Towards healthy, productive genotypes

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Consequences of selection for high productivity

Selection for high productivity has been the long term focus of pig breeding programs worldwide, however, Rauw *et al*. (1998) highlighted that selection for productivity alone has unfavourable consequences for a number of metabolic, reproduction and health traits across species. More recently, Prunier *et al.* (2010) reviewed relationships between high physiological demands and the health and welfare in pigs, concluding that highly productive pigs have increased difficulties in coping with environmental challenges and are more susceptible to stress and disease through increased behavioural, physiological and immunological problems. As a consequence, it is becoming more important to implement breeding programs that optimise productivity across a variety of environments without any compromises in animal health and welfare of pigs. This approach relies on a balance between the resources available to pigs given environmental constraints and the requirements of the genotype for performance. In addition, heightened immunity levels and increased disease resistance can significantly reduce the undesired impact of environmental constraints on performance, health and welfare of pigs.

In current pig breeding programs, selection candidates are raised in superior environments characterised by good housing, high health, low pathogen load and good management practices, in contrast to the more challenging environmental conditions that may be more prevalent in commercial herds. However, models indicate that selection for productivity in a non-limiting environment increases environmental sensitivity of the animals (Kolmodin *et al*. 2003) supporting results by Schinckel (1999) who compared performance of fat and lean genotypes in two environments with different health status. The leaner genotype grew faster in the high-health environment but its performance was inferior to the fatter genotype in the low-health environment, demonstrating higher environmental sensitivity. In our Australian commercial data, an increase in the difference in performance between winter and summer periods over the last ten years has been observed (Hermesch, unpublished results). This indicates that pigs have become more environmentally sensitive and are less able to cope with heat and other undefined stressor during summer, as typically experienced in Australia. Therefore, genetic improvement strategies have to be developed to select robust pigs which are highly productive across a variety of environments without compromises to their health and welfare.

Selection for reduced environmental sensitivity

1. Environmental sensitivity

Environmental sensitivity is the ability of an organism to change its phenotype in response to changes in the environment. Not all genotypes respond to environmental stressors in an identical manner, giving rise to a genotype by environment interaction. Usually, the genotype by environment interaction has been accommodated by defining a trait like growth rate as a separate trait in each environment. This approach is only feasible when there are few distinct environments, such as could be defined solely by different feeding regimes, for example (Hermesch, 2004). However, this approach is not appropriate when many factors contribute to differences between environments. In this scenario, an environmental continuum or gradient may be described on a continuous scale using a range of descriptors including temperature, microbial load and air quality.

2. Reaction norm models

There are statistical models (reaction norm models) that can express performance of a genotype as a function of the environment. These reaction norm models are random regression models that relate repeated records of an animal, or the performance of multiple offspring of a sire with a descriptor of the environment, thereby determining the genetic contribution to environmental sensitivity of animals. Key parameters of these models are the reaction norm intercept and slope for each genotype, which enables selection of highly productive animals (high reaction norm intercept) with low environmental sensitivity (flat reaction norm slope). Procedures to incorporate these new traits in pig breeding programs have been outlined by Knap (2005) and first applications of reaction norm models in pigs have been presented by Hermesch *et al*. (2006) and Knap and Su (2008).

3. Genetic relationships between productivity and environmental sensitivity

Genetic associations between productivity and environmental sensitivity of animals are ignored in current pig breeding programs. However, unfavourable correlations between the reaction norm intercept and slope have been found in sheep (Pollott and Greef, 2004) and cattle (Kolmodin *et al*. 2002). Ignoring positive genetic correlations between intercept and slope of the reaction norm model in breeding programs will increase environmental sensitivity. Therefore, these studies provide further evidence for increased environmental sensitivity in livestock populations due to current selection practices. In pigs, Knap and Su (2008) also found a positive genetic correlation between the reaction norm intercept and slope for litter size using large data sets. Reaction norm estimates differed between data sets and reliable estimation of these parameters require a large quantity of appropriate data. Knap and Su (2008) concluded that reaction norm slopes represent 'a-hard-to-measure' trait. Despite these challenges, reaction norm slopes provide new information about environmental sensitivity of animals towards stressors of the environment, which is useful for the selection of consistently highly productive pigs. Development of reliable reaction norm models relies on an accurate description of changes in environmental constraints, sufficient variation in environmental conditions, and good representation of sire-progeny groups across the whole trajectory of the environment. When these conditions are met, then it is possible to obtain accurate heritability for the reaction norm intercept and slope even in relatively small data sets used for genetic analysis (eg 2,400 records, see Hermesch *et al*. 2006). Therefore we want to have an objective description of the environment which can be consistently applied across farms.

4. Descriptors of the environment

Descriptors of the commercial environment include, but are not limited to, factors such as climate or micro-climate within the shed, number of pigs per pen, floor area and air volume per pig, air quality, microbial load and incidence of diseases. The negative effects of these stressors on performance seem to act cumulatively, such that removal of one factor should lead to improved performance (Black *et al*. 2001). The logical extension of this assumption is that individual stressors can be combined into one single value which quantifies the overall stress-load of a particular environment.

Selection of more disease and stress resistant pigs

Selection of more disease resistant pigs will benefit from a better understanding of metabolic and immunological parameters and their genetic associations with a) feed intake, growth and carcase performance of the growing pig, b) robustness-traits describing survival, health and welfare of the growing pig as well as reproductive performance of sows and c) reaction norm traits that quantify environmental sensitivity of pigs.

1. The role of feed intake

Following the high emphasis on selection for improved productivity, research focus has moved to genetic improvement of animal health, welfare and disease resistance during the last decade. Rauw (2007) outlined the similarity of resource allocation and residual feed intake, which is the difference between actual feed intake and that predicted on the basis of requirements for production and maintenance, proposing to use residual feed intake to quantify the amount of 'buffer' resources an animal has available to combat environmental stressors. Resource allocation theory assumes that proportionally more resources are allocated towards production and away from fitness under artificial selection resulting in decreased health, fertility and less energy available for maintenance (Beilharz *et al*. 1993). However, Doeschl-Wilson (*pers. communication*) pointed out that information from molecular biology indicates only a weak association between feed intake and immunity and highlighted the problem of anorexia as a by-product of infection, which has been illustrated for feed intake of sows during lactation by Bunter *et al*. (2009). Feed intake is a key parameter in regard to quantifying the response of pigs to infections and existing models for residual feed intake will have to be extended to better quantify the pigs ability to cope with environmental stressors.

2. Generalised immunity

Selection for disease resistance is difficult since the incidence of diseases differs between environments and husbandry practices attempt to minimize the incidence and impact of diseases in commercial conditions. Genetic improvement of 'generalised immunity' was suggested by Bishop and Woolliams (2004) as an opportunity to increase pig performance and to reduce the impact of subclinical diseases by improving the pig's ability to respond effectively to pathogenic challenges. General immunity depends on innate and adaptive immunity. Breed differences and heritability estimates have been presented for traits quantifying innate and adaptive immunity demonstrating that these traits can respond to selection (Henryon *et al*. 2006, Clapperton *et al.* 2009). In addition, unfavourable genetic associations between some immune traits and growth have been reported, which were affected by the health status of the environment (Clapperton *et al.* 2009). Estimates of genetic correlations were generally more unfavourable in pigs carrying various pathogens in comparison to specific pathogen free (SPF) pigs. These first results demonstrate that information about the disease load of the environment is required for pigs tested for immune traits in order to accommodate potential genotype by environment interactions for immunological parameters.

3. The role of stress

Stress affects immune response and the resulting interactions were reviewed by Salak-Johnson and McGlone (2007). They outlined that "stress can suppress, enhance, or have no effect on the immune status of animals" and concluded that a better understanding of the complex interactions between social and environmental stressors and immunity is required. The interacting factors that may affect the immunological response of an animal to a stressor include the duration of stress, genetics, age and social status of the animal. The review demonstrates that selection for highly productive, healthy pigs will benefit from a better understanding of these complex relationships between stress and immunity and their potential genetic basis.

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