The Old School, Brewhouse Hill, Wheathampstead,
Hertfordshire AL4 8AN, UK

Animal Welfare 2010, 19(S): 39-49
ISSN 0962-7286

The impact of genetic selection for increased milk yield on the welfare of dairy cows

PA Oltenacu*[†] and DM Broom[‡]

[†] Department of Animal Science, Oklahoma State University, Stillwater, OK 74074, USA
[‡] Centre for Animal Welfare and Anthrozoology, Department of Veterinary Medicine, University of Cambridge, Madingley Road, Cambridge CB3 0ES, UK
* Contact for correspondence and requests for reprints: toni.oltenacu@okstate.edu

Abstract

Milk yield per cow has more than doubled in the previous 40 years and many cows now produce more than 20,000 kg of milk per lactation. The increase in production should be viewed with concern because: i) the increase in milk yield has been accompanied by declining fertility, increasing leg and metabolic problems and declining longevity; ii) there are unfavourable genetic correlations between milk yield and fertility, mastitis and other production diseases, indicating that deterioration in fertility and health is largely a consequence of selection for increased milk yield; and iii) high disease incidence, reduced fertility, decreased longevity and modification of normal behaviour are indicative of substantial decline in cow welfare. Improving welfare is important as good welfare is regarded by the public as indicative of sustainable systems and good product quality and may also be economically beneficial. Expansion of the Profitable Lifetime Index used in the UK to include mastitis resistance and fertility could increase economic response to selection by up to 80%, compared with selection for milk production alone. In the last 10 years, several breeding organisations in Europe and North America followed the example of Nordic Countries and have included improving fertility and reducing incidence of mastitis in their breeding objectives, but these efforts are still timid. A multi-trait selection programme in which improving health, fertility and other welfare traits are included in the breeding objective, and appropriately weighted relative to production traits, should be adopted by all breeding organisations motivated in their goal of improving welfare.

Keywords: *animal welfare, dairy cattle, fertility, mastitis, milk yield, selection*

Introduction

Farm animals have been undergoing human-managed selection ever since their original domestication. Initially, selection was probably limited to docility and manageability, but in the last 60 years breeding programmes have focused on the genetic improvement of production traits, such as milk yield, growth rate and number of eggs.

From the beginning, selection was based on animals' phenotype with the hope that their offspring would also exibit superior phenotype. A major advance in selection practice occurred in the mid-20th century, with the advent of quantitative genetics based on principles of heredity and modern statistical theory (Hazel 1943). In practice, the phenotype of an individual and a substantial number of its relatives is recorded to compute the likelihood that the individual is transmitting a favourable set of alleles for the trait of interest. Although the method is still based on phenotypic selection, it more easily identifies variation at loci having a relatively small effect and represents an important advance. Essentially, the statistical genetics method calculates an average of all genetic loci contributing to a trait as transmitted by the individual, and reports it as an estimated breeding value (EBV) (Lynch & Walsh 1998). As a result, the animal production industry has undergone dramatic change during the last century (Ensminger & Parry 1996).

In response to changes in dietary preference of consumers, the selection emphasis has changed from just increased output to increased production efficiency and product quality. In the early 19th century dairy production focus shifted from milk quantity, which was very successfully increased by intense selection, to milk quality and quantity (Van Raden 2004). The concept of quality has now broadened greatly to take account of the effects of production systems on human health, animal welfare and the environment.

A key issue is the extent to which genetic selection for increased production affected the ability of the animals to adapt to the environment in which they find themselves.

At the individual level, adaptation is the use of regulatory systems, with their behavioural and physiological components, to help an individual to cope with its environmental conditions (Broom & Johnson 2000; Broom 2006).

Animals have limited resources for carrying out adaptation processes. A series of publications by Rolf Beilharz and colleagues proposed the Resource Allocation Theory (eg Goddard & Beilharz 1977; Beilharz *et al* 1993). The resources an animal has are limited and, as a result, if output is increased through one biological process, such as producing more milk, other functions such as fertility, maintenance, movement, immune defence, etc will be affected. The availability of resources that one process demands can be increased to a certain extent. Management factors, such as increasing access to feed and nutrients, could increase the fitness of the animal until resources became limited again. Any further increase in fitness would imply a reallocation of resources and thus modify other outputs such as disease resistance or behaviour (Beilharz *et al* 1993). Reviewing the negative side-effects of selection for high production, Rauw *et al* (1998) concluded that "when a population is genetically driven towards high production, … less resources will be left to respond adequately to other demands like coping with stressors". The key problem as noted by Rauw (2008) is that high productivity in farm animals could mean that there are insufficient resources for adequate coping and hence poor welfare whenever resources are limiting.

In this paper, the effects of selection for increased production on health and other welfare indicators in dairy cattle is discussed.

Selection for increased yield

Improved plant and animal production, largely as a result of genetic selection, was one of the greatest achievements of the last century (Broom 1994, 2004).

The dominant dairy breed in Europe is the Holstein. The North American Holstein breed began with imports from Northern Europe in the late 1800s. The breed was largely limited to North America until the early 1970s when large-scale exports began, initially of live animals followed by semen and embryos. Over a 25-year period, US Holstein semen exports grew from about 400,000 units in 1973 to almost 8 million units in 1997. Early exports were mainly to EU member countries, particularly Italy, The Netherlands, Germany and France. In addition, several countries, such as The Netherlands, France and others, implemented an embryo import programme as a source of breeding stock for their internal genetic improvement programmes. The major factors responsible for this trend were: (i) it became known worldwide that Holsteins gave higher milk yields than most breeds; (ii) dairy farmers' breeding objectives worldwide became increasingly focused on income from sale of milk; and (iii) technology existed to import Holsteins from the USA into other countries.

The Holstein has spread rapidly in much of Europe. In the UK, as an example, in the last 30 years, what was predominantly a Friesian dairy cattle population is now 90% North American Holstein in origin.

The high-nutrient-input high-milk-output systems are the most widely used dairy production systems in most of the EU. These systems, characterised by large average herd sizes, use of specialised dairy breeds (95% Holstein/Friesian), high stocking rate made possible by high use of fertilisers and with cows fed to yield using diets with high energy density, account for 83% of all EU dairy cows and 85% of all EU milk production (OECD 1999).

The dairy industry's goal has always been to produce quality milk for the consumer market. In many countries yield per cow has more than doubled in the last 40 years. This dramatic increase in yield per cow is due to rapid progress in genetics and management. The average energy corrected milk (ECM) yield for Swedish dairy cows (Figure 1) increased from 4,200 to 9,000 kg between 1957 and 2003 (SHS Annual reports 2003; Oltenacu & Algers 2005). Changes in dairy cows in Austria from 1988 to 2007 show that the mean yield per lactation in Holsteins increased from 5,500 to 8,200 kg and in Simmentals from 4,500 to 6,600 kg (Knaus 2009). Data from National Milk Records in the UK show an increase in average yields of dairy cows of about 200 kg per year from 1996 to 2002 and 50% of the progress in milk yield is attributed to genetics (Pryce & Veerkamp 2001).

The picture is similar in the US where between 1957 and 2007 the average milk production per cow increased by 5,997 kg, with 3,390 kg of this increase (or 56%) due to genetics (Van Raden 2004). Until the mid-1980s most of the increase in milk yield was the result of improved management, in particular better application of nutritional standards and improved quality of roughage. Since then, genetics has become the major factor due to effective use of artificial insemination (AI), intense selection based on progeny-testing of bulls and worldwide distribution of semen from bulls with high genetic merit for production.

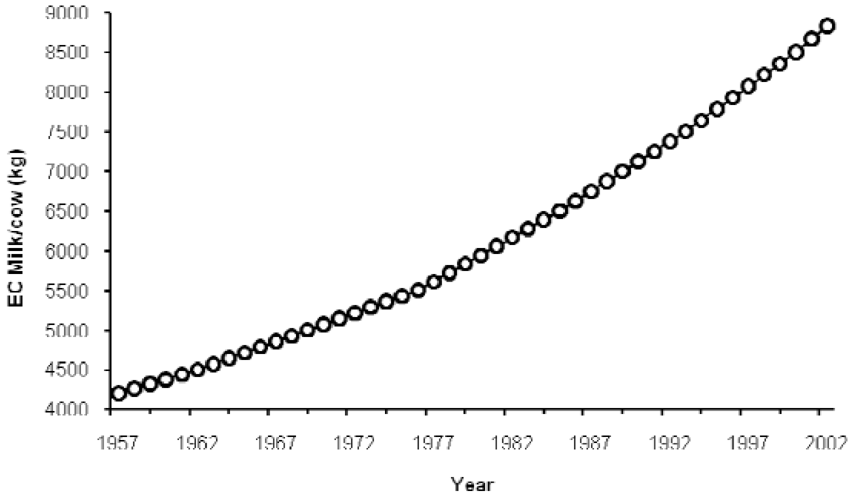
The dairy cow is producing considerably more milk than its ancestor would have produced. The amount is ten times the beef cattle average of 1,000–2,000 kg (Webster 1993). However, the product of daily energy output and duration of lactation is very high indeed. Hence, as we would predict according to resource allocation theory, long-term problems are the most likely to occur in high-producing animals (Broom 1995, 2001b; Nielsen 1998).

Consequences for the welfare of high milk producing dairy cattle

The consequences of selection and breeding can be judged on the basis of its impacts on health and the welfare of individual offspring and future generations. Ingvartsen *et al* (2003) reviewed 14 genetic studies on the relationship between milk performance and health in dairy cattle. These studies showed an unfavourable genetic correlation between milk yield and incidence of ketosis (0.26–0.65), ovarian cyst (0.23–0.42), mastitis (0.15–0.68) and lameness (0.24–0.48), indicating that continued selection for higher milk yield will increase lactational incidence rates (LIR) for these production diseases and reduce the welfare of dairy cows. A discussion of these consequences follows.

Figure 1

Average energy-corrected milk yield for Swedish dairy cows over time (from Oltenacu & Algers 2005).



Metabolic stress

As the genetic ability to produce milk increases, more cows have production diseases, ie those whose causation includes some aspects of changes directly associated with the level of production. The associations between increased milk production and increased risk of production disease, as well as decreased fertility, are well documented, but less is known about the biological mechanisms behind these relationships.

To address the growing perception that the pursuit of ever-increasing milk production is detrimental to cow welfare, Ingvartsen *et al* (2003) developed a framework for future research. The framework links the genotype, nutritional environment and management of the cow through its metabolic status to fertility and disease susceptibility and suggests that mobilisation of body reserves could be a key factor.

High-producing dairy cows have a high demand for energy and need to mobilise body reserves to support this demand. In the first third of the lactation period, until energy intake catches up with the requirements, high-producing cows enter a state of negative energy balance during which time they mobilise body reserves and lose excessive amounts of body condition. The terms 'metabolic load' and 'metabolic stress' are used (Clarkson *et al* 1996) to describe the effects of high production on dairy cows. The metabolic load is defined as 'the burden imposed by the synthesis and secretion of milk' and metabolic stress as 'that amount of metabolic load which cannot be sustained, such that some energetic processes, including those that maintain good fertility and general health, must be down-regulated'. The extent and type of down-regulation would be indicative of the degree of metabolic stress. Where the negative energy balance is substantial, there are insufficient body reserves available and the cow starts to metabolise functional body tissue, such as muscle. Mobilisation of functional tissue is considered indicative of starvation and the extent to which a high-producing cow may experience significant starvation can be assessed by detection of combinations of metabolites (Agenäs *et al* 2006).

Selection for milk production also changes the partitioning of available energy by increasing the priority with which energy is allocated to support milk synthesis. Selection for production also increases feed intake but, with a genetic correlation between yield and feed intake ranging from 0.46 to 0.65 (Veerkamp 1998), the gap between energy input and output during early lactation is increasing. There is little evidence for more efficient digestion or utilisation of metabolisable energy in high-genetic-merit cows; so, the correlated response to selection for yield is increased body-tissue mobilisation and increased metabolic load to bridge the gap between energy available through feed intake and energy needed to support increased milk production. Furthermore, an increasing demand for energy may lead to time constraints since cows have insufficient time in the 24 h per day to allocate to different activities, including eating behaviour.

Lameness

In the UK, in 1980, lameness in dairy cows was estimated to be less than 10% per lactation (Russell *et al* 1982) but by 1990 it was more than 20% (Clarkson *et al* 1996). Cubicle houses are associated with many welfare problems (Potter & Broom 1987, 1990) and the more widespread use of cubicle houses was one of the causes of the increase (Broom 1997). Publications of careful studies in various high-producing countries show leg and foot problems to be 25–59 cases per 100 cows per annum (Barkema *et al* 1994; Philipot *et al* 1994; Greenough & Weaver 1997; Boettcher *et al* 1998). For the US, Guard (1999) reported a 38% prevalence whilst Espejo *et al* (2006) report a mean prevalence in the country of 25%. Lameness decreases milk yield and is an important cause of culling (Rajala-Schultz *et al* 1999).

Guard (1999) estimated direct cost due to lameness in a 100-cow herd to be US$7,600.

Mastitis

Mastitis has also been increasing in many countries during the last 30 years, despite improvements in veterinary treatment. Ingvartsen *et al* (2003) reported that after a high-yield lactation there was more mastitis in the following lactation.

The genetic antagonism between mastitis resistance and production traits has been well established. In their review, Mrode and Swanson (1996) reported a weighted-average genetic correlation between Somatic Cell Score (SCS) and milk yield in first lactation of 0.14. Pryce and Brotherstone (1999) and Rupp and Boichard (1999) reported similar results.

The genetic antagonism between yields and clinical mastitis is more pronounced. Based on Scandinavian data, Emanuelson *et al* (1988) indicated an average genetic correlation of 0.30 and, 12 years later, Heringstad *et al* (2000) reported genetic correlations ranging from 0.24 to 0.55 with an average of 0.43. Pryce *et al* (1998), Rupp and Boichard (1999), and Kadarmideen *et al* (2000) reported genetic correlations in the same range, ie 0.29, 0.49 and 0.35, respectively.

The higher incidence of clinical mastitis is also associated with lower reproductive performance. Pryce *et al* (1998) and Kadarmideen *et al* (2000) reported genetic correlations with calving interval ranging from 0.16 to 0.41 and with conception rate to first service ranging from –0.21 to –0.58. Castillo-Juarez *et al* (2000) also reported that high somatic cell counts were correlated with reduced conception rate at first service and longer calving interval with genetic correlations of –0.21 and 0.14, respectively.

Mastitis resistance is found to be an important component of cows' longevity. Sander-Nielsen *et al* (1999) reported genetic correlations between udder health and survival from first calving to the end of second lactation ranging from –0.37 to –0.75, according to the breed. Pryce and Brotherstone (1999) reported genetic correlations of lifespan with somatic cell counts and clinical mastitis ranging from –0.11 to –0.32.

Up to the mid-1990s, in most countries, the breeding objective primarily included production traits (mainly protein and fat yield), milk composition (protein and fat contents), and several morphological traits, particularly udder capacity and form. The Scandinavian countries were an exception with selection based upon broader breeding objectives that included many functional traits and, particularly, mastitis resistance (Heringstad *et al* 2000). The inclusion of resistance to mastitis in selection objectives proved to be effective. In Norway, incidence of clinical mastitis (CM) increased from 0.15 cows treated per cow-year in 1975 to 0.44 in 1994, and then decreased to 0.23 in 2002 (Osteras *et al* 2007).

In the previous five years, the continuous and unfavourable trend for fertility and mastitis susceptibility led most European dairy populations to update their breeding objective and to increase the weight of non-production traits relative to production traits in their selection indices. Evaluating some of the recently defined breeding objectives put forth by Colleau and Le Bilan-Duval (1995) and by Pedersen *et al* (2002) shows that mastitis resistance accounts for 10 to 30% of the total weight applied to all traits combined. This weight is large enough to insure that selection using the index would substantially decrease SCC and to stop any deterioration of CM frequency, even if SCC is the only available information.

There are some concerns that continuous selection for low SCC may influence the cows' capacity for leukocyte recruitment and, therefore, the ability to respond to intramammary infection. Further research is needed to clarify whether this concern is indeed justified.

Reduced fertility and longevity

There is some debate as to whether reduced or impaired fertility is a welfare problem. We are of the opinion that a cow that cannot reproduce is clearly failing to cope with her environment, therefore reduced reproductive performance of modern dairy breeds is a welfare concern.

Many of the reproductive problems associated with highly productive dairy cows result from disease, such as uterine infections or other disorders (Bell & Roberts 2007; Dobson *et al* 2007; Sheldon *et al* 2008) or from metabolic stress associated with milk production.

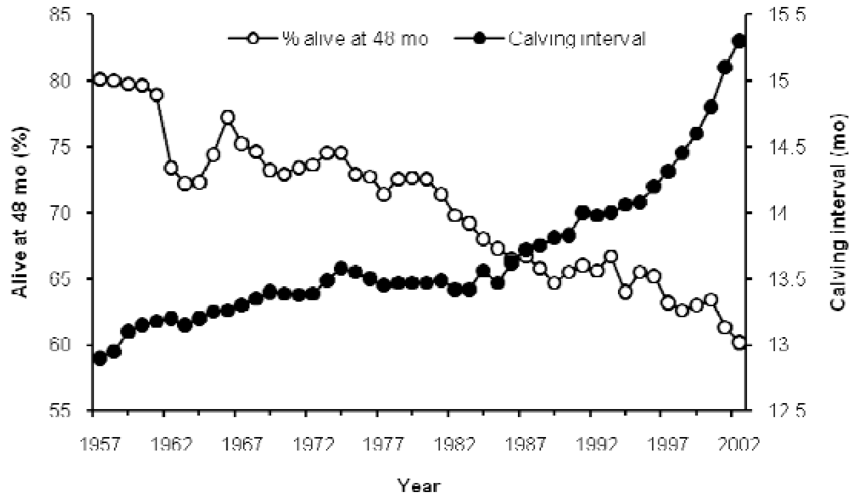
In the US, calving interval increased from < 13.0 months to > 14.5 months and number of inseminations per conception from 2.0 to > 3.5 from 1980 to 2000 in 143 US commercial herds (Lucy 2001). A decline in pregnancy rate to first service of 0.5% per year between 1975 and 1997 was reported in the US (Beam & Butler 1999). In the UK (Royal 2000), pregnancy rate to first service decreased from 56% in 1975–1982 to about 40% in 1995–1998, a decrease of about 1% per year. Similar decreases in conception rate and other reproductive measures have been reported in Sweden (Roxstrom 2001) and many other countries.

Behaviour may also play a critical role in the declining reproductive performance of genetically high-producing cows. In a study of 17 commercial herds that used an electronic oestrus-monitoring system, Dransfield *et al* (1998) showed that a higher proportion of cows with production above herd average exhibited only low intensity and short duration oestrus relative to lower-producing cows (24 vs 16%). Lopez *et al* (2004) also reported an unfavourable association between milk production and oestrus behaviour with shorter oestrus periods (5.5 vs 11.1 h) in high (> 40 kg per day) relative to low (< 30 kg per day) producing cows. Emanuelson and Oltenacu (1998) found an extended interval to first breeding and to conception in herds with poorer oestrus detection. The decline in fertility also has economic consequences and several studies reported increasing reproductive costs for dairy cattle (Lindhe & Philipsson 1999; Royal *et al* 2000; Lucy 2001).

Poor reproductive performance often leads to premature culling and decreased longevity of dairy cows. The association between the declines in fertility, reflected in increased calving interval, and decrease in longevity, measured by the proportion of cows still alive at 48 months of age (staya-

Figure 2

Average calving interval and proportion of cows alive at 48 months of age over time for Holstein cows in the North-eastern United States (from Oltenacu & Algers 2005).



bility) in Holstein cows in the North-East US from 1957 to 2002 are shown in Figure 2. Reduced longevity is also reflected in the mean number of calves produced during lifetime by Holstein dairy cows in Austria, which decreased from 3.59 in 1988 to 3.26 by 2007, whilst Simmentals still produced 3.87 in 2007 (Knaus 2009). The optimal profitability in dairy production has been calculated to occur if the cows live for six lactations (Essl 1998).

Body form

Although selection for yield traits has received primary emphasis in the selection goals of dairy cattle, substantial emphasis has been placed on other traits, particularly in North America. Many of these non-yield traits are related to the outward appearance of cows, such as overall conformation or 'type', udder-type traits, body size (including height, chest width and body depth), and angularity. Consequently, selection for increased milk production has also increased the body size and weight despite evidence that smaller cows have advantages for longevity, and welfare (Hansen 2000). Emphasis on angularity (or dairy type) may have also contributed to increased metabolic stress, particularly in early lactation, resulting in cows that are more prone to metabolic problems. Similar changes occurred in other Holstein-Friesian populations. In the Dutch Holstein-Friesian dairy population, average hip height of heifers increased from 130 cm in 1981 to 144 cm in 2007 while the 305-days milk yield of the pedigree cows in the same population increased from 5,765 kg in 1985 to 8,720 kg in 2007 (NRS Statistics 2007).

Changes in body form, size and weight affect the mechanics of movements of the cow in two major respects: i) the space that is needed to execute her movement freely and ii) the scale of forces to be exerted for the movement. Udder shape and volume are of specific concern with respect to normal locomotion and prevention of lameness, and for the resting comfort of the cows in the most common barn types (Webster 1993). The changes in body size and weight are changing the environmental requirements needed to maintain good welfare in cows.

It is clear that when we look for long-term consequences of selection for high milk production we find that: i) the increase in milk yield has generally been accompanied by declining ability to reproduce, increasing incidence of health problems, and declining longevity in modern dairy cows, all of which are indicative of reduced animal welfare; ii) substantial antagonistic genetic correlation exists between milk yield and fertility and between milk yield and several production diseases indicating that a proportion of the observed decrease in reproductive performance and of the increase in incidence rate of production diseases are correlated responses associated with past one-sided selection for increase yield; iii) with increasing production cows need to spend more time eating and thus have less time available for other activities, and may not be able to allocate time enough to fulfil their need for important activities such as resting; and iv) the selection for high milk production has produced a cow that is dependent on a high level of management in order to maintain its health, and which requires certain management practices to maintain its high milk output, which may themselves lead to poor welfare, eg high-starch, grain-based diets, and minimal grazing.

Interaction of genetics and environment

As animals tend to adapt to the environment they are selected in, it is likely that selection for increased yield may also lead to environmental sensitivity. Castillo-Juarez *et al* (2000) and Kearney *et al* (2004) showed that the magnitude of the unfavourable genetic correlations between milk yield and somatic cell score and between milk yield and conception rate were significantly higher in a poor environment relative to a good environment. Dairy producers in several grazing countries have expressed concern regarding the declining fertility of cows with an increased proportion of Holstein genes. Harris and Winkelman (2000) and Verkerk *et al* (2000) reported significant differences between cows of New Zealand origin and those of North American origin for conception rate, services per conception, and days to first service. These studies indicate that the negative genetic correlations between production, fertility and health in modern dairy cows, already large when producing in an intensive production environment, are even larger when cows are producing in a less intensive production environment. The increase in negative genetic correlation between production and fitness traits in less favourable environments is indicative of a decline in adaptability associated with selection for increased yield in the modern dairy cow.

Inbreeding

Inbreeding results from the mating of related individuals and is also increasing. Inbreeding in the UK currently stands at around 3% and has been rising at 0.17% per year (Brotherstone & Goddard 2005). The Holstein and Jersey breeds in the US have rates of inbreeding of 0.2% per year (Thompson *et al* 2000) corresponding to an 'effective' population size (or *Ne*) of 50, ie population size which, under random mating, would produce the same rate of inbreeding, and the picture is relatively similar in all Holstein populations across Europe. Movement of genes between countries and focus on similar breeding objectives has meant the selection of the same cattle everywhere. Low *Ne* causes inbreeding and loss of genetic variation in a population. The current *Ne* of 50 in the US Holstein is lower than required to maintain genetic diversity in a population, but the decrease in *Ne* of Holstein and other dairy breeds is a recent phenomenon so little genetic variance has been lost to date.

Inbreeding may itself have direct negative effects on animal welfare, eg an increased risk of retained placenta and dystocia in cattle with greater inbreeding (Adamec *et al* 2006). Smith *et al* (1998) reported a reduction in lifetime milk production of 177 kg per 1% increase in inbreeding.

Although inbreeding is not currently considered a serious problem, if it continues to rise it will become a real problem in the future. Inbreeding has three major undesirable effects. It causes inbreeding depression, including an increase in the incidence of abnormalities caused by recessive alleles, loss of genetic variance and random drift in the population mean. Inbreeding depression reduces the value of many traits, particularly those related to fitness, such as fertility, ability to remain healthy, and other traits indirectly affecting welfare.

Breeding organisations should implement strategies designed to maintain the genetic variability and prevent the increase of inbreeding in the dairy population. This can be accomplished by: (i) broadening the breeding objectives to include health, fertility and other fitness traits along with production traits; (ii) considering the genotype by environment interactions; (iii) implementing selection strategies that minimise the average relationship of selected individuals with the rest of the breeding population; and (iv) taking advantage of the molecular genetics tools already available or in the developmental phase. It should be acknowledged that several of these strategies are already adopted by many breeding organisations in the EU and other countries.

Other factors that would contribute to conservation of within- and between-breed genetic variance are a more realistic payment system for the meat value of cull dairy cows that would encourage more crossbreeding with beef breeds and better knowledge of breed differences that may decrease the dominance of the Holstein breed. For instance, breed differences in fertility, disease resistance and feed conversion have not always been known or considered when choosing the Holstein over other breeds. Crossbreeding of dairy cattle should benefit from heterosis in many traits contributing to profit, and for two breeds of similar profit, it is likely that crosses between them will be more profitable than either. Until now, crossbreeding has not been used much in dairy cattle but, recently, it has received more attention. In New Zealand, an across-breed genetic evaluation for profit indicates that, under their conditions, Jerseys are at least as profitable as Holsteins (Montgomerie 2004). In the US, crossbreeding of Holstein cows with Montbeliard, Swedish and Norwegian Red as well as other dairy breeds, is gaining in popularity and a three-breeds crossing system is generally recommended. The use of crossbreeding automatically leads to a demand for cattle of more than one breed. Therefore, a rational use of crossbreeding should, in the long run, support the conservation of a variety of breeds.

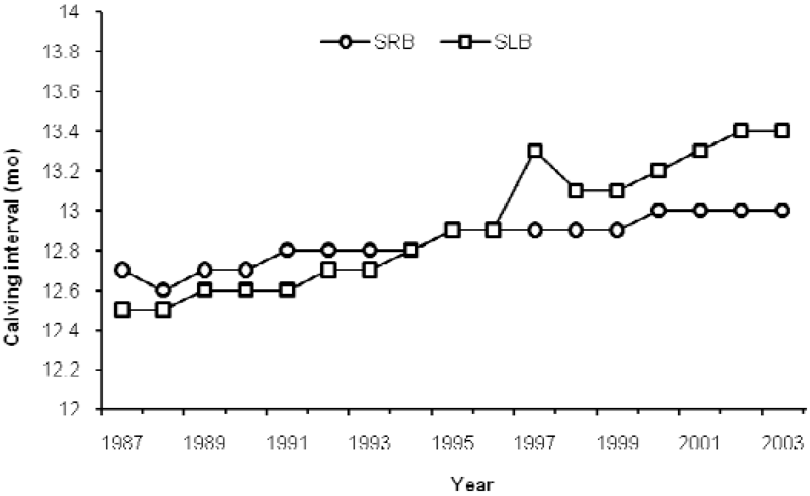
Genetic improvement of welfare in dairy cattle

In regard to breeding programmes, The United Kingdom's Farm Animal Welfare Council (FAWC 1997), in its report on dairy cow welfare, recommended the following:

> "Achievement of good welfare should be of paramount importance in breeding programmes. Breeding companies should devote their efforts primarily to selection for health traits so as to reduce current levels of lameness, mastitis and infertility; selection for higher milk yield should follow only once these health issues have been addressed".

Breeding organisations play a major role in determining what type of dairy cows will populate our dairy farms in the future and, therefore, the ethical responsibility for the welfare of future populations of cows (Sandøe *et al* 1999). The major advantages of genetic improvement for any trait are that changes are cumulative, permanent and cost-effective (Christensen 1998; Simm 1998). This is true for the selection trait as well as for correlated responses on

Figure 3



Average calving interval (in months) for Swedish Red and White (SRB) and Swedish Holstein (SLB) breeds from 1987 to 2003 (from Philipsson 2003).

other traits. As pointed out, these very advantages have facilitated a rapid increase in milk yield per cow and detrimental effects on the welfare of the animals when breeding objectives have centred on production, with little attention given to fitness traits, such as fertility and health.

The unfavourable genetic relationship between milk production and welfare indicators means that the most effective route to stop the decline or even improve welfare is by developing and adopting a selection index in which welfare-related traits are included and appropriately weighted. With such an index, the genetic progress for any of the traits considered is smaller than if selection is for a single trait, but overall economic response is greater than in single trait selection.

Efforts to improve animal welfare are often portrayed as increasing the cost of production (Rushen & de Passillé 1998) and selecting for welfare traits is assumed to be uneconomical. This is not always the case. As an example, the current breeding goal in the UK includes increasing milk, fat and protein yields plus lifespan. These traits are combined into Profitable Lifetime Index, or £PLI, designed to maximise the economic return from a cow during her expected productive life. Calculations suggest that expansion of £PLI to also increase resistance to mastitis and decrease calving interval could increase economic response to selection by up to 80%, compared with selection for milk production alone (Pryce *et al* 2000). Selection on such an index could also halt the decline in fertility and mastitis resistance, compared with selection for milk production alone. Sandøe *et al* (1999) evaluated the use of several selection indices combining selection for increased production with selection for increased resistance to mastitis for the Danish situation. They showed that, after 10 years of selection with zero relative weight on resistance to mastitis (selection for milk alone), production per cow increased by 1,179 kg and number of mastitis treatments per 100 cows by 12.9. Using an index in which resistance to mastitis is given double weight relative to yield, production increased by 964 kg and number of mastitis treatments per 100 cows decreased by 5.5. In a herd of 100 cows, this translates to 21,500 kg less milk and 18.4 fewer mastitis treatments compared with selection for milk yield only, ie the loss in milk yield gain is equal to 1,168 kg per avoided treatment of mastitis. In the above calculations, the weights were calculated based on genetic (co)variances and genetic correlation between traits. If the cost of mastitis relative to milk price is considered, the weighting of the two traits in the selection index can be chosen to maximise profit. These two examples illustrate that it should indeed be possible, through genetic selection, to improve welfare without a reduction in profitability.

One example of successful multi-trait selection comes from Sweden and other Nordic countries where breeding goals have been formulated to include not only production but also fertility and health for the last 20 years. The average calving interval from 1987 to 2003 is shown in Figure 3 for the two major Swedish dairy breeds.

By implementing more balanced selection goals it has been possible to limit the decline of fertility in the Swedish Holstein breed to about half of what has been observed in other Holstein populations and minimise it in the Swedish Red and White which is much less influenced by germplasm from outside Scandinavia. Resistance to mastitis follows similar trends. There have also been recent genetic improvements in the health of cows in Norway (Osteras *et al* 2007).

In Nordic countries, records are available such that fertility and health traits can be included in selection decisions. The progeny testing of bulls is performed with large progeny group size (> 120 daughters per bull) to allow traits with low heritability to be accounted for. The programme has a positive impact on smaller breeds, such as the red and white breeds in the Nordic countries (Philipsson & Lindhe 2003). It is also clear that, as long as the majority of the black and white dairy bulls tested in the Nordic countries originate from sires outside Scandinavia, where no estimates for genetic merit for health and fertility traits are available, the Nordic effort to improve these traits will only have limited impact (Christensen 1998). An active international germ plasm market makes breeding of dairy cattle truly global.

For the Holstein/Friesian breed, which is the dominant dairy breed in the world and accounts for about 80% of all dairy cows in Europe (van Arendonk & Liinamo 2003), increased emphasis on selection for fitness traits should occur in all countries, particularly those that dominate the international germplasm market. Since the mid-1990s, several breeding organisations in Europe as well as North America have included fertility and health (at least mastitis) in their breeding objectives. Recently, several Nordic Countries included lameness in the breeding objectives and their lead should be followed by other breeding organisations: a multi-trait selection programme in which health, fertility and welfare traits are properly weighted, relative to production traits and included in the breeding objectives, in order to improve welfare.

Sustainability of the dairy industry

Are current trends in dairy farming leading to a sustainable industry? A system is sustainable if it is acceptable now and if its effects will be acceptable in future, in particular in relation to resource availability, consequences of functioning and morality of action (Broom 2001a). Animal welfare is one of the factors that determines whether or not a system is sustainable (McGlone 2001). There are two other factors that may make some dairy farming unsustainable: the efficiency of production in relation to human food requirements and greenhouse gas production.

How efficient is dairy production in relation to human food requirements? Dairy cattle can utilise pasture plants, a resource unavailable to humans as food. This is a major long-term advantage to the industry. However, many dairy cattle are fed concentrates that humans could utilise. If cows are to produce 9,000 kg per lactation in an intensive production system, 40% of their diet is likely to be from concentrates and 96% of the protein they eat could have been used by humans. This is a serious net loss of nutrients for humans. However, if their diet would consist of 70% forage plants and the 30% concentrates of which 70% would come from by-products, there is a net food benefit for humans. Therefore, a mainly pasture-based diet is desirable for the future. Dairy cows produce methane, a greenhouse gas. Whilst there should be efforts to minimise this, the value of cattle as utilisers of pasture that we cannot otherwise use can be balanced against it. The cows' greenhouse gas production should be expressed per unit of milk production. Hence, an increase in longevity and lifetime production should be pursued for its environmental benefits, increased efficiency and animal welfare reasons.

What could be the reactions of consumers if they believe that something is wrong with dairy production? Some could stop eating dairy products. Some could eat some of the products but not others. Some could write to retail organisations to tell them what they will not buy. A 5% increase in vegetarianism or 5% of consumers ceasing to buy milk and other dairy products would have very serious effects on the dairy industry. Compared to the consequences of any of these possible consumer reactions, the cost of effectively addressing the animal welfare issues and improving the image of an industry would be small. It is clear that the industry should be proactive and adopt changes before consumers reduce consumption. Although some actions are being taken by the industry, it is our opinion that more needs to be done.

All dairy cattle breeding organisations should address the animal welfare and sustainability issues in their programmes to avoid public condemnation of breeding and management practices for dairy cows.

Conclusion

Traditionally, breeding programmes for farm animals have focused on genetic 'improvement' of economically important production traits. Consequently, productivity in farm animals rose dramatically during the second half of the twentieth century and effective selective breeding programmes were a major factor. The milk yield per cow in dairy and growth rate and feed conversion efficiency of broiler chickens illustrate these changes vividly. However, the combination of selective breeding narrowly focused on production traits and the intensification of animal production system have had consequences for the animals which have become more at risk of behavioural, physiological, and immunological disorders, ie poor welfare.

Farm animal welfare has become increasingly important and relevant from the societal point of view and its importance is now recognised by all stakeholders in the farm animal production chain. Breeding organisations working with farm animals cannot neglect these public concerns and must develop and implement breeding goals designed to improve animal welfare.

There is evidence that several welfare aspects have a genetic basis and that selective breeding for a better animal welfare, be it in combination with selection for production or not, could be successful. Broader selection goals have been implemented in some dairy cattle breeding programmes. Nordic dairy cattle breeding programmes combine production, health, fertility and longevity traits optimally combined in a 'total merit index', or TMI. More generally, it is clear that many breeding companies are working towards developing more balanced breeding goals by incorporating functional traits.

In order for breeding organisations to implement a selection for improvement of welfare in farm animals, the traits related to welfare need to be clearly defined, their heritabilities and genetic (co)variances need to be known, and recording of those traits on individual animals need to be feasible. One approach is to breed for animals that are better suited for current farming methods (Christiansen & Sandøe 2000). Another approach is to reverse some recent trends in genetic selection and to modify the farming systems so that it is easier for the animals to adapt to it. The challenge is to define a limited number of welfare traits with a sufficiently large genetic component and for which information on individual animals can be obtained routinely. Multidisciplinary research programmes should be developed, therefore, to provide the necessary information for successful implementation of selection for these societal important traits.

In order to improve the welfare and adaptability of dairy cows through genetic selection long term, the co-operation of breeding experts, geneticists, epidemiologists, nutritionists, ethologists and others concerned with animal welfare problems is required. Sustainable breeding goals aimed at improving fitness and robustness is necessary to prevent the decrease in the quality of life of the animals and, perhaps, enhance it. The effectiveness of a selection programme to improve welfare should be enhanced if selection acts directly on causes of poor welfare and not only on its symptoms. To implement such a programme, research is needed to clarify the relationship between production, negative energy balance, metabolic stress and welfare indicators and to develop practical methods for measuring negative energy balance and metabolic stress. This research should identify traits directly related to welfare status, such as negative energy balance, body condition score, onset of cyclicity after calving etc and, ultimately, provide better selection tools to improve welfare status in dairy cows.

At present, considering the severity of the effect on welfare, the duration of the effect and the number of individuals involved, after broiler chickens, dairy cow welfare is the worst animal welfare problem in Europe. This is the most important current problem for the dairy industry. Urgent action to change genetic selection and management of dairy cows is needed.

References

Adamec V, Cassell BG, Smith EP and Pearson RE 2006 Effects of inbreeding in the dam on dystocia and stillbirths in US Holsteins. *Journal of Dairy Science 89*: 307-314

Agenäs S, Heath MF, Nixon RM, Wilkinson JM and Phillips CJC 2006 Indicators of under nutrition in cattle. *Animal Welfare* 15: 149-160

Barkema HW, Westrik JD, van Keulen KAS, Schukken YH and Brand A 1994 The effects of lameness on reproductive performance, milk production and culling in Dutch herds. *Preventitive Veterinary Medicine 20*: 149-259

Beam SW and Butler WR 1999 Effects of energy balance on follicular development and first ovulation in postpartum dairy cows. *Journal of Reproduction and Fertility 54S*: 411-424

Beilharz RG, Luxford BG and Wilkinson JL 1993 Quantitative genetics and evolution: Is our understanding of genetics sufficient to explain evolution? *Journal of Animal Breeding and Genetics 110*: 161-170

Bell MJ and Roberts DJ 2007 The impact of uterine infection on a dairy cow´s performance. *Theriogenology 68*: 1074-1079

Boettcher PJ, Dekkers JC, Warnick LD and Wells SJ 1998 Genetic analysis of clinical lameness in dairy cattle. *Journal of Dairy Science 81*: 1148-1156

Broom DM 1994 The effects of production efficiency on animal welfare. In: Huisman EA, Osse JWM, van der Heide D, Tamminga S, Tolkamp BL, Schouten WGP, Hollingsworth CE and van Winkel GL (eds) *Biological Basis of Sustainable Animal Production. Proceedings of the 4th Zodiac Symposium EAAP Publication* 67. Wageningen Pers: Wageningen, The Netherlands

Broom DM 1995 Measuring the effects of management methods, systems, high production efficiency and biotechnology on farm animal welfare. In: Mepham TB, Tucker GA and Wiseman J (eds) *Issues in Agricultural Bioethics* pp 319-334. Nottingham University Press: Nottingham, UK

Broom DM 1997 Animal behaviour as an indicator of animal welfare in different housing and management systems. In: Saloniemi H (ed) *Proceeding of the 9th International Congress in Animal Hygiene* pp 371-378. Tummavnoren Kirjapaino Oy: Helsinki, Finland

Broom DM 2001a Effects of dairy cattle breeding and production methods on animal welfare. *Proceedings of the 21st World Buiatrics Congress* pp 1-7. Punta del Este, Uruguay

Broom DM 2001b *Coping with Challenge: Welfare in Animals: Including Humans.* Dahlem University Press: Berlin, Germany

Broom DM 2004 Future food animal production efficiency and acceptability. In: Shamsuddin ZH (ed) *Agriculture Congress: Innovation Towards Modernized Agriculture* pp 17-21. Universiti Putra Malaysia: Serdang, Malaysia

Broom DM 2006 Adaptation. *Berliner und Münchener Tierärztliche Wochenschrift 119*: 1-6

Broom DM and Johnson KG 2000 *Stress and Animal Welfare.* Kluwer/Springer: Dordrecht, The Netherlands

Brotherstone S and Goddard M 2005 Artificial selection and maintenance of genetic variance in the global dairy cow population. *Philosophical Transactions of the Royal Society Biological Sciences 360*: 1479-1488

Castillo-Juarez H, Oltenacu PA, Blake RW, McCulloch CE and Cienfuegos-Rivas EG 2000 Effect of herd environment on the genetic and phenotypic relationships among milk yield, conception rate, and somatic cell score in Holstein cattle. *Journal of Dairy Science 83*: 807-814

Christensen LG 1998 Possibilities for genetic improvement of disease resistance, functional traits and animal welfare. *Acta Agriculturae Scandinavica, Section A, Animal Science. 29*: 77-89

Christiansen SB and Sandøe P 2000 Bioethics: limits to the interference with life. *Animal Reproduction Science 60-61*: 15-29

Clarkson MJ, Downham DY, Faull WB, Hughes JW, Manson FJ, Merritt JB, Murray RD, Russell WB, Sutherst JE and Ward WR 1996 Incidence and prevalence of lameness in dairy cattle. *Veterinary Records 138*: 563-567

Colleau JJ and Le Bihan-Duval E 1995 A simulation study of selection methods to improve mastitis resistance of dairy cows. *Journal of Dairy Science 78*: 659-671

Dobson H, Smith R, Royal M, Knight C and Sheldon I 2007 The high-producing dairy cow and its reproductive performance. *Reproduction in Domestic Animals 42(2)*: 17-23

Dransfield MB, Nebel RL, Pearson RE and Warnick LD 1998 Timing of insemination for dairy cows identified in oestrus by a radiotelemetric oestrus detection system. *Journal of Dairy Science 81*: 1874-1882

Emanuelson U, Danell B and Philipsson J 1988 Genetic parameters for clinical mastitis, somatic cell counts, and milk production estimated by multiple-trait restricted maximum likelihood. *Journal of Dairy Science 71*: 467-476

Emanuelson U and Oltenacu PA 1998 Incidences and effects of diseases on the performance of Swedish dairy herds stratified by production. *Journal of Dairy Science 81*: 2376-2382

Ensminger ME and Parry RC 1996 *Beef Cattle Science*. The Interstate Printers and Publishers: Illinois, USA

Espejo LA, Endres MI and Salfer JA 2006 Prevalence of lameness in high-producing holstein cows housed in freestall barns in Minnesota. *Journal of Dairy Science 89*: 3052-3058

Essl A 1998 Longevity in dairy cattle breeding, a review. *Livestock Production Science 57*: 79-89

FAWC (Farm Animal Welfare Council) 1997 *Report on the Welfare of Dairy Cattle*. http://www.fawc.co.uk/repors /dairycow/dcowrtoc.htm

Goddard ME and Beilharz RG 1977 Natural selection and animal breeding. *Proceedings of the 3rd International Congress SABRAO* pp 4.19-4.21. February 1997, Canberra, Australia

Greenough PR and Weaver AD 1997 *Lameness in Cattle, 3rd Edition*. WB Saunders: Philadelphia, USA

Guard C 1999 Control programmes for digital dermatitis. *The Tools for Success in the new Millenium: Volume II, Advances in Dairy Technology* pp 235-242. University of Alberta, Edmonton, Canada

Hansen LB 2000 Consequences of selection for milk yield from a geneticist´s viewpoint. *Journal of Dairy Science 83*: 1145-1150

Harris BL and Winkelman AM 2000 Influence of North American Holstein genetics on dairy cattle performance in New Zealand. *Proceedings of the New Zealand Large Herds Conference 6*: 122-136

Hazel LN 1943 The genetic basis for constructing selection indexes. *Genetics 28*: 476-490

Heringstad B, Klemetsdal G and Ruane J 2000 Selection for mastitis in dairy cattle: a review with focus on the situation of the Nordic countries. *Livestock Production Science 64*: 95-106

Ingvartsen KL, Dewhurst RJ and Friggens NC 2003 On the relationship between lactational performance and health: is it yield or metabolic imbalance that causes diseases in dairy cattle? A position paper. *Livestock Production Science 83*: 277-308

Kadarmideen HN, Thompson R and Simm G 2000 Linear and threshold genetic parameters for disease, fertility and milk production in dairy cattle. *Journal of Animal Science 71*: 411-419

Kearney JF, Schutz MM and Boettcher PJ 2004 Genotype × environment interaction for grazing vs confinement II. Health and reproduction traits. *Journal of Dairy Science 87*: 510-516

Knaus W 2009 Dairy cows trapped between performance demands and adaptability. *Journal of Science of Food and Agriculture 89*: 1107-1114

Lindhe B and Philipsson J 1999 The Scandinavian experience of including reproductive traits in breeding programmes. In: Diskin MG (ed) *Fertility in the High-Producing Dairy Cow. Occasional Pub 26*: 251-261

Lopez H, Satter LD and Wiltbank MC 2004 Relationship between level of milk production and oestrous behaviour of lactating dairy cows. *Animal Reproduction Science 81*: 209-223

Lucy MC 2001 Reproductive loss in high-producing dairy cattle: where will it end? *Journal of Dairy Science 84*: 1277-1293

Lynch M and Walsh B 1998 *Genetic Analysis of Quantitative Traits*. Sinauer Associates: Sunderland, MA, USA

McGlone J 2001 Farm animal welfare in the context of other societal issues: toward sustainable systems. *Livestock Production Science 72*: 75-81

Montgomerie WA 2004 Future genetic progress of dairy cattle in New Zealand. *New Zealand Society of Animal Production 64*: 96-100

Mrode RA and Swanson GJT 1996 Genetic and statistical properties of somatic cell count and its suitability as an indirect means of reducing the incidence of mastitis in dairy cattle. *Animal Breeding Abstracts 64*: 847-857

Nielsen B 1998 Interspecific comparison of lactational stress: is the welfare of dairy cows compromised? In: Veissier I and Boissy A (eds) *Proceedings of the 32nd Congress of the International Society for Applied Ethology*. INRA: Clermont Ferrand, France

NRS (The Royal Dutch Cattle Syndicate) 2007 *NRS Statistics Handbook*. NRS: Arnhem, The Netherlands.

OECD 1999 *OECD Agricultural Outlook, 1999-2004*. OECD: Paris, France

Oltenacu PA and Algers B 2005 Selection for increased production and the welfare of dairy cows; are new breeding goals needed? *Ambio 34*: 308-312

Osteras O, Solbu H, Refsdal AO, Roalkvam T, Filseth O, and Minsaas A, 2007 Results and evaluation of thirty years of health recordings in the Norwegian dairy cattle population. *Journal of Dairy Science 90*: 4483-4497

Pedersen J, Sander-Nielsen U and Aamand GP 2002 Economic values in the Danish total merit index. *Interbull, Bulletin 29*: 150-154

Philipot JM, Pluvinage P, Cimarosti I, Sulpice P and Bugnard F 1994 Risk factors of dairy cow lameness associated with housing conditions. *Veterinary Research 25*: 244-248

Philipsson J and Lindhe B 2003 Experiences of including reproduction and health traits in Scandinavian dairy cattle breeding programmes. *Livestock Production Science 83*: 99-112

Potter MJ and Broom DM 1987 The behaviour and welfare of cows in relation to cubicle house design. In: Wierenga HK and Peterse DJ (eds) *Cattle Housing Systems, Lameness and Behaviour: Current Topics in Veterinary Medicine and Animal Science* pp 129-147. Martinus Nijhoff: Dordrecht, The Netherlands

Potter MJ and Broom DM 1990 Behaviour and welfare aspects of cattle lameness in relation to building design. In: Murray R (ed) *Proceedings of the Vth International Symposium on Ruminant Digit* pp 80-84. British Cattle Veterinary Association: Liverpool, UK

Pryce JE and Brotherstone S 1999 Estimation of lifespan breeding values in the UK and their relationship with health and fertility traits. *Interbull, Bulletin 21*: 166-169

Pryce JE, Esslemont RJ, Thompson R, Veerkamp RF, Kossaibati MA and Simm G 1998 Estimation of genetic parameters using health, fertility and production data from a management recording system for dairy cattle. *Animal Science 66*: 577-584

Pryce JE, Simm G, Amer PR, Coffey MP and Stott AW 2000 Returns from genetic improvement of dairy cattle. *Proceedings of 2000 British Society of Animal Science Winter Meeting*. March 2000, Scarborough, UK

Pryce JE and Veerkamp RF 2001 The incorporation of fertility indices in genetic improvement programmes. In: Diskin MG (ed) *Fertility in the High-Producing Dairy Cow. British Society of Animal Science, Galway, Ireland, Occasional Publication 26*: 237-249

Rajala-Schultz PJ, Grohn YT and McCulloch CE 1999 Effects of milk fever, ketosis, and lameness on milk yield in dairy cows. *Journal of Dairy Science 82*: 288-294

Rauw WM, Kanis E, Noordhuizen-Stassen EN and Grommers FJ 1998 Undesirable side effects of selection for high production efficiency in farm animals: a review. *Livestock Production Science 56*: 15-33

Rauw WM 2008 *Resource Allocation Theory Applied to Farm Animals*. CAB International: Wallingford, UK

Roxstrom A 2001 *Genetic aspects of fertility and longevity in dairy cattle*. PhD Dissertation, Swedish University of Agricultural Sciences, Uppsala, Sweden

Royal MD, Darwash AO, Flint APF, Webb R, Woolliams JE and Lamming GE 2000 Declining fertility in dairy cattle: changes in traditional and endocrine parameters of fertility. *Animal Science 70*: 487-501

Rupp R and Boichard D 1999 Genetic parameters for clinical mastitis, somatic cell score, production, udder type traits, and milking ease in first lactation Holsteins. *Journal of Dairy Science 82*: 2198-2204

Rushen J and de Passille AM 1998 Behaviour, welfare and productivity in dairy cattle. *Canadian Journal of Animal Science 78(S)*: 3-21

Russell AM, Rowlands GJ, Shaw SR and Weaver AD 1982 Survey of lameness in British dairy cattle. *Veterinary Records 111*: 155-160

Sander-Nielsen U, Pedersen GA, Pedersen J and Sørensen P 1999 Genetic variation in disease traits and their relationships with survival in Danish dairy cattle. *Interbull, Bulletin 21*: 170-177

Sandøe P, Nielsen BL, Christensen LG and Sørensen P 1999 Staying good while playing God: the ethics of breeding farm animals. *Animal Welfare 8*: 313-328

Sheldon IM, Williams EJ, Miller AN, Nash DM and Herath S 2008 Uterine diseases in cattle after parturition. *Veterinary Journal 176*: 115-121

SHS Annual Reports 2003 *Swedish Association for Livestock Breeding and Production.* SHS; Eskilstuna, Sweden

Simm G 1998 *Genetic Improvement of Cattle and Sheep*. Farming Press: Ipswich, UK

Smith LA, Cassell BG and Pearson RE 1998 The effects of inbreeding on the lifetime performance of dairy cattle. *Journal of Dairy Science 81*: 2729-2737

Thompson JR, Everett RW and Hammerschmidt NL 2000 Effects of inbreeding on production and survival in Holsteins. *Journal of Dairy Science 83*: 1856-1864

van Arendonk JA and Liinamo AE 2003 Dairy cattle production in Europe. *Theriogenology 59*: 563-569

Van Raden PM 2004 Invited review: selection on net merit to improve lifetime profit. *Journal of Dairy Science 87*: 3125-3131

Veerkamp RF 1998 Selection for economic efficiency of dairy cattle using information on live weight and feed intake: a review. *Journal of Dairy Science 81*: 1109-1119

Verkerk GA, Morgan S and Kolver S 2000 Comparison of selected reproductive characteristics in Overseas and New Zealand Holstein-Friesian cows grazing pasture or fed a total mixed ration. *Proceedings of the New Zealand Society of Animal Production 60*: 270-274

Webster J 1993 *Understanding the Dairy Cow, 2nd Edition*. Blackwell: Oxford, UK