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THE ROLE OF PHENOTYPIC PLASTICITY IN ANIMAL BREEDING

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Introduction

The term phenotypic plasticity means the ability to alter the phenotype in response to environmental influences (Bradshaw, 1965). Genotype by environment interaction (GE) is an expression of genetic variation in phenotypic plasticity. When there is genetic variation in phenotypic plasticity, or GE, some breeds or individuals are more tolerant to harsh conditions than others, i.e. they are less sensitive to changes in the environment. In the following the terms phenotypic plasticity and environmental sensitivity will be used synonymously.

A brief overview of methods to analyse phenotypic plasticity, results from previous studies and the implications of phenotypic plasticity for animal breeding will be given in this paper.

Why should animal breeders care about phenotypic plasticity?

GE is an important issue for maintenance of genetic diversity and for trade of genetic material. When significant GE is present the ranking of animals, or breeds, may differ between environments. Consequently, the choice of parents for the next generation, or breed for a specific farm, should be based on evaluations in an environment similar to that, in which the offspring or the breed will be kept. If selection decisions differ between environments, more genetic diversity may be maintained.

Within a country, or a group of countries with similar climate and conditions of animal husbandry, there are seldom significant effects of GE. Between countries that differ considerably, e.g. in climate or management

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system, significant GE has been found. Estimated genetic correlations between the same milk production traits evaluated in different countries is an example. The correlations are lower between New Zealand and Australia on the one hand, and the western European countries, USA or Canada (the northern hemisphere group) on the other (r_g 0.75-0.84), than between any two countries within the hemisphere group (r_g 0.85-0.9)(Emanuelsson et al, 1999).

In an intensive farming system, where the environment can be kept adequate, a high sensitivity (responsiveness) towards improvements of the environmental could be beneficial. In environments that are unfavourable, unpredictable and/or uncontrollable low sensitivity of production traits could be useful (Ceccarelli, 1994).

There are indications that environmental sensitivity may increase as a correlated response to selection for high phenotypic value (Eberhart & Russell, 1966; Taylor & Aarsen, 1988; Kolmodin et al, 2002a,b). These indications call for a discussion about whether to accept, enhance or counteract this increased sensitivity towards environmental change.

Methods for the analysis of phenotypic plasticity

When analysing experimental or field data, the existence of GE can be detected as a significant interaction term in a two-factor ANOVA, where the genotype and the environment are the two class factors.

For further analysis of phenotypic plasticity, there are two classes of models that are commonly used: character state models and reaction norm models. The two models are often, but not always, mathematically interchangeable (de Jong, 1995).

Character state models

When character state models are used the trait averages in different environments and the correlations between these 'character states' are analysed. Phenotypic plasticity is measured as the difference between the phenotypic values in different environments. Change in phenotypic plasticity is described as a correlated response to selection on phenotypic values within environments (Via et al., 1995) or a response to selection on the difference between character states (Scheiner & Lyman, 1991).

When the correlation is high between the phenotypic values in different environments, the character states are to large extent controlled by the same set of genes. A low correlation means that the phenotypic expressions in the different environments should be considered as separate traits, determined by partly different sets of genes (Falconer & Mackay, 1996, p. 322).

The character state method, as the ANOVA-analysis, requires classification of environments into groups, e.g. herds, countries, or production levels. Clustering methods can be used to group the observations with reference to several environmental factors (e.g. Weigel & Rekaya, 2000). The character state model can be modified to describe, by a covariance function, an infinite number of separate traits over a continuous gradient of environmental states. Covariance functions can be used to describe e.g. growth trajectories, lactation curves and reaction norms (Kirkpatrick & Heckman, 1989; Kirkpatrick & Lofsvold, 1989; Kirkpatrick et al, 1994).

Reaction norm models

A reaction norm describes the phenotype expressed by a genotype as a continuous function of the environment. A regression of phenotypic values expressed in different environments on the environmental values estimates the reaction norm. Phenotypic plasticity is commonly defined as the slope of a linear reaction norm or, more generally, as the first derivative of the reaction norm function (de Jong, 1995).

In the reaction norm model phenotypic plasticity can change as a correlated response to selection on phenotypic values within environments or as a result of selection acting on the reaction norm parameters (Via et al., 1995).

The reaction norm approach is useful when phenotypes change gradually and continuously over an environmental gradient (de Jong, 1995). The environments do not have to be classified into groups, but ordered as a gradient. Examples of environmental gradients are temperature and feeding intensity. If the environmental value is measured as the population mean performance in each environment, any environmental descriptor can be ordered along a gradient (e.g. Falconer & Mackay, 1996 p.133).

Theoretically, a reaction norm may have any shape, unless restricted by genetic correlations with other traits or other costs and limits to plasticity (De Witt et al, 1998). Within the range of environments normally encountered, it is often reasonable to assume that the reaction norms are linear. Linear reaction norms have been described e.g. for gall size in the gall fly (Weis and Gorman, 1990) and for milk protein production and female fertility in dairy cattle (Kolmodin et al, 2002a). However, a linear increase in the phenotypic value would not likely be found, for biological reasons, over very large environmental ranges. Extrapolation of estimated reaction norms outside the environmental range of the data should therefore be done with caution.

Non-linear reaction norms have been described for several traits in relation to temperature in Drosophila (e.g. David et al, 1997; Morin et al, 1999; Gibert and de Jong, 2001). Second degree polynomial functions are used to describe situations where there is an optimal environmental value. A sigmoid shaped reaction norm may describe a threshold character with two phenotypic classes (Fairbairn & Yadlovski, 1997) or any situation, where there are an upper and a lower limit to the phenotypic value.

Results of studies on phenotypic plasticity

This section will focus on the genetic variation of and selection effects on phenotypic plasticity. The molecular genetics of phenotypic plasticity will not be discussed. Neither will the occurrence of GE for different traits, species and environments be summarised here.

Genetic variation

Reported estimates of genetic variation and heritability of plasticity in several species vary from non-significant to highly significant (e.g. Scheiner and Lyman, 1989; Weis and Gorman, 1990; Holloway and Brakefield, 1995; Scheiner and Yampolski, 1998; Kolmodin et al, 2002a). Some of the differences between estimates of genetic variation may be explained by differences in the traits and species studied, the experimental procedure and the method of statistical analysis. In general, genetic variation of the plasticity of a trait is considerably lower than the genetic variation of the mean value of the trait (Scheiner, 1993).

Selection effects

Empirical studies show that phenotypic plasticity can change as a result of direct selection on phenotypic plasticity and also as a result of selection on phenotypic values in different environments (Scheiner & Lyman, 1991; Hillesheim & Stearns, 1991; Perez & Garcia, 2002). However, there have been other experiments, where the response in plasticity was not significant (Holloway & Brakefield, 1995; Wijngaarden &

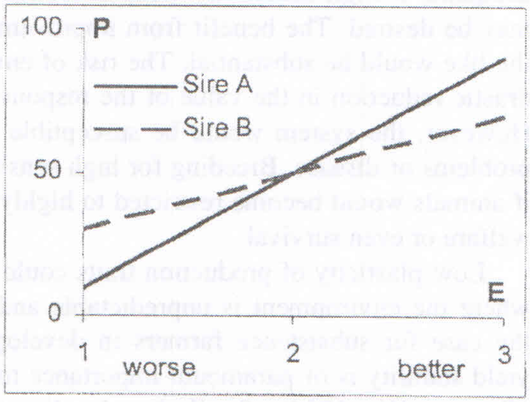
Brakefield, 2001). An algebraic description of selection on a phenotypically plastic trait and the effects on phenotypic plasticity has been given by de Jong and Bijma (2002).

Some studies (Eberhart & Russell, 1966; Taylor & Aarssen, 1988; Kolmodin et al, 2002a) have found a positive correlation between the magnitude of performance and the slope of the reaction norm. In such situations, phenotypic plasticity may increase as a correlated response when selection is for higher yield/level/performance.

In a recent simulation study the average phenotypic plasticity of a population was shown to increase with selection for high phenotypic value in presence of GE and a continuously improving environment, even though no correlation between the level of performance and the phenotypic plasticity was simulated (Kolmodin et al., 2002b). The principle can be illustrated with an example:

Assume a population of animals having linear reaction norms with individual variation in slope. The two sires in Figure 1 have equal phenotypic values in environment 2. If, in a later generation, the environmental value has improved, the progeny of sire A will be favoured over the progeny of sire B. The progeny of sire A, having the steeper reaction norm, respond more strongly to the changes in the environment. Consequently, if the population is selected for high phenotypic value, and the environment is continuously improving, there is reason to believe that the average phenotypic plasticity, or environmental sensitivity, of the population will increase. The described situation may be typical for domestic animals in an intensive production system, where feeding and management are continuously improved, in addition to the genetic improvement.

Figure 1. - REACTION NORMS OF TWO SIRES



P is the phenotypic value. E is the enviromental value. Arbitrary units.

In our simulation the average phenotypic plasticity increased with selection in an improving environment for linear and quadratic (described by a second degree polynomial function) reaction norms. Sigmoid reaction norms were described by an exponential function to approximate threshold characters. For sigmoid reaction norms phenotypic plasticity increased in the environmental range encompassing the threshold and the difference between the upper and the lower limits increased (Kolmodin et al., 2002b).

Implications

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., 2002a). The reaction norm function can be used to predict breeding values for a trait, given a certain environment.

The reaction norm parameters can be used to monitor the phenotypic plasticity of a trait in a population, or to select for high or low phenotypic plasticity of a trait, in parallel to genetic improvement of the mean level of the trait.

In an intensive farming system, where the environment can be kept adequate, a high sensitivity (responsiveness) towards environmental change may be desired. The benefit from improvements of management, feeding and the like would be substantial. The risk of environmental deterioration, causing drastic reduction in the value of the responsive trait, would be relatively low. However, the system would be susceptible to disturbances, e.g. feed quality problems or disease. Breeding for high sensitivity could be of ethical concern, if animals would become restricted to highly controlled environments for their welfare or even survival.

Low plasticity of production traits could be useful in agricultural systems, where the environment is unpredictable and cannot be controlled, as may be the case for subsistence farmers in developing countries. In such situations yield stability is of paramount importance to minimize the risk of crop failure (Ceccarelli, 1994). Similarly, the livestock must be tolerant to harsh conditions.

The disadvantage of breeding animals for low phenotypic plasticity would be a lesser incentive for actions to improve animal husbandry, because of the less sensitive animal's small response to improved conditions. Also, breeding for low sensitivity could be of ethical concern, if animals would lose their ability to react and respond to stressful treatment.

In conclusion, knowledge is needed about the amount and pattern of phenotypic plasticity and GE of important traits over different time horizons and for different environmental descriptors. With this information the decision can be made whether to include phenotypic plasticity in the breeding goal and whether the effects of GE are important enough to affect selection decisions.

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ULOGA FENOTIPSKE PLASTIČNOSTI UZGOJA ŽIVOTINJA

Sažetak

Vrijednosti uzgoja za parametre reakcijske norme mogu se predvidjeti ako su dostupne fenotipske vrijednosti velikog broja potomaka u razmjerno širokom rasponu okoline (Kolmodin et al., 2002.a). Za predviđanje uzgojne vrijednosti obilježja može se upotrijebiti funkcija reakcijske norme u određenoj okolini.

Parametri reakcijske norme mogu se upotrijebiti za praćenje fenotipske plastičnosti obilježja u populaciji ili za selekciju visoke ili niske fenotipske plastičnosti obilježja uporedo s genetskim poboljšanjem prosječne razine obilježja.

U intenzivnom sustavu gospodarenja gdje se okolina može održavati prikladnom, visoka osjetijivost (reagiranje) na promjenu okoline je poželjna. Korist poboljšanja upravljanja, hranidbe i sličnog bila bi znatna. Rizik pogoršanja okoline, što bi prouzročilo drastično smanjenje vrijednosti odgovarajućeg obilježja bio bi relativno malen. Međutim, sustav bi bio sklon poremećajima, npr. problemi kakvoće krmiva ili bolesti. Uzgoj na visoku osjetljivost stvar su etike kad bi životinje bile ograničene na visoko kontroliranu okolinu za svoju dobrobit ili čak i opstanak.

Niska plastičnost proizvodnih obilježja mogla bi biti korisna u poljoprivrednim sustavima gdje je okolina nepredvidiva i ne može se kontrolirati kao što može biti slučaj farmera koji rade za

vlastite potrebe u zemljama u razvoju. U takvim okolnostima stabilnost prinosa je najvažnija da se smanji rizik propasti uroda. Slično tome stoka mora biti tolerantna na grube uvjete.

Loša strana uzgajanja životinja za nisku fenotipsku plastičnost je slabiji poticaj za rad na poboljšanju stočarstva zbog slabog reagiranja manje osjetljivih životinja na poboljšane uvjete. Isto tako, uzgajanje za nisku osjetljivost moglo bi biti etički problem ako bi životinje izgubile sposobnost reagiranja i odgovora na stresni postupak.

Na kraju, potrebno je znanje o količini i uzorku fenotipske plastičnosti i GE-a važnih obilježja kroz različita vremenska razdoblja i za različite deskriptore okoline. S ovakvim podacima može se odlučiti da li uključiti fenotipsku plastičnost u cilj uzgajanja i da li su učinci GE-a dovoljno važni da djeluju na selekcijske odluke.

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