

Breeding for robustness in cattle



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Genetic concepts to improve robustness of dairy cows

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Abstract

The past decade has revealed unfavourable trends in udder health, fertility and locomotion in dairy cattle. More recently, dairy herds are increasing and the availability of skilled labour per animal is decreasing. This has increased the interest in more robust dairy cows. Robustness of a cow was defined as 'the ability to maintain homeostasis in commonly accepted and sustainable dairy herds of the near future'. Robustness is largely an acquired characteristic. Adaptive systems never cease to develop. Success of adaptation also depends on available resources and opportunities from the environment. Genotype merely gives an individual an advantage or disadvantage in becoming robust. Several concepts of breeding for robustness exist. These include avoiding inbreeding depression, utilising heterosis, using multi-trait selection, reducing environmental sensitivity in the target range dairy production systems and breeding for group performance. Environmental sensitivity may be reduced through natural selection, using genetic correlations between environments, using reaction norms or using genetic variation in residual variance within progeny groups of sires.

Keywords: adaptability, animal breeding, genotype environment interaction

Introduction

Cannon (1932) first used the term homeostasis to indicate that a body continuously acts to maintain a stable internal environment by responding to external environmental stimuli. In the last two decades, there have been concerns that high-yielding dairy cows struggle to maintain homeostasis. Several studies reported unfavourable genetic correlations between milk yield and reproductive problems, locomotive problems and udder health problems (Pryce *et al.*, 1997; Rauw *et al.*, 1998; Royal *et al.*, 2000), and there is general consensus that selection for milk fat and milk protein yield alone may give an unfavourable correlated response in these traits (Dechow *et al.*, 2002). The magnitude of these correlated responses is rather small, compared with the effects of environmental disturbance, albeit when the effects of breeding are accumulated across years these might be substantial. The gradual reduction in genetic levels for fertility and health will put more pressure on management to maintain performance at acceptable levels. Such cows require more management attention.

At the same time, the level of management is increasingly coming under pressure from other directions. For example, due to economic pressure, herd size is increasing and therefore the amount of labour available per animal is decreasing. The shortage of labour is aggravated by the fact that it is increasingly difficult to find suitably skilled labour. Also, pressure on management increases because previously simple and effective management tools, such as the use of antibiotics, are now perceived as potential risks for human health and therefore regulated much stronger.

These two trends, i.e. negative effects from selection for yield and increasing pressure on management, have fuelled the demand for more robust cows. These two trends may amplify each other in practice, as correlations with yield vary across environments (Windig *et al.*, 2005, 2008). A popular description of robust cows could be something like productive dairy cows that:

1. maintain homeostasis in an increasingly dynamic production environment;
2. are suitable for a wider range of dairy production systems;

3. only need the basic individual care; and
4. are easy to manage.

However, here we describe a more formal concept for robust cows first, and then describe the contribution that genetics can make to robustness. Robustness of a system is dependant on the chosen system level (e.g. cow, farm or sector), but here we restrict ourselves to the level of the cow.

The concept of robust cows

Robustness: control or adaptation

From a farm management point of view, there are essentially two ways to control the impact of disturbances on an animal (Ten Napel *et al.*, 2006). They are not mutually exclusive, but go together well. The one approach is called the Control Model and is characterised by maintaining stability through keeping away disturbances. Typically a strategy is used of protecting animals from disturbances as much as possible, constantly monitoring animals, whether a disturbance occurs, and interventions targeted at the disturbance, when it does occur. When taken to the extreme, the homeostasis of the animal is dependent on proper and timely functioning of humans and technical equipment.

The other approach is called the Adaptation Model. This approach is characterised by maintaining stability through minimising the impact of disturbances in the presence of the disturbance. The design of such a production system seeks to utilise the intrinsic capacity of animals to adapt where possible, and use the Control Model approach where necessary (Ten Napel *et al.*, 2006).

Definition of robustness

In the Netherlands, we gradually developed a concept of robustness of farm animals in the course of three to four years, based on discussions with many groups of stakeholders. This process resulted in the following definition of a robust dairy cow: 'A robust dairy cow is a cow that is able to maintain homeostasis in the commonly accepted and sustainable dairy herds of the near future'. It is clear from this definition that robustness is not just a matter of the average level of management being suitable for the cow. Dairy herds are dynamic and fluctuations in temperature, air speed, humidity, disease pressure, fodder quality, stocking density, social interaction with other cows, aggression, interaction with stockmen, among other factors, occur. Over time or across herds, common fluctuations largely fit in a certain band width. A cow that is robust is able to maintain homeostasis in a range of production environments with a band width that is wider than the common band width of fluctuations. It does not mean that a robust cow must be able to cope with anything. It is acceptable to look for ad-hoc solutions to unlikely disturbances and freak incidents.

To interpret the current situation, as described in the Introduction, in terms of band widths, it appears that the band width that cows can handle is gradually reducing, while the band width of fluctuations in dairy production systems is gradually increasing again, after decades of reducing the bandwidth by reducing the standardisation and improving the level of management following the Control model.

Intrinsic factors for robustness of cows

The genotype of a cow is a major determinant of the robustness of a cow. There are many examples that illustrate the role of genetics in susceptibility to disease (Morris, 2000; Owen *et al.*, 2000) and traits of the immune system (Dettileux *et al.*, 1994). In some cases, the genotype merely gives an

individual an advantage or disadvantage in becoming robust. In other cases, the genotype conveys complete resistance or susceptibility to particular threats.

However, apart from genotype, there is another important factor for robustness, i.e. the development of adaptive systems, such as the immune system and the nervous system. These adaptive systems develop in response to environmental signals throughout an animal's life, and this development is unique for every individual. As illustrated by (Tada, 1997): 'These systems engender their own elements from a single progenitor. The diverse elements thus generated form relationships by mutual adaptation and co-adaptation, and thus create a dynamic self-regulating system through self-organisation. They are closed self-satisfied systems, yet open to the environment, receiving outside signals to transduce them into internal messages for self-regulation and expansion'.

The adaptive systems of a newborn are primed for the environment in which the calf is born, for example through maternal antibodies and circulating maternal cortisol. In humans, maternal antibodies attenuate most infections in early life and turn them into effective vaccines. If this 'natural vaccination' does not occur, the infections may be severe, unless the child is actively vaccinated in synchronisation with the immune system's maturation (Zinkernagel, 2003).

The intrinsic robustness of a cow depends on the genotype, the early development of adaptive systems in the body and the challenges experienced in life.

Expression of robustness

Robustness of cows not only depends on the intrinsic robustness of the individual animals, but also on the opportunity for a cow to use the ability at farm level. For example, a diseased cow may have a different feed and temperature requirement and may want to temporarily isolate itself from the social group. Expression of robustness is not so relevant in the design of systems based on the Control Model, as it is focused on keeping away disturbances. Therefore, using the Adaptation model may require a re-design of the common dairy production systems, to allow for utilising the intrinsic capacity of animals to adapt.

Another aspect is the temporary vulnerability of a cow. For example, a cow that experiences a severely negative energy and protein balance during the peak of lactation may not have the resources to successfully combat an infection. So whether a cow is successful in maintaining homeostasis not only depends on the genotype and the development of adaptive systems, but also on the resources and opportunities offered by the environment to mount a response.

Breeding for robust animals

Robustness of an animal in a production environment is related to the genetic fitness in a natural environment. Genetic fitness of an individual is the contribution of genes that it makes to the next generation, or the number of its progeny represented in the next generation in absence of artificial selection (Falconer and Mackay, 1996). The characteristics that determine the contribution to the next generation in a natural environment may largely make up robustness in a livestock production environment. Animal breeding aims to use the genetic variation present for fitness and different strategies to do so will be discussed here.

Heterosis and inbreeding depression

Overcoming or avoiding inbreeding depression and maximising heterosis is a relatively easy way to improve genetic fitness and is widely utilised in pig and poultry breeding programmes. These effects come from the observation that characteristics associated with genetic fitness often reveal

overdominance, that is the phenotype of heterozygotes is superior to the phenotype of any of the two types of homozygotes. In studies of national subpopulations of 2.2 to 3.7 million heads of the largest dairy breed in the world, the Holstein, the effective population size has been estimated to be between 46 and 68, as reviewed by Taberlet (2008). The consequence is a high rate of inbreeding, associated with possible reduced fitness due to inbreeding depression. Widening the pool from which bulls are selected and limiting the use of individual bulls would reduce the rate of inbreeding significantly. This might lead to a loss of genetic progress, but this can be limited by optimising gain and inbreeding (Meuwissen and Sonesson, 1998). Although common in pig and poultry breeding, crossbreeding is rarely practiced in a structured manner in dairy cattle breeding. The first main reason is that a breeding programme with a pyramid structure is not possible, except when using super-ovulation and embryo transfer. Without these reproductive technologies, the average number of replacement heifers available per cow per year is between 0.4 and 0.5. So only when the replacement rate is around 20% per year, can a purebred herd support a crossbred herd of the same size. The second main reason is the unfavourable recombination that counteracts the favourable heterosis for milk production traits (Dechow *et al.*, 2007, Pedersen and Christensen, 1989), which reduced the need to look for feasible ways to utilise heterosis in dairy cattle breeding. However, for maintaining overall robustness, crossbreeding has become of interest again (Heins *et al.*, 2008). Rotational crossing, as sometimes practiced in beef cattle breeding (Marshall *et al.*, 1990), may be suitable for this purpose (McAllister, 2002).

Multi-trait selection

The most common way to breed for robustness, is to include fitness traits in the breeding goal, breeding value estimation and the selection index. This has been practiced in many dairy countries (Miglior *et al.*, 2005). One example of multi-trait selection being effective is shown in Figure 1, where the unfavourable trend in calving interval disappeared in progeny-tested bulls of both the Dutch Black and White and Red and White Holstein breed after inclusion of the trait in the selection index in 2001 (Van Drie, 2007). Philipsson and Lindhé (2003) provided similar examples for mastitis and fertility in the Nordic countries.

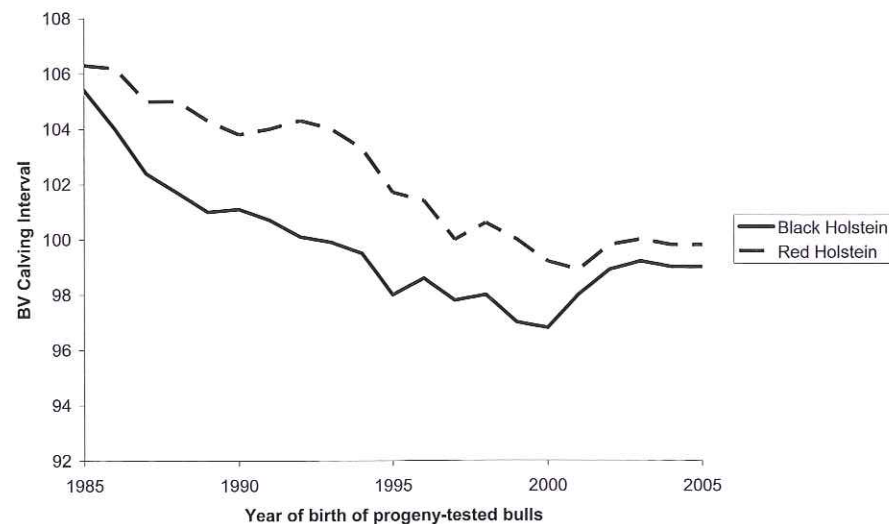


Figure 1. Genetic trend for calving interval for progeny-tested Dutch Black and White and Red and White Holstein bulls. Reproduced from Figure 3 in Van Drie (2007).

Although multi-trait selection clearly works and is better than single trait selection, there are four reasons why the commonly applied approach multi-trait index might not be satisfactory enough to maintain or improve robustness. Firstly, it is difficult for the many aspects of fitness to clearly define a trait to be measured. For example, mastitis may be caused by a large number of pathogens and may or may not result in clinical symptoms. If all pathogens are combined, the trait may be insufficiently discriminative, resulting in a very low heritability, but if groups of pathogens are distinguished, there may be insufficient observations for each trait to be meaningful. An additional issue is to identify the most relevant traits from the very large number of problem states that are potential indicators of (lack of) robustness.

Secondly, the data for fitness traits is often incomplete or censored. This may take several forms. For example, a cow that was culled after insemination, does not have a record for the success of that insemination. A highly productive cow may get a second and third chance to breed or recover from an infection, whereas a below-average productive cow may be culled after the first appearance of the problem. Further, as the nature of many recorded fitness traits is the presence of a problem, it is often not clear whether the absence of a record should be interpreted as absence of the problem or a missing record. Often it is assumed that herds either do not submit information or submit complete information, but there is no way to verify this assumption. For example, herds without records of clinical mastitis may genuinely not have had clinical cases, but may also not have recorded clinical cases that occurred. Testday SCC is more readily available in practice and provides information on intra-mammary infections

Thirdly, it has been suggested to include traits of the adaptive systems in the multi-trait index, like antibody and cell-mediated immune responsiveness (Groves *et al.*, 1993; Wagter *et al.*, 2000). These systems, however, are highly integrated life systems with a high degree of unpredictability and ambiguity observed (Tada, 1997). There are no mathematically linear cause-effect relationships in many of the important immune phenomena. Although genetic variation exists in immune components, it is unlikely that genetic selection for changes in the adaptive systems will improve robustness in the foreseeable future, except for the rare cases where complete resistance is conveyed through simple inheritance. In practice, it means that breeding for robustness is likely to be more successful when it concerns the result of adaptation (i.e. effective coping), rather than the adaptation process itself.

Fourthly, from the perspective of population biology, fitness traits are expected to exhibit genotype by environment interaction, causing animals to rank differently in different environments. In this way, after any major change in living conditions, there is at least a part of the population that is able to survive in the new environment. For milk production traits, genotype by environment is largely limited to scaling effects, when comparing North-American and Western European production environments, causing the difference between the best and the worse animal to increase with the average level of production, but without affecting the ranking of animals (Mark, 2004). For this reason, breeding value estimation generally includes a correction for heterogeneous variances for milk production traits. However, this is not a guarantee that fitness in all environments is improved (Mark, 2004). When following the definition of robustness given above, robustness is about maintaining homeostasis across environments and environmental challenges, and not only about having a high fitness on average across environments. Clearly environmental sensitivity and genotype by environment interaction play an important role when breeding for robustness.

Environmental sensitivity

Some animals respond to a change in environment for some characteristics in a much stronger way than other animals. Such animals are more environmentally sensitive for these traits. In population biology terms, these animals are called 'specialists' as they have a very high fitness only in specific conditions. Less environmentally sensitive animals are called 'generalists'. These qualifications are

not absolute, but relative to the range of environments considered. A cow may be a 'specialist' when considering all possible environments, but a 'generalist' when considering the range of acceptable production systems in a country. A robust cow is more of a 'generalist' as it has a reasonable fitness across relevant production environments (Bryant *et al.*, 2006).

If animals rank differently in different environments, then there is a risk of selecting environmentally sensitive individuals, if selection mainly takes place in the favourable environments. The question is how to identify the 'generalists' for the target range of environments. We distinguish four situations, (1) natural selection, (2) production environments fall into a limited number of categories, (3) production environments differ on a continuous environmental parameter and (4) production environments differ on a large number of aspects with a relatively small effect each.

Natural selection

An implicit way to breed for 'generalist' cows, is to create conditions in which cows that are environmentally sensitive in the target range of environments have a selection disadvantage. In natural populations without artificial selection, genetic fitness is maintained through a self-structuring force, called natural selection. If through a change in the environment, variation in genetic fitness arises, then the increase in fitness in the population is equal to the additive genetic variance of fitness at that time (Falconer and Mackay, 1996). Translated to production environments, genetic variation in fitness at an average level of management may be masked in environments with high-level management. Selecting bull dams in the latter group of herds will increase the dependency on high-level management and hence increase environmental sensitivity, if not accounted for.

Natural selection can not be utilised easily in breeding programmes for practical reasons. Breeding animals are often kept under strict biosecurity control in order to be able to sell semen or breeding stock. However, an option is to ensure that the target range of production environments is properly represented in the environments in which the progeny of the bulls are evaluated to improve general adaptability by selecting on an index based on the EBV of the specific environments (Mulder *et al.*, 2006). Natural selection in livestock production is particularly relevant for the very large number of fitness traits that are not recorded and included in a selection index.

For small, deviating production environments, such as low-input farming or organic farming, it may also be worthwhile to consider a breeding strategy that is radically different from using proven bulls with high-reliability indices and relies on bull dams that have proven to thrive in the specific production environment.

Limited number of environmental categories

For example, the distinction between organic and non-organic dairy herds is discrete. Grouping herds on prevailing soil type may yield five or six categories. Other examples are grouping by geographical region, type of production system or presence or absence of a major disease. If there is evidence of a change in ranking between groups of environments, the most obvious way is to define the trait of interest within groups and estimate genetic correlations between measurements of the trait in different environments. With these genetic parameters it is possible to carry out a multi-trait breeding value analysis for each trait measured in different groups of environments. In fact, this is how Interbull operates with its world wide breeding value estimation. A separate breeding programme for a challenging and a non-challenging environment may be considered if the genetic correlation between the two groups of environments is lower than 0.70 – 0.80 (Mulder, 2007; Mulder *et al.*, 2006).

Continuous environmental parameter

The performance of a genotype across the range of the environmental parameter is called the reaction norm. If a change in a certain environmental parameter affects some genotypes more than others, then there is genetic variation in environmental sensitivity. Conceptually, this could apply to a wide range of environmental parameters, such as temperature, stocking density, bacterial load, concentrates consumption, etc., but in practice, it is very difficult to collect reliable information. Hence, the specific environments are usually quantified by the mean performance of all genotypes, which then becomes the environmental parameter. An example of estimated breeding values for survival being dependent on the herd-year average of fat-protein ratio is shown in Figure 2 (Calus *et al.*, 2005). Each line in this graph represents the reaction norm of one bull. Random regression models have been used successfully in dairy cattle data to estimate reaction norms (Calus, 2006; Kolmodin *et al.*, 2002; Schaeffer and Dekkers, 1994; Windig *et al.*, 2006). The results of these analyses indicate that the genetic correlation between two traits may also be dependent on the level of the environmental parameter (Windig *et al.*, 2006).

Many small differences between environments

In practice, dairy herds differ in many ways and discrete or continuous environmental parameters describe these differences only in part. These unexplained micro-environmental differences may lead to genetic differences in micro-environmental sensitivity, which is observed as differences in residual variance. When bulls have at least 50-100 progeny, breeding values can be estimated for the size of the residual variance (Mulder *et al.*, 2007). Bulls with progeny that exhibit a large residual variation across herds are the ones that are environmentally sensitive. Bulls with progeny that exhibit a small residual variation across herds are the ones that are not environmentally sensitive. Figure 3 shows the distribution of residual variance of broiler sires for body weight, showing a large variation between sires in residual variance (H.A. Mulder, unpublished data).

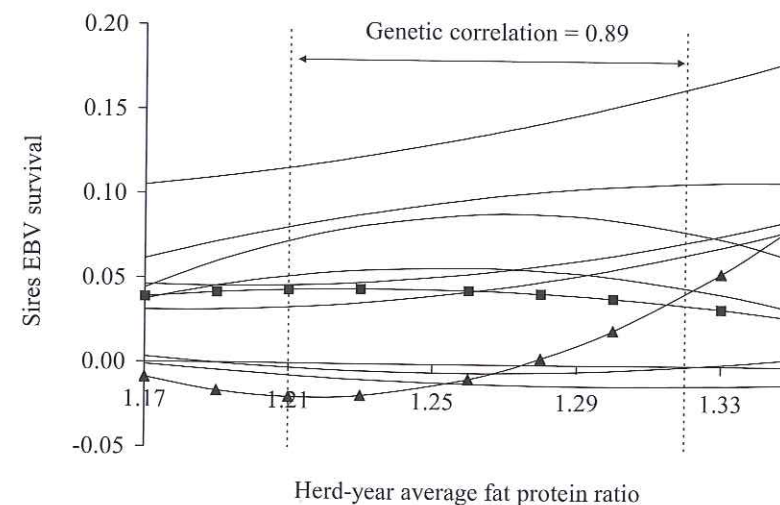


Figure 2. Breeding values for survival of the 10 sires with most daughters in the heifer data, estimated as function of herd-year average fat-to-protein ratio (squares and triangles mark breeding values of 2 particular sires). Tenth and 90th percentiles of the data are shown as dotted lines (reproduced from (Calus *et al.*, 2005)).

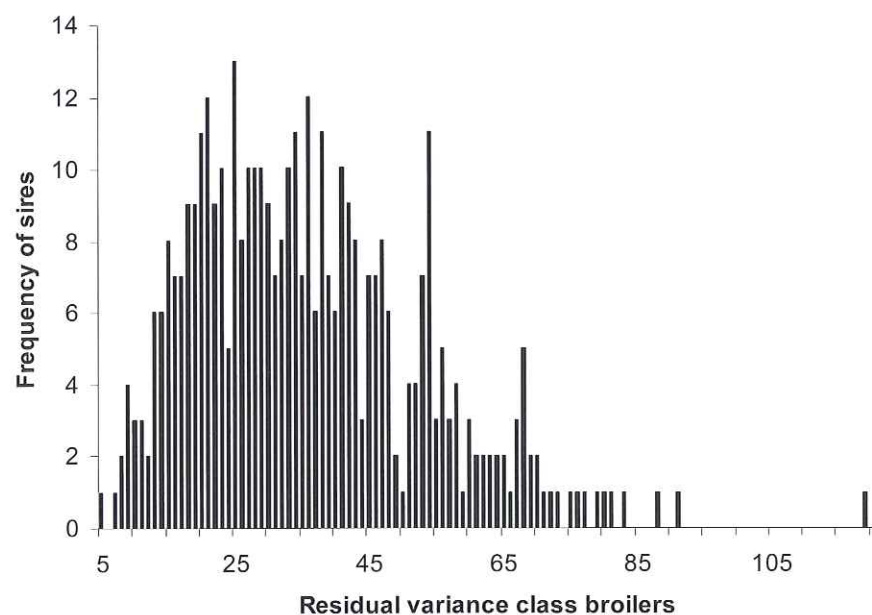


Figure 3. The frequency of sires per class of residual variance for body weight in broilers (H.A. Mulder, unpublished data).

Reduced environmental disturbances through breeding

Virtually all animals in animal production are kept in groups. It means that the genotype of an individual cow not only affects the performance of the cow itself, but it also determines part of the environment of its group mates. Hence, selecting the fittest animals directly, might have deleterious effects on its group mates (Muir, 2005), for example in the form of dominant social behaviour or aggressive behaviour, but also in the form of the amount of pathogens or parasites shed during an infection. The theory of simultaneously estimating direct genetic and associative effects has been developed by Bijma *et al.* (2007a,b). Work in layers showed that these models reveal more genetic variation in survival, which will enhance selection responses in comparison to selection on only direct effects (Ellen *et al.*, 2008). Hence, this work is a good example how selecting more robust animals at the individual level does not always lead to a higher robustness at pen or system level.

Conclusions

A robust dairy cow is able to maintain homeostasis in the commonly accepted and sustainable dairy herds of the near future. Robustness is largely an acquired characteristic through building up experience from exposure to a very large number of minor and major environmental signals. Breeding may give animals an advantage in acquiring robustness. Several methods have been discussed to improve robustness through breeding in practice.

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Robustness as a breeding goal and its relation with health, welfare and integrity²

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Abstract

The combination of breeding for increased production and the intensification of housing conditions have resulted in increased occurrence of behavioural, physiological, and immunological disorders in production animals. These disorders affect health and welfare of production animals negatively. For future livestock systems, it is important to consider how to manage and breed production animals. In this paper we develop the concept of robustness as a breeding goal. Improving robustness by selective breeding will increase (or restore) the animals' ability to interact successfully with the environment and thereby to make the animal better able to adapt to an appropriate husbandry system. This, in turn, is likely to improve both welfare and productivity, although this also depends on management and housing conditions. Therefore, in order to breed for sustainable and social acceptable production systems, animal production should accept robustness as a breeding goal.

Keywords: health, integrity, robustness as a breeding goal, welfare, future of livestock production

Introduction

From the 1960's onwards, animal husbandry became more and more intensive. This was supported by agricultural policy and the quest for sufficient, safe and cheap food. Animal breeding – in this context – was directed at an increase in production. The combination of breeding for increased production and the intensification of housing conditions have not been without consequences, especially for agricultural animals. And, despite of the economical and food-policy successes of these new husbandry systems, animal production created societal discussion on the way animals were treated. It was said that animals in animal production systems suffered; not only because of direct injuries, but also because of the confinement that made it impossible for them to behave in certain species-specific ways. In several countries public protests incited inquiries into the welfare of animals kept under intensive husbandry systems, for example the Brambell-report in the UK in 1965.

The traditional strategy to reduce these problems is preventive management. Besides the traditional strategy of preventive management, another possibility is to adapt animals by selective breeding or even genetic modification. Selective breeding can be used to improve health and welfare related traits in production animals. Health can be enhanced by selective breeding for disease resistance. This may be effective in resistance to a wide range of pathogens and can be used to protect animals under different environmental conditions (Lamont, 1998). Welfare can be enhanced by selection against expression of undesirable behaviour.

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