, fertility, calving ease
USA	TPI Net Merit	Udder score, leg score, conformation Longevity, somatic cell count

It is clear from Table 1 that these indices are similar in that they are combining similar groups of traits. The weighing of these categories varies among countries and to some extend may reflect differences in markets, but no doubt also is a consequence of marketing strategies of different breeding organisations. International comparisons of breeding values by Interbull were started some ten years ago for milk production traits. Correlations of these predicted breeding values across countries are high which leads to international focus on similar bulls. Differences in rank order will be larger for total merit indices, partly due to differences in weighing of groups of traits. Partly these larger differences in ranking are temporary and of a purely statistical nature. Initiatives are underway to improve the comparability of procedures and measures involving functional traits which gradually again will lead to higher rank correlations of bull's breeding values across countries. These initiatives are GIFT, the European Concerted Action on "Genetic Improvement of Functional Traits in Cattle" and the Working Group on Functional Traits of the ICAR (the International Committee on Animal Recording). The approach followed by GIFT (Interbull bulletin no 25, page 221) is to define groups of functional traits to be included in the breeding goal, and to predict each of those by combinations of measurements and (conformation)scores (Groen et al. 1997). There is considerable theory on the weighing of traits to be combined in aggregate breeding goals. An overview of this was given by Groen et al. (1997). Generally, effects on farmers' profit is used to derive the size of economic weights keeping in mind that the weights should reflect the relative relevance of traits under future production circumstances. Brascamp et al. (1998) discussed this rationale in the context of environmental factors affecting animal production world wide. They suggested that these factors either may limit input (for example feed or water, in some regions of the globe) or may be considered as accessible by trade. In the first case breeding goals should be expressed per unit of input, which means that breeding aims at more profitable production restricting inputs to a certain level. In the second case environmental factors will affect relative economic weights through the inclusion of costs, like in Steverink et al. (1994) who included effects of nitrogen and phosphorus legislation in The Netherlands on a dairy cattle breeding goal. In that case inputs are varied in such a way that profitability is optimised. This rationale also can be used to derive weights of traits in total merit indexes, but in that case contributions of functional traits on farm profitability should be derived. Recently, Olsen et al. (2000) argued not to limit weighing of traits to economic arguments alone, but to include ethical and social considerations. This particularly may affect weights of functional traits that enhance animal welfare and consumer acceptance of products and probably contributes to goals being sustainable.

LONG TERM GENETIC CHANGE

Relationships between production and functional traits and fitness traits tend to be unfavourable (Rauw et al., 1998, Hill, 2000). This would limit long term genetic change if reduction of fitness becomes a limiting factor. In case of total merit index it is likely that the relationship between breeding goal and fitness becomes less negative or even zero. In that situation, fitness still may diminish by inbreeding and accompanied inbreeding depression. Recent developments in theory (Woolliams and Bijma, 2000) enables optimisation of breeding programmes jointly predicting genetic change and rate of inbreeding. Also operationally recently dynamic selection algorithms were developed to minimise inbreeding in bull selection (Meuwissen and Sonesson, 1998). In their analyses, these strategies realised up to 44% more genetic gain with the same rate of inbreeding as compared to BLUP alone. Additional limitation of mating of relatives further increases genetic gain given the rate of inbreeding (Sonesson and Meuwissen, 2000). The question remains, however, which rate of inbreeding is acceptable. Meuwissen and Woolliams (1994) chose the approach where natural selection was taken as the mechanism to balance the effect of inbreeding depression. In absence of negative correlation between fitness and the trait under selection they found rates of inbreeding ranging from 0.2 to 1.6% per generation. Goddard (1992) found similar inbreeding levels when studying optimum effective population size of a global black and white population. Another approach was followed by Hill (2000), taking mutation to balance loss of variation and concluded that a rate of inbreeding of 1% per generation seems acceptable to maintain heritability on reasonable levels. Taking all these arguments together Bijma (2000) concludes that a rate of inbreeding per generation between 0.5 and 1% seems acceptable. Current rates of inbreeding in various *commercial* populations seem to be around 0.1% per year, which is some 0.6% per generation (Brascamp, 1998). Future rates are expected to pass these levels because of current small effective size of the internationally integrated *breeding* population. For example, in The Netherlands, Prins (1999) analysed the contribution of particular sires to the genes of female candidates for selection. Carlin M Ivanhoe Bell contributed some 50% of all genes to these female candidates. Using the approach of genetic contributions developed by Wray and Thompson (1990), the dominant contribution of this sire alone would lead to a rate of inbreeding per generation of 1.56%. It is important to mention that this would only occur when breeders select bull dams and bull dams without taking into account the pedigree. As indicated above, methods were developed to combine continued genetic change with a limited rate of inbreeding and these methods are applied in some dairy cattle breeding schemes. However, current international competition of dairy cattle breeding programmes combined with exchange of genetic material among them stimulates strategies primarily aimed at short term response. Wickham and Banos (1998) showed that narrowing the genetic base is a phenomenon common to many programmes. Among the almost 5000 bulls from 18 countries born in 1990, evaluated by the Interbull Center, 50% were bred by only five sires. As a conclusion it seems that maintaining a sufficiently large genetic base deserves attention.

CONTRIBUTION OF MOLECULAR BIOLOGY

Molecular genetic techniques have made it possible to identify differences between individuals at the DNA level . In particular the development of microsatellite markers as an abundant source of polymorphic and convenient markers has boosted the generation of linkage maps in the most important livestock species. These maps provide the basis for detection and exploitation of genes segregating at loci that have an effect on important traits. These are referred to as quantitative trait loci (QTL). Environmental factors as well as an undefined number of QTL influence the majority of economically important traits in livestock. Dissecting these traits into their Mendelian components is an important driving force behind the ongoing efforts to map QTL in livestock. Information from phenotypes and marker genotypes can be utilized to pinpoint chromosomal areas that explain a substantial amount of genetic variation. A number of publications have reported on mapping of QTL for production traits (e.g. Georges et al., 1995; Spelman et al., 1996) and functional traits (e.g. Schrooten et al., 2000).

Molecular genetics offers the opportunity to dissect phenotypic differences at the molecular level, which provides more detailed genotypic information on individuals as well as information on which alleles or chromosomal segments are transmitted by a parent to its offspring. As summarized by Van Arendonk et al. (1999), molecular genetic information can be used to improve the genetic evaluation of animals in several ways: 1) incorporating known genotypes; 2) marker-assisted genetic evaluation; 3) construction of a marker-based relationship matrix and 4) genomic model. Molecular genetic information offers the opportunity to better exploit phenotypic information but collecting phenotypic information remains important in order to identify the genetically unique individuals.

Although currently there is still only limited impact of molecular biology on dairy cattle breeding programmes, considerable research is underway. Current applications are limited to some mono-genetic traits like BLAD, DUMPS, Factor XI-deficiency, coat color and double muscling. Nevertheless, the current state of the cattle gene map is quite impressive (Gellin et al., 2000) with some 1500 microsatellite markers and some 800 genes. Genetic markers are currently used on a small scale in dairy cattle breeding programmes in The Netherlands and New Zealand, as examples. In The Netherlands, genotyping of animals is limited to bulls and to cows which are kept in nucleus herds, and marker information is used to predict breeding values simultaneously using phenotypic and marker information (Bink and Van Arendonk, 1999). In New Zealand current application builds on the routine DNA-sampling of all test daughters of young bulls carried out for pedigree verification (Spelman, 1999). In that case, within families marker-alleles are identified which positively associate with desired traits and progeny testing of a future generation of young bulls is limited to those inheriting these positive marker-alleles from their father (so called bottom-up approach).

Potential genetic benefits of marker assisted selection (MAS) are evaluated by in a large number of studies. The benefits of MAS largely depend on the amount of genetic variance explained by the marked chromosomal segments. Spelman et al. (1998), pointed out that a limitation of MAS is that linkage phase has to be estimated for each family. To overcome this problem, the genes themselves would have to be identified or marker haplotypes that are in disequilibrium with the genes. They reported increases in genetic gain ranging from 10 to 55% in different breeding structures when 50% of the genetic variances could be explained. These levels of genetic response are not what could be achieved today but possibly in 10 years time.

Optimizing the longer-term genetic gain results in putting a higher weight on the information from the selection candidate or its offspring, i.e. the Mendelian sampling term of the individual. Molecular genetic data might play an important role here because it provides information on genetic material that has been transmitted by the parent to its offspring. This provides opportunities for selection at a very early age or even the pre-implantation embryo. However, the effects of alleles that are transmitted in most cases need to be estimated from information on relatives. These estimates of allelic effects, in particular in schemes with short generation intervals, might be largely based on ancestral information, which puts more emphasis on ancestral phenotypic information. Consequently, predicted differences between individuals will be small. This can be avoided by collecting phenotypic information on selection candidates or their collateral relatives. This stresses the point made earlier that molecular genetic information offers the opportunity to better exploit phenotypic information but collecting phenotypic information remains important in order to identify the genetically unique individuals.

It is interesting to note that utilisation of genetic markers to limit the rate of inbreeding would be to equalise the contribution of both alleles per locus to progeny. Wang and Hill (1999) showed that with a limited number of two markers per chromosome the rate of inbreeding might be diminished with some 10-20% in random mating populations. In selected populations this decrease will be less. The bottom-up approach described above will have the opposed affect because it favours the contribution of specific alleles per locus.

CONTRIBUTION OF REPRODUCTIVE TECHNOLOGY

As discussed by De Boer (1994) the application of cloning would dramatically change the structure of dairy cattle production because it creates a sharp border between a nucleus population to improve the genetic level of the population and a commercial population utilising clones or semen. Most if not all arguments related to definition of breeding goal and long term genetic change hold similarly for the situation of clones. One new development may be anticipated, however. It is likely that the exchange of nucleus breeding stock among breeding programmes, as it takes place now, strongly will diminish, as it is the situation in poultry and pigs. Also, it may well be that marketing of crossbred clones will emerge, which even more enables to genetically close nucleuses. At first sight this may be a development which is negative for dairy producers because the trade in breeding stock on the basis of internationally comparable breeding values will disappear. On the other hand, commercial stock probably will be globally available. In contrast to the expectation of Ruane et al. (1997) for the long term maintenance of genetic variability this development may bear an advantage, however. Currently, the free exchange of breeding stock among breeding organisations advocates a strong weight on short term responses. It is likely, that in the situation of cloning, a limited number of closed programmes around the world more easily can aim for long term responses at nucleus level and concentrate marketing of crossbred commercial products.

REFERENCES

BIJMA, P., 2000. Long-term contributions: prediction of rates of inbreeding and genetic gain in selected populations. PhD Thesis, Wageningen University

BINK, M.C.A.M., VAN ARENDONK, J.A.M., 1999. Detection of quantitative trait loci in outbred populations with incomplete marker data. Genetics **151**: 409-420.

BRASCAMP, E.W., 1998. The development of animal breeding enterprises in the next decades: Reasons to change the structure of breeding programmes. Acta Agric. Scand. Section A. Anim. Sci. Suppl **28**: 61-67.

BRASCAMP, E.W.; GROEN, A.F.; DE BOER, I.J.M.; UDO, H., 1998. The effect of environmental factors on breeding goals. Proc. 6th World Congress on Genetics Applied to Livestock Production, Armidale, Australia. 27: 129-136.

DE BOER, I.J.M., 1994. The use of clones in dairy cattle breeding. PhD thesis, Wageningen University, The Netherlands.

GELLIN, J.: BROWN, S.:, MARSHALL GRAVES, J.A.; ROTHSCHILD, M.; SCHOOK, L.; WOMACK, J.; YERLE, M., 2000. Comparative gene mapping workshop: progress in agriculturally important animals. Mammalian Genome, 11: 140-144.

GEORGES, M., NIELSEN, D, MACKINNON, M., MISHRA, A., OKIMOTO, et al., Mapping quantitative trait loci controlling milk production in dairy cattle exploiting progeny testing. Genetics 139: 907-920.

GODDARD, M.E., 1992. Optimal effective population size for the global population of black and white dairy cattle. J. Dairy. Sci. **75**: 2902-2911.

GROEN, A.F.; STEINE, T.; COLLEAU, J-J.; PEDERSEN, J.; PRIBYL, J.; REINSCH, N., 1997. Economic values in dairy cattle breeding with special reference to functional traits. Report of an EAAP-working group. Livestock Production Science **53**: 1-21.

HENGEVELD, G.J., 1865. Het rundvee, zijne verschillende soorten, rassen en veredeling. page 3.

HILL, W.G., 2000. Maintenance of quantitative genetic variation in animal breeding programmes. Livest. Prod. Sci. **63**: 99-109.

MEUWISSEN, T.H.E.: SONESSON, A.K., 1998. Maximizing the response of selection with a predefined rate of inbreeding: overlapping generations. J. Anim. Sci. **76**: 2575-2583.

MEUWISSEN, T.H.E.; WOOLLIAMS, J.A., 1994. Effective sizes of livestock populations to prevent a decline in fitness. Theor. Appl. Genet. **89**: 1019-1026.

OLESEN, I.; GROEN, A.F.; GJERDE, B., 2000. Definition of animal breeding goals for sustainable production systems. Journal of Animal Science, **78**: 570-582.

PRINS, A., 1999. Optimalisatie van het nucleus programma gericht op de internationale markt. Msc. thesis, Animal Breeding and Genetics Group, Wageningen University, Wageningen, The Netherlands.

RAUW, W.M.; KANIS, E.; NOORDHUIZEN-STASSEN, E.N.; GROMMERS, F.J., 1998. Undesirable side effects of selection for high production efficiency in farm animals: a review, Livestock Production Science **56**:15-33.

RUANE, J.; KLEMETSDAL, G.; SEHESTED, E., 1997. Views on the potential impact of cloning on animal breeding and production, Acta Agric. Scand. Section A. Anim. Sci. **47**: 209-212.

SCHROOTEN, C., BOVENHUIS,H., COPPIETERS, W., VAN ARENDONK, J.A.M., 2000. Whole Genome Scan to Detect Quantitative Trait Loci for Conformation and Functional Traits in Dairy Cattle. J. Dairy Sci., **83**: 795-806.

SONESSON, A.K.; MEUWISSEN, T.H.E., 2000. Mating schemes for optimum contribution selection with constrained rates of inbreeding. Genet. Sel. Evol. (in press).

SPELMAN, R.J. , 1999. Integration of molecular and quantitative genetics in the New Zealand dairy industry. In proceedings “From Jay Lush to Genomics: visions for animal breeding and genetics”, Iowa State University, May 16-18: 160.

SPELMAN, R.J. COPPIETERS, W., KARIM, L., VAN ARENDONK, J.A.M., BOVENHUIS, H, 1996. Quantitative trait loci analysis for five milk production traits on chromosome six in the Dutch Holstein-Friesian population. Genetics **144**: 1799-1808

SPELMAN, R.J., GARRICK, D.J., VAN ARENDONK, J.A.M., 1999. Utilisation of genetic variation by marker assisted selection in commercial dairy cattle populations. Livest. Prod. Sci. **59**: 51-60.

STEVERINK, M.H.A.; GROEN, A.F.; BERENTSEN, P.B.M., 1994. The influence of environmental policies for dairy farms on dairy cattle breeding goals. Livestock Production Science **40**: 251-261.

VAN ARENDONK, J.A.M., BINK, M.C.A.M, BIJMA, P., BOVENHUIS, H., DE KONING, D.-J. , BRASCAMP, E.W., 1999. Use of Phenotypic and Molecular Data for Genetic Evaluation of Livestock. In proceedings “From Jay Lush to Genomics: visions for animal breeding and genetics”, Iowa State University, May 16-18: 60-69.

WANG, J.; HILL, W.G., 2000. Marker-assisted selection to increase effective population size by reducing mendelian segregation variance. Genetics **154**: 475-489.

WICKHAM, B.W.; BANOS, G., 1998. Impact of international evaluations on dairy cattle breeding programmes. Proc. 6th World Congress on Genetics Applied to Livestock Production, Armidale, Australia. 23: 315-322.

WOOLLIAMS, J. A.; BIJMA, P., 2000. Predicting rates of inbreeding in populations undergoing selection. Genetics **154**: 1851-1864.

WRAY, N.R.; THOMPSON, R., 1990. Prediction of rates of inbreeding in selected populations. Genet. Res. Camb. 55: 41-54.