SELECTION IN PRESENCE OF GENOTYPE BY ENVIRONMENT INTERACTION MAY INCREASE ENVIRONMENTAL SENSITIVITY

R. Kolmodin1, E. Strandberg1, H. Jorjani2,1 and B. Danell1

1Department of Animal Breeding and Genetics, PO Box 7023, S-750 07 Uppsala, Sweden
2Interbull Centre

INTRODUCTION

The reaction norm of a genotype describes the phenotype expressed by that genotype over a range of environments (e.g. Woltereck, 1909 in : Stearns, 1989). The two sires in figure 1 have equal phenotypic values in environment 2. If, in a later generation, the environmental value has increased, the progeny of sire 1, having the steeper reaction norm, will be favoured over progeny of sire 2. Assume a population of animals having linear reaction norms with individual variation in slope (i.e. genotype by environment interaction (GxE)). The environment is continuously improving. If the population is selected for high phenotypic value, there is reason to believe that the environmental sensitivity of the population will increase.

Within the range of environments normally encountered by the animal, it is often reasonable to assume the reaction norms to be linear. However, the linearity may not be valid for environments encountered after generations of environmental change. Biological restrictions, e.g. unfavourable correlations with other traits, may reduce the response to environmental improvements. In such cases, curvilinear reaction norms may be expected.

Our objective was to study the effect on environmental sensitivity of selection for high phenotypic value in combination with a continuously improving environment, and in presence of GxE. Our hypothesis is that the average environmental sensitivity of the population will increase.

METHODS

Simulation of records. Linear, quadratic and sigmoid reaction norms were simulated in 100 replicates of a population of 20 000 animals. Selection was practiced for 10 generations. In the base population the average environmental value $\bar{E}$ was zero. For each generation, $\bar{E}$ was increased ($\Delta E$) by 0.0, 0.1, 0.5, 5.0 or 10.0 units. The low levels of environmental change ($\Delta E$ 0.0-0.5) were assumed to be relevant for populations, wild or domestic, living under natural conditions. For farm animals in an intensive production system, $\Delta E$ was assumed to be high ($\Delta E$ 5.0-10.0), and approximately of the same magnitude as the genetic change.

Figure 1. Reaction norms of two sires. Arbitrary units
Two alternative selection schemes were used to select individuals to breed the next generation: A) Mass selection scheme: 10% of both males and females were selected in each generation based on their phenotypic values, B) Progeny test scheme: 5% of the males were selected based on their expected phenotypic value in the average environment of each generation (imaginary offspring average), and there was no selection among females. Mating of selected sires and dams was at random and each mating resulted in equal number of offspring. Genetic variances for the parameters of the linear reaction norms corresponded to estimated variances of reaction norm parameters for milk protein production of Nordic red dairy cattle (Kolmodin et al., 2002). The variances of the parameters of the non-linear reaction norms were chosen to result in approximately the same phenotypic variation. The reaction norm parameters in the base population, and the individual environmental deviations $x_i$ and the residuals $e_i$ in all generations, were simulated to be independently normally distributed with expectations zero. The environmental and residual variances were 900 and 500, respectively.

Linear reaction norms were simulated as $y_i = a_i + b_i (\bar{x}_i + x_i) + e_i$, where $a_i$ was the intercept (level) of the reaction norm, $b_i$ was the random regression coefficient of a regression of phenotypic value on environmental value (slope), $\bar{x}_i$ was the average environment in generation $t$, $x_i$ was the individual random deviation from average environment, and $e_i$ was the residual. Base population variances for $a_i$ and $b_i$ were 100 and 0.02, respectively.

Quadratic reaction norms were simulated as a second grade polynomial function, $y_i = a_i + b_i (\bar{x}_i + x_i) + c_i (\bar{x}_i + x_i)^2 + e_i$, where $a_i$, $b_i$ and $c_i$ were the reaction norm parameters, and $\bar{x}_i$, $x_i$ and $e_i$ were the same as before. Base population variances for $a_i$, $b_i$ and $c_i$ were 80, 0.02, and 0.00001, respectively. A restriction $c_i \leq 0$ was imposed on the curvature of the reaction norms, to ensure that a maximum phenotypic value existed. Hence the parameter $c_i$ had a truncated normal distribution.

The sigmoid reaction norms were simulated as $y_i = a_i + b_i \frac{\exp^{-d_i (\bar{x}_i + x_i)}}{1 + \exp^{-d_i (\bar{x}_i + x_i)}} + e_i$, where $a_i$, $b_i$, $c_i$, and $d_i$ were the reaction norm parameters, and $x_i$, $\bar{x}_i$, and $e_i$ were the same as before. Base population variances for $a_i$, $b_i$, $c_i$, and $d_i$ were 50, 180, 1.5, and 0.02, respectively.

**Estimation of environmental sensitivity.** Environmental sensitivity was defined as the weighted average of the absolute value of the first derivative of the reaction norm function. The average was weighted by the probability density function of the environmental distribution in the interval of $\pm 3$ environmental SD units (i.e. $\pm 90$ units) from the generation mean. For the sigmoid reaction norms we also discuss an alternative definition: the range of phenotypic values from the base generation’s mean environment - 3 environmental SD units to the tenth generation’s mean environment + 3 environmental SD units.

**RESULTS AND DISCUSSION**

Figure 2 shows the change of the average reaction norm over generations for linear, quadratic and sigmoid reaction norms.
Linear reaction norms. The average environmental sensitivity and the average phenotypic value of the population increased from base to tenth generation for both selection schemes and for all levels of environmental change (including $\Delta E 0.0$). The increase was larger with higher levels of environmental change, though there was no significant difference between $\Delta E 0.0$ and $0.1$.

Quadratic reaction norms. The shape of the reaction norm remained quadratic with the peak performance within the environmental range for each generation. The major change over generations was in the maximum phenotypic value (figure 2b). The average environmental sensitivity increased significantly from base to tenth generation for all levels of environmental change (including $\Delta E 0.0$). With the mass selection scheme, the increase was larger with higher levels of environmental change, though there was no significant difference between the three lower levels of environmental change ($\Delta E 0.0-0.5$). With the progeny test scheme the increase in environmental sensitivity was smallest with $\Delta E 5.0$, and highest with $\Delta E 10.0$.

Sigmoid reaction norms. Without environmental change the average reaction norm remained more or less flat over generations, though there was substantial variation in environmental sensitivity. With environmental improvement, the reaction norms assumed a sigmoid shape (figure 2c). With $\Delta E \leq 0.5$, the average environmental sensitivity increased over generations. With $\Delta E \geq 5.0$, the environmental sensitivity increased for some generations and then decreased. Most of the environmental sensitivity in the later generations occurred in less frequent environments, resulting in a relatively low weighted average environmental sensitivity. Given the range of environments that this generation is expected to encounter, the average reaction norm in generation 10 was flat, resulting in phenotypes at the upper limit of the reaction norm function (figure 2c).

Environmental sensitivity by the alternative definition for sigmoid reaction norms increased over generations for all levels of $\Delta E$ and for both selection schemes (illustrated by dotted lines in the figure).
in figure 2c). A large decrease in the environmental value, beyond the normal range of environments for the population to encounter, could have drastic effects on the average phenotypic value of the population.

**Implications.** The reaction norm function can be used to predict breeding values for a trait, given a certain environment. Breeding values for reaction norm parameters can be predicted, if phenotypic values of a large number of offspring in a reasonably wide range of environments are available (Kolmodin *et al.*, 2002). These breeding values could be used to monitor the environmental sensitivity of a trait in a population, or to select for high or low environmental sensitivity of a trait.

In an intensive farming system a large response to environmental improvements would often be advantageous. On the other hand, the system would become very susceptible to disturbances, e.g. climatic change, feed quality problems, or disease. Low sensitivity could be useful for low-input agriculture and in harsh climates. The disadvantage would be a lesser incentive for actions to improve animal husbandry, because of the less sensitive animal’s response to improved conditions. Before making the decision whether to include environmental sensitivity for a trait in the breeding goal, more knowledge is needed on the shape and variation of reaction norms for important traits over different time horizons and for different environmental descriptors.

**CONCLUSION**

The results showed increased environmental sensitivity in response to selection for high phenotypic value in presence of GxE. The environmental sensitivity increased with or without a simultaneous improvement of the environmental conditions. The increase was in general larger when selection was combined with an improving environment. Environmental sensitivity of the linear and the quadratic reaction norms increased more at higher levels of environmental change. The definition of environmental sensitivity could be an issue for discussion, especially for the sigmoid reaction norms. With more knowledge on the shape and variation of reaction norms for important traits, breeding evaluation of reaction norm parameters could be possible. Breeding values of reaction norm parameters could be used to select for high or low environmental sensitivity of a given trait, or to predict a breeding value of the trait, given a specific environment.

**REFERENCES**
