

## BIOLOGICAL LIMITS TO SELECTION AND ANIMAL WELFARE

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### SUMMARY

The paper is describing and discussing relationships between genetic selection for an improved production, biological limits to selection and animal welfare. Resource allocation theory has been used to underline the different aspects of biological limits.

**Keywords:** Animal welfare, stress, selection, animal breeding, resource allocation

### INTRODUCTION

Over the past centuries, humans have gradually increased their control over food-producing domestic animals. Improvements in production efficiency have been especially dramatic during the last fifty years. These advances can be attributed largely to improved nutrition and the introduction of highly mechanised and intensive farming systems. The productivity of these intensive farming systems has been further enhanced by the development of highly efficient breeding systems. These changes have benefited human consumers in the form of higher production, lower food prices, more efficient utilisation of feed resources, decreased manure production and decreased environmental pollution. However, during the last 20 years, opinion makers and scientists have raised critical questions and initiated a debate concerning animal welfare in these production systems. The debate includes ethical issues related to animal rights (e.g. Singer, 1990), our moral responsibility to ensure that animals are treated properly (Hagelsø and Krohn, 1993), and the animals' mental coping with their situation. Many have expressed the opinion that when considering animal welfare one should also include the animals' feelings and how they perceive their situation (Dawkins, 1990; Duncan and Petherick, 1991). However, our ability to assess an animals' mental experience is currently limited; thus scientific assessments have had to rely on more measurable welfare indicators.

The welfare discussion has largely focused on problems related to housing, management, genetic engineering and breeding practises that directly affect animal welfare. Examples in the last-mentioned category include reproduction problems, e.g. calves that are too large for normal parturition to occur safely in some strains of beef cattle, leg problems in broiler chickens and turkeys, and mating problems in male turkeys selected for large breast muscles (Dunnington, 1990; Duncan et al., 1991; Broom, 1993). However, less attention has been given to more general side-effects from selection for increased production efficiency.

## DEFINITIONS OF WELFARE

Animal welfare is defined in a number of ways. It varies from the individual perception of the ideal relationship between human and animals, where evaluation of welfare standards may be based on their subjective feelings to more objective definitions that focus on the animals and their ability to cope with their environment. A frequently cited definition of welfare is given by Broom (1986): “the welfare of an animal is its state as regards its attempts to cope with its environment”. A failure to cope implies a reduction of fitness and, hence, stress (Broom, 1991). When an animal is confronted with an environmental stressor, adaptation involves a range of behavioural and physiological responses where the endocrine, immune and central nervous systems respond to the stimuli in a co-ordinated manner to restore homeostasis (DeSouza, 1993). Corticotrophin-releasing hormone (CRH) appears to play a central role in many of the observed changes during stress (Dunn and Berridge, 1990). CRH is released a few seconds **after** the animal perceives a **stressor** and stimulates the pituitary gland to release adrenocorticotrophic hormone which in turn stimulates the adrenals to release glucocorticoids. CRH not only activates the hypothalamic-pituitary- adrenal axis, but, by its neurotransmitter function in the brain, CRH may also be involved in the activation of the other main branch of the stress response, the **sympatho-adrenal** medullary (SAM) system, resulting in a increased level of catecholamines. Both the **HPA** and SAM systems alter biological function in the animal in an attempt to mobilise **biological resources** (glucose, fatty acids and amino acids) at the cost of the immune system and ongoing biological activities (e.g. growth) necessary to cope with a critical situation. Such responses may be entirely appropriate when the behaviour stress response permits the animal to escape the stressor. However in our farming system animals frequently are unable to remove themselves from the stressor. Thus, the stress response may continue and involve a substantial adjustment of both autonomic and neuroendocrine systems and place the animal at risk for pathologies such as disease, failure to reproduce, reduced growth or aberrant behaviour (Moberg, 1985).

As mentioned above, the welfare status of individuals is related to the animals perception of stressors, the frequency of perceived stressful events and the animals ability to respond to them. Considerable variation exists between individuals in term of their psychological and physiological makeup. Among factors that can affect the welfare status are genetic make-up, prenatal stress and experiences during juvenile development, behaviour strategies, competition capacity, the individuals’ success or lack of success in their behavioural strategy and interactions between two or more factors (i.e. Henry, 1982; Hohenboken, 1986; Gray 1987; Von Holst, 1986; Benus, 1988; Becker et al. 1991; Toates, 1995; Bakken, 1994, 1995, 1997; Braastad et al., 1997; Weinstock 1997) As a consequence, behavioural, physiological, health and reproduction data should all be used as criteria when assessing animal welfare (Broom, 1993).

## **RESOURCE ALLOCATION THEORY AS A WAY OF UNDERSTANDING SELECTION LIMITS**

A simple model for studying the relationship between selection for increased production efficiency and adaptation ability and welfare can be derived from the resource allocation theory (Beilharz et al., 1993). Beilharz et al. (1993) stated, in two equations, that fitness,  $F$ , is a product of many major fitness component (say  $A, B, C$ , etc., i.e. number of parities, litter size, survival, survival of progeny, etc.). The metabolic resources ( $R$ ) used by the fitness component (say  $a, b, c$ ) as well as all other traits (i.e. growth, production, general activity, and resources necessary to cope with stressful situation) sum to no more than the animal can obtain **from** its environment. Resources consumed by one process are not available for other processes. Hence, in a environment with a restricted amount of resources, when  $R$  reaches its maximum value, natural selection will, if **successful**, lead to an optimal resource allocation to all traits so that the product of the major fitness components is **maximised**, with intermediate optimal values (Beilharz et al., 1993). The result is an animal with a behaviour and physiology highly adapted to their environment.

Intensive production and management systems provide food, shelter and protection **from** predators and have largely decreased or removed the animals' need to cope with stressors such as food shortage, predators and **unfavourable** weather conditions. All resulting in making more resources available, either in total by an increase in the amount of food available or an improvement in the quality of the food, or by a reduction in the amount of resources needed for traits previously important (Beilharz et al., 1993). Under such conditions rapid genetic progress in many traits, including fitness and other resource-demanding production traits, can be achieved without any negative side effects until a level is reached at which the environment by  $R$  again constrains further rise (Beilharz et al., 1993). The theory predicts that at this point any further rise in a given resource-demanding production trait would result in a negative response in one or more of the other traits owing to a reallocation of resources from these traits to the production trait.

Based on this theory at least four important relationships between animal welfare and artificial selection for improved production can be derived: 1) In a resource unrestricted environment, artificial selection will tend to favour animals with a strong ability to obtain and convert resources to the production trait and only to some degree disfavours animals with a high demand for resources owing to high stress sensitivity, level of activity, etc. Selection against the latter will be enhanced when the environment by  $R$  starts to become limiting. At a limit this may lead to an animal population adapted to their production environment but with fewer resources or to a genetically determined lower ability to cope with environmental change. 2) In an environment limiting by  $R$  further progress in selection for production will have negative side effects on the animals and may reduce their welfare. 3) Environmental improvements will relax environmental constraints and may reduce the severity of any negative side effects of selection. 4) Relaxed selection in a population showing negative **side-effects** will by natural selection restore a new optimal resource allocation to all traits so that

the product of the major fitness components again is **maximised** and by this may reduce negative side effects of selection. Experiments, nicely illustrating the first point, are shown both in Luiting et al. (1994) and in Beilharz and Mitpaiboon (1994)

## **SELECTION LIMITS AND PRODUCTION ENVIRONMENTS**

### **Long time experiments**

Long-term selection experiments with laboratory animals have been performed for almost half a century. One way to better understand selection limits and animal welfare is to look for general trends in the results of the large number of experiments carried out in laboratory animals as well as farm animals. Falconer and Mackay (1996) stated that selection limits normally are reached after 20-30 generations of selection and that reproduction is often reduced in selected lines. Eisen (1980) showed that selection limits in mice were reached **after** around 30 generations and that the total response was around 2.4 standard deviations for gain and 1.9 standard deviation for litter size. Several experiments have shown that after a period of intensive selection followed by relaxed selection, populations are able to stabilise at higher levels compared with those existing before the selection started (for example, see Yoo, 1980, ref. by Falconer and Mackay, 1996). This indicates that selection has altered certain of the animals' biological processes, allowing them to reach a higher production level even if the environment has not changed. In most selection experiments the response seems to have been higher for productive traits than for reproductive ones, and reproduction appears to have been heavily reduced in lines selected for production traits.

One of the most **well-known** selection experiments, performed on a beetle, was reported by **Enfield** (1979). Selection for pupa weight in *Tribolium* was performed for 140 generations, and changes in reproductive performance, incidence of sterility and number of progeny per fertile mating were measured and analysed. The experiment included several lines and replicates, periods of relaxed selection and crossing between lines. Some of the most interesting results in terms of biological limits to selection were as follows: There was a steady response to selection in the first 50 generations but little response **after** generation 75. However, heritabilities for pupa weight were constant throughout the selection period. It was possible to separate the up and down lines by more than 17 phenotypic standard deviations, which is indicative of a dramatic long-term response to selection. There was a marked increase in sterility in the period of rapid selection response and a steady decrease in number of progeny per fertile mating. The results proved that there was a negative genetic correlation between the selection criterion and fitness.

### **Selection limit and maternal effects**

Vangen (1993) presented results from 40 generations of selection for litter size in mice. The experiment examined the possibilities of improving litter size in a **standardised** maternal environment and measured direct and correlated traits to selection for litter size. To examine the effects of different maternal environments on selection response, selection for high litter size was performed in different lines where litter size was **standardised** to different levels (4, 8,

12 pups and unstandardised litter size) in another part of the experiment (Vangen, 1990). The main results can be summarised as follows: Realised heritabilities were around .16 in the first 20 generations and zero in the next 20 generations of selection. The reason for the plateauing was a combination of reduction in genetic variation and presence of recessive alleles at low frequencies. Additionally the maternal environment was assumed to be limiting for further response. Standardisation level had great impact on realised parameters in the first 10 generations of selection, however no clear effects after generation 15. Maternal effects were important for the immediate response, but of limited importance for the long term response. It was possible to obtain average litter sizes of some lines of more than 21 pups, 4 standard deviations above the level of the unselected population 60 generations earlier.

### **Life time performance**

Another question addressed was how long-term selection for large first-parity litter size affected litter size in later parities. Did selection for high early reproductive performance change the normal curve for lifetime reproductive performance. The results presented by Vangen (1990) were as follows: Lifetime performance was only measured through parities 1-4 since most females, quite unexpectedly, were not able to produce more than four litters. All high lines showed a drop in litter size beginning at parity one, and the number of empty females increased with parity number. This supported one element of the resource allocation theory (Beilharz et al., 1993); i.e. that allocation of resources to first-parity litters will decrease resources for later parities. However, overall lifetime performance was higher in the high lines than in the control lines.

### **CHANGES IN PRODUCTION TRAITS**

Selection has proved to be an efficient way of changing the genetic merit of farm animals for thousands of years. However, the quantitative genetics theory applied in animal breeding from the 1950s created dramatic changes in performance of the animals. In a bit more than 30 years, the production performance of Norwegian farm animals have increased by 84 percent of the mean in 1959; an increase in performance of about 2.5 percent of the 1959-level per year (Vangen et al., 1994). Slaughter weights of broiler chickens in the Netherlands increased from 1250 g in 1965 to 1900 g in 1996, whereas age at slaughter in the same period decreased from 59 to 44 days. Growth rate in Dutch meat type pigs increased from 606 g/d in 1974 to 729 g/d in 1995, and milk production per lactation in Dutch dairy cattle increased from 4029 kg in 1950 to 7605 kg in 1996. (Rauw et al., *subm.*). Similar figures can be found in other breeds and species. The question is if these trends will continue with the same speed and at which expenses in others, for example welfare traits.

### **SIDE EFFECTS OF SELECTION**

It is obvious that genetic selection for high production efficiency in livestock species has increased production levels considerably. However, apart from desired effects of genetic selection, selected animals seem to be more at risk for behavioural, reproduction and health problems. Examples of over 100 references on undesirable side-effects of selection for high

production efficiency in broilers and turkeys, pigs and dairy cows are presented in the review paper by Rauw *et al.* (submitted). In the following some examples of these side effects are presented: Results of Burkhart *et al.* (1983) and Barbato *et al.* (1984) suggest that selection for fast growth rate in broiler chickens has resulted in a hypothalamic failure to diminish the hunger drive leading to overconsumption: selected chickens consume feed above their metabolical requirements until they reach a limit set by the gastrointestinal capacity. Selection for high production efficiency has resulted in antagonistic relationships with several reproduction traits. Broilers breeder hens selected for high body weight showed an increased 'erratic ovulations and defective egg syndrome' (Anthony *et al.*, 1989) and a higher percentage of dead and abnormal spermatozoa (Marini and Goodman, 1969) compared with a low body weight line. In pigs, an unfavourable genetic relationship between breeding value for high lean tissue growth rate and incidence of prolonged intervals from weaning to farrowing has been found (Ten Napel, 1996). Growth rate and leanness had opposite effects on several oestrus traits (Rydhmer *et al.*, 1994). Genetic correlations between milk yield and reproduction traits in dairy cattle show that on average high producing dairy cows are bred later, show more days open, require more services per conception (e.g. Berger *et al.*, 1981), have a lower rate of non-return at 56 days (e.g. Van Arendonk *et al.*, 1989), and have a longer calving interval than low producing cows (e.g. Hoekstra *et al.*, 1994). Selection for high production efficiency also shows antagonistic relationships with several health traits. In broiler chickens a higher mortality rate has been reported with selection for high growth rate, which was mainly associated with sudden death, ascites and leg problems (Havenstein *et al.*, 1994). Controversy exists concerning the relationship between production and health traits in dairy cattle (Rauw *et al.*, submitted). High producing cows seem to be at higher risk of mastitis and ketosis (e.g. Lyons *et al.*, 1991). Henckel (1992) found a surprisingly low proportion of oxidative slow twitch muscle fibres in chickens, which is related to increased stress susceptibility and, due to the higher growth potential, may very well be a result of selection for high growth rate. Similar results have been found in pigs: Landrace pigs showed a higher percentage of glycolytic white muscle fibres (76%) than wild pigs (none) (Rahelic and Puac, 1980), suggesting a decreased ability to sustain environmental stresses.

## DISCUSSION

Results from selection experiments and experience gained in practical breeding indicate that there is great potential for further improving production traits in farm animals. This potential is connected to the improvement in the traits selected for. Even though the experiments levelled off at different plateau's, selection has improved the animals' potential for higher production during relaxed selection periods as well. However, negative side effects in parameters of importance for the animals' welfare and fitness are often found. Though it would be naive to evaluate animal welfare status based on a single welfare parameter, these results, nevertheless, call attention to the need for carefully controlled studies to evaluate the consequences of selection for high production with regard to animal welfare. Such studies should include measures of behaviour, physiological, health, genetic correlations between welfare and production traits and changes in genetic correlations across generations.

Based on the results from long-term selection experiments it is evident that periods of relaxed selection will increase possibilities for achieving further genetic responses if plateaus are reached. It would be interesting to evaluate the usefulness of including such a strategy in intensive industrial breeding programmes to obtain a better balance in terms of progress and long-term responses. Another possible strategy would be to include welfare parameters in the breeding objectives along with the production traits. Comprehensive research has been initiated in several species, including pigs and foxes, in order to develop genetic parameters for welfare traits.

Biological limits will often be more pronounced in selection experiments than in practical breeding work, since more traits are included in practical breeding work than in strict selection experiments. Still, the extent to which biology limits genetic progress seems to be greater than quantitative genetic theory indicates. This is due to the existence of threshold values for important biological functions and optimum values for body composition traits, as well as to the fact that the magnitudes of genetic correlations can change with the levels of the different traits. A better understanding of the biological aspects of animal breeding is essential to achieving further progress in the livestock industry. Welfare and stress aspects will be important not only in their own right but also as components of a balanced biological production of animal products in the future.

The agricultural industry has devoted great effort to improving nutrition and the physical environment for farm animals, however, less attention has been placed on aspects of their social environment and behaviour. Nor has the animals' perception of their situation or their ability to cope with confinement been given serious consideration. However, from an animal welfare point of view it is of great importance to increase knowledge about environmental components recognised as stressors in farm animals, causes of variation between individuals and use of this knowledge in order to introduce appropriate measures for decreasing the total burden of stress on the animals. In a systematic study with 20 putative environmental stressors on farm silver foxes social factors and human attitude were found to be the two main group of stressors for the animals (Bakken et al. 1994). It has also been shown that both these parameters strongly affect fox reproduction as well as their offspring's growth and behavioural ontogeny (Bakken 1993, 1994, 1995, 1997). Social factors have also been shown to be of great importance for animal production in both pigs and cows (Barnett and Hemsworth, 1990; Douglas et al., 1993). These studies indicate that farm systems and management practices designed with the animals' biology and social structure in mind will strongly benefit the animals' welfare. According to the resource allocation theory, this should also increase the amount of resources available for fitness or improved production by selection, relax environmental constraints and probably even improve the public image of the animal production industry.

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