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ABSTRACT

Selection programs for increasing milk production per cow have been very successful over time. This success has been partially due to the consideration of few other traits. Unfortunately, many traits related to costs of production and cattle functionality (i.e., “functional traits”), such as fertility and health, are antagonistically correlated with milk yield. Therefore, the average merit for these traits has decreased over time. The decline in functionality, along with increased awareness of the costs of production and animal well-being, has spurred interest in breeding for improvement in functional traits. Unfortunately, factors such as low heritability and lack of data make the selection for functionality more difficult than for production. Research has been able to overcome some of these limitations, at least to some extent, through the development and application of advanced statistical analyses and through indirect selection on genetically correlated traits. Possibilities exist in the future for additional refinement of selection procedures for improvement of functional traits. Computing capacities are continually increasing and more complex but statistically appropriate analysis methods are being developed. Furthermore, genome scans have identified chromosomal regions that have putative associations with functional traits. The bovine genome has been recently sequenced, so the possibility to identify the genes affecting functional traits exists, at least in theory. With low heritabilities and difficulties in measurement, functional traits are the ideal candidates for the application of marker-assisted selection.

Key words: Dairy cattle, Breeding, Functional traits.

RIASSUNTO

SELEZIONE PER IL MIGLIORAMENTO DEI CARATTERI FUNZIONALI NELLA VACCA DA LATTE

I programmi di selezione finalizzati all’aumento della produzione di latte vaccino hanno sempre avuto un grande successo, in parte dovuto al limitato numero di altri caratteri considerati. Sfortunatamente, molti dei caratteri legati al costo di produzione e quelli funzionali, come la fertilità e la salute, sono negativamente correlati con la produzione di latte. Pertanto il loro valore medio è diminuito nel tempo. La riduzione dell’efficienza riproduttiva, insieme all’aumentata attenzione verso i costi di produzione e il benessere animale, ha stimolato l’interesse verso una selezione per i caratteri funzionali. Purtroppo fattori come una bassa ereditabilità e una carenza di dati rendono la selezione per questi caratteri più difficoltosa di quella per la produzione. La ricerca è stata capace di superare alcuni di questi limiti, almeno fino a un certo grado, attraverso lo sviluppo e l’applicazione di analisi statistiche avanzate e attraverso una selezione indiretta sui caratteri geneticamente correlati. In futuro, esistono delle possibilità per un ulteriore perfezionamento delle procedure di selezione finalizzate al miglioramento dei caratteri funzionali. Le capacità di calcolo stanno continuamente aumentando e si stanno sviluppando dei metodi di analisi più complessi, ma statisticamente più appropriati. Inoltre, analisi del genoma hanno identificato regioni cromosomiali che hanno apparenti associazioni con i caratteri funzionali. Il genoma bovino è stato recentemente sequenziato così che la possibilità di identificare i geni che condizionano i caratteri funzionali esiste,
Introduction

For many years, genetic improvement of dairy cattle was based almost exclusively on increased production per cow. Some selection decisions considered conformation traits, especially in the final choice of dams of sires, but many of the formal indexes produced by national agencies placed most, if not all, of the emphasis on milk production traits. For example, prior to 1994, the official selection indexes published by the United States Department of Agriculture (USDA, 2005) considered only production traits (Van Raden, 2004). The strong emphasis on production was easily justifiable: 1) Milk sales are the primary source of income for most dairy producers; 2) the infrastructure for recording of milk production was available and programs for data collection and storage were active, and 3) genetic improvement is maximized when only a single trait is considered, so selection for functional traits would have decreased the responses obtained for yield traits. Genetic gains in the productive capacity of dairy cattle were remarkable. For example, the yearly genetic trend in the US Holstein population was more than >110 kg per year during the 1990’s (USDA, 2005). However, things have changed in the past 10 years. More and more dairy farmers and breeding organizations are becoming concerned not only with how much milk a cow gives, but how she does it. The way a cow functions has gained considerable attention. The term “functional” traits has been coined to refer to the phenotypic characteristics that affect or indicate a cow’s well-being, and such traits are now being actively included in selection indexes. The functional traits are a diverse group, including measures of reproductive performance, health and disease resistance, feed consumption, and longevity.

The objective of this manuscript is to discuss breeding for improvement of functional traits, including reasons why they have recently gained in importance, special limitations with functional traits that have affected their rate of adoption, and procedures that have or can be used to allow for their incorporation into breeding programs.

General discussion

Importance of Functional Traits

The reasons for the relatively recent interest in functional traits (and past emphasis on production) are many and diverse. Many of these reasons are indirectly tied to adoption of new technologies and increased production per cow. As production per cow increased, production per farm has increased as well. Thus, a single farmer can now produce a quantity of milk sufficient for many people. The size of farms has increased and the number of farms has decreased. These factors have changed management approaches. In the past, one farmer with a small herd was responsible for all aspects of dairy farming, including milking, feeding, health care, and breeding decisions. In today’s large farms, the owner may act primarily as a supervisor and financial manager. In this role, the farmer may be more aware of the costs of production rather than on income. With larger herds, computer software will likely be used for management of financial information, and costs of veterinary intervention, reproductive management and feeding can be organized for simple evaluation. The effects on profit of a particular health problem, mastitis for example, may be more obvious than for a small farm without computerized health records. In large farms, cattle are often housed and managed in groups and the farmer may lack the time or facilities to care for the needs of individual cattle. In small herds, individual cows with functional problems can more easily receive special treatment to allow them to remain productive and profitable. In large herds, such cows may simply be culled, resulting in a loss. In some ways, cattle have become more like machines and trouble-
free cows are important, because individuals with a problem can affect profit by not only directly increasing costs associated with treatment (increased labor, drugs, etc.), but also by disrupting the routine procedures of daily management of rest of the herd.

The increase in production per cow has had other influences on the importance of functional traits, in addition to the indirect effects associated with increased farm size. First of all, breeders may be satisfied with the current genetic trends for production and see improvement of functional traits as a more pressing concern. This is particularly true in countries where the introduction of milk quotas has limited the marginal returns from increasing yield. Furthermore, many health and reproductive traits have negative genetic correlations with production (Pryce et al., 1997). Experiments with lines of cattle selected for increased production have demonstrated that genetically superior cattle for production require more health care and higher treatment costs (Dunklee et al., 1994; Jones et al., 1994). Therefore, the great achievements obtained in genetic improvement for milk yield have been obtained at the cost of diminished fertility, disease resistance and general functionality (Pryce and Veerkamp, 1999). Intense selection for production has had other effects on functional traits in addition to those due to antagonistic genetic correlations between the respective traits. The genetic gains in milk yield were obtained by identifying a few superior animals and using technologies such as artificial insemination and embryo transfer to increase family sizes. This approach to selection has led to a great reduction in the effective population size of most dairy cattle breeds (Weigel, 2001) and increased rates of inbreeding (Kearney et al., 2004). Inbreeding depression is likely to be more severe for functional traits like fertility and survival than for production and has probably contributed to observed phenotypic decreases in these traits.

Producers are more likely to become aware of a health or management problem as the rate of its incidence increases. The threshold of awareness has apparently been crossed by many producers with respect to reproductive efficiency. Phenotypically, measures of fertility have declined markedly in the past 20 years (Beam and Butler, 1999; Van Raden et al., 2004). Many breeders of Holstein cattle in the US have begun experimenting with crossbreeding (McAllister, 2002). It is clear that these breeders currently place a higher value on improved functional traits than on increased production.

Finally, some of the reason for increased awareness of functional traits may be due to the influences from outside forces. The general public is continually becoming more concerned about the source of their food. Many people want to be sure that the animals whose products they are consuming were well treated during the production phase. This concern is due to both a desire to see animals treated well and for concerns about food safety, since healthy animals are likely to produce more healthful food, which is free from pathogens, antibiotics and other drug residues.

Obstacles to Selection for Functional Traits

Breeding for improvement of functional traits presents some difficulties, and this fact may also help to explain why functional traits have only recently gained what seems now to be well-deserved attention. First of all, functional traits generally have much lower heritabilities than do the typical production traits. Table 1 has estimates of heritabilities for production and functional traits from a group of studies in which both types of traits were evaluated together. The estimated heritabilities for the production traits ranged from around 0.20 to nearly 0.50 for the yield traits, averaging around 0.30. The heritabilities reported for fat percentage were generally greater than for yield from the same study (Uribe et al., 1995). In contrast, reported values for the heritabilities of the functional traits were much lower. Among the traits evaluated in these studies, the interval between calving and first estrous or first insemination had the highest heritability estimate (from Royal et al., 2002). The reported value was 0.16, which was lower than the lowest reported heritability for the production traits. In addition, other studies found much lower values for the same trait. Heritability estimates for the other traits ranged from 0.01 to 0.15 (Table 1). With heritabili-
Table 1. Heritabilities of production, functional, and indicator traits.

| Trait type | Trait                        | Heritability       |
|------------|------------------------------|--------------------|
| Production | Milk yield                   | 0.17 to 0.45       |
| Functional | Fat yield                    | 0.25 to 0.47       |
|           | Protein yield                | 0.20 to 0.34       |
|           | Fat %                        | 0.31 to 0.41       |
|           | Calving interval             | 0.02 to 0.07       |
|           | Interval for return to estrous | 0.02 to 0.16     |
|           | Number of services           | 0.02               |
|           | Mastitis incidence           | 0.03 to 0.15       |
|           | Cystic ovaries               | 0.02               |
|           | Retained placenta            | 0.01 to 0.02       |
|           | Ketosis                      | 0.08               |
|           | Milk fever                   | 0.04 to 0.09       |
|           | Longevity                    | 0.04 to 0.10       |
| Indicator | Body condition               | 0.10 to 0.58       |
|           | Change in body condition     | 0.07 to 0.10       |
|           | Somatic cell count           | 0.14 to 0.20       |
|           | Udder depth                  | 0.18 to 0.33       |
|           | Teat length                  | 0.21 to 0.33       |
|           | Foot angle                   | 0.09 to 0.15       |
|           | Lactation persistency        | 0.18               |

1 From Short and Lawlor (1992); Jairath et al. (1995); Uribe et al., (1995); Van Dorp et al., (1998); Dechow et al., (2001); Royal et al., (2002); Berry et al., (2003); and Muir et al., (2004); Carlén et al. (2005).
from the perspective of data recording and statistical analysis. In some cases, obtaining an objective measurement is difficult, expensive, or almost impossible. For example, mastitis is the most important disease economically for dairy production. Thus, a genetic evaluation based on its incidence could be of great value in a selection program, especially considering its antagonistic genetic relationship with production. In theory, such a program could be based on farmers recording mastitis incidence. However, one problem with this approach may be that different farmers likely have ideas about what constitutes an infection. In Scandinavia, this problem has been avoided somewhat, as the genetic evaluation is based on treatments by veterinarians. However, variability is still likely to exist among veterinarians (Kelton et al., 1998) and, in the end, the farmer makes the decision on whether or not to call the veterinarian. These factors may, in part, be responsible for the low estimates of heritability for mastitis incidence (Table 1). Extending the example, mastitis exists in both clinical and subclinical forms. The selection program in Scandinavia is based on the clinical form, but subclinical mastitis is actually responsible for the majority of economic losses from udder infections (Raubertas and Shook, 1982). Considering this factor, the ideal data collection procedure should probably be based on tests for the presence of bacteria pathogens in the udder, to detect both clinical and subclinical mastitis, but such a system would require enormous costs.

Another advantage that production traits have over many functional traits is that the data for yield are continuous and tend to be normally distributed. Lactational production per cow can take just about any values between 5000 and 25,000 kg, with most of the data centred around a population average. Data with these properties are easy to analyse statistically with a standard linear model. Most of the statistical procedures commonly used for genetic evaluation assume that the dependent variables (or at least the residual effect) are normally distributed. Furthermore, the genetic model generally believed to be correct is an infinitesimal model, which assumes that the genetic effect contributing to an animal’s phenotype is the sum of the effects of many genes. This leads to a continuous and normally distributed genetic effect.

In contrast, many functional traits are not normally distributed. Many are dichotomous, taking one of two possible values. For example, cows can be either sick or healthy, pregnant or open, dead or alive. In other cases, ordered categories have been created, to help assign a numerical phenotype to a trait that is otherwise ambiguous. For instance, a cow may have no problem calving (y = 1), a few problems (y = 2), a lot problems (y = 3), or surgery (y = 4). Even when traits values are continuously distributed, they may not be normally distributed. For instance, the average herd life of a dairy is around 36 months (Short and Lawlor, 1992), but many animals will be culled quite early and thus survive only a month or two after their initial calving. Still others can be quite long lived and surpass 100 months. This results in a skewed distribution. In all of these cases, either a special statistical model should be applied or the data should be transformed to yield a statistically appropriate analysis. In general, the special statistical model requires more complicated software and increased computing time and expense. Transformation can yield estimates that are difficult to interpret on the original phenotypic scale. For these reasons, the standard linear model is often applied for genetic evaluation, regardless of the distribution. Such a procedure results in decreased estimates of heritability and lower potential selection accuracy (Gianola, 1979). Estimates of breeding values (EBV) from the linear model and statistically appropriate model are usually highly correlated (Boettcher et al., 1999), but can still result in significant re-ranking of sires. The most appropriate method is thus recommended, although a simple evaluation is superior to no evaluation. A final shortcoming is that even when traits are continuously distributed and can be relatively easily recorded, such as for the interval from calving to first estrous, official recording would nonetheless be of the “B” type, according to the International Committee for Animal Recording (ICAR, 2005).

Practical Approaches to Selection for Functional Traits

Despite the aforementioned difficulties associated with many functional traits, many countries
have been able to start implementing national genetic evaluations for selected traits and, in some cases, international evaluations (Interbull, 2005). In many cases, the inherent problems with functional traits have been overcome or circumvented by imaginative approaches. The first of these is taking advantage of the opportunities for indirect selection. Indirect selection is based on the recording and genetic evaluation of a trait that is genetically correlated with a trait of interest, rather than the trait itself. This approach is often used when the trait of direct interest has low heritability, is difficult or expensive to measure, or both. Response to indirect selection can be greater than to direct selection if the two traits are highly correlated and if the correlated trait has a markedly higher heritability than the trait of interest (Falconer and Mackay, 1996). A classic example of this approach is the use of somatic cell count (SCC) to select for mastitis. As mentioned previously, collection of data for mastitis incidence is challenging. First, in many countries, mastitis incidence is not routinely recorded. In instances where mastitis data is recorded, the phenotype is usually dichotomous and is based on veterinary treatment, as requested by the farmer. Heritability thus tends to be quite low, usually less than 0.10 (Table 1). However, SCC is often recorded as part of the management data offered by milk recording agencies and large historical databases exist in many countries, as it can have a direct economic value, by influencing the price of milk. The genetic correlation between mastitis incidence and somatic cell count is in the range of 0.60 to 0.80 (Carlén et al., 2002). The phenotype can be recorded objectively and is continuous and normally distributed following a logistic transformation (Ali and Shook, 1980). As a result, estimates of heritability for SCC tend to be 2 to 3 times higher than for mastitis incidence (SCC). In addition, somatic cell score is an indicator of both clinical and subclinical mastitis.

Other possibilities for indirect selection can be identified. Examples of heritabilities for indicator traits are in Table 1, and most tend to be higher than heritabilities for the functional traits. Persistence of lactation has been suggested as a trait to be considered for indirect selection. In theory, cattle that have relatively low peak yield and maintain production at a reasonably high level may be less subject to metabolic problems associated with negative energy balance (Sölker and Fuchs, 1987). Although this relationship has yet to be fully demonstrated, the possible use of persistence has gained attention because the recent adoption of test day models has opened up the possibility to calculate EBV for persistency. Heritability estimates for persistency can tend to be at least 5 times greater than estimates for metabolic and fertility traits (Table 1). Body condition score (BCS) has also been proposed as a criterion for indirect selection against metabolic disorders and to help improve the reliability of genetic evaluations for reproductive traits (e.g., Dechow et al., 2001). Estimates of heritability for BCS range from moderate to high, whereas heritability estimates for metabolic disorders and fertility traits tend to be low (Table 1). Although BCS, unlike SCC, is measured subjectively, evaluators can be trained together and a reasonably cohesive system can be developed. In many countries, the scoring of BCS has been assigned to classifiers for type traits. These experts will generally score tens of thousands of cows in a given year. Change in BCS during a lactation may be a more informative trait than average BCS and random regression could be used to develop EBV for specific parts of the lactation where loss of body condition is especially detrimental.

The more traditional type traits can also be used for indirect selection. Feet and leg traits are associated with lameness and other locomotive disorders (Boettcher et al., 1998b). A selection index that considers multiple feet and leg traits can yield higher selection accuracy than direct selection against lameness and some countries currently include such an index in the national breeding goal (e.g. Canadian Dairy Network, 2005). In addition to SCC, udder traits are also genetically correlated with mastitis incidence. In general, genetic correlations between udder traits and mastitis incidence tend to be lower than between mastitis and SCC, but heritability estimates are usually greater (Boettcher et al., 1998a). For maximum accuracy, information on SCC and udder traits can be combined into an index for selection against mastitis (e.g. Boettcher et al.,
Traits related to body dimension can be used to help to select for increased feed efficiency. Large cows need to consume more feed for maintenance than do small cows and this difference can be accounted for in an index to select for total economic merit (e.g. Van Raden, 2002). Increased size also tends to be negatively associated genetically with longevity.

In fact, many type traits have a significant genetic relationship with longevity (Short and Lawlor, 1992). This fact allows for the possibility to create a multi-trait index to select indirectly for increased longevity. In some respects, longevity does not seem to be as obvious a candidate for indirect selection as do certain other functional traits. For example, the heritability for longevity is not as low as typically observed for fertility or disease resistance traits. Also, longevity can be measured accurately and objectively, using only the information routinely recorded by milk recording agencies. However, the problem with longevity data lies in the timing of data recording. Cows do not fully express longevity until they leave the herd.

Considering the currently high genetic trends for production, many bulls will be removed from active service due to low EBV for milk before they have enough daughters with recorded longevity to obtain an accurate progeny test. Type traits, however, are usually recorded during a cow’s first lactation and can thus be used to give an immediate indirect EBV for longevity.

Although longevity has a tangible economic value (unlike some traits used for indirect selection), it can also be considered a trait for indirect selection. Cows can be culled for a wide number of reasons, ranging from high disease incidence to low fertility to behavioural problems. In some respects, longevity can be considered an implicit index for selection for all of these additional functional traits, each weighted by its relative importance as informally assigned by the breeder. In animal breeding circles it has been discussed whether a more detailed index, formally calculating EBV and economic values for the component traits underlying longevity, is even needed, or if longevity is a reasonable and efficient proxy for general health and profitability.

Technologies leading to faster and more efficient computers and new algorithms have allowed for the introduction and adoption of more appropriate statistical methods and software for non-linear estimation of genetic parameters and genetic evaluation of functional traits. A specific example can be cited for longevity. The Survival Kit, a software package developed by Ducrocq and Sölkner (1998), applies survival analysis for evaluation of longevity. Survival analysis analyses the effect of an animal’s genetics on the probability that she will be culled at time t, given she has survived up to time t. It has the particularly attractive quality of being able to correctly account for animals that have not yet finished their productive lives at the time of data collection (and thus have not fully expressed their longevity). The records from these animals are considered to be censored on the date of data collection and are used only to evaluate risk of culling at time points up to the time of censoring. Many countries, including most of Europe, have adopted this methodology for their respective national genetic evaluations for longevity (Interbull, 2005). In addition, survival analysis has also been used to analyse other functional traits based on times to a given event, such as fertility (Schneider et al., 2005) and mastitis infection (Carlén et al., 2005).

The relatively recent developments in statistical analysis have also been particularly helpful for the evaluation of functional traits. The introduction to animal breeding applications of Bayesian analysis with Markov Chain Monte Carlo (MCMC) methods (e.g. Wang et al., 1993) and the use of generalized linear mixed models (e.g. Tempelman, 1998) have been especially useful. The former uses iterative procedures to generate samples from the distribution of genetic parameters, conditional on the data available. This process decreases the amount of computer memory required for an analysis, relative to other methods that require maximization of complex likelihood functions. These approaches have been used primarily to analyse traits with categorical distributions, by implementation of the threshold model. The threshold model assumes that the variability underlying a categorical trait is determined by continuous variable called “liability”, and there exist thresholds that determine into which category the observed phe-
notype falls (Fulconer and Mackay, 1996). The MCMC procedures continually sample liability values, conditional upon the observed categories and other parameters in the model, and these “augmented” data are then analysed with a standard linear model. Threshold models have been applied for the analysis of fertility (Averill et al., 2004), mastitis (Rekaya et al., 2003), longevity (Boettcher et al., 1999), calving ease (Luo et al., 2002), and lameness (Boettcher et al., 1998b), among other functional traits.

**Future Possibilities for Functional Trait Selection**

The future holds further opportunities to refine selection on functional traits. At the current time, MCMC methods are primarily used for estimation of genetic parameters, but generally not for routine genetic evaluation. Although they demand relatively little memory to implement, MCMC approaches can require significant time, due to the need to generate many samples from the respective posterior distributions. They also would (or could) produce posterior distributions of EBV for all animals, which could involve the need for great deals of data storage, depending on the implementation of the evaluation. However, technological advancements in computing hardware may soon eliminate such obstacles. These advancements may also enable the application of more complex statistical models for the analysis of functional traits. For example, Detillieux and Leroy (2000) noted that SCC data are a combination of data from two distributions, from healthy and infected cattle, and proposed the use of a finite mixture model for genetic analysis. This concept was further developed by Ødegard et al. (2003) and Boettcher et al. (2005). In these studies, the mixture model was found to be superior to the standard linear model, at least based on statistical measures of fit to the data. More research is still required, however, to refine the model and to understand the results and implications on a biological basis.

Molecular genetics may also provide a useful tool for selection to improve functional traits. According to Meuwissen and Goddard (1996), the traits that stand to reap the most benefits from marker assisted selection are those that have low heritabilities, are difficult or expensive to measure, can measured only after the desired age for selection, or can be measured in only one sex. Most functional traits have at least one of these characteristics. Genome scans have already identified numerous chromosomal regions where possible quantitative trait loci for functional traits seem to be located (e.g. Schroen et al., 2000). The bovine genome has been recently sequenced and is available in public databases. Different research projects are underway for the discovery of single nucleotide polymorphisms. These tools, along with genetics maps and databases from other species should allow for the eventual identification and characterization of multiple genes that have influences on functional traits.

**Conclusions**

For many years, the genetics of functional traits of dairy cattle were largely ignored as breeding programs emphasized increasing production per cow. Functional traits were either considered less important or more difficult to evaluate and phenotypic improvement was based on environmental modification rather than breeding. This trend has changed in recent years, as producers have become more concerned about the costs of production and advancements in data recording and statistical analyses have made genetic evaluation of functional traits more feasible. The interest in breeding for functionality is likely to increase in the future as new and existing analysis procedures become routinely adopted and opportunities for marker assisted selection for functional traits become available.

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DAIRY CATTLE BREEDING AND FUNCTIONAL TRAITS

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