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SUSTAINABLE LIVESTOCK GENETIC IMPROVEMENT

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SUMMARY

This paper argues that potential for livestock genetic improvement will be largest in directions not explored by natural selection. In particular, *i*) improving group performance by including social interactions in breeding schemes, and *ii*) exploiting trade-offs between past and present environments.

INTRODUCTION

Quantitative genetics and animal breeding are well developed disciplines, and past selection, focussed primarily on production traits, has been successful, particularly in species with short generation intervals and many offspring, such as broilers. Large improvements in yield have been achieved, while trade-offs in functional traits have been limited, partly by improvement of the production environment. Nevertheless, there has been a trend for aspects of fitness to decline, and breeders are concerned whether current practices can be sustained in the longer term. Moreover, there is increased societal concern about animal welfare, in particular in Europe. This paper discusses the opportunities to increase sustainability of livestock genetic improvement, partly in the light of evolution.

BASICS OF BREEDING

In principle, livestock genetic improvement is straight forward. The breeding goal (aggregate genotype) should include all traits of importance, either as a sum of traits weighted by economic values, or expressed as desired gains. Breeding value estimation should utilize all available information, ideally in multi-trait animal model evaluations, and selection decisions should maximize response while restricting the rate of inbreeding by using optimal contribution selection (Meuwissen 1997). Selection index theory and stochastic simulations can be used to optimize the structure of breeding schemes. Further improvement can be obtained by mating least related individuals and applying factorial mating when possible (Sonesson and Meuwissen 2000), and by using molecular information in particular for traits not recordable on selection candidates.

In principle, the above applies equally well to production traits as to health and welfare traits. Therefore, when the above aspects of a breeding scheme are well-organised, prospects for further improvement may seem limited at first glance. The above, however, is a very statistical approach which is maybe sufficient in the short term, but gives limited insight in the long-term consequences of selection. A better understanding of the biological organisation resulting from long-term natural selection may give us a better understanding of opportunities and threats in livestock genetic improvement.

OPPORTUNITIES LEFT OVER BY NATURAL SELECTION

Dobzhansky (1973) argued that “Nothing in biology makes sense except in the light of evolution”, which suggests that animal breeders can gain insight into the prospects for genetic improvement by looking at natural selection. This does not mean, however, that breeding strategies should resemble natural selection, but rather the opposite. Before domestication, our livestock species have been under natural selection for a very long time. Denison *et al.* (2003), therefore, argued that as a consequence of long term natural selection, any genetic modification that can contribute to fitness under natural circumstances will either have been exploited by natural selection already, or is too complex to be achieved by natural selection, and therefore probably also beyond the reach of artificial selection. To a large extent, our current species have been optimized by natural selection for individual fitness in the natural environment of the past (Price, 1970). (Though interactions with relatives and selection acting at multiple levels appears to have resulted in phenotypes beneficial to groups of individuals, instead of to the individual itself. Such systematic cooperation, however, in which individuals sacrifice personal fitness for the benefit of the group is largely restricted to social insects; *e.g.* Clutton-Brock, 2002.). Though one may argue that our current livestock species differ considerably from their wild predecessors, it follows from the large similarities in physiological organisation observed even between species that the fundamental biological organisation has been little affected by artificial selection in the past. Rather than creating new biological mechanisms, past artificial selection has mainly altered the magnitude of processes, such as increasing resource uptake and shifting resources towards productivity. Prospects in directions explored extensively by natural selection, *e.g.* to further improve basic biological processes, such as efficiency of enzymatic conversions or general disease resistance, therefore, seem to be limited. Instead, opportunities for improvement will come from utilizing trade-offs between *i*) fitness in past versus present environments, and *ii*) between individual performance and performance of entire groups of individuals (Denison *et al*. 2003). In other words, opportunities for artificial selection are greatest in directions not explored by natural selection. Two such directions are adaptation to the current instead of past environment, and selection for group instead of individual performance. Thus, in livestock genetic improvement we will necessarily have to accept a reduction in individual fitness that would be observed under natural circumstances, i.e. in the wild. In the following, prospects to improve traits affected by social interactions and GxE-interaction are discussed.

SOCIAL INTERACTIONS

Natural selection usually selects for individual fitness, and may therefore increase competition among individuals. As a consequence, natural selection may have resulted in (social) interactions among individuals that are beneficial to the individual, but detrimental to the entire group or population of individuals. Breeders, however, are interested in performance of groups of individuals, a direction of selection that may not have been fully exploited by natural selection. Prospects to improve livestock populations by improving social interactions among individuals will depend on the relevance of such interactions to group performance, which is largely unknown at present. Social interactions can affect performance in at least three ways. First, interactions may directly affect health, welfare and productivity of individuals. Examples are cannibalism in layer chickens, tail biting in pigs and fighting behaviour in mink. In those cases, accounting for social interactions in selection decisions may have large impacts on response to selection. For example, results in layer chickens indicate that including social interactions in the selection decisions may more than double response to selection against cannibalism (Muir 1996; Bijma *et al*. 2007b). Second, interactions may indirectly affect performance of individuals. In humans, for example, social interactions on the work floor are an important cause of stress affecting productivity and health of employees (Krantz and Mccenney, 2002). Similar effects may occur, for example, in pigs. Our preliminary results in growing pigs kept in groups indicate that social effects contribute substantially to the heritable variation in growth rate and *ad libitum* feed intake. Finally, competition for finite resources may depress performance of a herd. When the total amount of feed is fixed, for example, herd production can increase only by an increase of efficiency. Still, individuals may spend energy competing for feed intake, which will reduce herd productivity and probably also decrease uniformity within herds. Such phenomena may play a role, for example, with restricted group-feeding in pigs.

The relevance of social interactions for livestock genetic improvement may be judged by their contribution to the heritable variance in traits. Social interactions may increase the total heritable variation to a value substantially larger than the classical additive genetic variance in a trait. With social interactions, the total heritable variation is given by (Bijma *et al.* 2007a)

$$\sigma^2_{TBV} = \sigma^2_{A_D} + 2(n-1)\sigma_{A_{DS}} + (n-1)^2\sigma^2_{A_S} \ ,$$

in which TBV denotes the total breeding values of individuals, $\sigma^2_{A_D}$ is the usual (direct) additive genetic variance, $\sigma_{A_{DS}}$ is the additive genetic covariance between direct and social effects, $\sigma^2_{A_S}$ is the additive genetic variance in social effects of individuals, and n denotes group size. Bijma *et al.* (2007b) showed that the total heritable variation for mortality due to cannibalism in layer chickens was three-fold greater than the additive genetic variance, indicating that social interactions may hide heritable variation.

By using extended mixed model equations, the variance components involved in σ^2_{TBV} can be estimated from field data without the need to record the social interactions *per se*. The extended mixed model is

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_D\mathbf{a}_D + \mathbf{Z}_S\mathbf{a}_S + \mathbf{e}$$

in which $\mathbf{a}_D$ is a vector of direct breeding values, with incidence matrix $\mathbf{Z}_D$ linking phenotypic values of individuals to their direct breeding values; $\mathbf{a}_S$ a vector of social breeding values, with incidence matrix $\mathbf{Z}_S$ linking phenotypic values of individuals to the social breeding values of their group members; and $\mathbf{e}$ a vector of residuals. The covariance structure of genetic terms is: $Var\begin{bmatrix}\mathbf{a}_D \\ \mathbf{a}_S\end{bmatrix} = \mathbf{C}\otimes\mathbf{A}$, where $\mathbf{C} = \begin{bmatrix}\sigma^2_{A_D} & \sigma_{A_{DS}} \\ \sigma_{A_{DS}} & \sigma^2_{A_S}\end{bmatrix}$ and $\otimes$ indicates the Kronecker product of matrices. Residuals of group members are correlated due to non-heritable social effects (Bijma *et al.*, 2007b). The variance matrix of the residual is block diagonal, $Var(\mathbf{e}) = \mathbf{R}\sigma^2_e$, with $R_{ii} = 1$; $R_{ij} = \rho$, when i and j are in the same group, and $R_{ij} = 0$ when i and j are in different groups. This structure can be fitted in software such as ASREML.

Ellen *et al.* (2007) discuss methods to improve traits affected by social interactions. They show that traits affected by social interactions can be improved efficiently by using information of relatives *that are kept in family groups*. When relatives are kept in family groups, the mean performance of relatives includes both the direct and the social effect of the family, which avoids deterioration of social performance. Ellen *et al* (2007) show that asymptotic accuracies of selection for traits affected by social interactions are the same as for conventional traits (*i.e.* 0.5 for half sibs, 0.71 for full sibs and 1 for progeny).

GxE-INTERACTION

Utilizing trade-offs between past and present environments implies utilizing GxE-interaction. Compared to the past, present environments usually have higher resource availability, absence of natural predators, reduced environmental variance in species kept indoors, limited or no need for individuals to raise their offspring, and absence of natural mate selection. Such GxE-interaction may give the opportunity to improve performance by means of breeding without compromising productivity, health and welfare in current environments. Apart from GxE-interaction due to differences between past and present environments, GxE-interaction due to variation among current environments is an important factor in breeding. Genotype by environment interaction has a number of consequences for livestock genetic improvement. On the negative side, *i*) GxE-interactions involving the breeding and commercial environment can reduce the response to selection observed in the commercial environment, and *ii*) when the overall commercial environment consists of a number of sub-environments, GxE-interaction between those sub-environments reduces the total additive genetic variance in the trait in the entire population, which in turn reduces response to selection. On the positive side, GxE-interaction is equivalent to the existence of genetic variation in the slope of reaction norms, meaning that environmental sensitivity of a population can be altered by selection.

A difficulty in livestock improvement is to identify the environmental parameters contributing to the GxE-interaction. A classical solution in dairy cattle breeding is to treat countries as environments, even though environmental fluctuations within countries may be equally large as between countries. An alternative approach is to use average herd performance for a certain trait as an environmental parameter in a random regression model. Still the problem remains which parameters to choose. The so-called AMMI-models, which are used in plant breeding, may offer a solution (Mulder 2007). AMMI stands for Additive Main effects and Multiplicative Interactions (Gaugh 1988). In AMMI-models, the interaction is described in terms of differential sensitivity of genotypes to the most discriminating environmental variables that can be constructed. These environmental variables are hypothetical and estimated from the data (e.g. Van Eeuwijk 1995). Thus the data still need to contain variables explaining GxE-interaction, but the linear combinations of those variables do not have to be specified *a priori*, as they are derived from the data in an optimum manner. Hence, compared to the reaction-norm models currently used in livestock genetic improvement, AMMI models may solve the problem of identifying the (linear combination of) environmental variables that best explain the GxE-interaction.

The problem of reduced response due to GxE-interaction between breeding nucleus and commercial environment may be largely overcome by setting up data recording in commercial environments (Mulder and Bijma 2005), which may be combined with the use of molecular genetic information. For example, when the commercial population consists of crossbred beef cattle, performance data and molecular data on a limited number of markers may be collected from commercial individuals at the slaughter houses. Several thousands of markers may be collected from breeding individuals in the nucleus. The limited molecular data may be used to reconstruct the pedigree links between commercial and nucleus animals, and the large number of markers may be used in the nucleus to breed for commercial performance, e.g. using genomic selection (Meuwissen *et al*. 2001). Thus, dealing with GxE-interaction between nucleus and commercial populations may require substantial data collection, but does not present a fundamental biological problem.

GxE-interaction occurring when distinct commercial environments are supplied by a single breeding program directly reduces the response to selection, because it reduces the total additive genetic variance. Hence, the genetic variance in mean performance across environments is less than the mean of the genetic variances within each separate environment. As long as those environments are supplied by a single breeding population, there seems to be no solution for this problem. When the overall population is large enough, an approach may be to use crossbreeding with a limited number of pure lines to create a larger number of crossbred products. For example, four purebred breeding lines may be used to produce six types of crossbreds, and each pure line may be selected for performance of the crossbreds it produces, e.g. using genomic selection. Alternatively, each sub-environment may be supplied by separate pure line breeding program (Mulder *et al*., 2006). Such strategies, however, are often costly and will require substantial market share.

The existence of GxE-interaction implies that environmental sensitivity (ES) is heritable. Thus, ES may respond to selection, either intentionally or unintentionally. In many livestock species, genetic improvement has been accompanied by improvement of husbandry systems. In the presence of GxE-interaction, such combined genetic and environmental improvement increases ES for the trait under selection. (Essentially, this is an adaptation of our breeds to the good environment we provide them.) Increased ES for productivity is often seen as undesirable, because it decreases uniformity and may cause sudden fluctuations in productivity due to changes, for example, in the weather. Analysis of resource allocation models, however, suggests a trade-off between ES for productivity and ES for traits related to fitness, in particular when the amount of feed is limited. Thus, breeding programs targeting high and constant productivity are likely to result in decreased robustness for traits related to fitness. When profit is linear in productivity but non-linear for traits related to fitness, it may be better to sacrifice ES for productivity so as to gain ES for traits related to fitness. This requires knowledge of genetic correlations between ES for productivity and fitness.

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