FINAL REPORT


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Genotype-by-Environment Interactions and Farm Animal Adaptation on Phenotypic and Molecular Levels

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NordGen Farm Animals

Final Report

GENOTYPE-BY-ENVIRONMENT INTERACTIONS AND FARM ANIMAL ADAPTATION ON PHENOTYPIC AND MOLECULAR LEVELS

1. SUMMARY

NordGen, the Nordic Genetic Resource Center, organized in collaboration with the University of Helsinki a two-day scientific workshop "Genotype-by-Environment Interactions and Farm Animal Adaptation on Phenotypic and Molecular Levels". The workshop was held in Tuusula, Gustavelund Hotel and Conference Center on the 7th-8th of November 2012. The overall goal of the workshop was to deepen the understanding of genotype-by-environment interactions and adaptation potential of farm animal genetic resources (AnGR) in the face of climate change, and to stimulate networking between stakeholders for future research strategy building. This workshop also served as a mid-term seminar for the Nordic project "Nordic Research Network on Animal Genetic Resources in the Adaptation to Climate Change" (AnGR-NordicNET). This is a project funded by NordForsk with participation from the Nordic countries.

The workshop was organized in three sessions: 1) Genotype-by-Environment Interactions, 2) Farm Animal Adaptation on Phenotypic and Genetic Levels and 3) Genotype-by-Environment Interactions in Practical Breeding and Conservation Programs. Each of the sessions had three or four invited speakers. Additionally, a poster session was arranged where11 posters were presented.

The workshop provided a multidisciplinary view merging state of the art knowledge on quantitative, population and molecular genetics within both domestic and natural populations to increase understanding of the climate change impacts, adaptation and mitigation with respect to the sustainable use of farm AnGR. More specifically, the first session presented genotype-by-environment interactions in the model organism *Drosophila melanogaster* as well as summarized examples of GxE from farm animal populations with the focus on heat stress. Status report from AnGR-NordicNET presented the data available for the assessment of GxE effects on alternative fertility traits based on activity recordings of individual cows together with production data and traditional fertility data using reaction norm methods. Session II focused on adaptation potential and signs of adaptation of both natural and domestic animal populations, introducing the development of theory for studies of adaptation, by using experiences from natural populations. Participants were introduced to landscape genomics and shown how this method provides new and structured knowledge on the environmental forces acting on the genome. Results from AnGR-NordicNET summarized results from a study utilizing SNP data to examine population stratification and possible genome-wide signals of selection. Session III offered a broad overview on challenges and solutions of tackling genotype-by-environment interactions in practical breeding programs for plants, fish and pigs. The last lecture of the workshop put the goals and efforts of the AnGR-NordicNET into the context of the workshop. Furthermore, the future challenges of animal breeding in the face of climate change and population growth were discussed.

Poster session successfully supplemented the topics discussed during the three sessions, with a high and very active participation. Abstracts of the invited talks as well as papers presented as posters have been published in the Proceedings, edited by Anne Præbel and Torsten Nygård Kristensen. Electronic versions of the proceedings, presentations and posters are available on NordGen's homepages http://nordgen.org/index.php/skand/content/view/full/2249

2. SCIENTIFIC CONTENT OF THE WORKSHOP

Session I: Genotype-by-environment interactions

Three invited talks were presented in Session I. In this session definition of GxE and investigations done using the model organism *Drosophila melanogaster* as well as examples of GxE from farm animal populations with the focus on heat stress and genetic stress (inbreeding) were presented.

GxE interactions are defined as different performance of genotypes (breeds or individuals within a breed) in different environments. The way that trait expression varies over an environmental gradient for a given genotype is called its norm of reaction. The main question of GxE and AnGR in the face of climate change is whether the genotypes and breeds we have selected in the past are still superior in the future where the environment will be different from the past and present. To be able to answer this question, it is imperative to 1) investigate whether significant GxE effect exists in the traits of interest, 2) quantify GxE, 3) estimate its effect in the current production systems and 4) find solutions how to overcome (utilize) the impediment of (the benefit of) a particular GxE in livestock production to guarantee sustainable use of AnGR. The talks in this session concentrated on the questions 1) and 2). Questions 3) and 4) were discussed in Session III.

First invited talk was given by Torsten Nygård Kristensen on investigations of GxE interactions using the model organism *Drosophila melanogaster. Drosophila* has its genome mapped and sequenced, extra copy and knock-out lines are also available. *Drosophila* has a short life cycle and is handled easily and in high numbers. Additionally, despite of different genome size, chromosome number and physiology etc., there is high degree of similarity between *Drosophila* and mammals at the genetic level. Investigations with this model organism have shown significant GxE in locomotor activity and metabolic rate over a range of temperatures, and egg to adult viability in benign and hot environments. Genome wide association studies have revealed that many SNPs explain significant amount of variation only under specific environmental conditions. Additionally, environmental temperature has been shown to affect heritability estimates for egg to adult viability of both temperate and tropical populations. Lowest estimates were obtained in the most stressful environment. A special case of GxE, namely IxE (inbreeding-by-environment interaction), where inbreeding depression is more severe under stressful conditions, has been detected in *Drosophila*.

Ignacy Misztal summarized numerous investigations of GxE in dairy cattle with a special focus on heat stress. It has been shown that temperate and heat tolerance genetics are moderately antagonistic (r_g ~ 0.40). This means genetic re-ranking of animals in regular and warm environments. It has also been shown that selection of fluid milk on hot areas will result in use of less heat-tolerant sires and detrimental selection in long-term. Genetic variance of milk, protein and fat production increases up to three-fold from first to third parity under heat stress (increase of 5 °C from regular). Selection has resulted in a strong genetic improvement in milk yield and simultaneous genetic deterioration in heat tolerance relative to milk yield (weak effect) and number of days open and conception rate (large effect). In dairy cattle (trait: days open) the opposite relationship between heat stress and magnitude of heritability estimates has been shown than in *Drosophila*: higher h^2 estimates were obtained under heat stress conditions.

Analysis of GxE is not straightforward and careful modeling is important to conclude whether detected GxE is reality or relict from the statistical analysis. Heat stress related GxE is detected, both in model organism *Drosophila* and various livestock species, in production traits and especially in fitness traits. Incomplete knowledge of GxE may undermine successful breeding programs through use of biased estimates of genetic parameters, genetic deterioration of economically important traits under unfavourable conditions or existence of unidentified components of GxE such as IxE. Response to climate changes should

be tackled by both management and genetics. Selection for future challenges is possible with careful modeling and genomic selection.

Session II: Farm Animal Adaptation on Phenotypic and Genetic Levels

First talk of Session II was given by Scott McCairns. He used examples from natural populations to illustrate how adaptive population divergence through natural selection occurs over environmental gradients and may be verified in laboratory conditions as maximized fitness in native conditions (or reduced fitness in the reciprocal treatment/environment). F_{ST} can define a baseline of neutral population divergence, whereas divergence in quantitative traits can be expressed by Q_{ST}. Q_{ST} values larger than F_{ST} infer directional selection. New predator community, novel host or food resource or a new biophysical environment may promote adaptive evolution. It has been predicted with natural populations that phenotypic plasticity alone is unlikely to be sufficient to compensate for predicted environmental changes. Cairn's presentation underlines the importance of genetic diversity for maintaining the adaptive potential of farm AnGR.

Stéphane Joost gave a talk on landscape genomics: an approach where a set of environmental variables describing specific locations are regressed on the genetic profile of each sampled individual. The association between alleles and climatic variables gives information on the environmental forces acting on the genome and permits to seek genomic regions influencing the ability of animals to cope with and adapt to specific environmental conditions. Joost's results from a large collaborative project on goats using landscape genomics approach (ECOGENE) showed four AFLP loci possibly under selection; these loci were coupled with climatic variables such as solar radiation, frequency of precipitation and diurnal temperature range. If the genotype of an animal shows signatures of selection for traits significantly associated with an animal's habitat, more attention could be paid to choosing animals/breeds that are adapted to specific climatic conditions.

In the third presentation Terhi Iso-Touru showed results from a study where whole-genome SNP data was used to investigate 1) population structure among 10 Eurasian cattle breeds and 2) to detect signs of selection. Population structure analysis demonstrated the genetic difference of Yakutian cattle from other breeds. Additionally, several previously found QTL-regions showed high SNP-wise F_{ST} values inferring to directional selection. One interesting gene, *ELOVL0*, is situated within such a region, but further molecular level studies are needed to verify whether this or other genes in the region are involved in cold adaptation in cattle.

Session III: Farm Animal Adaptation on Phenotypic and Genetic Levels

The aim of the third session was to present challenges and solutions of tackling genotype-by-environment interactions in practical breeding and conservation programs.

In plant breeding GxE can be coped with using three alternative strategies. The first strategy is to develop a variety which performs consistently well in a range of environments ("Jack of all trades, master of none" genotype). This is equivalent to a selection of multiple traits and the rate of progress is determined by the divergence of the environments. The second strategy is to subdivide environments into groups so that there is little GxE within each group. This means setting up multiple breeding programs. The third strategy is to evaluate a common set of breeding material across environments but make specific recommendations for each environment. Rognli also gave an overview of the statistical methods used to estimate GxE in plant breeding and how these methods are utilized in strategy selection.

Bjarne Gjerde summarized the GxE investigations done within fish selective breeding programs. Fish are often reared in different environment than their parents, and individuals from the same year-class are

exposed to a set of environmental conditions during different life stages. Therefore, GxE may be more important in fish farming than in species reared under more controlled and stable condition. Many studies show substantial GxE in various fish species in economically important traits (growth, sexual maturity, disease resistance), but more studies are required for most species and traits. In his talk Gjerde emphasized the importance of analytical evaluation whether it is enough that breeding evaluation is based on testing at several commercial environments, or is it necessary to establish a separate breeding nucleus for a particular type of environment.

Pieter Knap presented the overview of scenarios of relating variation originating from genotype, environment and GxE and their implications on AnGR. In the cases where the effect of environment is greater than that of interaction, there is an incentive to improve the environment. If the effect of interaction exceeds that of the environment there is an incentive to match the genotype to the environment either by selecting in or selecting on data from the response environment. To take into account the environmental sensitivity of productivity, in addition to the conventional EBV, a new type of a breeding goal is actually set up. Average performance in commercial conditions combines the genetic potential of the nucleus with the environmental sensitivity of productivity in commercial conditions deviating from those experienced in nucleus. Although optimal, inclusion of sensitivity EBVs in the total merit index is not feasible in modern pig breeding and alternative methods have to be used to match the selection to the response environment. Individual reaction norm slopes show that better individuals perform "increasingly better" in better environments. Thus genetic variation can be detected, exploited and valuated more easily in a good environment.

In the last presentation, by Theo Meuwissen, the climate change and population growth challenges to livestock production were summarized. Production increase and improvement of cost effectiveness of livestock production are imperative to meet the challenges in the future. Additionally, there is an increased need to utilize waste products as input as well as marginal land. In the future, more focus will be on animal welfare and health and reduction of greenhouse gas emissions originating from livestock production. A great challenge for animal breeding lies ahead as the animals need to be adapted to these challenges. Rapid changes are required. This necessitates envisagement of new breeding directions as soon as possible. Animal breeding must work towards both mitigation and adaptation issues (including investigations of GxE) through sustainable and effective use of AnGR, genomic selection (GS) and GS-introgression.

Postersession

Eleven posters were presented in the poster session that was arranged in addition to the invited talks. Posters successfully supplemented the contents of the sessions on different aspects of GxE on different terrestrial livestock species as well as in fish. The full titles of the posters together with main results/conclusions of each poster were as follows:

Effects of genotype-by-environment interactions on lameness and pneumonia incidences in Dorper, Turcana and F_1 cross-breeds lambs during heat stress exposure

- Genotype (two breeds and their cross) plays a major role in the incidence of both lameness and pneumonia in fattening lambs reared extensively during heat stress exposure.

Are responses to selection in lines divergently selected for residual feed intake in growing pigs affected by GxE interactions when bred in a tropical environment?

- Tropical stress had major impacts of on the metabolism. Depressive effect of tropical environment was especially pronounced in early stages of growth for pigs selected for reduced residual feed intake.

Genetic variation in heat stress tolerance of Holsteins producing under a continental temperate environment

- It is possible to select for reduced thermal sensitivity using any of the six indicators of heat stress evaluated in this study.

Genetics of microenvironmental sensitivity in body weight of farmed rainbow trout

- Genetic improvement for body weight does not cause a concomitant increase in microenvironmental sensitivity. There may be high potential to simultaneously improve weight gain and increase its uniformity if both criteria are included in a selection index.

Genotype by environment interactions of claw health in Swedish dairy cattle in tie stalls and loose-housing

- There are only weak indications of genotype-by-environment interactions for claw health in these two housing systems (loose housing and in tie stalls).

Diseases induce genotype-by-environment interactions in production traits of farm animals

- Genotype-by-environment interactions induced by tolerance should be accounted for in breeding programs with multiple testing and nucleus environments having different levels of pathogen pressure.

A method to define environmental groupings for UK sheep farms to allow the assessment of genotype x environment (GxE) effects

- Multivariate analysis (Principal Coordinate and Cluster Analysis) of the results identified 5 homogenous clusters of farm environments.

A Europe-wide experiment for assessing the impact of genotype-environment interactions on the vitality of honey bee colonies

- The local bee strains showed overall higher fitness in local environments underlining the value of the conservation work of local honey bee breeds as a resource for successful and profitable bee keeping in the future.

Breed by environment and gender by environment interaction effects affect pre-weaning mortality in two Norwegian sheep breeds

- There was substantial re-ranking of risks for males and females in the different environments.

Challenges of estimation of international breeding values due to genotype-by-environment interactions in dairy cattle

- Random regression model facilitating exploitation of principal component and factor analytic approaches provides a highly parsimonious structure for the (co)variance matrix compared to the standard multi-trait model and a decrease in the estimation time and standard errors of the estimates.

Environmental stability of responses created by line selection: Finnish rainbow trout Growth vs. Delayed Maturity -lines in Vietnam

- Estimates of genetic correlations for growth and survival revealed substantial GxE, but showed clearly that there exist genotypes that are superior in all environments.

3. ASSESSMENT OF THE RESULTS AND IMPACT OF THE EVENT ON THE FUTURE DIRECTIONS OF THE FIELD

During the meeting it was clearly shown that a substantial GxE exists in many of the economically important traits in plants, terrestrial farm animals as well as in aquaculture species. As long as the production environment can be controlled, relative to the practical and economical aspects, effects of GxE can be overcome simply by adjusting the environment to the animals' optimum. Nevertheless, disregarding existing GxE may have a great negative effect on the profitability of agricultural businesses. Genetic parameters are dependent on the environment they are estimated in. Use of biased estimates of genetic parameters for the genetic evaluation of a particular group of selection candidates may negatively affect the genetic progress. Furthermore, if selection and production are performed in different environments, existence of GxE strongly deteriorates the production predictions and impairs the profitability.

Degree of control and stability of production environment vary between species (e.g., broilers vs. sea water aquaculture) and production systems (intensive vs. extensive). Furthermore, future challenges brought by population growth and climate change are likely to demand substantial strategy changes in livestock production. In an animal breeding framework this will call for adjustments or total overhaul of breeding programs, re-definition of breeding goals, utilization of fastest breeding techniques available. A profound understanding of GxE is indispensable. In conclusion, more GxE investigations in most of the species are necessary to understand, quantify and utilize or solve the GxE challenges in livestock production.

To increase the sustainability and robustness of animal production systems to the harmful effects of climate change, an increased accessibility to a wide diversity AnGR is needed. Without a delay, envisioning a future strategy for conservation, utilization and investigation of AnGR within adaptation and mitigation issues which focus on the potential of farm animal species and breeds to adapt to a changing environment is imperative. This includes interdisciplinary collaboration with climate researchers, economists etc. to understand the predicted climate change scenarios and their effects on the whole agriculture business, and specifically on farm animal production. Similar value should be put on education, relevant dissemination of research knowledge and maintenance of already established research networks.

Abstracts of the invited talks as well as papers presented as posters have been published in the Proceedings, edited by Anne Præbel and Torsten Nygård Kristensen. Electronic version of the proceedings, presentations and posters are available on NordGen's homepages
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4. FINAL PROGRAM OF THE WORKSHOP

Wednesday, 7th of November, 2012

09:30 - 11:30	Registration of the participants
11:30 - 12.30	Lunch
12:30 - 13:00	Opening of the workshop (*Prof. Jarmo Juga, University of Helsinki and Section Leader NordGen Farm Animals, Peer Berg*)

SESSION I: Genotype-by-Environment Interactions

Chair: Jarmo Juga

13:00 - 13:30	Genotype by environment interactions investigated using the model organism *Drosophila melanogaster* (*Torsten Nygård Kristensen*)
13:30 - 14:15	Genotype-by-environment interactions in fram animals with focus on heat stress (*Ignacy Misztal*)
14:15 - 15:00	Environmental sensitivity in dairy cattle with focus on fertility traits (*Peter Løvendahl*)
15:00 - 15:45	Coffee break

SESSION II: Farm Animal Adaptation on Phenotypic and Genetic Levels

Chair: Juha Kantanen

15:45 - 16:30	Adaptive population divergence: what have we learned and what challenges lie ahead? (Scott McCairns)
16:30 - 17:00	Livestock landscape genomics to detect adaptive loci in 43 European and Near-Eastern goat breeds (*Stéphane Joost*)
17:00 - 17:30	Whole genome scanning in cattle breeds to detect selection signatures (*Terhi Iso-Touru*)
17:30 - 19:00	Poster session
19:00	*Dinner*

Thursday, 8th of November, 2012

08:00 - 09:00	Coffee

SESSION III: Genotype-by-Environment Interactions in Practical Breeding and Conservation Programs

Chair: Peer Berg

09:00 - 09:30	Challenges and solutions of genotype-by-environment interactions (GEI) in plant breeding (*Odd Arne Rognli*)
09:30 - 10:00	Importance of genotype-by-environment interactions in fish selective breeding programs (*Bjarne Gjerde*)
10:00 - 10:30	GxE in commercial pig breeding: reaction norms and selection for the response environment (*Pieter Knap*)
10:30 - 11:00	Strategy building in AnGR-NordicNET, look into the future (*Theo Meuwissen*)
11:00 - 11:30	Summing up and closing (*Peer Berg*)
11:30 - 12:30	*Lunch*