

**Genetic progress and inbreeding rate in complex
breeding programmes**

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Applications to sport horses and laying hens

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Genetischer Fortschritt und Inzuchtrate in komplexen Zuchtprogrammen – Zuchtplanungsbeispiele für Sportpferde und Legehennen

Die vorliegende Arbeit befasst sich mit der Optimierung von Zuchtprogrammen. Zum einen wurde eine neue Methode zur Berücksichtigung der mittleren Inzucht in Zuchtplanungsrechnungen entwickelt. Zum anderen werden zwei gänzlich unterschiedliche Zuchtprogramme modelliert und aktuelle Optimierungsansätze validiert. Dabei werden sowohl der naturale als auch der monetäre Zuchtfortschritt und der diskontierte Züchtungsgewinn berücksichtigt. Im Projekt FUGATO+brain wurde die Zuchtplanungssoftware ZPLAN neu programmiert und mit weiteren zuchtplanerischen Werkzeugen versehen. Als Ergebnis des Projektes entstand die Software ZPLAN+. Diese ermöglicht die Modellierung von komplexen Zuchtprogrammen und kann zur Optimierung von Zuchtprogrammen genutzt werden. Die Software ist anwenderfreundlich und umfasst alle Bereiche der Zuchtplanung.

Zur Berechnung der mittleren Inzucht wurde eine neue Methode für die Implementierung in der Zuchtplanung entwickelt. Die Methode basiert auf der mittleren Kinship in einer Zuchtpopulation. Die Kinship ist definiert als die Wahrscheinlichkeit, dass innerhalb einer Gruppe am gleichen Locus zwei zufällig gewählte Allele herkunftsgleich sind. Die Berechnung der Kinship erfolgt auf Grundlage der Genflussmethode. Zur Validierung der Methode wurde eine früher beschriebene Schafpopulation verwandt, die in unterschiedlichen Weisen modifiziert wurde. Insgesamt wurden drei verschiedene Szenarien modelliert, wovon das erste von einem Populationswachstum ausging. Im zweiten Szenario wurde angenommen, dass die Populationsgröße durch einen Flaschenhals verringert wird und sich dann wieder erhöht. Für die dritte Modellierung wurde die Population über einen Zeitraum getrennt und dann wieder zusammengeführt. Es konnte gezeigt werden, dass sich mit der vorgeschlagenen Methode in sämtlichen komplexen Populationsstrukturen die mittlere Inzucht und die effektive Populationsgröße berechnet lässt.

In einer Zuchtplanungsrechnung für Reitpferde sollte der gezielte Einsatz von Embryotransfer in einem Pferdezuchtprogramm validiert werden. Hierfür wurde ein Zuchtprogramm in ZPLAN+ modelliert, welches das aktuelle Zuchtprogramm des Hannoveraner Verbandes e.V. näherungsweise abbildet. In ver-

schiedenen Szenarien wurde eine schärfere Selektion auf der Stutenseite modelliert, wobei die besten Stuten des Zuchtprogramms als Spenderstuten für den Embryotransfer eingesetzt wurden. Es wurde davon ausgegangen, dass die zur Selektion zur Verfügung stehenden Stuten sowohl Ergebnisse in der Eintragung, als auch Ergebnisse einer Leistungsprüfung haben. Die Anzahl der zur Selektion verfügbaren Stuten wurde ebenso variiert wie die Anzahl der selektierten Stuten und die Anzahl der geborenen Fohlen je Spenderstute. Deutlich wurde, dass der Embryotransfer die Möglichkeit bietet den Zuchtfortschritt in einem Pferdezuchtprogramm stark zu steigern, wobei dies mit einer Steigerung der Kosten für die Züchter einhergeht. Mit dem vorgeschlagenen Ansatz zur Inzuchtberechnung konnte gezeigt werden, dass die scharfe Selektion und der starke Einsatz der Spenderstuten eine Erhöhung der mittleren Inzucht und daraus folgend eine geringere effektive Populationsgröße nach sich zieht.

Im dritten Abschnitt der Arbeit sollten die Auswirkungen der Einbeziehung von genomischen Informationen in ein Legehennenzuchtprogramm gezeigt werden. Dafür wurde in enger Kooperation mit der Lohmann Tierzucht GmbH ein Zuchtprogramm zur Produktion von 500 Mio. Legehennen in ZPLAN+ nachgebildet. Die Produktion der Elterntiere basiert auf einer Kreuzung von vier Nukleuslinien, die konventionelle Selektion stützt sich vor allem auf die Leistungsprüfung von Hennen in den einzelnen Linien. Zur Nutzung der genomischen Informationen wurde von unterschiedlich großen Kalibrierungstichproben ausgegangen. In einem ersten Schritt wurden die genomischen Informationen der Hähne zusätzlich zu allen konventionellen Selektionskriterien genutzt. Dabei wurde die Anzahl der getesteten Hähne variiert und in einem weiteren Schritt wurde davon ausgegangen, dass die Hennen ebenfalls genotypisiert sind. In einem weiteren Szenario basierte die Selektion nur auf Pedigreedaten und genomischen Informationen. Deutlich wurde, dass in der zweiten Variante das Generationsintervall massiv gesenkt werden konnte. Der Zuchtfortschritt konnte in allen modellierten Varianten erhöht werden, wobei es Unterschiede in den Einzelmerkmalen gab. Die Einführung der genomischen Informationen in die Legehennenzucht ist verbunden mit einem massiven Kostenanstieg. Inwieweit der gesteigerte Zuchtfortschritt den Kostenanstieg rechtfertigt bedarf einer Marktanalyse seitens der Zuchtunternehmen.

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The main focus of this thesis is the optimization of breeding programmes. On the one hand a new method to account for the average inbreeding in the design of breeding programmes has been developed. On the other hand two entirely different breeding programmes have been modelled and current optimization approaches are validated using these reference programmes. When calibrating the programmes potential natural and monetary genetic gains as well as the discounted profit are taken into consideration. In the project FUGATO+brain the software ZPLAN for optimization of breeding programmes was re-programmed and further tools were added. The result of the project is the software ZPLAN+. This software enables the user to model and optimise complex breeding programmes. In addition, the software is user friendly and covers all areas of breeding programmes and hence can be used in various contexts.

To calculate the average inbreeding and effective population size in complex breeding programmes, a new method has been developed. The method is based on the average kinship in breeding populations. The kinship is defined as the probability that within a group at the same locus two randomly chosen alleles are identical by descent. The calculation of the Kinship is based on the gene flow theory. To validate the method, a sheep population described earlier was used and modified in different ways. Three different scenarios were modelled. The first scenario assumes population growth. In the second scenario it is assumed that the population size is reduced by a bottleneck and then increased again. For the third scenario the population was divided in two parts over a period and then brought together again. The results of this validation exercise show that average inbreeding and effective population size can be calculated in all three scenarios.

In a breeding programme for sport horses usage of embryo transfer was validated. A basic breeding programme in ZPLAN+ was modelled, which reflects the current breeding programme of the Hannoveraner Verband e.V. approximately. Using different scenarios, a more rigorous selection on the mares' side was modelled. The best mares in the breeding programme were used as donor mares for embryo transfer. It was assumed that for selection of

the donor mares information of stud book inspection as well as results of a mare performance test are available. The number of mares available for selection, the number of selected mares and the number of born foals per donor mare were varied in order to validate the methodology. The results show that the usage of embryo transfer offers one possibility to increase genetic gain in a breeding programme strongly. However using embryo transfer implies a steep increase in costs for the breeders. The proposed approach for calculating inbreeding showed that the rigorous selection and the intensive usage of donor mares results in an increase of the average inbreeding and consequently a reduction of the effective population size.

The third section of this thesis examines the effects of including and using genomic information in a layer breeding programme. A breeding programme to produce 500 million laying hens has been modelled using ZPLAN+ in close cooperation with the Lohmann Tierzucht GmbH. The production of the parents is based on a crossing of four nucleus lines. The conventional selection is based primarily on performance testing of hens of the different lines. In order to utilise the genomic information two different calibration sets were used (500 and 2`000 animals). In a first step, the genomic information of the cocks has been used in addition to all conventional selection criteria. The number of cocks was varied and in a further step it was assumed that the hens are also genotyped. In another scenario, the selection was based on pedigree and genomic information only. It became clear that the generation interval could be strongly reduced in the second variant. The genetic gain could be increased in all modelled variants, but there were differences in individual traits. The implementation of genomic information into layer breeding programmes is connected to a massive increase in costs. Whether the increased genetic gain justifies the increase costs requires a market analysis by the breeding companies.

1st CHAPTER

General Introduction

Preface

Since the beginning of domestication, humans have been selecting breeding animals on the basis of their potential in different traits. For thousands of years it has been attempted to enrich desired characteristics and to eliminate undesired ones. The selection only relied on phenotypic performances and the selection, as well as the breeding, were made undirected and not even systematically (Lush, 1945).

The pre-conditions for a systematic breeding have first been created in the United Kingdom with the foundation of associations to register purebred animals. One of the oldest herd books which is conducted till now was published for Thoroughbred horses in 1791 (Weatherby, 1791). One of the oldest herd book associations in cattle breeding was founded in 1875 for the breed of Shorthorn (Perry, 1982). These herdbooks and associations were used as a model for many other breeds. Most of the present breeds were created in the 18th to the 20th century. With further developments in animal breeding the associations built specific and efficient breeding programmes.

Nowadays only few breeds per species are able to compete on the global market (Simianer, 2005). These breeds are specialized for economically significant traits. Breeding programmes for such world breeds are on a high standard. The breeding structures and organisations are deliberated and genetic gain as well as economic aspects have to be taken into consideration. The breeding programmes differ for the diverse species for various reasons. In general one can distinguish two types of organizational structures that engage in breeding activities: breeding associations with mostly pure bred animals organized in herd books and breeding companies which are breeding hybrids from nucleus lines. This dichotomy is reflected in the two species that will be studied in this thesis: breeding of horses is driven by associations whereas breeding of laying hens is dominated by few international companies.

Registered breeding associations have been created by private breeders and conduct a herd book with mostly pure bred animals. This is typical especially for cattle and horse breeding where the progeny is not a final product but is used

for breeding. 1871 the first herd book for Holstein dairy cattle was formed in the United States (Lush et al., 1936). This breed today is one of the most important dairy cattle breeds in the whole world and is continuing mostly in purebred.

Breeding companies which are producing hybrids use the effects of crossbreeding. These effects are well known in plant breeding as well as in animal breeding. A detailed and famous description of crossing different *Pisumsativum* ssp. was given by Mendel (1866). In animal breeding the crossing of different breeds or different lines has several purposes. First of all, different additive genetic effects could be used from different breeds. The crossproducts form an intermediate genotype which enables capitalizing on the merit in both sexes for specific characters. Because of heterosis, hybrid offspring often show superiority relative to the average of the two parental pure lines. These effects have been used in cattle (Gregory and Cundiff, 1980) as well as in pig breeding (Schneider et al., 1982). Nowadays especially in pig and poultry breeding crossing nucleus lines is the method of choice.

The introduction is structured as follows: The first section gives an introduction in the breeding of sport horses. The second part describes the characteristics of layers breeding programmes. The third part explains the software-based optimization of breeding programmes. When doing so, the breeding methods embryo transfer and genomic selection are considered separately. A further aspect of this introduction will be the implementation of inbreeding in the optimization of breeding programmes.

Breeding of sport horses

Horses were crucial for the military purposes, agriculture and locomotion until the mid-20th century. With the growing motorization in the 1950s, draft horses and workhorses were not needed anymore. Also in the army horses were replaced by machines. Since the beginning of the 1960s, horses have been predominantly used for sport and leisure activities. Over time these working horses became more and more light due to the crossing with Arabian and Thoroughbred horses and became the present sport horses (v. Stenglin, 2005).

Horse breeding has some unique characteristics compared to other livestock species. Regional and national horse-breeding associations breed sport horses with the same overall breeding goal and a similar genetic background. The breeding programmes are designed as purebreds, but there is an exchange of animals between the different breeding associations. The breeding goal for German sport horses includes several aspects. On the one hand breeders breed horses for sport competition up to Olympic level. On the other hand most of the horses are used for hobby without any athletic demand (Gille and Spiller, 2010). It is quite difficult to breed one horse which satisfies both objectives in multiple traits, which are often assessed subjectively, have to be considered. Hence, no economic weighting has been estimated for the single traits (Koenen et al., 2003).

The selection mainly takes place on the male side. Stallions have to pass licensing and a performance test. Mares only have to be registered in a studbook. Breeding values are estimated over the whole German population including results from equitation as well as results from performance test of stallions and mares (v. Velsen-Zerweck, 1998). Through the use of artificial insemination, the usage of stallions is possible at a national and even international scale. Especially famous young stallions without secure breeding values were used extensively all over Germany. Broodmares' selection is marginal and almost every registered mare in a breeding programme can be used for reproduction purposes. Mating is often made based on emotional decisions and not with a breeding goal in mind.

Modern reproduction techniques like embryo transfer or sperm sexing are not used systematically and modern selection strategies like using genomic information are still in the early stages. Most horses are bred by hobby breeders with no more than two registered broodmares (Klunker and Barth, 2008). This could be an advantage because the amortisation of the costs for breeding horses does not play an important role for these breeders.

Horse breeding and equitation are a considerable economic factor and a figurehead for Germany (IPSOS, 2001). Many of the most successful sport horses come from Germany. However, recently other European and

international breeds and breeding associations are getting more and more successful. Therefore, the German horse breeding programmes have to improve their breeding structures if they want to maintain their dominant position. For this reason the planning and optimization of breeding programmes plays an important role in the breeding not only of sport horses.

Poultry breeding

In contrast to horse and cattle breeding associations, breeding companies in pig and even more so in poultry are resident. For instance, the market of laying hens is mainly resulting of three companies worldwide (Thiruvankadan et al., 2010). Poultry meat represents 21% of the German meat consumption and every German eats 211 eggs a year (BMELV, 2010). The self-sufficiency rate of eggs is currently about 70%. Consumers are increasingly focused on a high product quality and animal welfare.

In poultry breeding, the breeding goals are well defined and consist of many economically weighted single traits. They are regularly adapted to changing market conditions. That can result in a need of different traits or new traits and in different weights of the single traits (Goddard, 1998). Companies hold a stock of breeding animals which were selected very rigorously and mated in purebred lines. The original breeds evolved towards advanced performance and the animals in the lines have a high relationship. Selection is based on an efficient performance testing, mainly on station. The recording of phenotypic information is objective and accurate. Crossbred animals are produced out of this breeding stock in one or more multiplication stages and sold.

In poultry breeding the marketable product is the parent stock for producing poultry for fattening or laying hens. Both sexes of the parent stock are generally crossbreds of two lines. Thereby the end products are four-way crosses. All breeding decisions are made in the company and the companies are profit-oriented.

For layers there are only few worldwide operating breeding companies (Thiruvankadan et al., 2010). These companies face international competitive pressure about their customers. The profit margins in poultry industry are very small and the farmers have been confronted in the last years with an increase of feed prices, which reduced the margins even more. Hence, the farmers need very efficient animals to keep their business profitable. Hence, the breeding companies have to offer optimal products at the lowest possible price. For this reason optimization of breeding structures and increased genetic gain has always been important for breeding companies. Before being implemented, new selection strategies, for instance relying on genomic information, have to prove empirically that they are generating the desired results for the breeding programmes.

Optimization of breeding programmes

The design of breeding programmes is an important element of the work in breeding companies as well as in breeding associations. On the one hand new breeding programmes can be set up. On the other hand established breeding programmes have to be adapted to new conditions like new breeding techniques, changing legal requirements or changing consumers' preferences. This clearly indicates that planning breeding programmes is not a one-time necessity but it is a permanent challenge and task to stay competitive in the market.

For the optimization of breeding programmes a common method is the use of computer-based modelling to find the best breeding strategies. ZPLAN (Karras et al. 1997) is one of the oldest software tools for optimization of the breeding programmes. It is written in FORTRAN and needs a complex and inscrutable input file. In the project FUGATO+brain, an evolution of ZPLAN called ZPALAN+ has been developed. ZPLAN+ includes all functionalities of the old ZPLAN and in addition some new tools, such as the prediction of inbreeding and the implementation of genomic information in the optimization of breeding

programmes. Another advantage is the user-friendly interface and the comprehensive documentation of ZPLAN+.

This piece of software is based on the selection index, the gene flow theory and a complex modelling of costs and returns. The selection index theory by Hazel and Lush (1942) makes it possible to select animals for different traits at the same time in an optimum member. Hill (1974) and Elsen and Mocquot (1974) introduced the gene flow which describes the transmission of genes within a breeding programme. Complex structures of selection groups with overlapping generations can be modelled while taking into account where and how often the genetic improvement of the selected animals is realized. Furthermore, a complex modelling of discounted costs and returns provides results for economic considerations in the breeding programme.

In a usual application, the present situation is often modelled first as a reference scenario. In a next step, the new breeding structures can be implemented to be compared to the reference scenario. New breeding structures can be for example the use of genomic information or new biotechnologies such as embryo transfer. Also questions about the traits in the breeding goal and their economic weights or changes in the intensity of selection through changes in the population sizes can be answered. The comparison of breeding programmes can rely either on the optimization of genetic gain or on economic aspects as well as a combination of both. Usually a combination of genetic gain and economic aspects is used to decide which scenario is the best and in what form the reference breeding programme could be optimized.

Embryo transfer

Using new reproductive technologies can change structures of breeding programmes to a large extent especially in dairy cattle and horses. The method of artificial insemination has been known since more than 200 years and revolutionized the breeding of cattle since the 1940s (Foote, 2002). Robertson and Rendel (1950) described a dairy cattle breeding programme which was based on progeny testing and the usage of artificial insemination to maximize

the genetic improvement. Skjervold and Langholz (1964) designed a cattle breeding programme based on artificial insemination which has remained basically up to the present day. Also in horse breeding artificial insemination is the oldest widely used reproduction biotechnology. However, in German horse breeding programmes the targeted use of artificial insemination started not until the beginning of the 1990s (Schade, 1996).

A further development was the use of embryo transfer (Betteridge, 2003). This technique, introduced especially in combination with multiple ovulations, offered new possibilities to improve the efficiency of dairy cattle breeding programmes (Nicholas and Smith, 1983). In German horse breeding programmes embryo transfer is permitted but only used by few breeders and mainly for mares with fertility problems (Squires et al., 2003). While in Germany embryo transfer is not routinely included in the breeding programmes, it is frequently used as a part of horse breeding programmes in Argentina, where the best mares in the breeding programme were used intensively (Losinno et al., 2000).

Other reproductive technologies such as invitro techniques (Hasler, 2003) or sperm sexing (Seidel, 2003) provide opportunities to optimize dairy cattle breeding programmes in different ways but are not established in horse breeding yet. In horse breeding embryo transfer has the potential to optimize the selection of mares, which still has to be validated before implementing it in existing breeding programmes.

Genomic selection

The initial idea for searching quantitative trait loci (QTL) via markers was developed by Thoday (1961). This was followed by the development of marker assisted selection (Lande and Thompson, 1990) and the mapping of QTL in different species. Reviews are available for cattle (Khatkar et al., 2004), pigs (Kerr et al., 2001) and chicken (Abasht et al., 2006). Many QTL were also found in horses (e.g. Lampe et al., 2009; Shakhsh-Niaei et al., 2012). But marker assisted selection did not always achieve the desired results in farm animal application (König and Simianer, 2007).

The era of genomic selection was heralded by Meuwissen et al. (2001). Searching for QTL was replaced by genomic breeding values estimated by the sum of all single nucleotide polymorphism effects. First calculations showed the potential to maximize genetic gain and reduce breeding costs in dairy cattle breeding programmes (Schaeffer, 2006; König et al., 2009). Nowadays genomic breeding values are successfully implemented in dairy cattle breeding programmes (Loberg et al., 2009). In pig breeding too first calculations showed a potential for advances in breeding programmes (Simianer, 2009).

Nowadays genomic selection is discussed as a potential method to optimize selection and breeding strategies for all livestock species. It is therefore essential to assess potential of using genomic information via software like ZPLAN+. The use of genomic information in livestock breeding programmes must be validated before implementing such new methods. In every species the genomic information can be used in different ways and therefore the best method has to be found to optimize the genetic gain but also economic aspects need to be considered.

Inbreeding in the optimization of breeding programmes

Inbreeding results from mating of related animals (Pearl, 1917). Lush (1945) defined inbreeding as the mating of animals which are more related to each other than the average relationship within the whole population. The mating of related animals is unavoidable in wild populations as well as in domesticated populations because the number of individuals is limited. Thus the increase of relationship and the probability of mating closely related animals is a natural process in populations of finite size. The consequence of inbreeding is an increase of the homozygosity in the populations (Wright, 1922) which can be a desired effect in line breeding (Lush, 1945), but also is often found to have negative effects.

A negative effect of inbreeding is the increased risk of homozygosity of deleterious alleles in monogenic diseases with a recessive expression. Important examples for this are the Hyperkalaemic Periodic Paralysis Disease

in horses (Rudolph et al., 1992), the Malignant Hyperpyrexia Syndrome in pigs (O'Brien, 1987) or the Complex Vertebral Malformation in cattle (Thomsen et al., 2004). Today gene tests are available for the genes determining all of these diseases (Bowling et al., 1996; Agerholm et al., 2001; Fujii et al., 1991).

Another disadvantage is the incidence of inbreeding depression. This may occur in many wild populations (Crnokrak and Roff, 1999) as well as in livestock populations. Morley (1954) showed negative correlations between inbreeding and performance traits in a breeding programme of Australian merino sheep. König and Simianer (2006) summarized the negative influence of an increase of one per cent inbreeding on functional and performance traits in dairy cattle. Furthermore there are several studies in pig breeding (e. g. Rodríguez et al., 1998; King and Roberts, 1959) and in horse breeding (e. g. Gandini et al., 1992; Gómez et al., 2009) which show a negative influence of increasing inbreeding coefficients on different traits. However, in poultry breeding, increasing inbreeding was reported to have no significant negative impact on traits in the breeding goal (Preisinger, 2000).

Further the increase of inbreeding reduces genetic variance which is directly associated with the genetic gain. Rendel and Robertson (1950) showed this with $\Delta G = ih\sigma_A$. The Genetic gain ΔG is directly linked to the selection intensity i , the square root of the heritability h and the additive genetic standard deviation σ_A . Since inbreeding reduces the genetic variance both h and σ_A will be reduced and genetic gain will be negatively influenced by increased levels of inbreeding in populations (Sorensen and Kennedy, 1984).

These are several important reasons to include the expected inbreeding rate in optimization of herdbook breeding programmes as well as line breeding programmes for the production of hybrids.

Scope of this thesis

The aim of this thesis is to assess the use of software ZPLAN+ in different breeding programmes and to answer current questions related to the optimization of breeding programmes for horses and poultry. To achieve these goals, reference breeding programmes for sport horses and laying hens were modelled based on the present breeding structures in the two species. Following this, typical current questions were modelled and the results were compared with the reference scenario. It was demonstrated that ZPLAN+ can help to answer current questions in all livestock species.

A new method for computing the development of inbreeding provides the opportunity to include this aspect in the optimisation of breeding structures with ZPLAN+. The results indicate that if the selection intensity were increased and only few animals were used intensively, inbreeding will rise and genetic variance will therefore be decreased in breeding programmes. The opportunities to calculate inbreeding coefficients and effective population size in complex and dynamic breeding programmes is shown in different examples (Chapter2).

In horse breeding programmes the effects of rigorous selection and the implementation of embryo transfer in order to use the best mares is investigated. This is an example of the implementation of a new reproduction technique in combination with rigorous selection of the breeding animals (Chapter 3).

In laying hens different ways of using genomic information are analysed and the consequences for the breeding programme were assessed. Using genomic information has triggered a new era in dairy cattle breeding programmes and also in pig and poultry breeding. However, the implementation of this new technique must be validated empirically (Chapter 4).

Finally, in Chapter 5 the results of the different parts are discussed and general conclusions are made.

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2nd CHAPTER

A recursive method for computing expected kinship and inbreeding in complex and dynamic breeding programmes

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A recursive method for computing expected kinship and inbreeding in complex and dynamic breeding programmes

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Abstract

In many livestock breeding programmes the development of inbreeding is of critical importance. Thus, the assessment of the expected development of inbreeding should be an essential element in the design of breeding programmes. We propose a new method to deterministically predict the rate of inbreeding based on the gene-flow method in well-defined complex and dynamic breeding programmes. In the suggested approach a breeding programme has to be structured in homogeneous age-sex-groups, so called cohorts, with a defined origin of genes. Starting from an initial setup (usually an unrelated and non-inbred base population) transition rules to calculate the kinship within and between cohorts originating from reproduction or aging, respectively, are defined. Using this approach recursively provides the expected development of kinship within and between all cohorts over time, which can be combined into average kinships for the whole population or defined subsets. From these quantities relevant parameters like the inbreeding rate or the effective population size are easily derived. We illustrate the method with a simple static example breeding programme in sheep. Based on this reference breeding programme we demonstrate the use of our approach for dynamic breeding programmes, in which cohort sizes or vectors of gene origin change over time: here we model the situation of exponential population growth and a bottleneck situation, respectively. The suggested approach does not account for the effect of selection on the development of inbreeding, but ideas to overcome this limitation are discussed.

Keywords

kinship, inbreeding, effective population size, gene-flow method, dynamic breeding programme

Introduction

The consequences of inbreeding in animal breeding were discussed first by Pearl (1917) and Wright (1922 and 1931). Crnokrak and Roff (1999) collected in a review many examples for inbreeding depressions in wild populations. But also in closed farm animal populations increasing inbreeding levels are unavoidable and even enforced under selection. The inbreeding coefficient of an individual is defined as the probability that the two alleles at one autosomal locus are identical by descent. The inbreeding coefficient is linked to both Wright's (1922) concept of relationship and Malécot's (1948) concept of kinship, in that the inbreeding coefficient of an animal is half the relationship coefficient of its parents or, which is identical, the kinship coefficient of its parents. Averaging the inbreeding coefficient over animals in a defined group yields the overall inbreeding level of this group. The practically most important quantity is the inbreeding rate, which is the first derivative of the average inbreeding level with respect to time and can be expressed as the increase in the level of inbreeding per year or per generation.

Morley (1954) shows negative correlations between inbreeding rates and performance traits in a breeding programme of Australian merino sheep. König and Simianer (2006) compiled ten papers including negative effects of an increase of inbreeding on productive as well as functional traits in dairy cattle populations. In pig breeding increasing inbreeding reduced the litter size significant (Rodrigález et al., 1998) and Fernández et al. (2002) showed negative effects of inbreeding on growth traits in different pig breeds. Also in horses height traits were influenced by increasing inbreeding (Gandini et al., 1992; Gómez et al., 2009). Besbes and Gibson (1998) and Sewalem et al. (1999) showed in laying hens low negative effects of an increase of inbreeding. In the design of breeding programmes it therefore is necessary to assess the expected inbreeding rate for the different alternative breeding strategies. A parameter that is directly connected with the inbreeding rate is the effective populations size (N_e) introduced by Wright (1931). The N_e describes the size of an ideal population which has the same inbreeding rate as the real population from which it is calculated. N_e is an important parameter to characterise a

population (Caballero, 1994) and reflects the available genetic diversity and also has a direct impact on the accuracy of genomic breeding value estimates (Daetwyler et al., 2010).

Hill (1974) and Elsen and Mocquot (1974) introduced a concept to represent a population by a defined number of sex and age specific groups of individuals to predict the response to selection in structured populations with overlapping generations. This approach, usually termed the 'gene-flow method' was later extended to reflect more complex breeding structures. Selection groups can be defined with respect to different levels of the breeding programmes, like splitting all bulls in bull sires and cow sires. In the gene-flow concept such a group is characterised by the fact that all members of the group have common characteristics. In the context of assessing response to selection this means that the expected genetic value is identical, that identical selection intensities are applied *et cetera*. For modelling the gene flow this implies especially that all members of the group receive their genes from the same source or combination of sources. In the case of a group originating from aging, this means that all members of the group at time t resulted from the aging of another group at time $t - 1$. In the case of a group originating from reproduction this means that all members of the group at time t stem from sires (dams) out of one or several groups at time $t - 1$ with the same probability.

Due to this basic principle the expected kinship is uniform within a group. Also, the expected kinship between all members of two different groups is identical.

The approach suggested by Hill (1974) exclusively focused on the prediction and evaluation of response to selection. In some studies (e.g. Johnson, 1977; Hill, 1979) the same basic concept was used to derive formulas for expected inbreeding rate or effective population size in well-defined breeding designs.

This study follows a different route. A breeding design is completely defined if it can be structured in age-sex-groups with a defined origin of genes. We call these age-sex-groups cohorts, and a full definition will be given below. The kinship within and between cohorts at time $T = t$ is set to a starting value. We will show that expected kinships within and between cohorts at time $T = t + 1$ are a function of the values at time t , and we will give the respective recursive

equations for all possible constellations of reproduction and aging. Based on this, we can project the development of kinship within and between cohorts over a defined planning horizon. This allows assessing the development of kinship and derived parameters, like expected inbreeding, relationship, and effective population size, both for the whole populations and for subsets, like breeding or production animals, sex groups *et cetera*. It also allows to model arbitrarily complex breeding structures without the necessity of a constant breeding design, assuming e.g. that number and size of cohorts may change over time in a dynamic way.

The structure of the paper is as follows: we first will introduce the basic definitions and then will give equations to calculate the kinship within and between cohorts at time t from the same quantities at time $t - 1$. We will illustrate this concept with a simple breeding design used by Hill (1974) and Johnson (1977). We then will demonstrate the flexibility of the concept with more complex dynamic designs. Finally we will discuss extensions of the method and suggest a modification to account for selection and unequal family size.

Methods

We define C_i^t as cohort i at time $t \geq 0$. A cohort is a group of animals with the same sex, the same age class, and with identical probabilistic origin of genes. This means that each member of cohort C_i^t has obtained its genes with the same probability from a set of cohorts at time $t - 1$. Thus, members of a cohort are by definition indistinguishable and have identical expected characteristics like e.g. inbreeding levels. The number of individuals in cohort i is n_i . The entire population consists of m contemporary cohorts, where the structure, not necessarily the size, is assumed to be constant over time.

Time is represented by a series of discrete time points $T = 0, 1, \dots, t, t + 1, \dots$, where the interval between subsequent time points t and $t + 1$ reflects the same time span. In most cases a time span of one reproduction cycle (e.g. average calving interval) or fractions thereof will be appropriate.

k_{ij}^t is the mean kinship of cohort C_i^t and C_j^t for $i, j \leq m$ at time t . This includes kinship within ($i = j$) and between ($i \neq j$) cohorts. We use kinship in the sense of Malécot (1948) as the probability that one allele sampled in cohort C_i^t and one allele sampled in cohort C_j^t at the same locus are identical by descent (IBD) and we restrict this to autosomal loci in diploid genomes only. Hence, $0 \leq k_{ij}^t$ and $k_{ij}^t = k_{ji}^t$.

The probabilistic origin of the genes in cohort C_i^t needs to be defined for two possible cases: reproduction and aging.

In the case that C_i^t originates from a reproductive event, i.e. individuals in C_i^t are in the youngest age class, then p_{ij} is the probability of a cohort j providing genes to cohort i . From these probabilities arises the vector $\mathbf{p}_i = \{p_{ij}\}$ of length m , which will be called the vector of origin of cohort i . Note that $\sum_{i=1}^m p_{ij} = 1$.

In the case of aging, individuals in C_i^t are identical to or a subset of C_i^{t-1} . Note that this implies $n_i \leq n_j$. If $n_i < n_j$ we assume that a random sample of C_j^{t-1} of size n_i becomes the cohort C_i^t .

The complete kinship structure of the population at time t is contained in the matrix \mathbf{K}^t of size $m \times m$ with elements $k_{ij}^t, i, j = 1, \dots, m$.

The development of the kinship in a population is a Markov process for which we need to define a starting constellation \mathbf{K}^0 and a set of transition rules to derive \mathbf{K}^t from \mathbf{K}^{t-1} .

In the design of breeding programmes an often made assumption is that the base population consists of animals which are not inbred and mutually unrelated. In the present parameterization this is equivalent to $k_{ij}^0 = 0$ for all $i, j \leq m$.

Transition rules will be defined for the following cases:

(i) Diagonal element k_{ii}^t for a cohort originating from reproduction

Cohort C_i^t originates from reproduction. The two alleles have a probability of p_{ij}^2 to come from the same parental cohort j , and a probability $2p_{ij}p_{ik}$ to

come from different parental cohorts j and k . When both alleles originate from the same cohort, they can be IBD either because the same allele has been sampled twice (probability $(2n_j)^{-1}$) or because they were already IBD in the previous generation (probability $(1 - (2n_j)^{-1})k_{jj}^t$). If the two alleles stem from different cohorts, they can only be IBD if they were IBD in the previous generation, which has a probability k_{jk}^t . Thus, when combining all the potential origins, one obtains:

$$k_{ii}^{t+1} | reproduction = \sum_{j=1}^m p_{ij}^2 \left[\frac{1}{2n_j} + \left(1 - \frac{1}{2n_j}\right) k_{jj}^t \right] + 2 \sum_{j=1}^m p_{ij} \sum_{k \neq j} p_{ik} k_{jk}^t$$

(ii) Diagonal element k_{ii}^t , originating from aging

Cohort C_i^t originates from aging of cohort C_j^{t-1} . In this case the average kinship remains unchanged, so that

$$k_{ii}^t | aging = k_{jj}^{t-1}$$

(iii) Offdiagonal element $k_{ii'}^t$, both C_i^t and $C_{i'}^t$ resulting from reproduction

It is assumed, that cohort C_i^t has the paternal and maternal vectors of origin s_i and d_i and cohort $C_{i'}^t$ has the paternal and maternal vectors of origin $s_{i'}$ and $d_{i'}$. In that case, the *ibd* probabilities are a function of the state of identity of the paternal (j) or maternal (m) allele sampled in cohort C_i^t with the paternal (j') or maternal (m') allele sampled in cohort $C_{i'}^t$, respectively. Table 1 gives the expected kinship for four different combinations of paternal allele origins. Note that new homozygosity can only arise if either two paternal or two maternal alleles are sampled and if the cohorts C_i^t and $C_{i'}^t$ have a paternal or maternal cohort of origin in common.

The offdiagonal element pertaining to cohorts C_i^t and $C_{i'}^t$ thus becomes

$$k_{ii'}^t | both\ reproduction = \sum_{x=j,m} \sum_{y=j',m'} p_{xy} k_{ii'}^t | xy$$

where the respective values $k_{ii'}^t | xy$ are listed in the right column of Table 1.

Table 1: Probability of paternal and maternal allele combinations and expected kinship conditional on the allele combination contributing to the offdiagonal element between two cohorts C_i^t and $C_{i'}^t$ stemming from reproduction.

| Cohort of origin of allele sampled in cohort | | Probability of allele combination | Expected kinship given the allele combination |
|--|------------|--------------------------------------|--|
| C_i^t | $C_{i'}^t$ | | |
| j | j' | $p_{jj'} = \frac{s_{ij}s_{i'j'}}{4}$ | $k_{ii'}^t mj' = \begin{cases} \frac{1}{2n_j} + \left(1 - \frac{1}{2n_j}\right) k_{jj'}^{t-1} & \text{if } j = j' \\ k_{jj'}^{t-1} & \text{otherwise} \end{cases}$ |
| j | m' | $p_{jm'} = \frac{s_{ij}d_{i'm'}}{4}$ | $k_{ii'}^t jm' = k_{jm'}^{t-1}$ |
| m | j' | $p_{mj'} = \frac{d_{im}s_{i'j'}}{4}$ | $k_{ii'}^t mj' = k_{mj'}^{t-1}$ |
| m | m' | $p_{mm'} = \frac{d_{im}d_{i'm'}}{4}$ | $k_{ii'}^t mm' = \begin{cases} \frac{1}{2n_m} + \left(1 - \frac{1}{2n_m}\right) k_{mm'}^{t-1} & \text{if } m = m' \\ k_{mm'}^{t-1} & \text{otherwise} \end{cases}$ |

(iv) Offdiagonal element $k_{ii'}^t$, C_i^t resulting from reproduction and $C_{i'}^t$ resulting from aging

Let us suppose that the genes constituting cohort i are transmitted through reproduction from any cohort l , and assume that cohort i' is the aging form of cohort j . Two situations can occur: j is the same cohort as l or not. If $j = l$, the genes can be IBD because the same gene has been chosen or because the two genes were previously IBD, leading to a probability $(2n_l)^{-1} + (1 - (2n_l)^{-1})k_{ll}^t$. If the two groups of origin are different ($j \neq l$), then the genes can only be IBD if they were already IBD in the two cohorts of origin, which has a probability k_{jl}^t . Thus,

$$k_{ii'}^{t+1} | \text{reproduction } i, \text{ aging } i' = \sum_{l=1}^m p_{il} \left[\frac{1}{2n_l} \left(1 - \frac{1}{2n_l}\right) k_{ll}^t \right] + \sum_{l=1}^m p_{il} \sum_{j \neq l} k_{jl}^t$$

(v) Offdiagonal element $k_{ii'}^t$, C_i^t and $C_{i'}^t$ both resulting from aging

If we assume that C_i^t results from aging of cohort C_j^{t-1} and $C_{i'}^t$ results from aging of cohort $C_{i'}^{t-1}$ then

$$k_{ii'}^t \mid \text{both aging} = k_{ji'}^{t-1}$$

With this the set of transition rules is complete. Given a starting constellation \mathbf{K}^0 and this set of transition rules, we can determine the development of the expected kinship in any population of defined cohort structure.

From the kinship matrix it is possible to calculate the weighted average inbreeding coefficient in a new generation:

$$F^{t+1} = \frac{2 \sum_i \sum_{j>i} n_i n_j K_{ij}^{t+1} + \sum_i n_i^2 K_{ii}^{t+1}}{2 \sum_i \sum_{j>i} n_i n_j + \sum_i n_i^2}$$

The level of kinship in the population at time t can be assessed in different ways: we can be interested in the average kinship of all individuals living at time t , of all new born individuals at time t , or of a subset (e.g. all animals in the breeding nucleus).

Based on the mean annual increase of inbreeding per generation the effective population size (N_e) can be calculated as

$$N_e = \frac{1}{2\Delta F} \text{ with } \Delta F = \frac{F^{t+1} - F^t}{1 - F^t}$$

Illustration of the method

To illustrate the method we use an example given by Johnson (1977). In a sheep breeding programme 20 rams are mated to a flock of 200 mixed-age ewes each year. Both sexes have their first offspring with two years of age. Rams are only used for one year, while ewes can be used up to an age of 5 years with variable lambing percentages and survival rates from one year class to the next. In the parameterisation of this study this is reflected by seven cohorts (two for rams and 5 for ewes), and one breeding cycle is equivalent to one year. The relevant parameters are displayed in Table 2.

The two cohorts resulting from reproduction, i.e. 1 (young rams) and 3 (young ewes) have an identical vector of origin, i.e. $\mathbf{p}_1 = \mathbf{p}_3 = \{0, 0.5, 0, 0.112, 0.126, 0.137, 0.125\}$. This reflects the fact that all newborn males and females have a two year old sire and with a probability of 0.224 a two-year old dam, with a probability of 0.252 a three-year old dam *et cetera*.

Table 2: Structure of example sheep population with overlapping generations as described by Johnson (1977)

| Cohort | sex | age class | number | contribution to next generation |
|--------|-----|-----------|--------|---------------------------------|
| 1 | ram | 1 | 22 | 0 |
| 2 | ram | 2 | 20 | 1 |
| 3 | ewe | 1 | 64 | 0 |
| 4 | ewe | 2 | 58 | 0.224 |
| 5 | ewe | 3 | 52 | 0.252 |
| 6 | ewe | 4 | 47 | 0.274 |
| 7 | ewe | 5 | 43 | 0.250 |

Figure 1 shows the development of the average kinship values for the different cohorts over 12 years and the overall kinship computed with the approach suggested above. Table 3 gives complete expected kinship in year 12, i.e. \mathbf{K}^{12} . It should be noted, that expectations within and between cohort 1 and 3 (and similar 2 and 4) are identical because these cohorts have exactly the same origin of genes. Due to the two-year-cycle on the paternal side female cohorts separated by an even number of reproduction cycles (e.g. cohort 2 and 4, 3 and 5 etc.) have a higher pairwise kinship than female cohorts separated by an odd number of reproduction cycles (e.g. cohort 2 and 5, 3 and 6 etc.).

Table 3: Expected kinship coefficients within and between cohorts after 12 years

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|--------|--------|--------|--------|--------|--------|--------|
| 1 | 0.0195 | 0.0101 | 0.0195 | 0.0101 | 0.0154 | 0.0105 | 0.0131 |
| 2 | | 0.0184 | 0.0101 | 0.0184 | 0.0089 | 0.0143 | 0.0093 |
| 3 | | | 0.0195 | 0.0101 | 0.0154 | 0.0105 | 0.0131 |
| 4 | | | | 0.0184 | 0.0089 | 0.0143 | 0.0093 |
| 5 | | | | | 0.0173 | 0.0078 | 0.0131 |
| 6 | | | | | | 0.0162 | 0.0067 |
| 7 | | | | | | | 0.0151 |

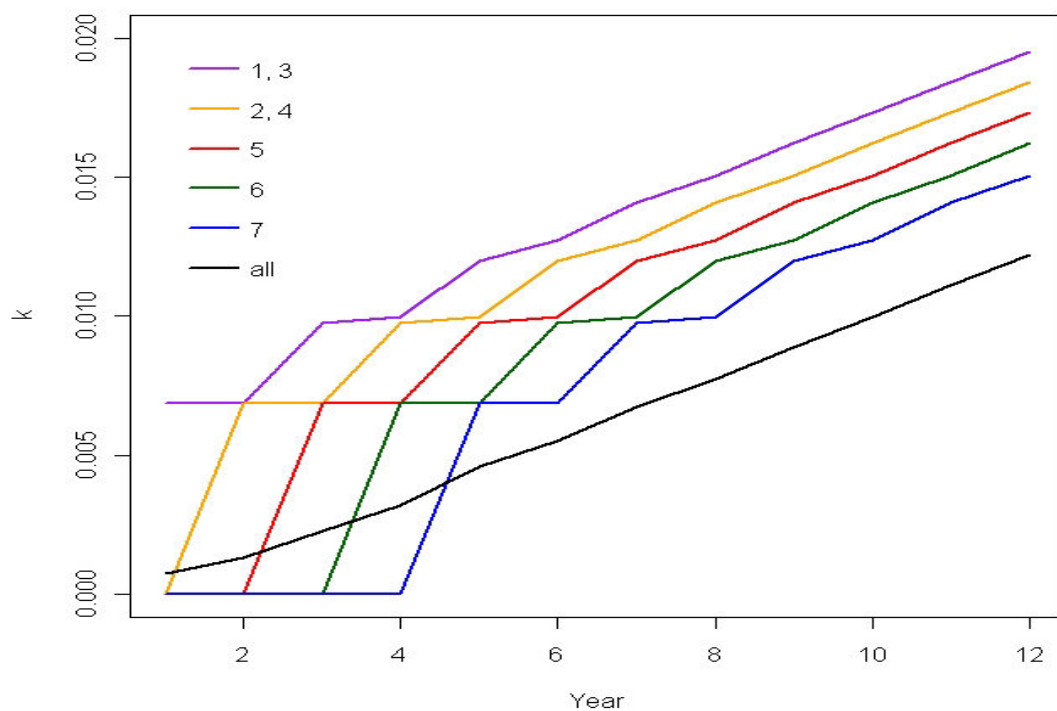


Figure 1: Kinship in the basic breeding programme within the cohorts 1 to 7 and the average inbreeding over a period of 12 years

The development of the overall average inbreeding F^t is smoother than the development of every single cohort, because the stepwise function of each

single cohort is averaged over all diagonal and offdiagonal elements. Also, this value is much lower than the within cohort kinships, because F^t takes into account all offdiagonal elements which are typically equal to (between cohorts of the same origin) or smaller than the diagonal elements. It should be noted that the overall average kinship in year 12 is $F^{12} = 0.0111$ which is close to the value which was obtained by Johnson (1977) with his approximate recurrence formula for the same year.

The corresponding inbreeding rate per year is $\Delta F = 0.00110$, which is equivalent to the annual effective population size $N_e = 455$. The generation interval in the described scheme is $\Delta T = 0.5 \times 2 + 0.5 \times (0.244 \times 2 + 0.252 \times 3 + 0.274 \times 4 + 0.25 \times 5) = 2.775 \text{ years}$, so that the inbreeding rate per generation is $\Delta F_G = 0.00305$ and the effective population size per generation is $N_{eG} = 164$ which is exactly the same value as obtained by Johnson (1977).

Application to dynamic breeding programmes

The suggested approach can be readily used to accommodate for situations where the structure of the breeding programme changes temporarily or permanently. Such a change can be reflected by (i) a change of cohort size over time, i.e. the number of individuals in a cohort n_i varies over time which, for year t , can be expressed as n_i^t ; (ii) a change of parental origin over time, indicated as vector $\mathbf{p}_i^t = \{p_{ij}^t\}$. In the extreme, the latter can result in a change of the cohort structure over time, i.e. some cohort is only present in certain years and thus can be either added or omitted at certain points of time. The flexibility of the approach will be demonstrated with the following two dynamic variants of the reference breeding programme suggested by Johnson (1977), where each of the breeding programme variants was run over 40 years.

First we modelled a continuous change of cohort size over time. For this, we assumed the cohort sizes of newborn animals (cohort 1 and 3) to increase with a rate of 5 per cent per year, so that $n_i^{t+1} = 1.05n_i^t$ for $i = 1$ and $i = 3$, respectively. The sizes of the cohorts originating from aging were calculated based on a survival rate of 0.9 per year. The vector of parental contributions was kept as in the reference scenario.

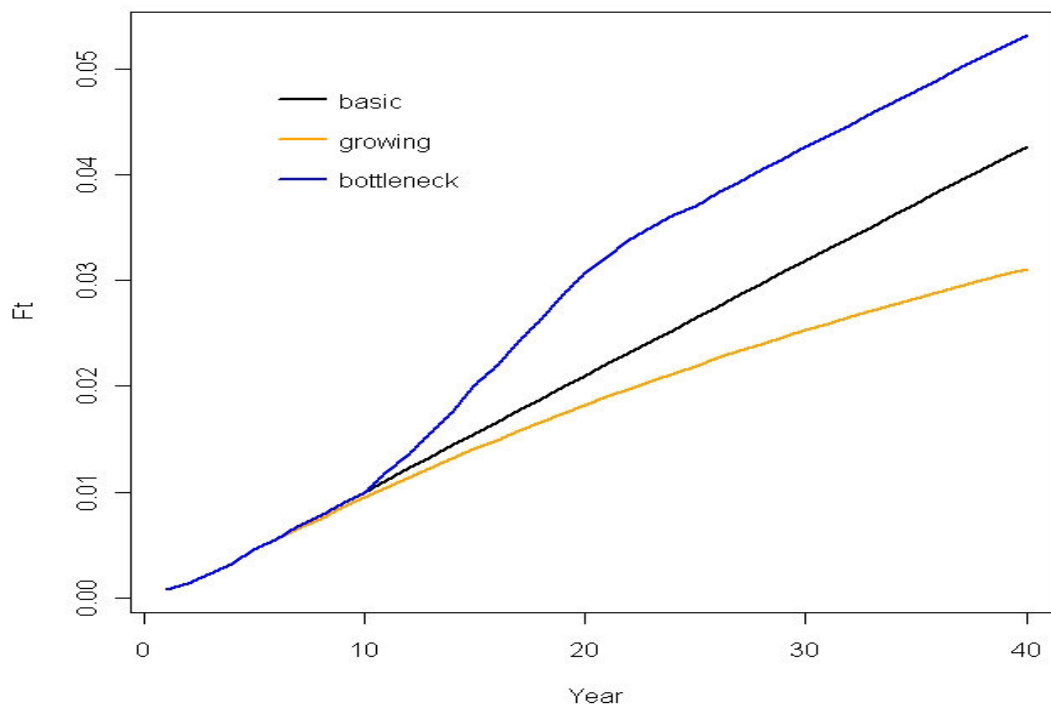


Figure 2: Development of the average inbreeding coefficient F^t in the different breeding programmes over 40 years

The result is shown in Figure 2 in terms of the average inbreeding coefficient relative to the reference scenario. As expected, the population growth leads to a reduction in the inbreeding level compared to the linear increase in the reference scenario. In the latter, the average level of inbreeding in year 40 is $F^{40} = 0.0426$ and the inbreeding rate per generation is $\Delta F = 0.00311$, which is equivalent to $N_e = 161$. Exponential growth of the population with a growth rate of 5 per cent per year over 40 years leads to a smaller average inbreeding level in year 40 ($F^{40} = 0.0311$) and also a reduced inbreeding rate ($\Delta F = 0.00054$) which corresponds to an effective population size $N_{eG} = 333$. Although the final actual population size is $1.05^{40-1} = 6.705$ times the actual population size in year 1, the final effective population size is only about doubled ($333/161 = 2.07$) relative to the reference scenario. In a population with size fluctuating over generations the overall effective population size is reflected by the harmonic mean of the population sizes (Iizuka, 2010). Using the harmonic mean in this case would suggest the effective population size to be ~ 2.6 times the effective size of the reference scenario. The deviation of the observed value (333) from

the expected value ($2.6 \times 161 = 419$) presumably is due to the fact that a number of assumptions underlying the theoretical expectation (Wright-Fisher-Model, discrete generations, stochastic fluctuation of population sizes) are not fulfilled.

In a second dynamic scenario an abrupt bottleneck situation is considered. For the first ten years the reference breeding programme is assumed. In year eleven the population size was halved by setting in each cohort $n_i^{11} = 0.5n_i^{10}$ and maintaining this reduced size for ten years. From year 21 onwards, the original population size was re-established.

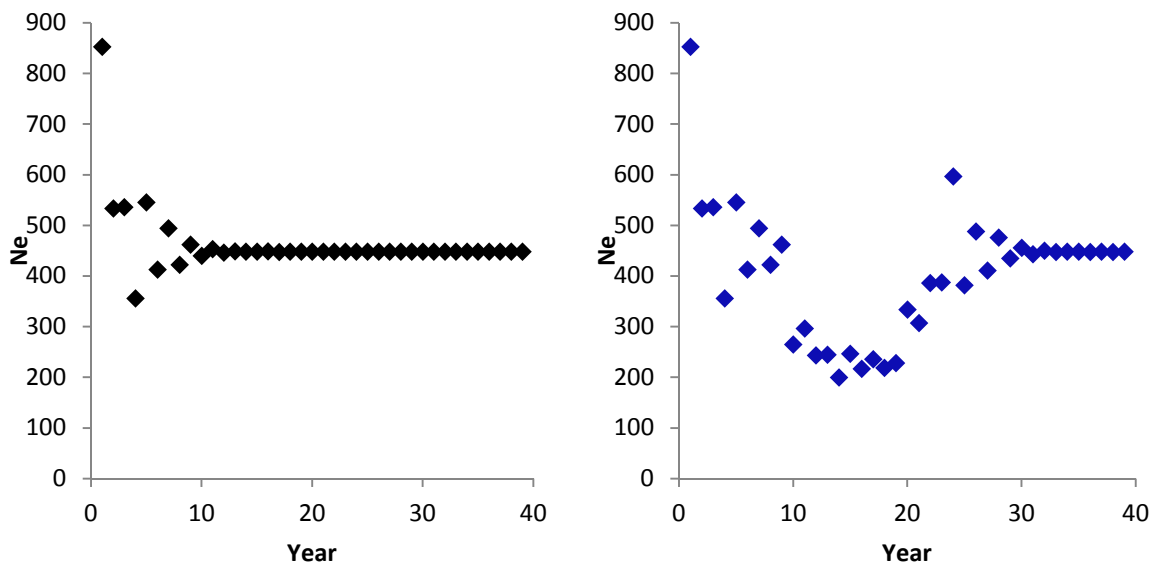


Figure 3: Development of the effective population size N_e in the basic breeding programme (black) and the breeding programme with bottleneck (blue)

Again the corresponding development of the average inbreeding coefficient is shown in Figure 2, and Figure 3 shows the development of annual effective population size over time. This figure nicely demonstrates the ‘fuzziness’ of the respective parameters when the structure of a breeding programme is changed. It then takes a number of generations until a new equilibrium state is reached. As expected the inbreeding rate is roughly doubled during the bottleneck phase in which the population size is halved. The effective population size in year 20 thus is $N_e = 82$. After the subsequent expansion to the original cohort sizes, the development of the inbreeding rate runs parallel to the reference scenario.

Despite the 70 per cent higher mean absolute level of inbreeding in the bottleneck ($F^{40} = 0.0532$) vs. the reference scenario ($F^{40} = 0.0311$) the exact same inbreeding rate per generation ($\Delta F = 0.00311$) and effective population size ($N_e = 161$) at the end of the considered time horizon is obtained in both cases, which is expected since at this point both populations have had the same structure for 20 years.

Discussion

As we could show our approach allows calculating the expected kinship, inbreeding coefficient and effective population size for arbitrary time-points in well-defined complex breeding programmes in a deterministic way. Since the approach is based on the gene-flow concept (Hill, 1974; Elsen and Mocquot, 1974), especially the sub-structuring of the population in cohorts and the definition of vectors of gene origin, it can be applied to structured breeding programmes of arbitrary complexity. Since expected kinship values within and between cohorts are explicitly computed for each point of time, the approach also allows a detailed analysis of the inbreeding pattern in highly structured populations with large numbers of different cohorts, possibly having various possible sources of genes.

The suggested approach is innovative in that it allows predicting the development of kinship, inbreeding and effective population size also in dynamic breeding programmes, which generally can be defined through time dependent vectors of parental origin and/or cohort size. Since these vectors can be defined externally and used as input for the algorithm, the approach is fully flexible and can be used to derive the expected inbreeding for a wide variety of situations. This is also a major advantage over alternative solutions (such as e.g. the approach of Johnson, 1977), which define a fixed recursion which cannot readily account for changes in the breeding programme structure over time.

In our approach the contribution to the next generation of all animals in one cohort is assumed to be stochastic, i.e. parental alleles from a cohort are randomly sampled with equal probability. In selective breeding programmes this assumption is often not fulfilled, since in one parental cohort (say, elite bulls)

often the very best individuals in that cohort (the bulls with the highest breeding values in that group) pass on their genes more often than genetically less favored cohort members. It also is assumed in our approach, that maternal and paternal alleles are drawn independently. Again, this assumption may be not realistic under selection and targeted mating, where elite matings try to merge the genetics of the best sires with the best dams but at the same time matings of highly related animals are avoided.

Wray and Thompson (1990a) showed that the rate of inbreeding is directly related to the contribution of the different families in the breeding programme. In selected populations genetically superior families will contribute more genes to the next generation than inferior families. For this reason the contribution of the different families will be unequal in selected populations (Wray and Thompson, 1990b), and this effect accumulates over time. The authors showed for simple breeding programmes with discrete generations that in selected populations the rate of inbreeding can increase by about 75% over what is expected in unselected populations. Wray et al. (1994) implemented their approach in an index selection framework, which is integrated in the *SelAction* (Rutten et al., 2002) software for predicting selection response in livestock breeding programmes. This software predicts the rate of inbreeding in static breeding programmes with discrete generations and single-stage selection using the method of Wooliams and Bijma (2000). In contrary to the approach suggested here this methodology accounts for the effects of selection by considering non-uniform long-term genetic contributions.

A possibility to implement elements of this concept into the approach suggested here would be to replace the number of individuals in a cohort i , n_i , by the *effective* number of individuals in cohort i , v_i . Here, p_j is defined as the number of individuals which under random sampling leads to the same probability of identity by descent as in the real unbalanced situation. We define

$$v_i = \frac{1}{\sum_{j=1}^{n_i} p_j^2}$$

where p_j is the probability that individual j in cohort i is sampled when contributions of this cohort to the next generation are calculated ($\sum_{j=1}^{n_i} p_j = 1$). Note that with $p_j = 1/n_i$ we obtain $v_i = n_i$. If, however, contributions of

individuals are different, then the effective number of individuals will be smaller than the true number $v_i < n_i$ and the corresponding *ibd* probability will increase. This is illustrated with the following example: consider a case where the true cohort size $n_i = 10$. In the balanced situation, each individual from this cohort is sampled with probability $p_j = 1/n_i = 0.1$ and the probability of two alleles being sampled independently from this cohort to be *ibd* is $1/(2n_i) = 0.05$.

Now assume that two of the ten individuals have a probability of $p_j = 0.4$ to be sampled, and the remaining eight individuals have a probability of $p_j = 0.025$ each. Then

$$v_i = \frac{1}{\sum_{j=1}^{n_i} p_j^2} = \frac{1}{2 \times 0.4^2 + 8 \times 0.025^2} = 3.077$$

and the probability of two alleles being sampled independently from this cohort to be *ibd* is $1/(2v_i) = 0.1625$. This result thus is about equivalent to a situation where the cohort size is $n_i = 3$ and all members of the cohort contribute with equal probability to the next generation.

Selection will cause unequal short- and long-term contributions which will result in different *effective* cohort sizes v_i^t over time. If it is possible to derive these quantities from an assumed selection scheme, the course of inbreeding in complex dynamic selection programmes can be assessed.

The methodology as it is described above is directly applicable in situations where we need to assess the impact of alternative scenarios on the development of inbreeding in breeds that are under no or very moderate selection pressure. A good case for this area of application may be the comparison of different Scrapie eradication strategies in sheep (Dawson et al. 2008). The main strategy was to exclude carriers of certain high-susceptibility genotypes from the breeding flocks, leading to a genetic bottleneck. This was not only implemented for large and highly selected commercial sheep breeds, but also for local breeds with moderate to low selection intensity, often small effective population size and, in some cases, high prevalence of the susceptible genotype. In such a situation, the suggested deterministic approach to assess the impact of different dynamic breeding strategies on the inbreeding level might have been useful as an alternative to, or possibly also in combination with, stochastic simulation approaches used for this purpose (Man et al., 2007).

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3rd CHAPTER

The potential of embryo transfer in a German horse-breeding programme

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The potential of embryo transfer in a German horse-breeding programme

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Abstract

A reference horse-breeding programme with 13'500 foals each year was modelled with ZPLAN+. This new software for the optimization of the structures in breeding programmes is based on ZPLAN. In two scenarios the implementation of a rigorous selection of mares was implemented. In scenario I the mare performance test was the point of selection while in scenario II further information on 20 competitions in two more years are available. These selected mares were used for embryo transfer (ET), partly in combination with multiple ovulation (MOET). The selection intensity and the number of foals out of (MO)ET were varied in both scenarios. It was expected that 250, 500 and 1'000 mares are available for selecting 20, 50, 100 or 200 donor mares each year. The number of foals out of (MO)ET was varied between one and six foals per donor mare and year. The donor mares were used for embryo transfer for four years. It became clear that with high selection intensities of donor mares and high reproduction rates of them the yearly genetic gain in a horse-breeding programme could increase over a large range. In scenario II the additional information on 20 competitions increased the accuracy of the selection index to 0.85. With 200 selected donor mares out of 1'000 available mares and six foals per year the genetic gain could almost be doubled compared to the reference scenario. The additional information on 20 competitions could increase the accuracy of the selection index on 0.85. The implementation of embryo transfer and a related higher usage of few selected mares entails rising costs and a reduction of the genetic variance. In the most extreme MOET scenario the effective population size was reduced by 19% relative to the reference scenario. Only if the increase in genetic gain can be converted into higher return for the breeders, the implementation of (MO)ET schemes is a realistic and sensible option for horse-breeding programmes.

Keywords

horse breeding, embryo transfer, breeding programme design, ZPLAN+

Introduction

Selection in German horse breeding programmes is focused on the competition traits dressage and show jumping. This selection is made in various steps in the breeding programmes. In stallions the selection is characterised by high selection intensity especially in the first stage of licensing. Only one per cent of the colts born in one year are licensed in the Hanoverian breeding programme (Niemann, 2008). In contrast, selection of mares is less intensive. Over 90% of all fillies per year are registered in the main studbook and are available for breeding purposes (Schade, 1996). The selection of broodmares is based on a judgment of conformation and movement during the studbook inspection and on the presence of four generations of recognised ancestry. The mare performance test, which 50% of the registered mares pass, has no influence on the authorisation for breeding (Hannoveraner Verband, 2010). This test could be used more effectively for selecting broodmares. Using modern reproduction technologies like embryo transfer (ET) and multiple ovulation in combination with embryo transfer (MOET) could increase the number of foals out of this selected mares. This would offer the opportunity to increase efficiently the return in a breeding programme (Bruns, 2005).

In horse breeding, ET is well suited to practical use since a long time (Leidl and Braun, 1987). The mean recovery rate for embryos is reported to be 64% and the mean adhesion rate is specified with 70%, resulting in a pregnancy rate of 45% for each flushing (Panzani et al., 2007; Squires and Mc Cue, 2007). While there is no commercially available method to stimulate multiple ovulations in horse breeding today (Squires et al., 2003), there are successful efforts to increase the number of ovulated ova in horses (Squires and Mc Cue, 2007). Furthermore the number of foals per donor mare could be increased with multiple flushings per year.

As shown in the dairy cattle context (Christensen, 1991; Nicholas and Smith, 1983) ET and MOET can increase the efficiency of breeding programmes in uniparous animals. When combined with other techniques like in vitro fertilisation, embryo splitting or semen/embryo sexing, the efficiency of ET and MOET nucleus programmes in dairy cattle can be increased even more

compared to conventional breeding programmes due to the higher selection intensity on the female pathways (Lohuis, 1995).

The nations resorting most on ET in horses are the United States, Brazil and Argentina (Squires et al., 2003). In Argentina embryo transfer is part of the breeding programme of Polo horses and over 9'000 embryos are transferred per year (Losinno et al., 2000). In Germany only some state studs and private veterinarians offer the procedure and it is just used by few breeders (von der Ahe et al., 2010). In 2009, the Fédération Equestre Nationale registered only 431 ETs in the various German breeding programmes for sport horses (Fédération Equestre Nationale, 2010). ET enables the use of especially high-quality mares that would otherwise be used only in competition. Without the usage of ET this mares would earliest used in breed after their career in equitation. At this late breeding use fertility problems often reduce the number of foals out of this high-quality mares.

When using fewer breeding animals in a more intensive way as envisaged with ET or MOET, the inbreeding rate can increase in a population. The Hanoverian population is at present classified as unproblematic with regard to genetic diversity (Hamann and Distl, 2008), providing a good basis for a more intensive use of the best mares in the breeding programme.

The aim of our study was to investigate how to improve the efficiency of horse breeding programmes by implementing a selection of donor mares for ET or MOET, respectively. We furthermore assessed the development of inbreeding for the considered scenarios. The present Hanoverian population was used as reference. This population was modelled as close to reality as possible.

Materials and methods

Modelling software

All breeding programmes investigated in this paper were modelled with ZPLAN+ (Täubert et al., 2010) software for the optimisation of breeding programmes. ZPLAN+ is suitable for modelling complex breeding programmes

considering all relevant structures and biological parameters of a breeding process. It is an evolution of ZPLAN (Karras et al., 1997) which was developed in the 1980's and conflates the geneflow theory by Hill (1974), the selection index by Hazel and Lush (1942) and a complex economic modelling.

Among the results provided by ZPLAN+, we focused here on the genetic gain and the costs. These results are relevant to compare the breeding programmes and are thus the decision keys. In ZPLAN+, for each selection path, the genetic gain is computed as the product of the index accuracy, the selection intensity and the standard deviation of the breeding objective. The return of a selection path is obtained as the monetary genetic gain weighted by its corresponding Standardised Discounted Expression (SDE). The SDE value of a selection path includes the number of animals that realize the genetic gain, the point in time of realization and the genetic gain. The overall return is the sum of all returns over all selection paths.

For modelling breeding programmes, ZPLAN+ requires precisely defined selection groups. A selection group combines contemporary animals of one sex and uniform breeding characteristics regarding the number of tested animals, the number of selected animals, the length of a reproduction cycle, the productive lifetime of an animal in this selection group and the selection index applied in this selection group (Täubert et al., 2010). The profit is defined as the discounted return minus the discounted costs, discounting being done over the time of investment. The return and thereby the profit is linked directly to the economic weighting of the single traits. These parameters are unsuitable for comparing different breeding strategies in horses because the economic weightings are only assumptions and cannot be reliably estimated. Variable costs, especially those cost components related to mare selection and (MO)ET, can be quantified much more precisely, so that different breeding programs using (MO)ET in different intensities can be reliably compared on a cost basis, which then is contrasted with the expected relative increase in genetic gain.

The costs are separated into two components, the fixed and the variable costs. Fixed costs are not linked to a precise selection group and are supposed to

evolve linearly with the number of individuals in the breeding programme. Variable costs are defined for each selection candidate in each selection group.

To model the gene flow in a breeding programme, the origin of the newborn animals has to be defined. This is done in a pedigree matrix. Each newborn selection group can inherit a proportion of genes from the present selection groups comprised between zero and one. On both the paternal and maternal side, the proportions have to sum up to one.

Modelled horse breeding programmes

In the German riding horse population the different traits in the breeding goal are defined as conformation and movements (CM), free jumping (FJ), ride-ability (RI) and the two traits dressage (DR) and show jumping (SJ) in competition. We reduced the complexity of the single traits in the breeding goal for our study because the breeding goal was not the main aim of this calculation and the correlations between the traits of performance tests and competitions are very high (Thorén Hellsten et al., 2006). Heritabilities and genetic and phenotypic correlations of the modelled traits (Table 1) are based on the results of Christmann (1996), Schade (1996) and the Fédération Equestre Nationale (2009).

Table 1: Heritabilities (diagonal), genetic correlations (above diagonal), phenotypic correlations (below diagonal), repeatability (w^2) and economic weighting in €/genetic standard deviation (EW).

| | CM | FJ | RI | DR | SJ | w^2 | EW |
|---------------------------------|-------------|-------------|-------------|-------------|-------------|-------|------|
| Conformation and movements (CM) | 0.21 | -0.20 | 0.70 | 0.40 | 0.10 | - | 500 |
| Free jumping (FJ) | 0.10 | 0.38 | 0.00 | 0.00 | 0.80 | - | 500 |
| Ride-ability (RI) | 0.60 | 0.00 | 0.37 | 0.70 | 0.20 | - | 500 |
| Dressage (DR) | 0.50 | 0.00 | 0.50 | 0.13 | 0.20 | 0.32 | 2000 |
| Show jumping (SJ) | 0.00 | 0.80 | 0.00 | 0.00 | 0.09 | 0.27 | 2000 |

The evaluation of these traits is made on a scale from one (worst) to ten (best). The phenotypic standard deviation was assumed to be two in all traits. The economic weighting for the two competition traits was set to €2'000 (four times weighted) and the three other traits had a modelled weighting of €500 (single weighted) per genetic standard deviation. This dimension should be a realistic assumption and was used for all modelled breeding programmes. More important than the absolute dimension is the relative weighting. Here it becomes obvious that the competition traits represent the main ones while the three other traits were not weighted in such a big range.

Reference scenario

The present state of the Hanoverian breeding programme was chosen as reference. This breeding programme is the biggest one in Germany with about 20,000 registered broodmares, 400 registered stallions and 9,000 foals each year (Schade, 2011). The reference horse-breeding programme is shown in Figure 1 and described thereafter. The origin of the genes of a new generation is modelled in accordance to Niemann (2008) and shown in Table 2.

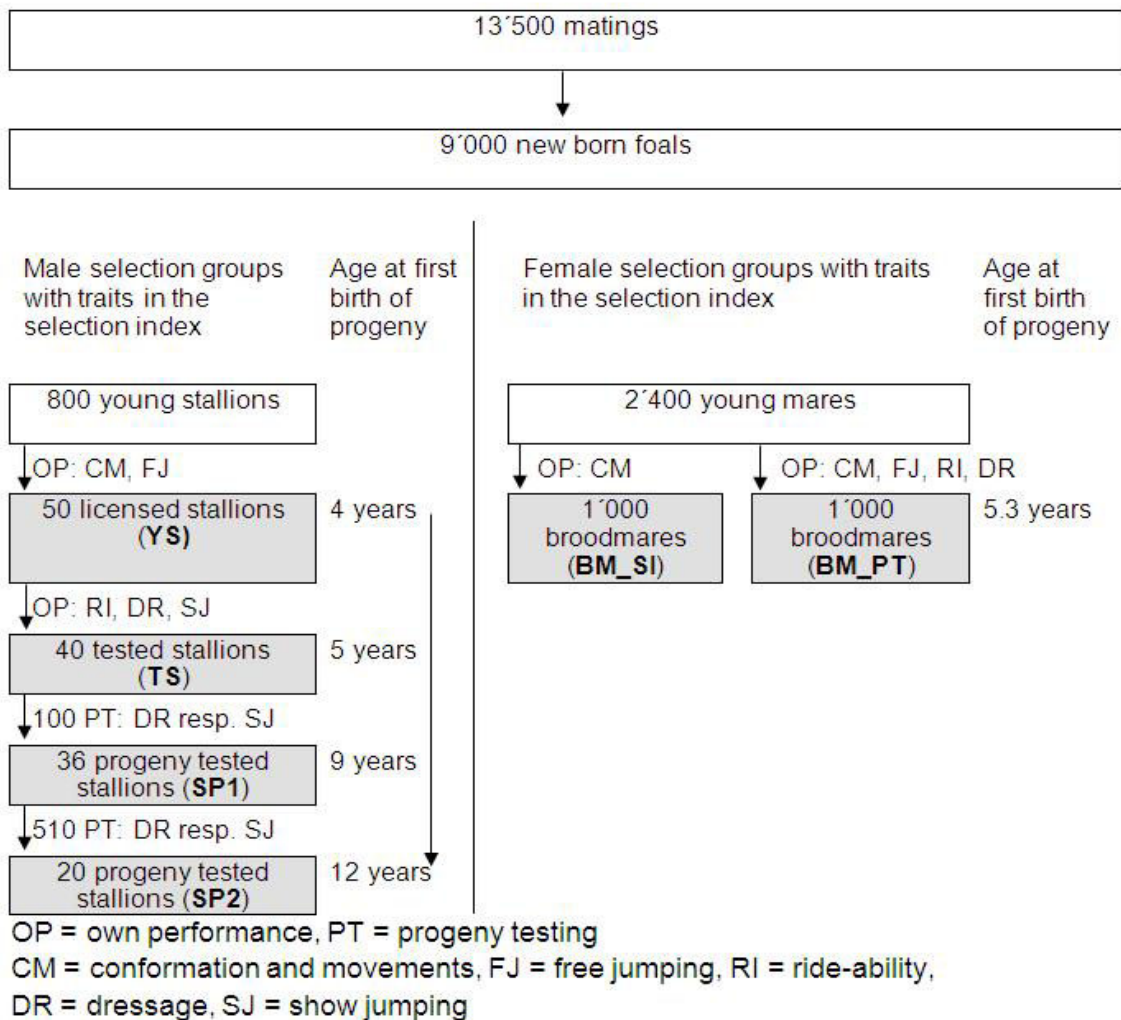


Figure 1: Schematic structure of the selection groups with the information in the selection index in the reference scenario.

Selection of the males

The selection of stallions was modelled as a multistep selection. The first selection step is the licensing, for which the traits CM and FJ are recorded. It was assumed that all young stallions also have pedigree information from their parents for the traits DR and SJ. Out of 800 two and a half year old stallions, 50 young stallions (YS) were selected and used for one reproduction cycle at the age of three years. At the age of four years, the young stallions passed their stallion performance test for the traits RI, DR and SJ. The 40 selected tested stallions (TS) were used for breeding purposes for four years. The next selection step was a progeny test based on the competition results in dressage and show jumping. It was assumed that half of the 40 eight-year old stallions had 20 progeny with five replicated performance records each for dressage and

the other half had 20 progeny with five replicated performance records each for show jumping, respectively. Out of the 20 stallions in each progeny tested group, 18 stallions were selected (SP1) and these 36 stallions were used for three breeding seasons. The final selection of 10 stallions (SP2) out of each group at the age of eleven years is based on 510 progeny information per stallion (30 progeny with 17 measures) in one performance trait according to the same scheme as SP1. The SP2 animals were used for breeding purposes for another five years. Overall the modelled breeding programme includes 418 stallions in the different selection groups. The contribution of paternal genes of the newborn foals is shown in Table 2.

Selection of the females

The selection of 1000 broodmares (BM_SI) is based on the studbook inspection of 1200 mares for the traits conformation and movements (CM). Another 1200 mares passed the studbook inspection and were in addition tested for RI, FJ and DR in a mare performance test to select 1000 broodmares (BM_PT). Like the stallions, all mares have pedigree information from their parents for the traits DR and SJ. The mares foaled at the age of 5.3 years for the first time and they were used for breeding for ten reproduction cycles. This results in a total female population of 20,000 mares. Each broodmare was mated every 1.48 years. Out of these 13,500 matings 9,000 foals were born each year (67% foal rate) in this horse-breeding programme and they originated equally from BM_SI and BM_PT (Table 2).

Table 2: Contribution of genes of the newborn foals (each line sums up to one) (Abbreviations see Figure 1).

| | YS | TS | SP1 | SP2 | BM_SI | BM_PT |
|----------------|------|------|------|------|-------|-------|
| Paternal genes | 0.03 | 0.45 | 0.26 | 0.26 | | |
| Maternal genes | | | | | 0.50 | 0.50 |

Alternative scenarios

For modelling the implementation of ET, the best mares were selected out of the BM_PT and were used as donor mares for four years. On one hand, the number of broodmares available for selection (250, 500 or 1,000) was varied because it cannot be assumed that all breeders participate in an embryo transfer programme. Also the number of selected broodmares was modified (20, 50, 100 and 200) in order to assume various selection intensities. On the other hand, the number of foals per donor mare was varied as well. The values for the number of offspring per broodmare could take 1, 2, 4 or 6 per year. The higher numbers of foals per donor mare require the use of multiple ovulation techniques in addition to ET and are included to study the effect of a very intensive use of the donor mares when MOET techniques become commercially available in horse breeding schemes. The information in the selection index was modified accordingly. For each combination of the number of broodmares and of the number of offspring per mare, two scenarios of selection were studied. In scenario I the selection of the donor mares (BM_ET) is based on the same information as in the selection index of the BM_PT. We supposed that the donor mares were flushed for the first time at the age of four years. Scenario II assumes a selection of BM_ET at the age of six years, where the broodmares are supposed to have additional own performances in 20 competitions for both DR and SJ.

Table 3: Proportion (%) of genes originating from BM_ET in different ET scenarios.

| Number of selected mares for BM_ET | Number of foals per BM_ET | | | |
|------------------------------------|---------------------------|------|-------|-------|
| | 1 | 2 | 4 | 6 |
| 20 | 0.90 | 1.78 | 3.56 | 5.34 |
| 50 | 2.22 | 4.44 | 8.88 | 13.34 |
| 100 | 4.44 | 8.88 | 17.78 | 26.68 |
| 200 | 8.88 | 3.56 | 35.56 | 53.34 |

In all breeding programmes, we supposed that an identical number of foals (9,000) are produced each year to ensure their comparability. The proportion of genes out of the different female selection groups was adjusted. In Table 3 the genetic proportion of the BM_ET on the newborn foals is shown. The gene proportions for each ET success rate and for the various numbers of selected mares out of the donor mares selection group (BM_ET) are calculated. The number of foals that were produced by the female selection groups BM_SI and BM_PT were thus changed in each scenario.

The fixed costs for horse-breeding programmes are not yet evaluated accurately and were assumed to be €10 per breeding animal and year in every scenario. The variable costs for a breeding programme are assigned to the different selection groups. In our horse-breeding programme, most of used variable costs are based on the values from the Hannoveraner Verband e.V. (2010). It should be noted that only costs linked to breeding progress have to be considered. For each mating, €200 veterinary fees were assumed. Additional costs were €85 for the creation of an equine pass and €28 for a DNA-based parentage test per foal. On the mare side, the studbook inspection and registration fee was set at €35 and the mare performance test at €87.50 per mare. Each registered mare had also an annual subscription fee of €25. On the stallion side, costs for licensing and registration in the stallion book were €70. The stallion performance test costs €2'500 for each stallion and the annual subscription was €300. For each performance information in a competition €20 were counted as breeding costs reflecting the proportion of the starting fee that can be attributed to the breeding programme.

To evaluate the success of ET for a horse-breeding programme, additional costs needed to be considered. According to the official veterinary fee schedule (GOT, 2008), the costs for medical examination of donor and recipient mare, flushing, searching and evaluating the embryo and the implementation of the embryo in the recipient mare were €270. The costs for the transport to the embryo transfer station were assumed to be €125. Multiplied with the adopted success rate of 45% for each foal out of ET the additional costs were rounded to €900. Furthermore it was assumed that selecting the donor mares induced costs of €10 per available mare. The costs for the recipient mares were not

considered because in both, the reference and the alternative breeding programmes, the recipient mares are getting foals. In all modelled breeding programmes the same number of foals per year was assumed. Thus the costs for the embryo recipients would also accrue for the regular foals of the broodmares in a breeding programme without ET. The costs for one performance test at a competition of the BM_ET in scenario II were assumed to be €20.

Average kinship and effective population size

The average kinship is the probability that, in a selection group or between two selection groups, two randomly chosen alleles are identical by descent (IBD) at the same locus (Malécot, 1948). We apply a deterministic method (Sitzenstock et al., 2013) to calculate the average kinship and following from that the effective population size on the basis of the gene flow theory (Hill, 1974). Each selection group is subdivided in age classes, so-called cohorts, with the information: (a) number of animals, (b) if the age class arises from reproduction or aging and (c) the paternal (resp. maternal) origin of alleles. The average kinship coefficients within and between all cohorts can then be computed with a recursion formula.

Out of the kinship matrix comprising all average kinship coefficients within and between cohorts it is possible to calculate the weighted average inbreeding coefficient F^{t+1} in a new generation:

$$F^{t+1} = \frac{\sum_i \sum_{j>i} n_i n_j K_{ij}^{t+1} + \sum_i n_i^2 K_{ii}^{t+1}}{2 \sum_i \sum_{j>i} n_i n_j + \sum_i n_i^2}$$

with

i =cohort i n_i = number of animals in cohort i

j =cohort j n_j = number of animals in cohort j

K_{ij}^{t+1} = Kinship between cohort i and j in a new generation

K_{ii}^{t+1} = Kinship within cohort i in a new generation

On basis of the mean annual increase of inbreeding the effective population size (N_e) can be calculated:

$$N_e = \frac{1}{2\Delta F} \text{ with } \Delta F = \frac{F^{t+1} - F^t}{1 - F^t}.$$

Results

Reference scenario

The mean generation interval in the reference scenario amounts to 10.6 years. ZPLAN+ calculates the mean generation interval based on the generation intervals in the different selection pathways weighted by the proportion of genes contributed to the progeny by this pathway. Table 4 shows an overview of the generation intervals, the selection intensities and accuracies for the selection groups. The genetic gain in the reference scenario was 0.019 in SJ, 0.016 in DR, 0.018 in CM, 0.033 in FJ and 0.032 points in RI per year. The variable costs in the breeding programme were €599.68 per animal. In addition, the fixed costs of €14.28 had to be added. Over all the total costs was €613.96.

Table 4: Selection intensity, generation interval and accuracy of the selection index in the single selections groups in the reference scenario (Abbreviations see Figure 1).

| Selection group | YS | PT | SP1 | SP2 | BM_SI | BM_PT |
|-----------------------------|------|------|-------|-------|-------|-------|
| Selection intensity | 1.97 | 0.35 | 0.20 | 0.71 | 0.30 | 0.30 |
| Generation interval (years) | 4.00 | 6.50 | 10.00 | 14.00 | 11.98 | 11.98 |
| Selection index accuracy | 0.42 | 0.63 | 0.80 | 0.98 | 0.32 | 0.63 |

Scenario I

In scenario I, the generation interval could be reduced even when the use of ET was moderate (up to 200 selected BM_ET and 4 foals per BM_ET) compared to the reference scenario (9.8 years vs. 10.6 years). In the most extreme case

(200 selected BM_ET and 6 foals per BM_ET), it was further diminished to 9.4 years. The evolution of the genetic gain relative to the number of foals for both performance traits (DR and SJ) and for all numbers of selected mares is presented in Figure 2. The genetic gain in these traits, as well as all others, increased with the number of foals. The largest gain was achieved for all traits when 200 mares were selected out of 1000 to produce 6 foals each. It then ranged between 158% (SJ) and 177% (DR) of the genetic gain in the respective trait compared to the reference scenario. The total costs are rising with the number of selected mares for BM_ET and the number of foals produced out of ET. While with one foal out of ET the total costs average from 101% (20 selected mares) to 110% (200 selected mares) of the reference scenario, the total costs rise up to 106% with 20 selected mares and six foals and to 158% with 200 selected mares and six foals.

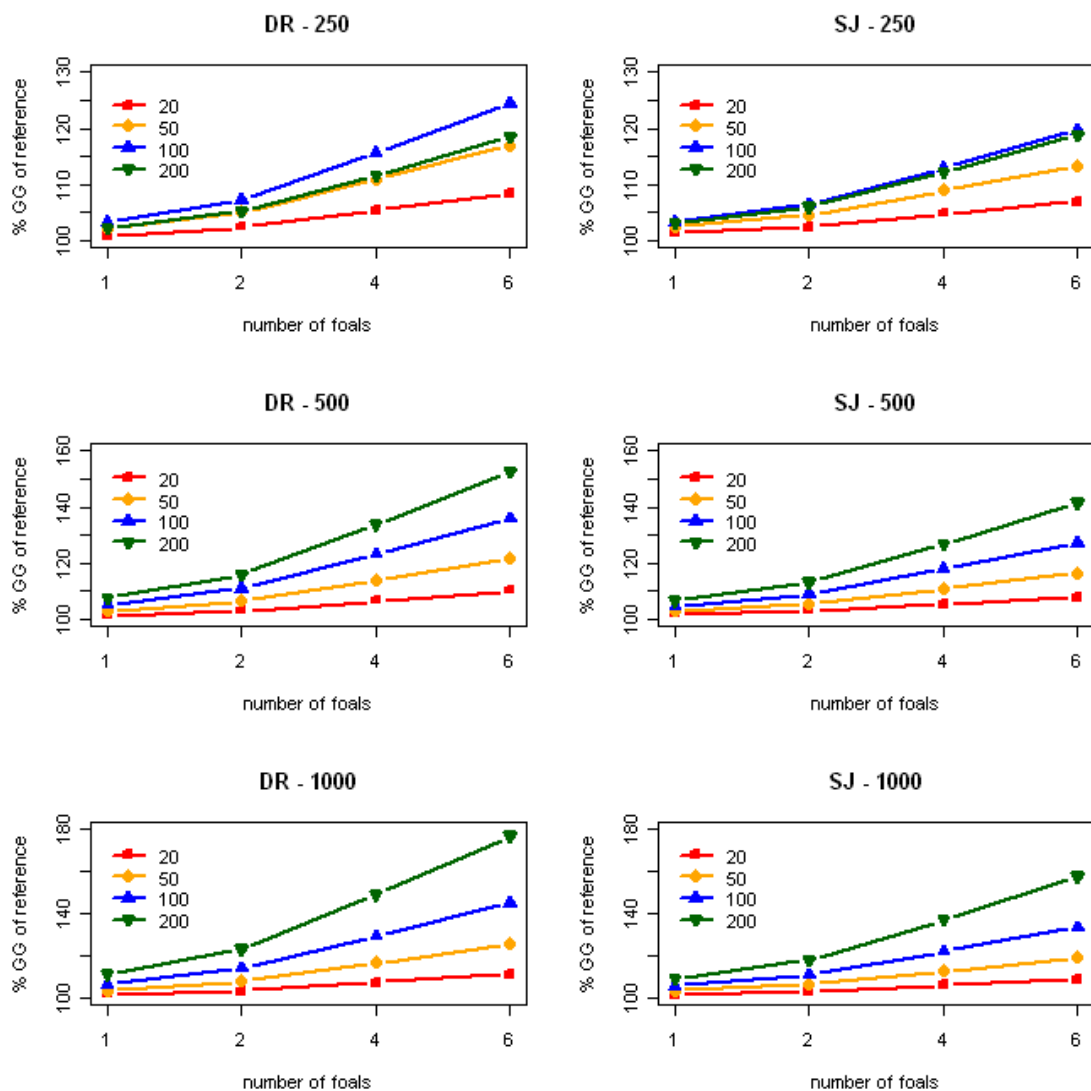


Figure 2: Genetic gain (GG) in the performance traits dressage (DR) and show jumping (SJ) in per cent of the reference scenario in scenario I depending on the number of foals of the BM_ET, the number of mares available for selection (250, 500, 1'000) and the selected mares for BM_ET (20, 50, 100, 200).

Scenario II

In this scenario, the generation interval could not be reduced as in scenario I and ranged between 9.8 and 10.6 years. However, the additional 20 own performances in tournament of the BM_ET increased the accuracy in the index up to 0.85 (against 0.3 in the reference scenario and in scenario I). The trait specific genetic gain showed the same pattern as in scenario I but increased to a higher level than in scenario I in all traits. The results for DR and SJ are

displayed in Figure 3. When at least 4 foals (6 foals) per BM_ET were produced, the genetic gain for example in DR was 15% (19%) higher than in scenario I. The total costs in the different cases of scenario II were in a similar range to those in scenario I. Only the additional costs for the own performance testing were added, but these costs were marginal when they are allocated over the whole breeding programme.

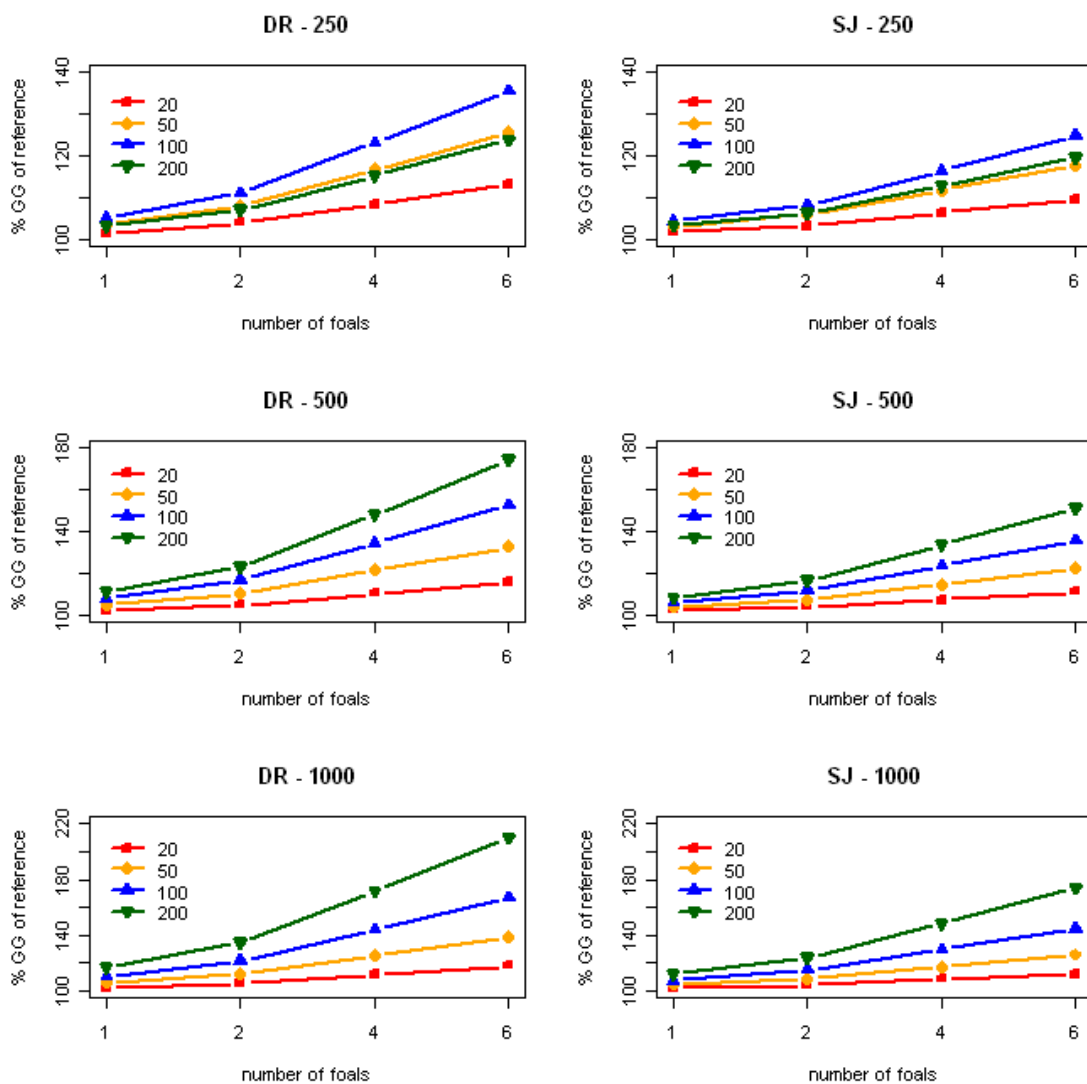


Figure 3: Genetic gain (GG) in the performance traits dressage (DR) and show jumping (SJ) in per cent of the reference scenario in scenario II depending on the number of foals of the BM_ET, the number of mares available for selection (250, 500, 1'000) and the selected mares for BM_ET (20, 50, 100, 200).

Kinship and effective population size

The growth rate of the kinship and thereby the N_e in scenario I and scenario II is not substantially different because the genetic structure in both scenarios is identical. The scenarios only differ in the fact that the ET mares are older in scenario II. In the scenarios with only 20 or 50 selected mares for ET, the BM_ET have a small genetic impact on the progeny as they do not contribute much to the newborn individuals (Table 3). The number of mares available for selecting the BM_ET has no significant effect on the kinship and the effective population size. For these reasons, only the results for the kinship and the effective population size of scenario I with 200 selected mares out of 1,000 available mares in the last year of the investment period are presented in Table 5. The final N_e per generation of the reference scenario is about 1,087 animals while in the most intensive scenario (200 BM_ET, 6 foals), the N_e reached only 882 animals. The kinship in the newborn foals' increased with a higher usage of the BM_ET.

Table 5: Kinship in the new born foals and effective population size in year 40 in scenario I with 200 selected BM_ET.

| | Number of foals per BM_ET | | | | |
|---------------------------|---------------------------|---------|---------|---------|---------|
| | reference | 1 | 2 | 4 | 6 |
| Kinship in new born foals | 0.00187 | 0.00192 | 0.00208 | 0.00230 | 0.00254 |
| Effective population size | 1'087 | 1'076 | 1'003 | 937 | 882 |

Discussion

In general, it could be shown that a complex conventional horse-breeding programme can be modelled with ZPLAN+. The reference scenario reflected approximately the Hanoverian horse population as described by Schade (1996) and Niemann (2008). Similar structures were described for the Trakehner horse breed by Teegen et al. (2008a) and for the French warmblood population by Dubois et al. (2008). While the computer-assisted design and optimisation of breeding structures are an inherent part of the optimisation of breeding

programmes in farm animals (Täubert et al., 2010), it is not used routinely in horse-breeding programmes. Furthermore there is no horse-breeding programme in Europe with an economically well-defined breeding goal. Therefore we had to choose economic weightings in this study in such a way that the breeding goals reflect the most important traits for sport horses (Koenen et al., 2003). These traits are part of most European breeding programmes; hence it is likely that the model is close to reality. An economic weighting of the single traits in sport horse breeding programmes is difficult to apply and different to other farm animals because there are no marketable products like eggs, meat or milk (Edel, 2005). Different approaches for deriving economic weights applied in horse breeding resulted in very different economic weights. While Bruns et al. (1978) estimated economic weights for sport horses using auction prices, Teegen et al. (2008b) estimated weights using a contingent valuation method. These two approaches result in completely different economic weights for the traits in the breeding goal, and no consensus is reached so far neither on the appropriate methodology to assess economic weights for performance traits in sport horses, nor on the values to be used.

The selection intensities in the male selection groups are high, while the selection intensity on the female side amounts to 0.3 in the reference scenario. With higher selection intensities on the female side and an additional implementation of ET in a horse-breeding programme, the genetic gain could be increased in both scenarios. But this increase is associated with higher costs.

Selecting the mares for embryo transfer is crucially important for the genetic progress and only the best mares should be used. Using additional information on the mares available for selection, the accuracy can rise substantially (scenario II). This is important because the costs for the ET technique are high and therefore only very good mares with high accuracies ought to be used as donor mares, as is the case in dairy cattle breeding for bull dams (Burnside et al., 1992). The total costs for the breeding programme in scenario II are only marginally higher than in scenario I. The generation interval could not be reduced in scenario II like in scenario I because the selection of mares for ET takes place at a later point in time.

In horse-breeding programmes, the private breeders who own one or more of the BM_ET also bear the costs for using this additional reproduction technique which generates an additional increase in genetic gain in the whole breeding programme. For this reason, the ET technique must also generate a monetary return to these private breeders. Therefore the breeding associations would have to build a network for trading embryos: (a) within the breeding programme to acquire recipient mares and (b) worldwide to export the embryos produced in the breeding programme to other national and international breeding associations. In this study, the recipient mares were randomly chosen in the remaining female selection groups. If one assumes that only genetically inferior mares were used as recipient mares, the ET breeding programme could become even more efficient. Furthermore, it is particularly important that as many mares as possible should be available for selecting the BM_ET. If only a quarter of the performance-tested mares are available (250 out of 1'000) the trait-specific genetic gain rises only marginally. This clearly shows that such modifications of horse-breeding programmes will only be efficient if a large number of private breeders support the changes. The comparison of scenario I and II shows that the genetic gain rises with more information in the selection index. Moreover it must be noted that such ET success rates as assumed are difficult to achieve (Hinrichs, 1993). A horse-breeding programme has to assess these points and subsequently has to determine the optimal selection strategy of mares for ET.

Squires et al. (2003) showed that there is no commercially available method to stimulate multiple ovulations in horses. But still health and reproductive management of donor mares as well as of the recipient mares could increase the success of ET horse breeding programmes (Losinno et al., 2000; von der Ahe et al., 2010). However, this is a field with substantial research activities (e.g. Alvarenga et al., 2001; Raz et al., 2011), and we included MOET scenarios in our study to assess possible consequences in case this technology becomes available to the industry. In this case ET could be more efficient so that the presented scenarios with up to four or six foals per donor mare and year could be realistic in intensive MOET programmes.

In the Hanoverian population, Hamann and Distl (2008) found an N_e of 372 animals and an average coefficient of inbreeding of 1.3% based on a pedigree analysis of the current generation. The yearly inbreeding rate is fluctuating, which means that the breeders attach no big value to these aspects. In the more closed and smaller population of the Trakehner horse, Teegen et al. (2008a) estimated N_e to be 150. The theoretical effective population size is much larger in our designed population. This mainly results from the assumption that the family sizes have a Poisson distribution and the animals are randomly mated. These requirements are not fulfilled in real horse populations (Niemann, 2008). The absolute figures are thus no definite descriptions and the development of kinship is certainly underestimated in this study. However, the relative differences between the various scenarios illustrate the impact of ET on N_e and genetic variability. With few foals out of ET, the impact of ET on N_e in comparison with the reference scenario is low but the impact rose with 4 to 6 foals because the 200 BM_ET have much more genetic influence on the newborn foals. In these scenarios the kinship grew faster and the N_e was reduced to 86% resp. 81% of the N_e in the reference scenario. We can conclude that in intensive ET programmes, the development of kinship and of N_e must be monitored in order to prevent a too large reduction of the genetic variance.

Conclusions

We have demonstrated that complex horse-breeding programmes can be modelled in ZPLAN+. Implementation of embryo transfer increases the genetic gain in all scenarios, and with more information for selection of the donor mares the genetic gain increases on a higher level. The increasing genetic gain is attached to higher costs for the breeders and therefore the breeders which own donor mares have to receive a monetary return. The efficiency of an embryo transfer programme depends on the number of foals born out of one donor mare per year. Under all embryo transfer schemes, a stringent selection on the mare side and a high reproduction rate of the best mares show a high potential for increasing the efficiency of horse-breeding programmes.

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4th CHAPTER

Efficiency of genomic selection in an established commercial layer breeding programme

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Efficiency of genomic selection in an established commercial layer breeding programme

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Abstract

In breeding programmes for layers the selection of hens and cocks is based on recording phenotypic data from hens in different housing systems. Genomic information can provide additional information for selection and/or allows to reduce the generation interval strongly. In this study a typical conventional layer breeding programme using a four line cross was modeled and the expected genetic progress was derived deterministically with the software ZPLAN+. This non-genomic reference scenario was compared with two different genomic breeding programmes to find the best strategy for implementing genomic information in layers breeding programmes.

In scenario I genomic information was used on top of all other information available in the conventional breeding programme, so that the generation interval was the same as in the reference scenario, i.e. 14.5 months. Here we assumed the alternative of genotyping only young cocks or young hens and hens as selection candidates, respectively. In scenario II we assumed that breeders of both sexes were used at the biologically earliest possible age so that at the time of selection only performance data of the parent generation and genomic information of the selection candidates was available. In this case the generation interval was reduced from 14.5 months to 8 months. In both scenarios the number of genotyped male selection candidates was varied between 800 and 4800 males and two sizes of the calibration set (500 or 2000 animals) were considered. All genomic scenarios increased the expected genetic gain and the economic profit of the breeding programme. In scenario II, the increase is much more pronounced and even in the most conservative

implementation leads to a 60 per cent improvement. This increase in all cases was connected with higher breeding costs.

It is argued, that the higher breeding costs are real, whereas a possible extra profit of the breeding company depends on the willingness of the customers of breeding stock to pay more for improved genetic quality. While genomic selection is shown to yield a high potential to improve the genetic gain in layer breeding programmes, its implementation thus remains a business decision of the management of a breeding company.

Keywords

genomic selection, breeding programme design, layers, ZPLAN+

Introduction

Breeding of layers for commercial egg production is an international business and is dominated by few breeding companies. The marketable product of these companies is the breeding stock that subsequently is used to produce laying hens for the various production systems. In egg production the profit margins are extremely tight, especially with increasing feed prices as well as changing production systems (Summer et al., 2011). The strong competition on the market for laying-hens also contributes to a substantial economic pressure. In such a highly competitive market, the strategy of a breeding company with regard to allocation of resources in the breeding programme needs to be continuously optimized and monitored in order to maintain its competitiveness and market share on the global market.

Breeding of commercial laying hens is based on the pool of nucleus lines of a breeding company. Selection is done within closed purebred lines and is based on a comprehensive phenotyping scheme both in pure line birds under highly standardized housing conditions, and in crossbred hens under housing conditions which are closer to the production environment of the end product. The time of selection in both sexes depends on the time the performance of the hens is recorded. In the presently established breeding schemes, cocks and hens usually are selected at an age of one year or slightly more. Biologically, both cocks and hens could be used for reproduction much earlier since they achieve their sexual maturity at an age of about five months.

The benefit of genomic selection in over conventional selection strategies was first reported for dairy cattle. This expected benefit is due the reduction of the generation interval, the increase of accuracies of the breeding values of young bulls and bull dams and a reduction of costs for testing the young bulls (Schaeffer, 2006; König et al., 2009). Based on these theoretical findings genomic selection was rapidly implemented in dairy cattle breeding programmes (Loberg et al., 2009).

The breeding structures and the biological conditions in layer breeding programmes in many aspects are strongly different from those in dairy cattle breeding programmes. Therefore optimum breeding strategies for the

implementation of genomic selection in layer breeding programmes need to be designed and their comparative advantage needs to be assessed.

Among all farm animals the genome of the chicken was the first to be completely sequenced (Wong et al., 2004). Abasht et al. (2006) already reviewed 50 articles on identified quantitative trait loci in chicken. However, in practical breeding programmes marker-assisted selection has only been implemented for few traits like the fishy taint in brown layers (Honkatukia et al., 2005) and susceptibility to Marek's disease (Taejoong et al., 2010). Currently an array comprising about 60'000 single nucleotide polymorphisms (SNPs) (60k Illumina SNP BeadChip) for chicken is available (Groenen et al., 2011).

In this study we try to assess the potential benefits of genomic selection approaches in a layer crossbreeding programme. A conventional breeding programme based on a four-line cross was used as a reference. We then implemented two genomic scenarios, the first using the genomic information only in addition to the phenotypic information available at selection, the second assuming an earlier selection based on a combination of progeny and genomic information. In both scenarios, additional parameters such as the size of the calibration set and the number of genotyped selection candidates were varied. We discuss the results both with respect to expected genetic progress on the level of single or combined traits as well as on an economic scale. Here, the balance of expected costs and returns is delicate, and different aspects of the practical implementation of genomic selection in commercial layer breeding programmes will be addressed.

Material and Methods

Modelling software

The software ZPLAN+ (Täubert et al., 2010) was used to compare conventional crossbreeding programmes with breeding programmes using genomic information. This software allows to model all relevant breeding structures while taking all biological, technological and economic parameters relevant for complex breeding programmes into account. ZPLAN+ is based on the gene flow theory (Hill, 1974), the selection index by Hazel and Lush (1943) as well as

on a complex modelling of costs and returns. ZPLAN+ is based on a similar conceptual approach as the software ZPLAN (Karras et al., 1997) but has many additional features (such as the possibility to model genomic information) and a more appropriate web-based user interface. Like ZPLAN it deterministically calculates the expected genetic trend as well as the discounted economic gain and profit over a defined planning horizon.

To model a breeding programme in ZPLAN+, input parameters to define properly the biological aspects and the breeding processes need to be specified. In the following section the input parameters required for modelling a breeding programme are briefly described.

Input parameters

All traits that either are recorded and/or are part of the breeding goal need to be specified. For each trait the heritability, the phenotypic standard deviation, an economic value and genotypic correlations to all other traits must be given. Phenotypic correlations are only required between those traits that are actually measured for the birds in the same environment. The breeding goal is implicitly defined by assigning economic weights to all or a subset of the defined traits.

For each trait, the different information source groups (e.g. full sib groups) and the traits that are recorded for these must be defined. This comprises to specify the number of individuals in the group, the number of repeated measurements of the traits, as well as the additive-genetic relationship within the group and with the selection candidates.

The animals in the breeding programme are divided into selection groups. A selection group is a group of animals having the same sex and ancestry. For each selection group the following information has to be provided: the breeding goal for the group, the information source groups available for each selection candidate, the number of tested and selected animals, the variable costs for each tested animal, the age at first reproduction, and the productive lifetime.

ZPLAN+ provides a comprehensive set of detailed results. For each selection path the genetic gain is computed as the product of the accuracy of the selection index, the selection intensity and the standard deviation of the respective breeding goal in this respective path. The discounted variable costs

are calculated across the selection groups. Discounted variable costs plus discounted fixed costs are resulting in the total costs. The discounted return of a selection path is obtained as the monetary genetic gain weighted by its corresponding Standardised Discounted Expression (SDE) value. The SDE value of a selection path includes the proportion of animals that realize the genetic gain, the point in time of realization and the amount of the genetic gain provided by this selection group over all generations within the planning horizon. The overall discounted return is the sum of returns over all selection paths.

The profit is the overall discounted return minus the total discounted costs and is expressed per animal unit in the breeding programme.

Conventional breeding programme

A commercial layer crossbreeding programme with four nucleus lines (A, B, C and D) was modeled in ZPLAN+ for a planning period of ten years (Reference Scenario). In these four lines the selection process relies on a combination of information measured in the purebred birds at the breeding unit and on information captured from crossbred half-sibs under commercial conditions. From the pure lines the grandparent generation (grandparents of the production hens) was hatched in a first multiplication step. In the parent generation, the cocks are a cross of lines A and B, while the hens are a cross of lines C and D. This results in 500'000 cocks and 5'000'000 hens in the parental generation. The cross of this parental generation finally produces 500'000'000 laying hens for the egg production. The complete breeding scheme is presented in Figure 1. Each pure line comprises the same number of animals. In each line and generation, 600 hens and 60 cocks were used. A pre-selection after rearing was carried out on the basis of parental information. 4000 female chicks were selected out of 4800 reared chicks to be housed on the breeding farms. The 4000 selected hens then were tested in single cages over 32 weeks from age 20 to 51 weeks of age to finally select 500 hens based on an index combining pedigree information with own, full- and purebred half-sib performance. In addition, 1500 hens per line are tested in group cages (3 full- or half-sib hens per cage) from which further 100 hens per line are selected.

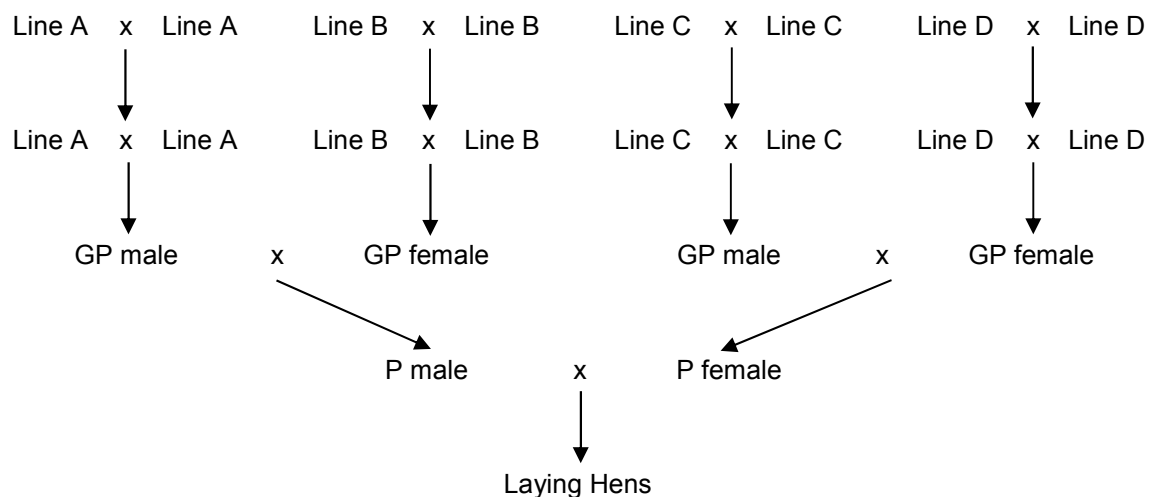


Figure 1: Schematically structure of the crossbreeding programme (GP: Grandparents, P: Parents)

The selection of 60 cocks per line out of 800 male chicks was based on parental information plus the following information on relatives:

- 8 purebred full-sibs and 65 pure-bred half-sibs in single cages,
- 4 purebred full-sibs and 20 pure-bred half-sibs in group cages,
- 30 crossbred half sibs in practical environment.

For the latter, cocks of the lines A and B were mated with hens of the lines C or D resulting in crossbred hens of genotype AC, AD, BC or BD, respectively, which were tested in practical environment.

These 60 selected cocks and 600 selected hens per line were used to produce the new pure bred generation. All the hens, not only the selected ones, were kept for the entire production cycle to have information on the late laying performance for the next generation.

The breeding goal comprised performance traits as well as functional traits. The selection indexes for the pure bred hens in the single cages, group cages and the hens in practical environment include in total 22 single traits (Table 1). The laying performance was split in four time periods. Table 2 provides the used relative economic weights (ew), the phenotypic standard deviations, heritabilities and genetic and phenotypic correlations of all single traits. These parameters were based on a breeding programme for laying hens from the Lohmann Tierzucht GmbH. Note that the sign of the economic weight indicates

the desired direction of genetic change in the respective trait (e.g. for feed consumption and mortality, a negative economic weight indicates that a numerical reduction of the trait level was desirable). While ZPlan+ requires economic weights in € per genetic standard deviation, the values in Table 2 are scaled to allow a direct assessment of the relative values of traits in the breeding goal.

Table 1: Single traits recorded in the different housing systems

| | single cage | group cage | practical environment |
|----------------------|-------------|------------|-----------------------|
| laying performance 1 | X | X | X |
| laying performance 2 | X | X | X |
| laying performance 3 | X | X | X |
| laying performance 4 | X | | X |
| egg weight | X | X | X |
| feed consumption | X | | |
| egg shell strength | X | X | X |
| hatchability | X* | | |
| mortality | X | X | X |
| feathering quality | | X | |

*only in C and D

The variable costs for rearing a cock or a hen over a period of 20 weeks were assumed to be €11.00 per animal. During production, daily feeding costs resulted from a feed consumption of 0.11 kilogram per day at a price of €0.30 per kilogram. For each cock and hen additional costs for the cage unit (€5.00) and animal care (€5.00) were assumed. Performance testing caused additional costs of €5.00 per hen. Since it was difficult to quantify fixed costs which are related to decisions on the breeding structures (e.g. the costs of a newly built performance test unit when the population size is increased), we included no fixed costs in the reference scenario. This has no influence on the comparison of alternative scenarios if we assume that they are indifferent with respect to the population size. It should be kept in mind, though, that the fixed costs have to be paid from the resulting profit. The considered time frame was set to ten years (i.e. ten breeding cycles) and the interest rate to calculate the discounted costs

was assumed to be seven per cent while the interest rate for the discounted returns was assumed to be two per cent.

As results we report the genetic gain in the single traits as well as the total monetary genetic gain, the generation interval and discounted economic parameters return, costs and the resulting profit to evaluate and compare the different scenarios for the breeding programmes. To allow a better comparison we set the values obtained for the reference scenario (conventional breeding programme) to 100% and express the results obtained with the alternative genomic scenarios relative to these reference values.

Table 2: Relative economic weight (ew), phenotypic standard deviation (SD), heritabilities (diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal)

| | | ew | SD | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | |
|--------------------|------------------------|----|-----|-------------|-------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------|-------------|-------------|-------------|
| Single cage | Laying performance 1 | 1 | 3 | 22.7 | 0.35 | 0.16 | -0.05 | -0.10 | -0.20 | -0.14 | -0.06 | 0.05 | 0.05 | 0.73 | 0.05 | 0.02 | -0.20 | -0.05 | -0.03 | -0.17 | 0.40 | -0.05 | -0.10 | -0.15 | 0.18 | 0.03 |
| | Laying performance 2 | 2 | 6 | 4.8 | 0.06 | 0.10 | 0.73 | 0.58 | -0.30 | 0.05 | -0.05 | 0.15 | -0.05 | 0.05 | 0.30 | 0.20 | -0.15 | -0.08 | -0.02 | 0.05 | 0.07 | 0.20 | 0.10 | -0.12 | -0.09 | -0.05 |
| | Laying performance 3 | 3 | 6 | 7.0 | -0.01 | 0.47 | 0.12 | 0.85 | -0.20 | 0.09 | -0.08 | 0.15 | -0.05 | -0.05 | 0.22 | 0.25 | -0.10 | -0.09 | -0.02 | 0.02 | 0.01 | 0.16 | 0.20 | -0.10 | -0.10 | -0.05 |
| | Laying performance 4 | 4 | 9 | 7.3 | -0.07 | 0.27 | 0.32 | 0.20 | -0.20 | 0.10 | -0.12 | 0.20 | -0.08 | -0.10 | 0.12 | 0.15 | -0.09 | -0.08 | -0.02 | 0.03 | -0.05 | 0.20 | 0.33 | -0.10 | -0.08 | -0.10 |
| | Egg weight | 5 | 18 | 3.8 | -0.18 | -0.08 | -0.04 | -0.06 | 0.75 | 0.64 | -0.20 | -0.40 | 0.02 | -0.18 | -0.15 | -0.14 | 0.80 | -0.22 | 0.01 | -0.03 | -0.10 | -0.20 | -0.15 | 0.70 | -0.15 | -0.04 |
| | Feed consumption | 6 | -12 | 10.0 | -0.05 | 0.08 | 0.07 | 0.01 | 0.43 | 0.50 | -0.05 | -0.24 | 0.01 | -0.05 | -0.08 | -0.05 | 0.55 | -0.01 | 0.00 | 0.00 | -0.10 | -0.10 | -0.05 | 0.45 | -0.05 | 0.00 |
| | Egg shell strength | 7 | 7 | 7.0 | 0.05 | 0.13 | 0.11 | 0.10 | -0.12 | -0.04 | 0.35 | 0.08 | 0.02 | -0.10 | -0.09 | -0.08 | -0.22 | 0.80 | 0.03 | 0.08 | -0.03 | 0.08 | 0.12 | -0.21 | 0.75 | -0.04 |
| | Hatchability | 8 | 2 | 25.8 | 0.05 | 0.13 | 0.09 | 0.07 | -0.25 | -0.13 | 0.09 | 0.26 | -0.01 | 0.06 | 0.05 | 0.05 | -0.52 | -0.07 | 0.00 | 0.00 | 0.08 | 0.05 | 0.05 | -0.40 | 0.08 | 0.00 |
| | Mortality | 9 | -3 | 0.2 | 0.02 | -0.03 | -0.04 | -0.05 | 0.01 | 0.01 | -0.01 | -0.01 | 0.03 | 0.02 | -0.15 | -0.10 | 0.08 | 0.01 | 0.10 | -0.09 | 0.08 | -0.10 | -0.05 | 0.05 | -0.03 | 0.05 |
| Group cage | Laying performance 1 | 10 | 2 | 18.9 | . | . | . | . | . | . | . | . | 0.24 | 0.15 | 0.10 | -0.25 | -0.06 | -0.10 | -0.15 | 0.60 | -0.07 | -0.05 | -0.10 | 0.05 | 0.05 | |
| | Laying performance 2 | 11 | 3 | 6.2 | . | . | . | . | . | . | . | . | . | 0.10 | 0.10 | 0.70 | -0.20 | -0.05 | -0.10 | -0.05 | 0.09 | 0.40 | 0.08 | -0.10 | -0.04 | -0.10 |
| | Laying performance | 12 | 3 | 7.5 | . | . | . | . | . | . | . | . | . | 0.15 | 0.80 | 0.10 | -0.20 | -0.03 | -0.15 | -0.05 | 0.08 | 0.50 | 0.08 | -0.08 | -0.05 | -0.08 |
| | Egg weight | 13 | 1 | 2.9 | . | . | . | . | . | . | . | . | . | -0.30 | -0.05 | -0.08 | 0.70 | -0.20 | -0.05 | 0.10 | -0.04 | -0.30 | -0.15 | 0.85 | -0.15 | 0.01 |
| | Egg shell strength | 14 | 2 | 6.2 | . | . | . | . | . | . | . | . | . | 0.05 | 0.03 | 0.05 | -0.05 | 0.35 | -0.04 | 0.11 | 0.05 | -0.05 | -0.05 | -0.15 | 0.78 | -0.03 |
| | Mortality | 15 | -3 | 0.2 | . | . | . | . | . | . | . | . | . | -0.09 | -0.20 | -0.30 | -0.01 | 0.01 | 0.05 | 0.05 | 0.02 | -0.14 | 0.03 | 0.15 | 0.01 | 0.20 |
| | Feathering quality | 16 | 3 | 1.5 | . | . | . | . | . | . | . | . | . | -0.10 | -0.08 | -0.09 | -0.02 | 0.01 | 0.09 | 0.40 | -0.05 | 0.04 | 0.04 | -0.02 | 0.02 | 0.08 |
| Pract. environment | Laying performance 1 | 17 | 1 | 18.5 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.26 | 0.15 | -0.10 | -0.21 | 0.05 | -0.05 | |
| | Laying performance 2 | 18 | 3 | 5.5 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.40 | 0.08 | 0.65 | -0.15 | 0.04 | -0.10 | |
| | Laying performance 3+4 | 19 | 5 | 6.2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.18 | 0.77 | 0.10 | -0.13 | 0.05 | -0.03 | |
| | Egg weight | 20 | 2 | 2.7 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | -0.17 | -0.06 | -0.09 | 0.60 | -0.21 | 0.02 |
| | Egg shell strength | 21 | 3 | 5.0 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | -0.06 | -0.04 | -0.01 | -0.08 | 0.29 | -0.05 |
| | Mortality | 22 | -5 | 0.2 | . | . | .. | . | . | . | . | . | . | . | . | . | . | . | . | . | -0.10 | -0.15 | -0.08 | 0.02 | -0.02 | 0.08 |

Genomic breeding programmes

In ZPLAN+ it is straightforward to define for each single conventional trait a genomic counterpart, which basically is the estimated genomic breeding value for this trait assuming a given calibration set size. The background for implementing genomic information in the selection index was suggested by Dekkers (2007) and was modified by Haberland et al. (2011). This approach requires to define the correlation of the true and the estimated genomic breeding value for every genomic trait $r_{Q\hat{Q}}$. This is done using the approach by Erbe et al. (2011) which builds on an equation suggested by Daetwyler et al. (2008 and 2010)

$$r_{Q\hat{Q}} = w \sqrt{\frac{Nr_{TI}^2}{Nr_{TI}^2 + M_e}}$$

where N is the assumed size of the calibration set, r_{TI}^2 is the reliability of the estimated breeding values of the animals used in the calibration set, and M_e is the number of independently segregating chromosome segments which was determined by Goddard (2009) as

$$M_e = \frac{2N_e L}{\ln(4N_e L)}.$$

The effective population size N_e per line was assumed to be 60 and the length of the genome in Morgan $L \approx 32$ was taken from Groenen et al. (2009), leading to an estimated $M_e = 429$.

The factor w reflects the accuracy of genomic breeding values that is hypothetically obtained with a calibration set of infinite size using the given SNP density. Erbe (2011) empirically determined this factor to $w \approx 0.9$ for different traits in dairy cattle for genomic breeding value estimation based on a 50k SNP chip. Since for layers this quantity is unknown, we also assumed $w = 0.9$ for this study, but w needs to be determined from empirical data once these are available.

The variable costs for genotyping an animal were assumed to be €150. The total costs for the implementation of a genomic breeding value estimation were €150 multiplied by the number of animals in the calibration set. We assumed

calibration sets of 500 and 2000 animals, respectively. These costs were fixed costs for the genomic breeding programmes and were divided by the modeled time period of ten years.

We modeled two different genomic scenarios:

In scenario I the genomic information was used just in addition to all other information in the reference scenario, but all selection decisions were made at the same time as in the reference scenario.

In scenario II, it was assumed that selection takes place at the biologically earliest possible point of time, so that only parental and genomic information is available for cocks as well as for all 6300 reared hens. Selected animals were used for breeding at the age of eight months. For the re-calibration of the genomic information and the production of the grandparental generation the hens were still kept and fully performance tested to the age of 72 weeks.

In both genomic scenarios, the number of genotyped cocks was varied between 800 and 4800 animals per purebred line in steps of 800 animals, while the number of selected cocks was kept constant at 60. While in the conventional scheme all fullsibs have the same estimated breeding values and drawing one animal from a group at random is the best one can do, it is possible to select between fullsibs when genomic breeding values are available. In a second step we assumed in scenario I that additionally all 6300 reared hens were genotyped too and this new additional information was used for dam selection. All incurred variable costs were accounted the same way as in the reference scenario.

Results

Reference Scenario

The generation interval in the reference scenario was 14.5 months within each line. The accuracy of the selection index at the time of selection was $r_{TI}^{\wedge} = 0.51$ for cocks, $r_{TI}^{\wedge} = 0.53$ for the hens selected tested in single cages, and $r_{TI}^{\wedge} = 0.51$ for the hens tested in group cages. The genetic gain per generation in all single traits is shown in Table 3.

The monetary results in ZPLAN+ are standardized to an animal unit and are given per year. For our breeding programme we defined the selected animals in the four lines and all grandparental animals as basis for the standardization unit. The total number of all animals amounted to 127'640 animals. The discounted return per animal unit was €282.17 per year. The variable costs were €17.19 per animal unit and this resulted in a profit of €264.98 per animal unit (remember that we don't account for fixed costs, which thus will have to be paid from this profit). This results in a profit per laying hen of €0.07.

Table 3: Genetic gain per year $\Delta G/a$ in genetic standard deviations (σ_g) in the reference scenario

| Housing system | Trait | GG in σ_g |
|--------------------|---------------------------|------------------|
| Single cage | Laying performance I | 0.074 |
| | Laying performance II | 0.389 |
| | Laying performance III | 0.497 |
| | Laying performance IV | 0.422 |
| | Egg weight | 0.116 |
| | Feed consumption * | 0.033 |
| | Egg shell strength | 0.240 |
| | Hatchability | 0.025 |
| | Mortality* | - 0.116 |
| Group cage | Laying performance I | - 0.008 |
| | Laying performance II | 0.215 |
| | Laying performance III | 0.199 |
| | Egg weight | 0.116 |
| | Egg shell strength | 0.166 |
| | Mortality* | - 0.041 |
| | Feathering quality | 0.116 |
| Pract. environment | Laying performance I | 0.091 |
| | Laying performance II | 0.174 |
| | Laying performance III+IV | 0.166 |
| | Egg weight | 0.116 |
| | Egg shell strength | 0.248 |
| | Mortality* | - 0.149 |

* *negative genetic gains are in the desired direction*

Scenario I

In this scenario the genomic information was just used on top of the information in the reference scenario. Neither the generation interval nor the costs for the performance testing of the hens were reduced in scenario I. The return increased with the number of tested cocks and with a higher number of animals in the calibration set (Figure 2).

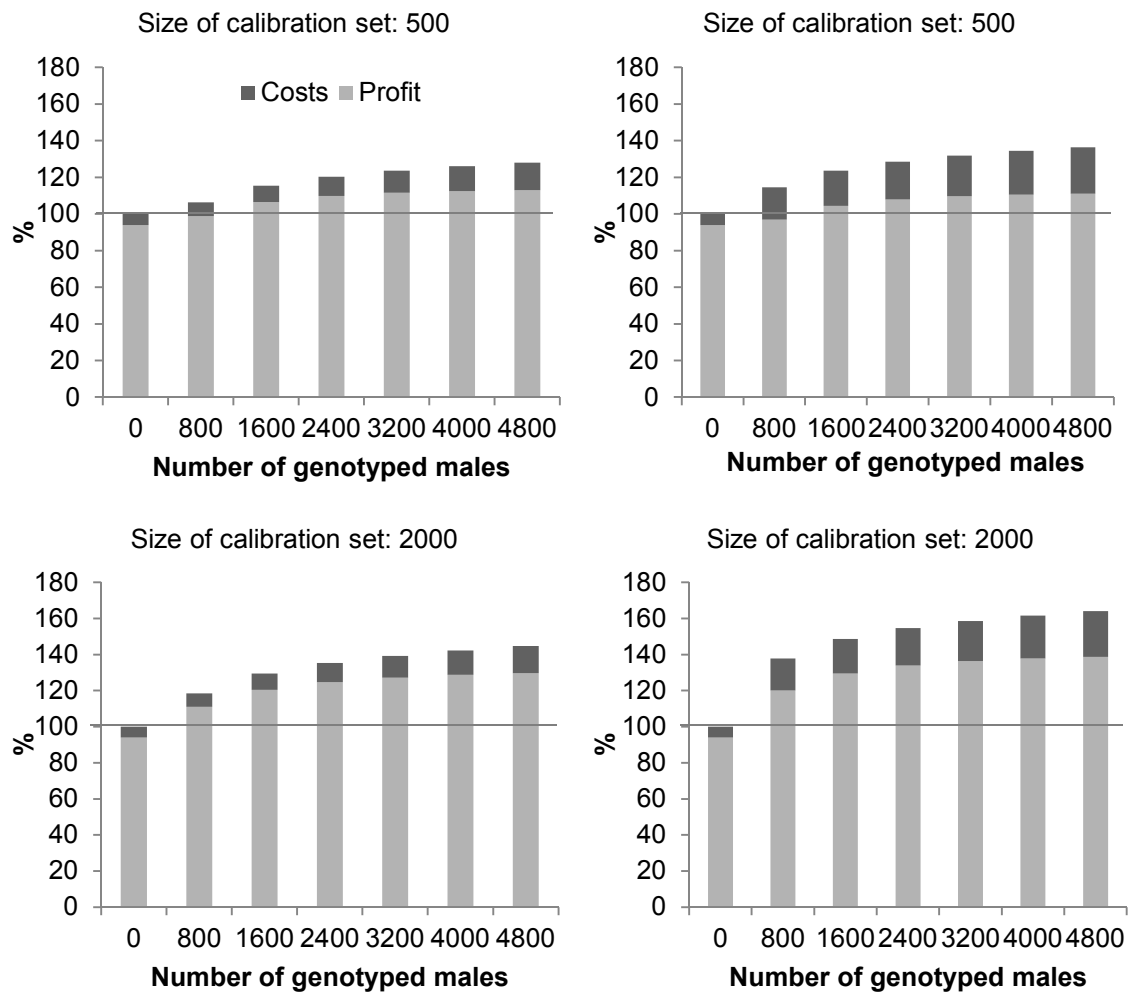


Figure 2: Profit and costs (collectively: return) in scenario I with genomic information of cocks (left side) or cocks and hens (right side) in relation to the return of the reference scenario (Number of genotyped males: 0)

Total costs scaled with the number of genotyped animals. The number of animals in the initial calibration set had no significant impact on the total costs, since these costs are distributed over the whole considered period of ten years

and all animals receiving genetic gain. Compared to the reference scenario the profit was higher with all numbers of tested cocks (€278.93 – €391.37) although there was a diminishing marginal utility with increasing numbers of genotyped cocks, since adding more cocks increases the genotyping costs linearly, while the extra benefit from selection intensity increases at a lower rate. With a calibration set of 500 animals, genotyping both sexes resulted in a marginally lower profit than genotyping cocks only.

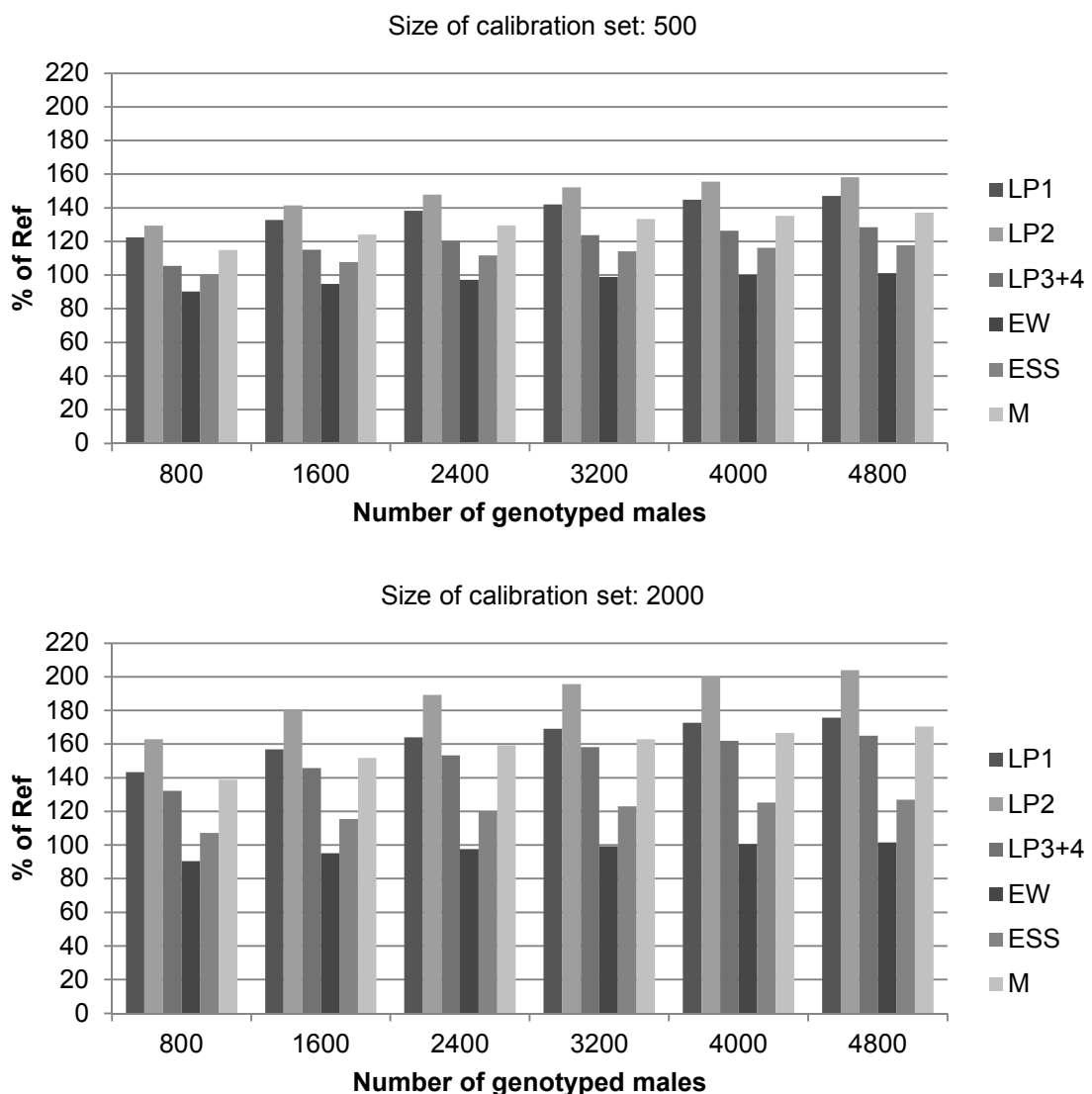


Figure 3: Genetic gain in crossbred hens in practical environment in laying performance 1 (LP1), 2 (LP2), 3 and 4 (LP3+4), egg weight (EW), egg shell strength (ESS) and mortality (M) in scenario I with genomic information of the cocks in relation to the reference scenario with different numbers of tested cocks and different sizes of the calibration set

To compare the expected genetic gain in different trait complexes across the different scenarios we used the six single traits of the crossbred hens in the practical environment, since this is the type of production that is closest to the production system for which the hens are selected.

In Figure 3 the predicted genetic change for these six traits is shown relative to the predicted change in the reference scenario. The laying performance increased in all laying periods with the highest gain in the second laying period. Here, the genetic gain was doubled when a calibration set of 2000 cocks was used and 4000 cocks were genotyped for selection. Genetic gain in the egg weight decreased slightly when few cocks were genotyped for selection and only reached the same level as in the reference scenario when 4000 or more cocks had been genotyped for selection. With 2000 animals in the calibration set, the genetic gain rose higher than with 500 animals, but the ranking between the single traits stayed the same. In all cases a considerable genetic improvement of mortality under production conditions was observed. The additional genotyping of all hens causes an increased genetic gain in all traits except the egg weight (data not shown). Especially the genetic gain in laying performance and mortality benefits from the additional genomic information. The additional increase in the egg shell stability was only marginal and the genetic gain in the egg weight was lower than in the scenario where only the cocks were genotyped.

Scenario II

In scenario II the generation interval was reduced to eight months. Assuming that performance testing of the hens was still done after the breeding period the costs related to performance testing were not reduced. The return, the costs and the profit are shown in relation to the reference scenario in Figure 4. It can be seen that with a calibration set of 2000 animals the return can be doubled even with very few (800) male animals genotyped for selection. With the initially more realistic number of 500 animals in the calibration set, the return was increased by 60 to more than 100 per cent with 800 to 4800 genotyped cocks, respectively. The costs were increasing with higher numbers of genotyped

animals. With the lowest number of genotyped cocks, the costs were three times as high as in the reference scenario (€48.84 per animal unit) and with the highest number of genotyped cocks the costs were more than quadrupled (€69.80 per animal unit).

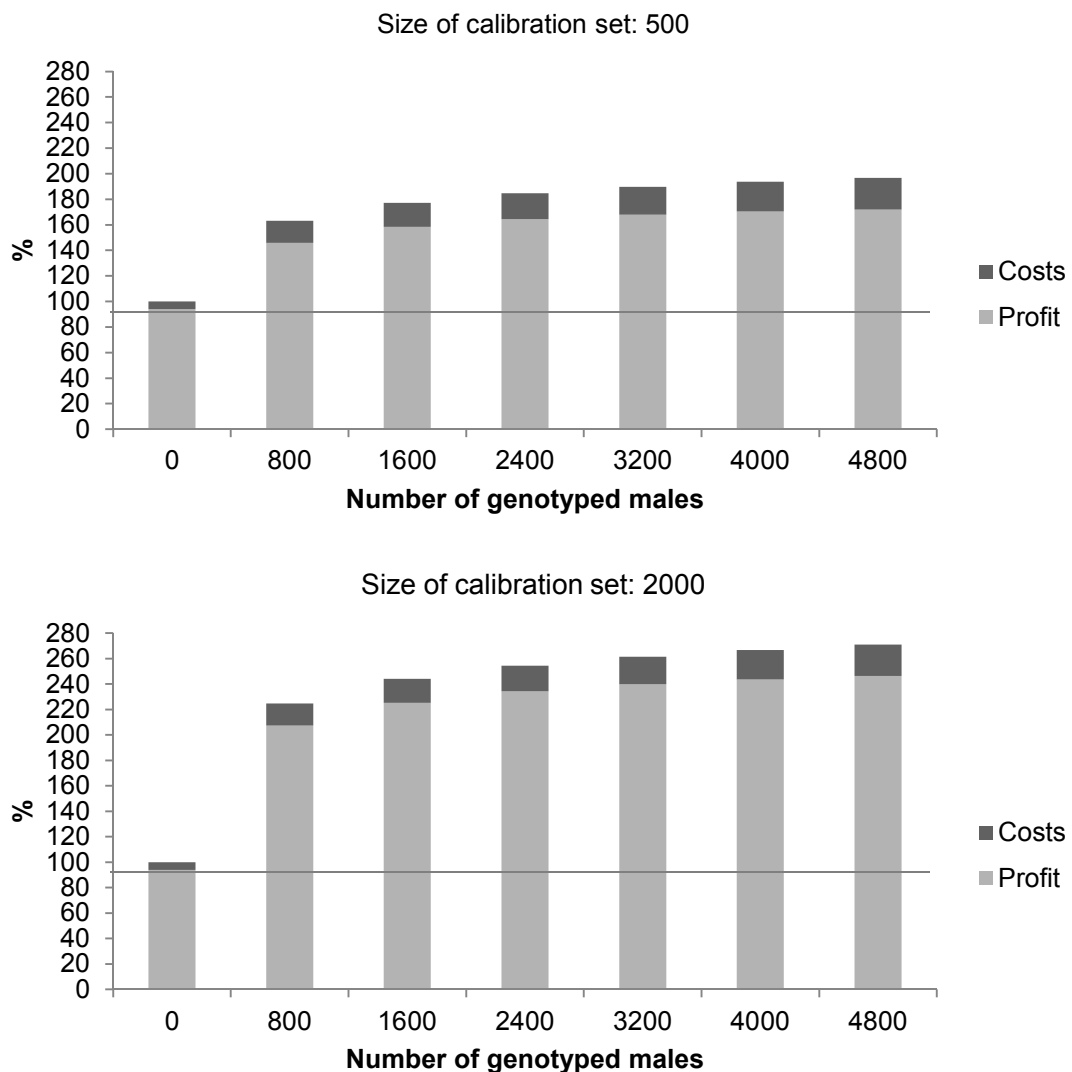


Figure 4: Profit and costs (collectively: return) in Scenario II with genomic information of cocks in relation to the return of the reference scenario (Number of genotyped males: 0) with different numbers of tested cocks and different sizes of the calibration set

The genetic gain in the six traits of the crossbred hens in practical environment is shown in Figure 5. While the genetic progress for most traits was substantially increased (partly doubled or tripled) the genetic gain in the trait

egg weight was lower than in the reference scenario. It should be noted, that egg weight in many breeding programmes is considered as a trait under stabilizing selection (i.e. neither an increase nor a decrease of the trait level is desired), so that a reduction in genetic trend appears acceptable for this trait. The result may also be a consequence of aiming at a higher laying performance with lower feed consumption, which must have consequences on the egg size produced.

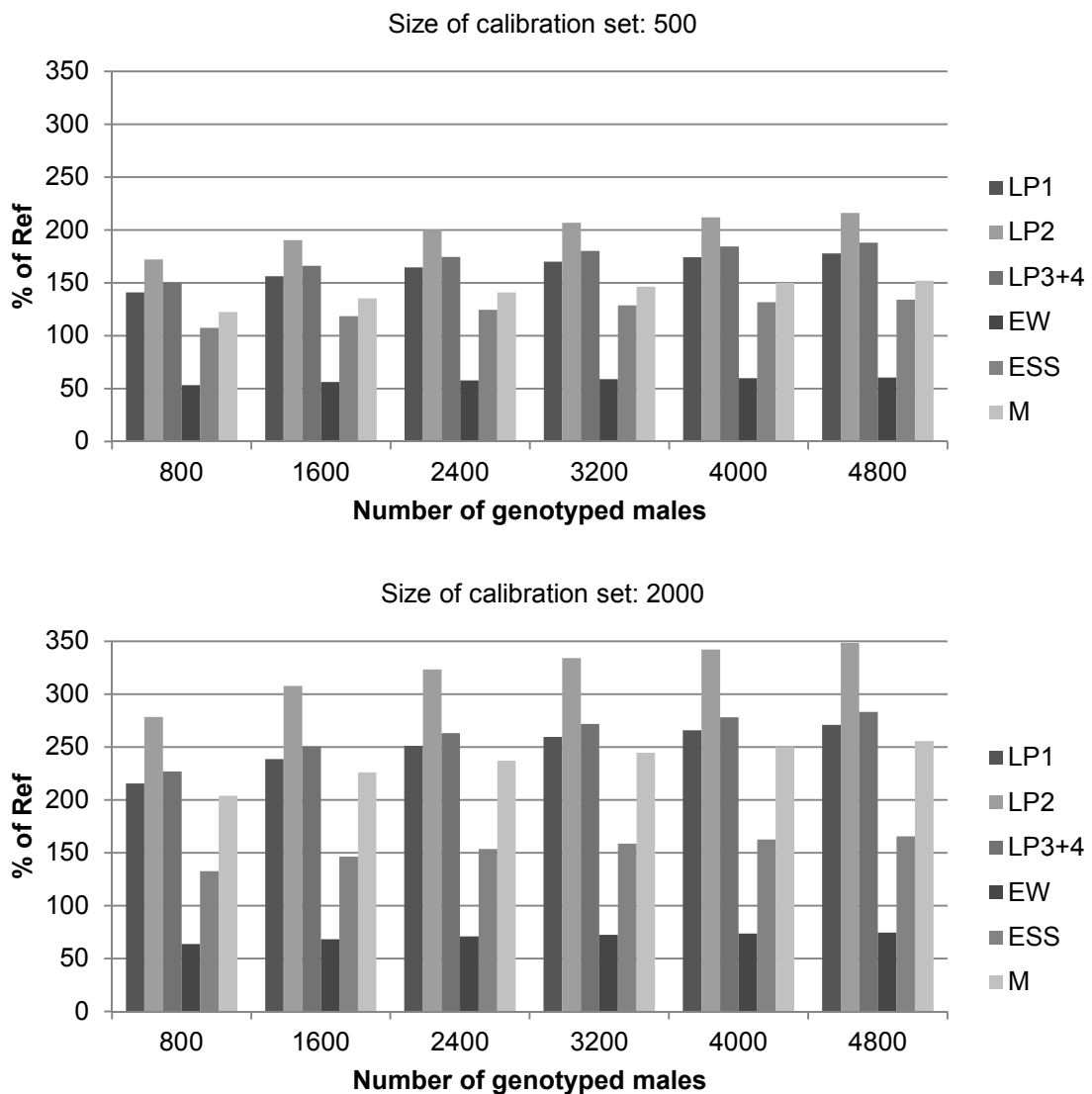


Figure 5: Genetic gain in crossbred hens in practical environment in laying performance 1 (LP1), 2 (LP2), 3 and 4 (LP3+4), egg weight (EW) egg shell strength (ESS) and mortality (M) in scenario II with genomic information of the cocks in relation to the reference scenario with different numbers of tested cocks and different sizes of the calibration set

Discussion

In general it can be noted that the complete breeding structures of a conventional commercial crossbreeding programme for laying hens can be comprehensively modelled with ZPLAN+. Although we still simplified the breeding structures to some extent compared to the ones implemented in a real breeding programme, we still ended up modelling 23 selection classes and 18 selection index variants in the different scenarios. ZPLAN+ allows for such a complexity by having e.g. no fixed limit regarding the number of traits or information groups in the selection index module which is a part of the software. However, the more complex a scenario becomes, the more challenging it is to define admissible parameters, e.g. positive definite variance-covariance matrices.

Based on a conventional reference scenario we evaluated different approaches to implement genomic information in the breeding strategies of laying hens. In scenario I the genomic information was used as additional information. In scenario II the selection in the purebred lines was based only on pedigree and genomic information which allows to shorten the generation interval substantially.

The genomic information was shown to have a positive effect on the increase of monetary genetic gain in all scenarios. The size of the calibration set and the accuracy of the genomic information were found to have a high impact on the efficiency of the implementation of genomic selection. The theoretical background for this dependency was given by Dekkers (2007), Daetwyler et al. (2008) and Erbe et al. (2011), and practical calculations for other farm animals with ZPLAN or ZPLAN+ show the same trend (König et al., 2009; Haberland et al., 2010; Sitzenstock et al., 2010). Over time, the number of animals available for the recalibration will grow, which will lead to a higher accuracy of genomic prediction, although the number of additional cocks with performance tested progeny will be small (60 per year and line). Our study focuses on the implementation and the short-term effects of incorporating genomic information in a layer breeding programme in the transition process. Therefore, we did not model the dynamics of this transition with changing population sizes (esp.

training set sizes) over time. In scenario II the advantage of genomic selection was particularly evident because the genomic information was the main basis for selection, so that the generation interval could be reduced substantially.

In the reference scenario the selection of cocks and hens was carried out at the age of one year, after the hens were progeny tested, and the reproduction of the new generation takes place only after selection. This leads to a generation interval of 14.5 months. Since in scenario I genomic information is only used on top of the phenotypic information, the generation interval is the same as in the reference scenario. The extreme case was shown in scenario II where the selection of cocks and hens relied only on genomic information, on performance of the mother as well as on the performance of full-sibs and half-sibs of the father. It is therefore possible to reduce the generation interval to the biological limit of about eight months, because the time of selection depends not on performance information of contemporary hens of the present generation. Similar effects were found in dairy cattle, where the use of genomic information replaces progeny information so that young bulls can be used immediately (Schaeffer, 2006; König et al. 2009). These studies suggested that in dairy cattle breeding programmes the variable costs per proven bull could be reduced substantially. In conventional dairy cattle breeding programmes, there are substantial costs of housing and feeding the bulls for several years until the performance test of their daughters are available, and also using a substantial proportion of the cow population to be mated to test bulls with an inferior average breeding value compared to progeny tested bulls causes economic losses, which together sum up to about 25'000 € per tested bull. In layer breeding programmes, costs of keeping a cock are marginal and the performance information of the hens is necessary anyway for a recalibration of the genomic breeding value estimation method. Also, the hens were used for producing the grandparental generation as well as the crossbred hens for performance testing. Thus, the benefit of scenario II is mainly due to the reduced generation interval, but not to a significant reduction of breeding programme costs, as it was suggested for dairy cattle (Schaeffer, 2006). Henryon et al. (2012) showed in pigs that only a small proportion of selection candidates which were preselected based on phenotype information need to be

genotyped to realize most of the benefits. This approach could not be used to reduce the generation interval because in layers the phenotypic information accrue at a later point in time than breeding maturity. In scenario I such an approach could reduce costs for genotyping, though.

The increase of the genetic gain in the genomic scenarios was associated with a strong increase of costs, mainly for genotyping. The higher expected returns could balance these increased costs, but it has to be noticed that the costs are real, i.e. they have to be paid by the breeding company while the expected benefits are just hypothetical in the first place and only turn into a realized economic benefit, if improved breeding products can be sold at a higher market price, or the genetic superiority allows to increase the market share in a competitive market.

The genotyping costs for the initial calibration study only have a very marginal effect in the calculations because they were assigned to 127'640 animal units over a time frame of ten years. However, taking into account the total costs of genotyping the calibration set (for 2000 animals the genotyping costs are €300'000) there is a conflict between a considerable investment to be done at one point of time to obtain an expected competitive advantage over a considerable period (ten years) which may or may not materialize and generate an economic profit. Just assume that competing breeding companies also invest into a calibration study and establish a similar genomic selection scheme. In this case there is no competitive advantage despite the fact that the investment was done. But then there would be a competitive disadvantage for the company if the investment had not been made.

A reduction of genotyping costs of the genomic selection scheme could be achieved by the use of low density chips containing a subset (e.g. 3k to 6k) of SNPs on the 60k chip. Thereby, genotyping of selection candidates in each generation would be cheaper, and almost the full genomic information content could be retrieved by using imputation strategies (Weigel et al., 2010; Dassonneville et al., 2011), so that only selected animals are re-genotyped with the 60k chip. In dairy cattle it was shown that by using such an approach the

quality of genomic information was not significantly affected (Dassonneville et al., 2011).

The expected genetic gain in the single traits differed substantially between trait complexes. Especially for the trait egg weight, the genetic gain was similar or even reduced compared to the reference scenario, while for the other five traits genetic gains increased with the amount of genomic information (size of the calibration set and number of genotyped selection candidates) used. The reasons for this were the low economic weight of the egg weight in all housing systems and the negative genetic correlation to many other traits, especially to the laying performance. This was particularly evident in scenario II where the information of the performance testing of the present generation was not used for selection. It must be noted that relative benefits were high for traits with low heritability like the mortality. Especially traits in the functional area are expected to benefit from the use of genomic information (Ytournal et al., 2011) but in our study also performance traits with moderate heritability and higher economic weights in the breeding goal profit from the genomic information. This could be confirmed by Wolc et al (2011). They showed in real data an increase in accuracy of the estimated breeding values when layers were selected on basis of genomic information and no phenotypic information is available.

Our study provides a basis to optimize layer breeding programmes from an economic point of view. Particularly the total abandonment of waiting for performance information of the hens could boost the genetic trend and increase the expected monetary genetic gain. But also a combination of genomic information with all available performance information of the present generation as modelled in scenario I would increase the monetary genetic gain compared to the conventional system.

For breeding companies it is basically a business decision whether an investment in a genomic breeding programme is expected to pay off through additional returns due to a higher genetic quality of the marketable products, or an increase in the market share in a competitive market. Market research has to assess the willingness of the direct customers to pay more for a higher quality of the breeding stock. The hen producers will base their final decision on the

willingness of the egg producers to pay a higher price for better laying hens. On the other side, failing to adopt a major innovation in an oligopolic situation may lead to a major competitive disadvantage if the competitors implement the innovation and realize the benefits combined with an appropriate communication strategy.

Genomic selection substantially can increase the efficiency of breeding programmes for layers as previously found for other livestock species. The breeding structures and biological conditions do not allow a cost reduction, but genomic information can be used either to increase the accuracy at selection (scenario I) or shorten the generation interval (scenario II), where the latter is shown to be the much more efficient strategy. The decision whether or not to implement a major technological innovation such as genomic selection in a competitive market with an oligopolic structure, however, does not only depend on expected genetic trends and breeding profits but primarily is a business decision taking into account the perceived consumers' willingness to pay for improved genetics as well as the assumed technological innovation strategy of the main competitors.

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5th CHAPTER

General Discussion

Modelling of breeding programmes with ZPLAN+

One focus of this thesis was the optimization of different breeding programmes with new a software called ZPLAN+. In Chapter 3 it was shown that building an actual reference breeding programme in sport horses is possible using this new software. The implementation of a stringent selection on the mares' side and a targeted usage of the best mares on a high level by using embryo transfer technique have been proven to be a valid approach to optimize the genetic gain. This optimization of genetic gain is associated with an increase in costs for the breeders which are using embryo transfer. Chapter 4 deals with the optimization of layer breeding programmes with the usage of genomic selection. The empirical results show that a complex hybrid breeding programme with four lines could be modelled with ZPLAN+. Genomic information can be integrated for every conventional single trait. The results show that the usage of genomic information in layer breeding programmes provides the opportunity to increase genetic gain as well as the return. This increase is also associated with an increase in costs for the breeding company.

In other studies reference breeding programmes for cattle (Ytournal, 2011) and pigs (Haberland, 2010) were modelled and current questions for optimizing these breeding programmes were answered. All these different and complex breeding programmes could be modelled in ZPLAN+. It is obvious that in every species different breeding strategies and breeding methods were used. Thus, software solutions for optimization of breeding programmes have to be very flexible. As shown, ZPLAN+ meets all of these requirements.

ZPLAN (Karras et al., 1997) was and is used for optimization of breeding programmes in many different aspects. Roessler et al. (2009) designed breeding programmes for pig producing smallholders in Vietnam taking account to economic aspects. Wurzinger et al. (2007) modelled in ZPLAN a breeding programme for llama population in Bolivia for increasing the fleece weight. König et al. (2009) evaluated the implementation of genomic selection in dairy cattle breeding programmes. SELECTION (Rutten et al., 2002) represents software for predicting selection response in livestock breeding programmes basing on the selection index. Swan et al. (2009) used SELECTION for

predicting genetic trends in a sheep breeding programme. In broilers there is a study comparing different selection strategies for body weight and reduced Ascites susceptibility (Padkel et al., 2005) using SELACTION. Another possibility to model and evaluate breeding programmes affords stochastic simulations (cf. Wensch-Dorendorf et al., 2011; Abdel-Azim and Freeman, 2002).

Breeding programmes for sport horses

Software-based planning of breeding programmes is not a standard tool for horse-breeding associations as it is in other livestock breeding programmes. However, several recent questions arising in the development of breeding structures can be applied in horse breeding programmes (Sitzenstock and Simianer, 2009). In the scope of the project FUGATO+brain it was tried to answer some of these questions using ZPLAN+. During the modelling of a reference breeding programme for sport horses some difficulties arose. A reference scenario should represent the present breeding structures and methods of the studied breeding programme very accurately. Because of the very complex structures in horse breeding many aspects had to be slightly simplified in order to obtain meaningful results. The clarification of this procedure is discussed in the following section.

In ZPLAN+ an economically weighted breeding goal and all genetic parameters have to be defined. In other livestock species this is unproblematic because clearly defined breeding goals based on economic weights are available. In horse breeding, however, the breeding goal is formulated opaquely. This and the fact, that most of the traits are assessed subjective, by economic weighting is very difficult to realize (Koenen, et al., 2003). Hence, a simplified breeding goal was suggested for the optimization of breeding programmes with ZPLAN+. The traits conformation and movements, free jumping, ride-ability and dressage as well as show jumping in competition were chosen. In Germany all of these traits are used for selecting mares and stallions for breeding programmes of sport horses. The economic weights of these traits were defined relative to each

other. While the competition traits were weighted four times (€2'000) the other three traits were weighted only once (€500). Genetic parameters are based on the results of Christmann (1996), Schade (1996) and the Fédération Equestre Nationale (2009). This so defined breeding goal provides a good basis for the optimization of breeding programmes with ZPLAN+.

The German horse breeding associations have to realise that particularly the implementation of new traits like radiographic findings (Stock and Distl, 2007; Sitzenstock, 2010a) or character and temperament (Graf et al., 2011) requires a transparent breeding goal and a rigorous selection. These new traits nowadays increase in importance and the implementation in the breeding programmes has to be validated. It is difficult to combine breeding goals for horses that will be used for different purposes. For instance, the requirements for horses that are supposed to join Olympic competitions will be different from the requirements for horses that that only serve for leisure purposes. In a calculation focusing the breeding programme on a single competition trait (Sitzenstock et al., 2010b) it was shown that the total return in a breeding programme can be increased and the return in the focused competition trait was also increased on a high level.

Many procedures in animal breeding are difficult to communicate from the breeding associations to the breeders. Estimated breeding values are available based on performance information of equitation as well as on mares' and stallions' performance tests (Jaitner and Reinhardt, 2003). This information is often not used for mating decisions of the breeders. Even the breeding associations do not use the breeding values for selection. In 2011 a new system for selecting stallions according to their stallions' performance test was implemented (Fédération Equestre Nationale, 2011). The selection is currently based on estimated breeding values calculated based on the own performance and the performance tests of all available related stallions. Before 2011 the selection was based on an index (Brockmann, 1998). This change was made to make the selection more objective so that all tested stallions in Germany are assessed on a comparable scale. But owners of stallions and breeders discuss this modification controversially because their aims are not primarily linked to

animal breeding or the maximization of the genetic gain in the breeding programmes at all.

Another problem in horse breeding programmes is the unilateral selection. This selection almost completely takes place on the stallions' side (Schade, 1996). In Chapter 3 it has been shown that the selection on the mares' side has a high potential for increasing the genetic gain. Horse breeding associations often cannot realize high selection intensities on the mares' side, because the owners of the mares which were not selected to be broodmares in the breeding programme change to other associations. This prevents horse breeding associations from stringent selection in order not to lose breeders and thereby financial backers. On the other hand, many breeders breed horses as a hobby and have no direct intentions of making profit or to increase the genetic gain of the whole breeding programme (SLU, 2001). However, taking into account the growing competition of other countries the success of German horse breeding associations depends on an increase of the number of successful sport and breeding horses.

Rigorous selection of mares and the targeted implementation of new reproduction techniques like embryo transfer show a great potential to achieve higher genetic gain in horse breeding programmes. In dairy cattle breeding programmes a combination of multiple ovulation and embryo transfer (MOET) has been suggested for using the best cows in the breeding programme in an optimal way (Nicholas and Smith, 1983). In horses inducing multiple ovulations is virtually impossible (Squires et al., 2003) and therefore high success rates as in cattle cannot be achieved.

Nonetheless, there are two alternatives in horse breeding for using embryo transfer in breeding programmes. First, mares which are intensively used in equitation could be used at the same time as donor mares for breeding. These mares often are among the best ones in the breeding programme and were even used for breeding just after their sport career. By this the generation interval is extended (Stout, 2006). Second, there is the possibility to produce several embryos from genetically superior mares which could either lead to a

higher genetic gain in the breeding programme or could be sold on the national or even international level.

It is obvious that horse breeding programmes have many stakeholders. Not all of these players are necessarily interested in the optimization of the breeding programme. It is therefore a difficult task to optimize the genetic gain and maximize the return of a breeding programme and to meet the different requirements of different persons at the same time. Nevertheless, it was shown that horse breeding programmes have a high optimization potential and design of breeding programmes a valid and valuable tool to optimize genetic and economic gain.

Breeding programmes for laying hens

The structures of layers breeding programmes are completely different from horse breeding programmes. All decisions are made in the breeding companies. The aims of the companies are to optimize breeding programmes and maximize the profit of the company at the same time. Only few companies operate on the global market and so they have to offer products for each regional market. The requirements of the regional markets depend on the usual housing systems and the market requirements of consumers. For all these special requirements breeding goals are adapted in different hybrids.

The breeding goal is not only well-defined, it also contains many traits. For all traits economic weights and genetic parameters are available. Hence, an current layer breeding programme was modelled in ZPLAN+ very close to reality. As a consequence, it is possible to model a meaningful reference scenario that enables the user to validate new breeding methods and selection strategies in layer breeding programmes.

In total over 20 traits were included in the breeding goal for layers breeding programme. The traits are defined in general for a long timeframe and have to adapt current market demands (Flock, 2005). Genetic correlations between the traits in the breeding goal only allow selection in particular directions. An

example is the negative correlation between laying performance and egg weight. This makes it necessary to breed two different laying hens for different market demands, one for markets desiring many small eggs and one for markets in which a premium is paid for larger egg size.

In the reference scenario, the breeding goal is focused on performance traits. The economic most important traits are laying performance and feed consumption (Thiruvankadan et al., 2010), but also functional and behaviour traits were accounted for. Such traits are becoming more and more important because of the change in the housing systems for laying hens in the European Union (van Horne and Bondt, 2003). Traits like nesting behaviour (Icken, 2006) as well as feather pecking and cannibalism (Kjaer and Sørensen, 2002) are economically interesting traits for barn and free range systems. These traits cannot be recorded in single-bird cages where the breeding flocks were kept. In this respect there is a need for optimization of the breeding goal and respectively of the whole breeding programmes. Information in these traits can be collected from crossbred animals which are kept in a practical environment and are half-sibs of the selection candidates.

Laying hens mostly are hybrids of four different lines. In these purebred lines the selection takes place and the genetic gain is generated. The number of breeding animals in a single line is low (König et al., 2009) because there is a multiplication stage in the production of the grandparental stock where the parental stocks of the laying hens are produced. With these multiplication steps it is possible to produce a high number of laying hens with only few breeding animals in the nucleus.

Because of the few breeding animals and the strong selection over 30 years within the lines a high level of homozygosity exists. Several studies showed that the increase of inbreeding has no significant or only a small negative impact on the genetic gain of traits in the breeding goal in poultry breeding (Savas et al., 1999; Sewalem et al., 1999; Besbes and Gibson, 1998).

The breeding programmes for laying hens are different from any other livestock species and especially from herd book breeding programmes like in horses.

Planning and optimizing breeding programmes is a continuous process in breeding companies to increase market share as well as profit. For this reason new breeding methods such as using genomic information have to be validated before implementation.

Implementation of genomic selection in breeding programmes

A further innovation in ZPLAN+ is the consideration of genomic information. The idea of genomic selection (Meuwissen et al., 2001) offers the possibility to revolutionize breeding programmes. This innovation is based on a high coverage of the whole genome with a new sort of markers, so called single nucleotide polymorphism (SNP). Especially in dairy cattle breeding programmes genomic selection allows a very accurate prediction of breeding values for young animals. The lengthy and expensive time of waiting for daughter information of young bulls can be reduced (Schaeffer, 2006; Hayes et al. 2009). In various livestock species it has been shown that ZPLAN+ could be used to assess the chances of integration of genomic information in breeding programmes (pig: Haberland et al., 2010; horses: Sitzenstock et al., 2011; cattle: Ytournal et al., 2011).

In Chapter 4 two different options for using genomic information for layers breeding programmes were compared. It is obvious that genomic information could be used in addition to all conventional performance information. Here the genetic gain as well as the return could be increased on a large scale. In a second scenario the genomic information can entirely replace the conventional information for selection. In that case the generation interval could be almost halved. In contrast to dairy cattle breeding genomic selection did not reduce the breeding costs directly. This is because most of the costs in layers breeding programmes occur for maintaining the breeding stock in the single lines. These costs accrue anyway and they are not directly associated with the performance testing. The costs for genotyping the calibration set and genotyping the selection candidates are also associated with high costs for the breeding companies. These costs are accompanied by an increase in genetic gain. Out

of this increase the breeding companies have to realize a higher return. For this, the customers of the companies have to be willing to pay more for an improved product. Similar considerations were made by Albers (2010) and Preisinger (2012).

One of the critical variables when using genomic information is the size of the calibration set. A large number of animals with accurate estimated breeding values are needed. In dairy cattle the calibration set for Holstein cattle was pooled together across associations and countries in Europe (Lund et al., 2010) as well as in North America (van Raden et al., 2009). By this it is possible to achieve high accuracy of the prediction of genomic breeding values, as the accuracy is linked directly to the calibration size (Daetwyler et al., 2010). In pigs as well as in poultry the calibration has to be made inside the breeds or lines. In both species the breeding companies are competitors and thus collaboration is not always possible. Another point is that the breeds and lines of the companies differ genetically. Hence, a combination of the calibrations sets is more difficult to establish and, arguably, less information than in cattle would be available. However, it might be possible to predict genomic breeding values across breeds and crossbred animals (de Roos et al., 2009; Toosi et al., 2010). Wolc et al. (2011) showed that the SNP-effects have to be re-calibrated in each generation for maintaining a high accuracy of the genomic information. It will be a challenge for breeding companies to reach sizes of their calibration sets which are big enough to get acceptable accuracies and desired effects when using genomic selection.

In pig breeding genomic information could increase the accuracy of the selection index and the genetic gain in breeding programmes (Haberland et al., 2010; Lillehammer et al., 2011). In this species similar problems and prospects as in poultry breeding are expected (Albers, 2010).

In horse breeding genomic selection is discussed as in any other livestock population. The question here is if the number of stallions with conventional estimated breeding values is large enough for building a calibration set. Further it is questionable if the current breeding values include all crucial traits. Calculations have shown that the implementation of genomic information for

functional traits has a high potential in horse breeding (Sitzenstock et al., 2010a and 2011). First genome-wide association studies in German sport horses for functional traits (Wulf et al., 2011) as well as for performance traits (Schröder, 2011) were carried out and yielded useful results. In Switzerland there are first results from association studies in Freiberger Horses (Hasler et al., 2011) aiming at the implementation of genomic selection in that breed. However, the successful implementation of genomic selection in horse breeding programmes will be heavily depends on the interests of the participants of the breeding programmes.

Inbreeding in planning breeding programmes

Another focus of the work was to generate a new method to assess for the average inbreeding rate and effective population size in the design of breeding progress (Chapter 2). Considering the development of inbreeding is a relevant tool for planning breeding programmes and for optimizing them. For this reason the calculation of kinship (Malécot, 1948) was implemented in the gene flow method (Hill, 1974; Elsen and Mocquot, 1974). It was shown that the approach is able to handle dynamic breeding programmes with changing population sizes and gene origins of newborn animals. The results are varying between different scenarios. Kinships within cohorts and between cohorts can be predicted at any time of interest. The average inbreeding coefficient of the whole breeding programme is calculated as well as the effective population size in every generation. This approach is a new tool for an all-embracing optimization of breeding programmes with ZPLAN+. Especially increasing selection intensity causes higher inbreeding rates in closed populations. In Chapter 3 it was shown that the implementation of an intensive selection and the usage of an effective reproduction technique like embryo transfer increases the inbreeding and decreases the effective population size.

Today, controlling parameters of inbreeding is of increasing importance. Especially the effective population size is one of the most relevant parameters in animal breeding. Daetwyler et al. (2010) showed that the accuracy of

genomic breeding values depends directly on the effective population size. With regard to the genetic diversity in livestock species inbreeding rates and effective population sizes provide valuable information for conservation of breeds (Groeneveld et al., 2009). The conservation of breeds and of genetic diversity in the different livestock species might be an important aspect for animal breeding under unknown future conditions (Rege, 1999).

One approach to control inbreeding in the optimization of genetic gain is to use the software SELACTION (Rutten et al., 2002) for predicting selection response in livestock breeding programmes. This software calculates the rate of inbreeding in breeding programmes with discrete generations and single-stage selection using the method of Wooliams and Bijma (2000). Padkel et al. (2005) compared five different breeding strategies in broilers with software SELACTION including the aspect of inbreeding and found very different inbreeding rates per year.

An approach to balance the rate of inbreeding and the genetic gain is presented by Meuwissen (1997). In this paper a new method was suggested to optimize the number of offspring per selected animal, the so-called optimum genetic contribution. Meuwissen (2002) introduced the software GENCONT which is based on this method. The software is based on a given detailed pedigree and not on an abstract breeding structure as in ZPLAN+. This approach was used for various livestock species. König and Simianer (2006) showed in different settings that using optimum genetic contribution is able to optimize genetic gain and inbreeding rate in dairy cattle breeding programmes. In layer breeding a higher genetic gain could be realized at the same level of inbreeding or a lower inbreeding rate could be achieved at the same level of genetic gain (König et al., 2010). Also in horse (Niemann et al., 2009) and pig breeding (Sonesson and Meuwissen, 2000) the concept of optimum genetic contribution has been validated. Schierenbeck et al. (2011) suggested to implement the genomic relationship instead of the pedigree-based relationship in optimum genetic contribution studies.

General perspectives and conclusions

With the modernization of software ZPLAN to ZPLAN+ a powerful tool for planning breeding programmes is now available. Questions on the optimization of breeding programmes in all livestock species can be answered with ZPLAN+. The optimization of existing breeding programmes or the conversion to new breeding programmes are an important aspect for breeding associations as well as breeding companies, especially in times of changes regarding technologies, consumer demands or regulatory frameworks. The validation of new breeding methods or new breeding tools is mandatory before implementing them in breeding programmes. In this thesis examples of such optimization of breeding programmes with completely different structures and requirements are shown.

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