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OPPORTUNITIES FOR ANIMAL BREEDING TO MEET THE CHALLENGES OF THE FUTURE

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Summary. The challenges for the next 50 years are to increase the productivity of major livestock species to address the food needs of the world, while at the same time minimizing the environmental impact and the loss in genetic diversity. This paper describes on a number of contributions of animal breeding to meet these challenges of the future. First it is discussed how to incorporate environmental impact in the breeding objective, i.e. the goal of an animal breeding program. Over the last two decades, breeding in poultry, pigs and dairy cattle has not only resulted in increased productivity but also in decreased emission of greenhouse gases per ton of animal product. Opportunities are discussed to further reduce the impact on the environment. Subsequent sections describe the impact of genomics, social interactions, and product quality on animal breeding programs. The final section deals with opportunities to use animal breeding in developing countries. The completion of genome sequences has generated the tools for whole-genome selection programs for a wide spectrum of traits which are now being applied in practise. Furthermore, research is increasing our understanding of the underlying biology of important traits such as animal welfare. Developments in the area of quantitative genetics and in recording of phenotypes are required to fully exploit the wealth of genomic information. For the developed world, new tools and techniques are now being implemented to increase the genetic gain from breeding programs. These techniques, however, also offer opportunities to better characterize and use indigenous breeds in developing countries. Through international collaboration in training, research and implementation, animal breeding can help in meeting the challenges for the next 50 years.

Key words: breeding program, genetic improvement, social interaction, methane emission, product quality

Introduction

On a global level, we are faced with increasing demands on natural resources from a growing population. To meet the growing demand, the food production needs to double in the coming 30 years while halving its environmental impact. Not only more and higher quality food is needed, but also renewable feed stocks for energy and other industrial uses are asked for. The increased demand for food and non-food products requires innovations in agricultural, aquaculture and forestry ecosystems (BECOTEPS 2011). In this paper, I will concentrate on the opportunities offered by farm-animal genetic improvement to meet these challenges.

There are many individuals on this planet who live relatively healthy lives consuming little or no animal protein and many would argue that the challenge of feeding the human population could be met by reducing the amount of livestock products in our diet (AP-PLEBY et AL. 1999). However, the demand for animal protein especially in developing countries is expected to grow as they become more affluent (SPEEDY 2003). Part the animals proteins are produced from feed such as grain that could be directly consumed by humans while another part is produced from feed that would not be available to humans such as grass and by-products from the human food industry. The challenge for livestock production is to meet the growing demand for animal product while at the same time reducing the environmental impact. This implies that the livestock production needs to improve the efficiency of production, robustness of animals and quality of animal products. Improvement of efficiency of animal production needs to focus on improving lifetime productivity which can be achieved by improving not only productivity but also by improving health, reproductive performance, length of productive life span, and robustness of animals (e.g. HUME et AL. 2011). Robustness of animals refers to the ability of animals to handle variation in the environment and face climate change. The quality of animal products refers not only to the food safety and taste but also to animal welfare.

A breeding scheme aims at genetic improvement in the breeding objective through the selection of parents to produce the next generation. The breeding objective reflects the combination of traits that the breeder aims at improving through selection. The amount of genetic improvement in the breeding objective (and the underlying trait) depends on the accuracy of the selection criteria, the intensity of selection and the generation interval.

Genetic variation has been found in most traits (production, reproduction and health) investigated in livestock species. Breeding programmes exploit this genetic variation to improve the mean level of the population by selecting the best animals as parents for the next generation. Livestock breeding is at the top of the animal production pyramid and hence defines the quality of all animals used in agriculture. Farm-animal selection has a great impact on livestock production as a whole, because the breeding response is cumulative and sustainable. The predicted rate of genetic gain from a breeding program generally lies around 1% per year. Efficient reproduction techniques, such as artificial insemination, allow genetic improvement to be rapidly disseminated throughout the productivity of pig, poultry and dairy cattle. The increase in productivity in these species in Western countries over the last 50 years lies around 1% per year (VAN DER STEEN et AL. 2005). Observed changes in productivity as reflected by annual statistics

result from the combined effect of genetic improvement and improvements in housing, nutrition and disease control.

In this paper, I will concentrate on a number of contributions of animal breeding to meet the challenges of the future. The selection of topics is based on activities of my research group in Wageningen. I will discuss the contribution of animal breeding to reduction of environmental impact and how to incorporate environmental impact in the breeding objective. Subsequently, I will discuss the impact of genomics, social interactions, and product quality on animal breeding programs. Finally, I will discuss opportunities to use animal breeding in developing countries.

Breeding objective to improve sustainability

The breeding objective can be thought of as the overall goal of the breeding program. The purpose of the breeding objective is to aid the following decision-making processes:

- 1) within-line or -breed selection, i.e. which animals to choose as parents,
- across line or breed selection, i.e. which lines or breeds to use in the production system,
- evaluation of investments in breeding programs and design of breeding programs, i.e. the breeding objective provides the criterion to quantify and maximize returns on investments in the breeding program.

An obvious and attractive economic breeding objective would be to maximize profit. Some people have argued that breeding objectives should be defined in terms of biological efficiency. More recently, a number of persons have argued that not only economic but also non-tangible effects should be incorporated in the definition of breeding objectives (OLESEN et AL. 2000, KANIS et AL. 2005). DEKKERS and GIBSON (1998) reviewed how best to ensure that breeding objectives and selection criteria are used in practice by taking into account the perceptions and wishes of the breeders for whom they are designed.

The discussion on how to best express the environmental impact in deriving a breeding objective has many similarities with the discussion at the end of the last century on the perspective to be taken in calculating economic values. The differences in economic values between perspectives disappear when using the same basis of calculation (BRAS-CAMP et AL. 1985, SMITH et AL. 1986, GODDARD 1998). VAN ARENDONK (2011 a) has shown that the same principles apply when incorporating an ecological constraint in the derivation of weights of traits in the breeding objective. Profit expressed per kilogramme of methane emission, for example, leads to exactly the same economic values as profit expressed at herd level with a constraint on total methane production. VAN ARENDONK (2011 a) further showed that maximizing profit per kilogramme of methane leads to different relative weights of productivity and longevity than minimizing methane emission per kilogramme of milk. This difference results from the difference in the implied perspectives.

Maximizing profit per kilogramme of methane refers to a situation where a maximum applies to the total emission of methane from dairy herds. Minimizing methane emission per kilogramme of milk refers to a situation where a maximum applies to the

total amount of milk that can be produced by dairy herds. It is not easy to choose the perspective that best represents the actual and future situation. We need to deal with that uncertainty. However, it is very important to be aware of the perspective that is taken in deriving economic weights and its consequences. To be able to do more detailed analysis on the breeding objective, more detailed knowledge on emission of methane and other greenhouse gases is needed. For example, BANNINK et AL. (2011) analysed how methane emission from a cow depends not only on milk production but also on other factors such as live weight and milk composition. Information on some of the relations is scarce due to the difficulty of measuring the emission of greenhouse gases on individual animals. There is an urgent need to join resources to develop detailed bio--economic models to enable evaluation of the ecological and economic analysis of various mitigation options including animal breeding. Further, a full assessment of the environmental impact requires the quantification of the emissions and resource use during the entire life cycle (DE VRIES and DE BOER 2010). The simple equations used in the analysis by VAN ARENDONK (2011 a), however, are sufficient to show how ecological constraints on animal production should be incorporated in determining the breeding objective. It can be concluded that the emission should be expressed per kilogramme of product rather than per animal in evaluating the ecological consequences of animal breeding.

Breeding to reduce environmental impact

Breeding in poultry, pigs and dairy cattle has not only resulted in increased productivity but also in decreased emission of greenhouse gases per unit of animal product (Table 1). BANNINK et AL. (2011) used a mechanistic model to predict the methane emission by dairy cows from data on productivity and composition of the average ration in The Netherlands. They found that the average methane emission per cow per year increased from 110 kg in 1990 to 126 in 2010. Expressed per kilogramme of milk, the methane emission decreased from 17.5 g in 1990 to 15.0 g in 2010. These results illustrate the importance of how environmental impact is expressed. Expressed per cow, methane production increased by 15% over the last 20 years while expressed per kilogramme of milk, the methane production decreased by 14% over the last 20 years. In a recent paper (VAN ARENDONK 2011 a), I argue that environmental impact should be evaluated per kilogramme of product. In analysing environmental needs to include not only the productive period of animal but needs to include the entire life cycle (DE VRIES and DE BOER 2010).

Measuring emission directly on animals under practical conditions is currently difficult and hampering direct selection. WALL et AL. (2010), recently, showed the potential to reduce emissions from dairy cattle by selection on correlated traits such as feed efficiency and longevity. De HAAS et AL. (submitted) found a heritability of 0.50 for predicted methane emission in dairy cows. Methane emission in that study was predicted using IPCC Tier-2 methodology (IPCC 2000) based on feed intake, milk production and weights records of the animals and diet composition to predict methane output. Development of measurement techniques will help to enhance the capability for reducing emissions through genetic selection.

Table 1. Proportional changes in greenhouse gas emissions and global warming potential (GWP_{100}) achieved through genetic improvement (1988-2007) as calculated by DEFRA (%) (HUME et AL. 2011)

Tabela 1. Proporcjonalne zmiany w emisji gazów cieplarnianych i ociepleniu globalnym (GPW₁₀₀) osiągnięte przez doskonalenie genetyczne zwierząt w latach 1988-2007 według obliczeń DEFRA (%) (HUME i IN. 2011)

	CH_4	NH ₃	N ₂ O	GWP ₁₀₀
Chickens-layers Kury nioski	-30	-36	-29	-25
Chickens-broilers Brojlery	-20	10	-23	-23
Pigs Trzoda chlewna	-17	-18	-14	-15
Cattle-dairy Bydło mleczne	-25	-17	-30	-16
Cattle-beef Bydło mięsne	0	0	0	0
Sheep Owce	-1	0	0	-1

Genomics assisted breeding

Over the past few years, we have seen spectacular advancements in molecular genetics. One recent advancement is high-density single-nucleotide polymorphism (SNP) technology, which enables genotyping of an individual at many thousands of SNPs at low cost. It is anticipated, that in a couple of years, an entire individual genome will be sequenced for less than 1000 US \$. These recent advancements in the field of molecular genetics have enabled revolutionary changes in genetic analysis of populations and in genetic improvement programmes. We are at the threshold of an era in which these advancements will require us to revise completely our assumptions about which traits can be addressed by breeding, how breeding values are estimated, and what impact breeding may have on populations. Paradoxically, current quantitative genetic models and tools to use molecular data lag behind the amount of genomic data accumulated.

In dairy cattle, genomics-assisted breeding has been implemented recently. The breeding structure of the dairy cattle population allows breeders to capitalize on the potential benefits from SNP information. This implementation is an important first step that is expected to lead to 50% higher rate of genetic gain in dairy cattle improvement (GODDARD and HAYES 2009). The increased rate of genetic gain originates from the ability to select better for traits that can be recorded only on females and for traits that are recorded late in life. In pigs and poultry, however, crossbreeding plays an important role, which hinders the adoption of methods currently used in dairy cattle. In pigs and poultry, genomics-assisted breeding offers even greater opportunities because molecular information offers unique opportunities to exploit data collected on a crossbred popula-

tion in a way that is no longer constrained by the need for pedigree registration. Further developments in quantitative genetics are needed to achieve these improvements.

Breeding and social interactions

Social interactions among individuals, such as cooperation and competition, are key factors in evolution by natural selection. As a consequence, evolutionary biologists have developed extensive theories to understand the consequences of social interactions for response to natural selection. Current genetic improvement programs in animal husbandry, in contrast, largely ignore the implications of social interactions for the design of breeding programs (BIJMA et AL. 2007).

At the same time, housing systems for farm animals are evolving to larger groups in which positive and negative social interactions have greater impact. This implies that animal breeders need to respond to welfare issues that are caused by negative social interactions in group-housed animals, such as cannibalism in laying hens, aggression in pigs and food competition in fish. MUIR (2005) clearly demonstrated that breeding programmes aimed at individual body weight failed to generate the desired response. He selected group-housed Japanese quail (Coturnix japonica) on individual body weight during 25 generations. After 25 generations of selection, there was no improvement in body weight. This was caused by the fact that individual selection for greater bodyweight resulted in a large increase in cumulative mortality at 6 weeks of age due to fighting and cannibalism (24% mortality vs. 6% in the initial population). This example illustrates that individual selection in group-housed animals does not necessarily lead to traits that are optimal for the whole group, but instead may lead to increased negative social interactions. Recently, theoretical and empirical tools have been developed to quantify the magnitude of heritable social effects, i.e. the heritable effects that animals have on traits of their group mates, in livestock populations, and to utilize those effects in genetic improvement programs (BIJMA et AL. 2007). In growing pigs, social effects contributed substantially to the heritability estimates of growth rate and feed intake, indicating that pigs can have significant effects on growth rate and feed intake of their group mates (BERGSMA et AL. 2008). Similarly, in laying hens, the total heritable variance for the trait survival increased from 7 to 19% due to heritable social effects (ELLEN et AL. 2008). These results show clearly that including social effects in genetic improvement programmes has the potential to substantially increase responses to selection in traits affected by social interactions. In laying hens, we applied selection between kin-groups to reduce mortality due to cannibalistic pecking. This resulted in a considerable difference in mortality between the low mortality line and the unselected control line in the first generation (20 vs. 30%). Furthermore, changes in behavioural and neurobiological responses to stress were detected in the low mortality line, pointing to reduced fearfulness and stress sensitivity (RODENBURG et AL. 2009). These first results indicate that including social effects into breeding programs is a promising way to reduce negative social interactions in farm animals, and possibly also to increase positive social interactions, by breeding animals with better social skills.

Animal breeding and product quality

Milk and dairy products are important components of the western diet. Content and composition of fat and protein determine the value of bovine milk for human nutrition and technological properties of milk and dairy products. In The Netherlands, selection on milk-production traits has contributed to an increase in milk-fat percentage, from 3.66% in 1950 to 4.37% in 2008 (NRS 2009). However, until recently little was known about the extent of or the basis of genetic variation in milk-quality traits, in particular milk-fat and milk-protein composition. The release of the dairy cattle genome opened new opportunities to uncover more information about individual genes and their effect on important traits in cattle. In 2005, the Dutch Milk Genomics initiative was started to unravel the natural genetic variation in milk-quality traits and to develop strategies for further improving the quality of milk. The program combined expertise in the fields of genomics, quantitative genetics, bioinformatics, proteomics and dairy science to increase our understanding of the genetic variation in milk composition. Milk and DNA samples on 2000 individual cows of the Dutch Holstein-Friesian population were collected and analysed. This created a unique database containing detailed information on milk composition.

STOOP et AL. (2008) found that there is considerable genetic variation for fatty acid composition, with genetic variation being high for C4:0 to C16:0 and moderate for C18 fatty acids. The moderate coefficient of variation in combination with moderate to high heritabilities indicates that fatty acid composition can be changed by genetic selection. SCHENNINK et AL. (2007) found that the *DGAT1* K232A polymorphism has a clear influence on milk-fat composition. The *DGAT1* allele that encodes lysine (K) at position 232 (232K) is associated with more saturated fat; a larger fraction of C16:0; and smaller fractions of C14:0, unsaturated C18 and conjugated linoleic acid. In a whole genome association analysis, BOUWMAN et AL. (2011) found a total of 54 regions that were significantly associated with one of more fatty acids. Medium chain and unsaturated fatty acids are strongly influenced by polymorphisms in *DGAT1* and *SCD1*. Other regions also showed significant associations with the fatty acids studied. This information helps in unravelling the genetic background of milk fat composition.

The genetic analysis revealed that variation between cows in content and composition of milk protein is to a large degree due to genetic variation between cows (SCHOPEN et AL. 2009). Part of this genetic variation can be attributed to milk-protein variants (HECK et AL. 2009). In a recent whole genome scan, a number of other genomic regions have been identified that contribute to genetic variation in milk protein composition (SCHOPEN et AL. 2011).

The results of the Dutch Milk Genomics initiative and other studies have shown that genetic variation between cows is an important source of variation in milk quality. A number of genes and genomic regions have been identified that contribute to the genetic variation. This is an important step towards a better understanding of the regulation of milk composition and will assist breeders in designing breeding programs that are tailored towards the production of milk that better meets the needs of the consumers.

Animal breeding in a global context

The global needs for better management of domestic animal genetic resources were highlighted in the FAO report "The state of the world's animal genetic resources for food and agriculture", based on information from 169 countries (FAO 2007). Breeds of domesticated farm-animal species (including fish) are the primary biological capital for livestock development, food security and sustainable rural development. Indigenous farm animals may appear to produce less than highly specialized exotic breeds, but they are highly productive in their use of local resources and are more sustainable over the long term. Developing breeding programs for conservation and sustainable use of domestic animal genetic resources requires knowledge and skills in all areas of animal breeding and genetics, and on the framework needed to implement breeding programs.

Local breeds can thrive with limited care and feeding, and they are often more tolerant or resistant to diseases. They are also better able to cope with drastic changes in food and water supplies as well as with harsh, variable and extreme weather and climatic conditions. By neglecting to develop locally adapted breeds for higher productivity, an opportunity is being missed to help the developing world feed its people. Genetic improvement of local breeds can help to improve the livelihood of the livestock keepers, to increase the production of animal products and to conserve genetic diversity.

Implementing breeding schemes in developing countries has proven to be difficult (MADALENA et AL. 2002, KOSGEY et AL. 2006). Genetic improvement is difficult due to the infrastructure and institutions required for collecting information and the time required for realising genetic improvement. Consequently, crossbreeding or breed substitution has been viewed as an alternative method of increasing animal productivity. However, numerous reports detail the failure of various crossbreeding and breed substitution projects. The success of genetic improvement programmes in developing countries is generally not determined by the anticipated rate of genetic gain, but by their compatibility with the breeding objective of the farming system and the involvement of farmers (KOSGEY et AL. 2006). Participatory approaches (e.g. GIZAW et AL. 2010) are recommended to involve the farmers and to avoid that breeding objectives are too narrow. VAN ARENDONK (2011 b) discussed opportunities to implement breeding schemes which minimize the need for extensive pedigree and performance recording. A number of authors have shown that genetic progress can be generated in a small population. Consequently, community-based breeding schemes offer a good starting point for involving farmers in improving local breeds.

Concluding remarks

The challenge for the next 50 years is to increase the productivity of major livestock species to address the food needs of the world, while at the same time minimizing the environmental impact and the loss in genetic diversity. The completion of genome sequences has generated the tools for whole-genome selection programs for a wide spectrum of traits (HUME et AL. 2011). For the developed world, these techniques are now being implemented to increase the genetic gain from breeding programs. These tech-

niques, however, also offer opportunities to better characterize and use indigenous breeds in developing countries. Traditional livestock systems are expected to evolve towards more intensive integrated farming systems that control inputs and outputs to minimize the impact on the environment and improve efficiency.

Meeting the challenges of the next decades requires international collaboration to develop the required human resources. In 2007, six European universities started with the European Master in Animal Breeding and Genetics (EMABG), a two-year master course that aims at building capacities in the fields of animal breeding and genetics. The EMABG aims to train students who can contribute to the development of sustainable farm animal breeding. Graduates find positions in and outside Europe, in training, research or development in a wide range of organisations related to animal breeding and genetics. This new generation of graduates are essential to realise the potential contribution of animal breeding to meet the challenges of the future.

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HODOWLA ZWIERZĄT WOBEC WYZWAŃ PRZYSZŁOŚCI

Streszczenie. W artykule omówiono problemy hodowli zwierząt stojącej wobec wyzwań przyszłości. Poruszono zagadnienia dotyczące możliwości włączania do celów hodowlanych oddziaływań chowu zwierząt na środowisko, a także wpływ genomiki, interakcji społecznych i jakości produktów zwierzęcych na programy hodowli zwierząt. Wskazano na aspekty wykorzystania hodowli zwierząt w krajach rozwijających się. Stwierdzono pilną potrzebę opracowania szczegółowych bioekonomicznych modeli w celu oceny skutków ekologicznych i ekonomicznych hodowli zwierząt. Wyzwaniem następnego półwiecza jest zwiększenie wydajności głównych gatunków zwierzat gospodarskich. Pomoże ono rozwiazać problemy żywnościowe na świecie, z jednoczesnym zmniejszeniem oddziaływania zwierząt na środowisko i utratą ich różnorodności genetycznej. Zakończenie sekwencjonowania genomu bydła mlecznego przyniosło narzędzia dla programów selekcji genomowej dla szerokiego spektrum cech. W krajach rozwinietych sa już one obecnie stosowane, zwiększając skuteczność programów hodowlanych. Techniki te umożliwiają także ocene i wykorzystanie rodzimych ras w krajach rozwijających się. Tradycyjne systemy utrzymywania zwierząt będą ewoluować w kierunku bardziej intensywnych systemów rolnictwa zintegrowanego. Dążąc do podnoszenia produkcyjności zwierząt hodowlanych, należy pamiętać o konieczności minimalizowania ich negatywnego wpływu na środowisko naturalne. Wielu autorów wyraża pogląd, że nie tylko ekonomiczne, lecz także inne wymierne efekty powinny być włączone do definicji celów hodowlanych. W artykule pokazano, że te same zasady stosuje się przy wprowadzaniu ekologicznych ograniczeń wag ekonomicznych dla cech także w hodowli zwierząt. Na przykład zysk w przeliczeniu na 1 kg emisji metanu prowadzi do uzyskania dokładnie tej samej wartości jak wartość wyrażona na poziomie stada, z ograniczeniem całkowitej produkcji metanu. Ujawnienie genomu bydła mlecznego otworzyło nowe możliwości, pozwalające na uzyskanie dalszych informacji o poszczególnych genach i ich wpływie na ważne cechy produkcyjne bydła. W 2005 roku powołano konsorcjum Holenderskiej Genomiki Mleka, które rozpoczęło badania nad naturalną zmiennością genetyczną cech jakościowych mleka oraz opracowało strategie dalszej poprawy jakości mleka. Celem tej inicjatywy jest zwiększenie wiedzy na temat zmienności genetycznej składu mleka przez wspólne działanie specjalistów z dziedziny genomiki, genetyki ilościowej, bioinformatyki, proteomiki i hodowli bydła mlecznego. Zgromadzono i przeanalizowano mleko i próbki DNA 2000 krów populacji holenderskiej holsztyńsko--fryzyjskiej. Stworzyło to unikalną bazę danych zawierającą szczegółowe informacje na temat

składu mleka. Zidentyfikowano znaczną liczbę genów i regionów genomu determinujących zmienność genetyczną. Jest to ważny krok w kierunku lepszego zrozumienia regulacji składu mleka, pomocny w projektowaniu programów hodowlanych, których celem jest produkcja mleka bardziej dostosowanego do oczekiwań konsumenta.

Slowa kluczowe: program hodowlany, doskonalenie genetyczne, interakcja społeczna, emisja metanu, jakość produktu

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