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Modelling genomic selection schemes in Bavarian pig breeding programs using ZPLAN+

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Abbreviations

AI	artificial insemination
AGG	annual genetic gain
AMGG	annual monetary genetic gain
ANGG	annual natural genetic gain
ADG	average life-time daily gain
AGF	number of weaned piglets per litter
BLUP	best linear unbiased prediction
BU	breeding unit
Conv	conventional selection scheme
$C_{p,t}$	average pedigree completeness of the cohort born in the *t*
DE	Bavarian German Large While
DG	daily gain in fields
DGAT1	diacylglycerol O-acyltransferase 1
DL	Bavarian German Landrace
EB	selection group of elite boars
EB-PS	selection group of elite boars that produce crossbred offspring in PU
EBV	estimated breeding value
EGZH	Erzeugergemeinschaft und Züchtervereinigung für Zucht- und Hybridzuchtschweine / Community of Producers and Union of Breeders for Breeding and Hybrid pigs in Bavaria
ES	selection group of elite sows
FCR	feed conversion ratio
$\bar{F}_t$	average coefficient of the cohort born in the *t*
FT1	field-test of the traits DG and SPECK
FT2	field-test of the litter size traits AGF and LGF
FT3	field-test of the trait inverted teats of farrowed piglets
GBLUP	genomic best linear unbiased prediction
GEBV	genomic estimated breeding value
GS	genomic selection

h^2	heritability
HB	selection group of herd book boars that combines the selection groups YB, EB and EB-SP
HS	selection group of herd book sows that unites the selection groups of YS and ES
IMF	intramuscular fat content
L	genome length in Morgans
LD	linkage disequilibrium
LfL	Bayerische Landesanstalt für Landwirtschaft / Bavarian Institute of Agriculture
LGF	number of live born piglets per litter
LMP	lean meat percentage of carcass
MAS	marker-assisted selection
M_e	effective number of independent chromosome segments
MFR	meat-fat ratio
MMP	muscular-meat percentage
N	size of reference population for marker effect calibration
N_e	effective population size
N_{gmc}	size of genotyped male candidates
pH_1	pH value in M. long dorsi measured 45 minutes post mortem
PI	Bavarian Piétrain
PRKAG3	protein kinase, AMP-activated, gamma 3 non-catalytic subunit
PS	selection group of piglets production sows
PU	production unit
q^2	proportion of genetic variance explained by genome-wide markers
QTL	quantitative trait locus
r_{AI}	theoretical accuracy of BLUP EBV for sires or dams
r_i	accuracy of breeding values for the trait i in the reference population
r_{mg}	predicted accuracy of genomic breeding value
$r_{\hat{Q}}$	accuracy of estimates of marker effects
r_{TI}	accuracy of (selection) index

σ_p	phenotypic standard deviation
SG	selection group
SME	spine-muscle expanse
SNP	single nucleotide polymorphism
SPECK	ultrasonic back-fat thickness
ST	station-test of the traits ADG, FCR, IMF, LMP and pH_1
STLP	number of inverted teats
w	economic weight
YB	selection group of young boars
YS	selection group of young sows

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1 Introduction

Over about 9,000 years of pig domestication (Giuffra et al., 2000), the quality standards for pork meat have evolved. Modern consumers expect lean, nutritious and healthy meat. To meet such demands, pig breeders need to breed high performance and healthy animals, and at the same time to cope with increasing economic pressures. Hence, establishing efficient breeding programs is vital for them, especially in a competitive market place. Efficient breeding programs generally enforce selection strategies for stock animals that enable maximum genetic gains with low breeding costs.

1.1 Traditional selection methods

Most of livestock breeding aims to genetically improve traits of economic importance through artificial manners. Artificial selection of elite individuals with high breeding values to be the parents of the next generation is considered effective. The methods for artificial selection have evolved over the past few decades. In the early period, selection was mostly based on own conformation or performance. This method may not be accurate when there is a large environment contribution to the phenotype. Since the 1990s, best linear unbiased prediction (BLUP) (Henderson, 1984) has been introduced in livestock breeding for breeding values estimation. By this statistical procedure, estimated breeding values (EBVs) are derived from phenotypic and pedigree records. This strategy has been evidenced to be successful in increasing reliability of EBVs, and thus is of prevalence in many livestock breeding projects. For instance, an increase of about 5000 kg in average milk yield has been achieved in the American diary cattle population over the past 40 years, and 60% can be attributed to this state of the art (Zhang et al., 2011). Nevertheless, for traits with low heritability, sex-limited traits, and traits that are difficult or expensive to measure (such as carcass traits), such phenotype- and pedigree-based methods are inefficient. Besides, application of progeny testing mostly leads to long generation intervals.

With the advance of molecular genetics, specific loci on the genome that explain a major genetic variation can be discovered. Fernando and Grossman (1989) proposed a method named marker-assisted selection for combining information from a relevant locus with a polygenic term when predicting EBVs. Industry application of MAS has been considerably successful, such as *DGAT1* gene for milk yield in dairy cattle (Grisart et al., 2002), *Callipyge* gene for growth and composition in sheep (Freking et al., 2002), *PRKAG3* gene for meat quality in pigs (Milan et al., 2000). In general, although molecular genetic information has been used in industry programs for several decades and is growing, the extent of use has not lived up to initial expectations (Dekkers, 2004). There may be two major reasons. Firstly, many economic traits are influenced by many quantitative trait loci (QTLs) across the whole genome. Tracking a small number of QTLs through limited detected markers will only explain a small proportion of the variance. Secondly, most of major QTLs were identified in experimental populations using crosses between breeds or lines (Andersson, 2001). Such studies identify QTLs that differ in frequency between breeds but results cannot be used directly for selection within breeds (Dekkers, 2004).

1.2 Genomic selection strategies

With the advance of animal genome sequencing, a large number of markers covering whole genomes have been discovered (Zhang et al., 2011). Meuwissen et al. (2001) proposed a method to select animals based on genotypes of genome-wide dense markers, a procedure which was termed genomic selection. Genomic selection can be considered as a variant of marker-assisted selection (Goddard and Hayes, 2007), assuming the dense markers covering the whole genome are in linkage disequilibrium (LD) with each QTL so that all the genetic variance is captured by markers. The criteria for selection are termed genomic estimated breeding values (GEBVs). GEBV is the sum of additive genetic effects of makers covering the whole genome that are estimated in the reference population. The reference population is a sample of animals that were both phenotyped and genotyped, used for calibration of the additive genetic effect of each marker. Compared to marker-assisted selection, genomic selection skips the difficulty of detecting individual QTLs, with either significant or fractional contribution on the phenotypic variation. Focusing on all the QTLs through genome-wide dense markers that are in LD with them, genomic selection is more accurate than marker-assisted selection. According to Hayes et al. (2009a), the accuracy of GEBV depends on four parameters: 1) the level of LD between the markers and the QTL, 2) the number of animals with phenotypes and genotypes in the reference population from which the SNP effects are estimated, 3) the heritability of the trait in question, or , if de-regressed breeding values are used, the reliability of these breeding values, and 4) the distribution of QTL effects. The first two are under the control of the experiments and the second two are not. The single markers should be in sufficient LD with the QTL so that the markers will predict the effects hold by the QTL across the population and across generations. The extent of LD between markers and QTL can be determined with the parameter r^2 (Hill, 1981), and r^2 measures the proportion of the variation explained by the alleles at a QTL. According to the simulation of Meuwissen et al. (2001), the level of LD between adjacent markers (haplotypes) should be $r^2 \geq 0.2$ as long as accuracies of GEBV of 0.85 are expected. Calus et al. (2008) used simulation to evaluate the effect of the average r^2 between adjacent marker pairs on the accuracy of genomic selection by using single SNP rather than haplotypes, and observed the accuracy of GEBV increased dramatically along with the average r^2 increased, from 0.68 when the average r^2 was 0.1, to 0.82 when the average r^2 was 0.2. The accuracy of GEBV will also be affected by the number of phenotypic records that are used for estimating the marker effects in the reference population. The more phenotypic records available, the more observations there will be per marker allele and the greater the accuracy of GEBV. In dairy cattle breeding, Hayes et al. (2009a) showed that reliabilities of GEBV for young bulls without progeny testing results in the reference population were between 20 and 67% in a world-wide investigation.

High extent of LD as reported by Uimari and Tapio (2011) and Badke et al. (2012) in the US and Finnish pig breeds respectively are comparative with those in North American Holstein cattle. These findings corroborate applying genomic selection in breeding programs with e.g. the 60k SNP chip. However, GS in pig breeding programs has still not been widely applied yet. There are several limitations. Establishing a large reference population consisting of progeny tested boars comparable to the cases in dairy cattle is extremely difficult by most of the pig breeding organizations. For instance, the reference population of the EuroGenomics project (Lund et al., 2010) is made up of 25,000 progeny tested bulls. Besides, pig breeding is much less dominated by the selection of male animals only, due to the much higher reproduction rates compared to cattle. Moreover, pig populations have relatively low generation intervals (2-2.5 years on average) in comparison to dairy cattle (ca. 5-7 years). Schaefer (2006) stated bull breeding companies can save up to 92% of their costs by avoiding progeny test. GS potentially can double the rate of genetic gain through selection and breeding from bulls at an age of 2 years rather than 5 years or later. Thus, the benefit resulting from substantial reduction of generation interval and the relevant breeding costs is not as distinct as that in dairy cattle. In light of such factors, the major potential for GS in pig breeding lies in the high accuracies of genomic breeding values and intensities of selection, not so much in the shortened generation interval.

Up to date, several initiatives have studied the potentials of GS in pig breeding programs. In studies of GS for fertility, Simianer (2009) showed that implementing GS in a two-line model breeding program can achieve an increase of 37% in the genetic gain per year relative to the conventional scenario and an extra return of 6.76 € per euro invested in genotyping. Forni et al. (2010) revealed an increase of 68% in the accuracy of breeding values of the training population over traditional selection (BLUP); Using training populations of individuals with high accuracy of EBVs in place of the phenotypes of total born and stillborn, Cleveland et al. (2010) obtained accuracies of 0.83-0.63, which is similar to those reported for a range of traits in dairy cattle when similar-size training populations (~3,000) were used. On the other hand, a few negative results were also observed mainly concerning the failure of consistency of accuracies across generations (Cleveland et al., 2010; Ibáñez-Escriche and Blasco, 2011; Toro and Varona, 2010). This indicates that a constant re-phenotyping and re-genotyping is required. This may lead an increase in the monetary costs of GS. However, with the decrease of genotyping costs GS may still be promising in pig breeding in the near future. Accurately predicting GEBVs plays an essential role for implementing GS, and so there have been a few methods proposed for this purpose such as GBLUP (Christensen and Lund, 2010; VanRaden, 2008) and Bayes-A or -B (Meuwissen et al., 2001).

1.3 Introduction of the software ZPLAN+

Since GS offers great opportunities for livestock breeding, how to desgin breeding programs incorporating GS becomes a practical issue. Up to date, most efforts have been concentrated on the development of tools to incorporate the large amount of genomic information into statistical analyses and genomic evaluations (Ibañez-Escriche and Gonzalez-Recio, 2011). ZPLAN+ is an easy-to-use software to evaluate and optimize animal breeding programs (Täubert et al., 2010), developed based on the gene flow method (Hill, 1974) and selection index theory (Hazel and Lush, 1942). It allows integration of genomic and traditional phenotypic information in breeding program designs. Prediction of selection response is deterministic and based on truncation selection assumption (Falconer and Mackay, 1996), that is

$$\Delta G = i * r_{TI} * \sigma_g^2 / GI \quad \text{(Equ.1)},$$

where i is the intensity of selection, r_{TI} is the accuracy of selection index, σ^2_g denotes the genetic variance and GI represents the generation interval.

It models breeding programs by simulating the biological parameters (e.g. the numbers of tested and selected animals, reproduction cycle, productive lifetime, age at first reproduction and survival rate) and the economic parameters (e.g. the economic values of breeding goal traits, breeding costs, interest and discounting rate etc.). ZPLAN+ has been first employed in developing practical breeding programs for Holstein populations (Täubert et al., 2011). Experimental studies on other livestock such as pig, horse and layer are ongoing in corporation with breeding companies.

Table 1 Mean performances of average daily gain (ADG), feed conversion rate (FCR), Spine-muscle expanse (SME), meat-fat ratio (MFR), muscular-meat percentage (MMP) and intramuscular fat content (IMF) for the dam line German-Landrace (DL) and sire line Piétrain (PI) and crossed line PI × DL in Bavaria (stMELF, 2010).

Line	ADG [g/day]	FCR [kg/kg]	SME [cm^2]	MFR 1:	MMP [%]	IMF [%]
DL	941	2.59	45.1	0.47	55.3	1.44
PI	784	2.25	68	0.13	67.7	1.15
PI x DL	834	2.3	60.9	0.20	64.3	-

1.4 Brief introduction of the lines of German Landrace and Piétrain in Bavaria

To use complementary attributes of different lines and heterosis effects (Habier, 2006), most pigs used for pork production are crossbred. In Bavaria, three major pig lines are kept. Piétrain (PI) boars sired 95% of all Bavarian fatteners and accounted for 16.7% of the total herd book animals (stMELF, 2010). The dam lines are mainly German Landrace (DL) (73.3%) and German Large White (DE) (9.9%). Characteristic for PI is the high flesh and ham proportion with very low intramuscular fat content (Sambraus, 1994). Unlike PI, DL shows very good fattening and meat performances as well as fertility attributes. In Bavaria it is used as a dominating dam line. The average daily gain of 941 g and feed conversion of 2.59 kg with 1kg weight of growth were observed in 2010 (Table 1). The annual report features DL on high fertility of 22 live born piglets per year with only 9.4% loss rate (LKV, 2010). The breeding goal of EGZH (Erzeugergemeinschaft und Züchtervereinigung für Zucht- und Hybridzuchtschweine / Community of Producers and Union of Breeders for Breeding and Hybrid pigs in Bavaria) in 2010 for the dam lines is primarily (70%) focused on the fertility of the sows. Another focus is on the level of weight gain (14%). Due to strong selection since 1986, the dam line DL is nearly completely stress resistant (Pausch, 2009). For the Bavarian pig production system, Piétrain boars are used to mate sows of the lines such as DL, DE and DL × DE. Table 1 shows the mean performances of purebred pigs of PI and DL, and crossbred pigs from intercross PI × DL.

Since the introduction of BLUP in the breeding value estimation for Bavarian pigs in 1995, the Bavarian institute of Agriculture (LfL) renews the breeding goal within either boar or sow line every five years. The renewal is preceded by several rounds of internal discussion among representatives of insemination stations, piglets producers, breeders and slaughtering companies, based on the current demands of the market. The last renewal was put into practice after the usual preliminary phase in summer 2010.

The purpose of this study was to model potential GS schemes in the breeding programs for the dam line German-Landrace and the sire line Piétrain in Bavaria, using the software ZPLAN+. The complex breeding goal and population structure for both lines were taken into account.

Ultimately, two GS schemes were established for each line. A number of evaluation parameters relevant to genetic trend and economic efficiency were compared to the conventional progeny-test-based scheme. By varying the size of the reference population for calibrating SNP effects and the number of genotyped male selection candidates, opportunities and limitations for applying the modelled GS schemes in Bavarian breeding programs were discussed. The thesis also aims to present a methodology for designing and evaluating GS schemes in pig breeding programs.

2 Data and methods

2.1 Data

The current breeding programs for DL and PI were provided by the Bavarian Institute of Agriculture (LfL). The programs contained essential information for performance testing, testing costs, selection practice and animal life cycle. The Bavarian pig herd book association renews the breeding goal every 5 years, where new breeding goal traits along with their economic weights are determined. The breeding goal updated in 2010 included five traits for DL. These were average daily gain (ADG) and feed conversion ratio (FCR) between 30 and 105 kg live weight, number of live born piglets per litter (LGF), number of weaned piglets per litter (AGF) and number of inverted teats (STLP). The breeding goal traits for PI were ADG, FCR, intramuscular fat content (IMF), lean meat percentage of carcass (LMP) estimated via a standard multiple regression equation used at all German testing stations (ALZ, 2003), and pH value in M. long dorsi measured 45 minutes post mortem (pH_1). Lifetime daily gain (DG) and ultrasonic back-fat thickness (SPECK) at an average live-weight of 115 kg were also recorded. For both lines, these traits routinely serve as the correlated traits for the breeding goal traits. Economic weights for breeding goal traits were available from LfL in a separate data sheet which also included the heritability, phenotypic standard deviation, genetic and phenotypic correlation for each trait (Table 2). In addition, the pedigree data for herd book animals born between 1980 and 2007 were provided.

Table 2 Overview of traits in terms of theoretical accuracy of BLUP estimated breeding value (r_{AI}) for sires or dams, heritability (h^2), phenotypic standard deviation (σ_p), economic weights (w), and phenotypic and genetic correlations (phenotypic correlations above and genetic correlations below the diagonal) in the current Bavarian German-Landrace **(a)** and Piétrain **(b)** breeding populations.

(a)

Trait	Unit	h^2	σ_p	w	r_{AI}		Genetic and phenotypic correlations									
				[€]	sire	dam	ADG	AGF	DG	FCR	IMF	LGF	LMP	pH_1	SPECK	STLP
ADG	g/d	0.39	85	0.10	0.7684	0.6590	-	0.0040	0.2370	-0.6880	-0.0420	0.0090	0.1157	0.0091	-0.0220	0.0119
AGF	piglets	0.10	1.8	20	0.7776	0.4007	0.0280	-	0.0190	0.0000	0.0970	0.8649	-0.1020	0.1020	-0.0060	-0.0820
DG	g/d	0.31	55	-	-	-	0.7430	-0.1520	-	-0.1500	-0.0410	0.0360	0.0150	0.0270	0.1360	-0.0030
FCR	kg/kg	0.27	0.20	-10	0.8508	0.5334	-0.3381	0.0000	-0.3000	-	0.1256	0.0000	-0.1422	0.0816	0.0500	0.0000
IMF	%	0.64	0.37	-	-	-	-0.1944	0.0190	-0.0920	0.2466	-	0.0490	-0.1336	-0.0459	0.0270	0.0572
LGF	piglets	0.11	1.8	10	0.7953	0.4081	0.0570	0.8840	-0.1500	0.0000	0.0110	-	-0.0500	0.0620	-0.0120	-0.0630
LMP	%	0.69	2.2	-	-	-	0.3165	-0.0210	0.0340	-0.2017	-0.1491	-0.0110	-	-0.0368	-0.2940	0.1291
pH_1	mol/L	0.20	0.20	-	-	-	-0.0796	0.0100	0.1200	0.1304	0.0082	0.0070	-0.0966	-	0.0230	-0.0048
SPECK	mm	0.30	1.9	-	-	-	-0.0730	0.1310	0.1850	0.1000	0.0630	0.1080	-0.6650	0.1090	-	-0.0410
STLP	%	0.19	33	0.45	0.7125	0.3722	0.0757	-0.0080	-0.0130	0.0000	-0.0286	-0.0070	0.0494	0.0056	-0.1860	-

(b)

Trait	Unit	h^2	σ_p	w	r_{AI}		Genetic and phenotypic correlations						
				[€]	sire	dam	ADG	DG	FCR	IMF	LMP	pH_1	SPECK
ADG	g/d	0.24	70	0.10	0.7658	0.4909	-	0.092	-0.342	0.089	-0.235	0.042	0.016
DG	g/d	0.19	49	-	-	-	0.460	-	-0.068	0.032	-0.041	0.044	0.129
FCR	kg/kg	0.20	0.17	-30	0.7470	0.4698	-0.380	-0.310	-	0.091	-0.166	0.003	0.029
IMF	%	0.43	0.26	9.1	0.8335	0.4549	0.170	0.220	-0.060	-	-0.065	0.000	0.101
LMP	%	0.40	2.1	2.1	0.8281	0.4996	-0.350	-0.170	-0.380	-0.150	-	-0.220	-0.078
pH_1	-	0.44	0.22	7.7	0.8397	0.5169	0.100	0.170	0.150	0.050	-0.390	-	0.108
SPECK	mm	0.32	0.14	-	-	-	0.120	0.160	0.230	0.270	-0.430	0.550	-

Abbreviations for traits: ADG = average daily gain; AGF = number of weaned piglets per litter; DG = daily gain (in fields); IMF = intramuscular fat content; FCR = feed conversion ratio; LGF = number of live born piglets per litter; LMP = lean meat percentage of carcass; pH_1 = pH value in m. long dorsi measured 45 minutes post mortem; SPECK = ultrasonic back-fat thickness; STLP = percentage of progenies for a boar that has no inverted teats.

2.2 Methods

For DL or PI, a conventional selection scheme (***Conv***) was established to reflect the current selection scheme for the male path with use of pedigree, own and progeny information. On the basis of ***Conv***, genomic selection (GS) schemes were modelled with attempts to integrate genomic information in the current breeding program. They were compared to ***Conv*** to evaluate the potentials on both genetic trends and economic efficiency. The software ZPLAN+ (Täubert et al., 2010), which is developed based on selection index (Hazel and Lush, 1942) and the gene flow method (Hill, 1974), were adopted to derive the evaluation parameters. The considered evaluation parameters included: overall generation interval within the investment period, accuracy of selection index (r_{TI}) in terms of correlation between selection index and aggregate economic breeding value, genetic trend in terms of annual natural genetic gain for individual breeding goal traits (*ANGG*), trend for aggregate economic breeding value in terms of annual monetary genetic gain (*AMGG*), discounted return and costs per animal in the whole population within an investment period of 10 years, and discounted profit as discounted return minus discounted costs. In addition to these parameters, the annual genetic gain (*AGG*, referring to *ANGG* or *AMGG*) relative to the magnitude under the ***Conv*** were compared between the GS schemes. Such relative annual genetic gain was calculated as

$$rel.AGG = \frac{AGG_{GS\,scheme}}{AGG_{Conv}} \times 100\,\% \quad .$$

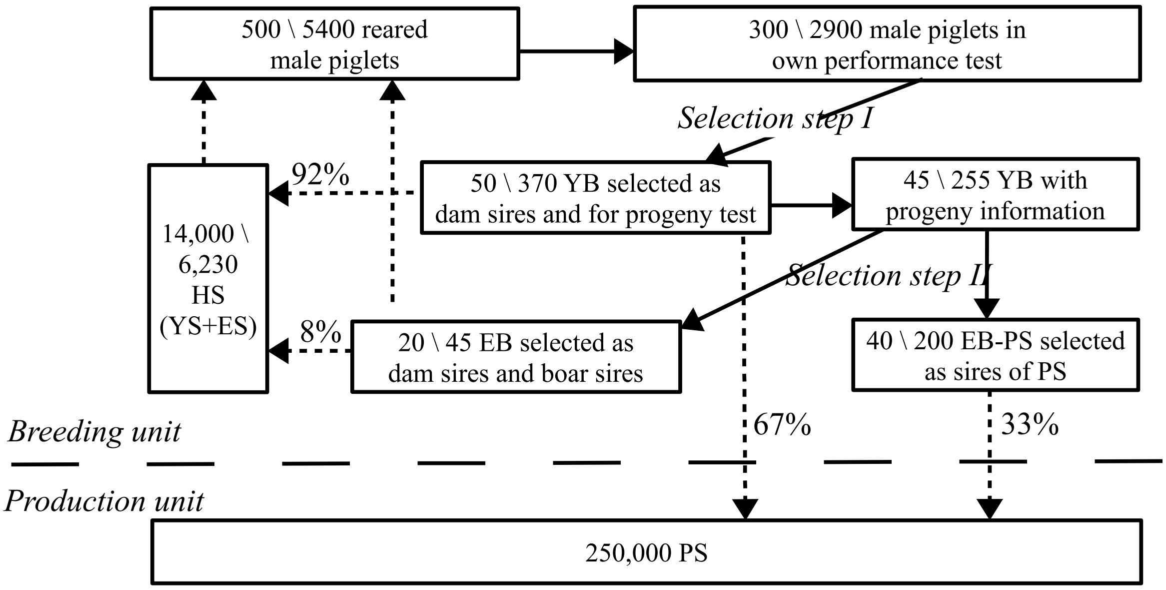


Figure 1 Selection steps for herd book boars in the conventional selection scheme. The figures prior to the "\" refer to German-Landrace, while the ones after that refer to Piétrain. The arrows with solid line refer to the selection steps and the arrows with dashed line refer to the selection paths. The proportions indicate the rates of gene contribution. YB = young boars; EB = elite boars; EB-PS = elite boars siring production sows; YS = young sows; ES = elite sows; PS = production sows.

2.2.1 Description of the modelled selection schemes

2.2.1.1 Conventional scheme

In the conventional selection scheme (Conv) for DL or PI, both the herd book population (breeding unit / BU) and the piglet production population (production unit / PU) were taken into account (Figure 1). Selection paths were partitioned characterizing the flows of genetic superiority (genes) of parents to offspring (Table 3). In ZPLAN+, a selection path is determined by two selection groups (SGs), whereby genes flow from one parental SG to the other offspring SG. A selection group (SG) comprises contemporary animals of the same sex with uniform selection and breeding characteristics: the number of tested and selected individuals, the information sources of selection index, the length of a reproduction cycle, age at first reproduction and the productive lifetime etc. (VIT, 2011). For both DL and PI, the BU was separated into three male SGs and two female SG. The male SGs were young boars (YB), elite boars that active in BU (EB) and elite boars siring production sows (EB-PS). YB and EB united to be herd book boars (HB). The female SGs were young sows (YS) and elite sows (ES). YS and ES united herd book sows (HS). In PU, only one female SG, the sows responsible for piglets production (production sows / PS), were considered. Because normally only females produce offspring that can be sold (VIT, 2011), YS, ES and PS played the roles to realize genetic gains generated within BU. The population sizes of YB, EB, EB-PS, YS and ES were 500, 40, 80, 12000 and 2000 for DL, and 5400, 255, 255, 5600 and 215 for PI, respectively (Table 5). A fixed size of 250000 was assumed for PS in both DL and PI.

Table 3 Pedigree matrices as the demonstrations of the selection paths for the conventional selection and genomic selection schemes. For a certain selection path, genes flow from a parental selection groups (Parental SG) to an offspring selection group (Offspring SG).

Offspring SG	Parental SG					
	YB	EB	EB-PS	YS	ES	PS
HB	0	1	0	0.4	0.6	0
HS	0.92	0.08	0	0.4	0.6	0
PS	0.67	0	0.33	0	0	1

YB = young boars; EB = elite boars; EB-PS = elite boars siring production sows; YS = young sows; ES = elite sows; PS = production sows.

Table 4 Breeding events for herd book boars and sows in the conventional selection scheme for German-Landrace **(a**, **b)** and Piétrain **(c**, **d)**.

(a)

Age	Breeding events for herd book boars
0	Birth
21 d	Reared candidates entering the field test of own performances
8 m	Completion of field test, 1st step selection for young boars (YB)
10 m	Completion of 2-month quarantine in AI stations, mating of YB
1.15 yr	Birth of the 1st offspring of YB assuming 114 days of gestation for sows
2 yr	Progeny information (on station-test-traits) is available
3 yr	Daughter information (on litter size) is available, the 2nd-step selection for elite boars (EB) and elite boars siring production sows (EB-PS), mating of EB or EB-PS
3.3 yr	Birth of the 1st offspring of EB and EB-PS assuming 114 days of gestation for sows
5.3 yr	Use time of EB and EB-PS for 2 years

(b)

Age	Breeding events for herd book sows
0	Birth
21 d	Reared candidates entering the field test of own performances
8 m	Information from half and full sibs on test station is available 1st step selection for young sows (YS), mating of YS
~1 yr	Birth of the 1st offspring of YS assuming 114 days of gestation for sows, litter size of YS is available, inverted teats of progeny is recorded
20 m	Progeny information (on station-test-traits) is available, the 2nd-step selection for elite sows (ES), mating of ES
~2 yr	Birth of the 1st offspring of ES assuming 114 days of gestation for sows
~5 yr	Use time of ES for 3 years

(c)

Age	Breeding events for herd book boars
0	Birth
21 d	Reared candidates entering the field test of own performances
8 m	Completion of field test, 1st step selection for young boars (YB)
10 m	Completion of 2-month quarantine in AI stations, mating of YB
1.15 yr	Birth of the 1st offspring of YB assuming 114 days of gestation for sows
2 yr	Progeny information (on station-test-traits) is available, the 2nd-step selection for elite boars (EB) and elite boars siring production sows (EB-PS), mating of EB or EB-PS
2.3 yr	Birth of the 1st offspring of EB and EB-PS assuming 114 days of gestation for sows
4.3 yr	Use time of EB and EB-PS for 2 years

(d)

Age	Breeding events for herd book sows
0	Birth
21 d	Reared candidates entering the field test of own performances
8 m	Information from half and full sibs on test station is available 1st step selection for young sows (YS), mating of YS
~1 yr	Birth of the 1st offspring of YS assuming 114 days of gestation for sows, litter size of YS is available, inverted teats of progeny is recorded
20 m	Progeny information (on station-test-traits) is available, the 2nd-step selection for elite sows (ES), mating of ES
~2 yr	Birth of the 1st offspring of ES assuming 114 days of gestation for sows
~5 yr	Use time of ES for 3 years

Table 5 Definition of selection groups (SGs) in the conventional selection scheme in ZPLAN+. The figures prior to the "\" refer to German-Landrace, while the ones after that refer to Piétrain.

SG [1]	Size [2]	Candidates [3]	Selected [4]	Prod. Lifetime (yr) [5]	1st offs. (yr) [6]	Surv. Rate [7]
YB	500 \ 5,400	300 \ 2,900	50 \ 370	2.15 \ 1.15	1.15	0.9
EB	40 \ 255	45 \ 255	20 \ 45	2	3.3 \ 2.3	0.9
EB-PS	80 \ 255	45 \ 255	40 \ 200	2	3.3 \ 2.3	1
YS	12,000 \ 5,600	10,800 \ 430	3,500 \ 250	1	1	0.7
ES	2,000 \ 215	2,450 \ 215	666 \ 210	3	2	0.7
PS	250,000	50,000	50,000	5	1	1

[1] Five selection groups were classified in the breeding unit (i.e. YB, EB, EB-PS, YS and ES) and one selection group in the production unit (i.e. PS); YB = young boars; EB = elite boars; EB-PS = elite boars siring production sows; YS = young sows; ES = elite sows; PS = production sows.

[2] Population size of the selection group.

[3] Number of candidates.

[4] Number of selected animals for replacement per time unit.

[5] Productive lifetime: use time of a selection group from the 1st reproduction to culling.

[6] Age of animals in a selection group when producing the 1st offsprings.

[7] Survival rate: The proportion of animals remained in a selection group after each reproduction.

Breeding events for boars and sows of both lines were summarized in Table 4, and the selection steps for herd book boars were illustrated in Figure 1. In ***Conv*** for DL, 500 weaned male piglets were reared per year after a preselection regarding growth, conformation and functional criteria. 300 of them were screened to enter own performance test in fields (field-test of DG and SPECK) according to breeding values of parents. They were considered as the selection candidates for herd book boars (YB and EB), which would be used for artificial insemination. At the 1st step, 50 YB were selected as dam sires entering artificial insemination (AI) stations (Table 5). The selection criteria were BLUP EBVs of the parents (i.e. pedigree information) and the own performances (Table 6 **(a)**). The costs for obtaining the parental EBVs were considered free of charge for the current round of selection. Field-test of DG and SPECK (FT1) costs 40 € per male candidate, and it was completed at the age of 8 months (0.67 yr) when the candidates reached the average final live-weight for pork industry (115 kg). The 1st step selection was followed by a quarantine period of 2 months in AI stations. Then, the new YB animals were mated to herd book sows (HS) via AI to produce the next generation of HS and for progeny testing. They also served production sows (PS) to produce the next generation of PS. This indicated two selection paths

YB>HS and YB>PS. With a gestation period of 114 days for sows, YB had their 1st offspring at ca. 1.15 years old. Then they continued to be used for 2.15 years (productive lifetime = 2.15 yr) (Table 5). In Bavaria, ADG, FCR, IMF, LMP and pH_1 was tested on stations. The costs for station-test (ST) were assumed 100 € per test animal. Litter size performances AGF and LGF were recorded for dams in fields, where inverted teats for the farrowed piglets were also observed. Herein, these two tests were termed FT2 and FT3 respectively. FT2 and FT3 were regarded free of charge because they can be done by the breeders themselves. The progeny testing for the 2nd step selection collected the information from 18 progenies (9 full-sib groups with 2 full sibs in each) on these station-test (ST) traits and inverted teats, as well as 40 daughter on AGF and LGF. The 2nd step selection for elite boars (EB) took place at the age of 3 yr when the considered information of all test progenies was available. At this step, 20 EB were selected as dam sirs and boar sires out of 45 YB survived in AI stations, and 40 EB-PS were selected as sires of production sows (PS). Immediately following the selection, EB served herd book sows (HS) for producing the next generation of herd book boars (HB) and herd book sows (HS), resulting in the selection paths EB>HB and EB>HS. EB-PS were mated to PS for producing the next generation of PS, leading to the selection path EB-PS>PS. EB and EB-PS subsequently generated their 1st offspring at the age of ca. 3.3 yr. Afterwards, EB and EB-PS continued their services in AI stations for 2 years (productive lifetime = 2 yr). For the female path, a two-step selection was also applied. 12000 weaned female piglets after a preselection based on the conformation and functional criteria were reared. 10800 of them were qualified according to breeding values of parents, as the candidates for young sows (YS) and elite sows (ES) (Table 4 **(b)**). At an age of 8 months, 3500 candidates were selected as YS at the 1st step based on the parental EBVs and the station-test results of 4 half sibs and 2 full sibs. Immediately, they were mated to herd book boars (HB) to produce the new generation of HB and HS (i.e. YS>HB and YS>HS) and for progeny testing. YS had their 1st offspring at the age of 1 yr and continued their service for 1 yr (productive lifetime = 1 yr). At the age of 20 months (1.67 yr), the station-test (ST) of progeny was completed. 666 ES were selected out of 2450 YS based on the above testing results as well as the information for the 1st step selection. These ES animals served herd book boars (HB) to produce the next generation in BU (ES>HB and ES>HS). Subsequently, ES farrowed the 1st offspring at the age of 2 yr, and then continued to be used in the herd book for 3 years (productive lifetime = 3 yr). According to the guideline, no effective selection was conducted on production sows (PS) (Table 5). The PS animals were 1 yr at their 1st farrowing and continued to be used for 5 years (productive lifetime = 5 yr). It was assumed that the survival rate after each reproduction cycle (survival rate) for YB, EB, EB-PS, YS, ES and PS was 0.9, 0.9, 1, 0.7, 0.7 and 1.0 respectively (Table 5). The studied selection paths were schematically demonstrated by the “pedigree matrices” constructed in ZPLAN+ (Table 3). In a “pedigree matrix”, the column header refers to parental SGs which contributed genes and the row header refers to offspring SGs that received genes. An intersection denotes a proportion of received genes that were transmitted from a particular parental group (VIT, 2011). For an offspring group, the proportions have to sum up to 100% on either the paternal or the maternal side. According to the latest population analysis, YB were supposed to sire 92% of the herd book sows (HS) and EB to sire 2%. Besides, YB sired two thirds of ES and EB sired one third. On the maternal side, 40% of herd book boars (HB) or HS originated from YS and 60% from ES. PS only transmitted genes to the next generation of its own.

Table 6 Cost parameters in terms of cost groups (or selection groups) in the conventional selection scheme for German-Landrace **(a)** or Piétrain **(b)**.

(a)

Cost group [1]	Cost parameters						
	Info. Source [2]	Test [3]	No. of tested groups	No. of ind. in tested groups	Relation between tested groups	Cost per ind. (€)	Mean age of cost group (yr) [4]
YB	Sire	EBVs	1	1	-	-	0
	Dam	EBVs	1	1	-	-	0
	Self	FT1	1	1	-	40	0.67
EB or EB-PS [5]	Progeny	ST	9	2	Half-sib	100	2
	Progeny	FT3	9	2	Half-sib	-	2
	Progeny	FT2	40	1	Half-sib	-	3
YS	Sire	EBVs	1	1	-	-	0
	Dam	EBVs	1	1	-	-	0
	PHS	ST	4	1	Half-sib	100	0.67
	FS	ST	1	2	-	100	0.67
ES [6]	Progeny	FT3	2	1	-	-	1
	Progeny	ST	1	2	-	100	1.67
PS	-	-	-	-		-	-

(b)

Cost group [1]	Cost parameters						
	Info. Source [2]	Test [3]	No. of tested groups	No. of ind. in tested groups	Relation between tested groups	Cost per ind. (€)	Mean age of cost group (yr) [4]
YB	Sire	EBVs	1	1	-	-	0
	Dam	EBVs	1	1	-	-	0
	Self	FT1	1	1	-	40	0.67
EB or EB-PS [5]	Progeny	ST	9	2	Half-sib	100	2
YS	Sire	EBVs	1	1	-	-	0
	Dam	EBVs	1	1	-	-	0
	PHS	ST	4	1	Half-sib	100	0.67
	FS	ST	1	2	-	100	0.67
ES [6]	Progeny	ST	1	2	-	100	1.67
PS	-	-	-	-	-	-	-

[1] Five selection groups were classified in the breeding unit (i.e. YB, EB, EB-PS, YS and ES) and one selection group in the production unit (i.e. PS); YB = young boars; EB = elite boars; EB-PS = elite boars siring production sows; YS = young sows; ES = elite sows; PS = production sows.

[2] PHS = paternal half-sibs; FS = full-sibs.

[3] EBVs = BLUP estimated breeding values for breeding goal traits; ST = station-test of ADG, FCR, IMF, LMP and pH_1; FT1= field-test of DG and SPECK; FT2 = field-test of LGF and AGF; FT3 = field-test of STLP; Abbreviations for the traits, see footnote Table 2.

[4] Mean age of cost group when the information source is available.

[5] The information sources for the 1st step selection for YB were also included in the selection criteria for the 2nd step selection for EB or EB-PS, but were not repeatedly listed.

[6] The information sources for the 1st step selection for YS were also included in the selection criteria for the 2nd step selection for ES, but were not repeatedly listed.

The conventional scheme for PI differed from that for DL in terms of breeding goal, breeding events (Table 4), selection group parameters (Table 5) and performance testing (Table 6). However, the selection steps for herd book boars were similar to DL (Figure 1). 5400 weaned male piglets were reared per year according to the conformation and functional criteria. 2900 of them that passed the a family selection based on parental breeding values were considered as the candidates for herd book boars (YB and EB). They finished their own performance test in fields at age of 8 months by which the 1st step selection was followed. 370 YB animals were selected based on parental EBVs and own performance on DG and SPECK. After a 2-month quarantine in

AI stations, YB served herd book sows (HS) for siring the next generation of HS and PS (i.e. YB>HS and YB>PS), and for progeny testing. Progeny testing in PI referred to a station-test of the traits ADG, FCR, IMF, LMP and pH_1. Until the information from 18 progenies (9 full-sib groups with 2 full sibs in each) was available (at ca. 2 yr old), the 2nd step selection was conducted. 45 EB and 200 EB-PS animals were identified out of 255 YB based on the progeny performances on stations and the criteria for the 1st step selection. EB and EB-PS had the 1st offspring in BU and PU respectively (i.e. EB>HB, EB>HS and EB-PS>PS) at the age of 2.3 yr old. Similar to DL, the productive lifetime for EB and EB-PS were supposed to be 2 yr. For the female path, after a culling against conformation and functional deficiency and the family selection, 430 weaned female piglets were kept for rearing. At about 8 months old, station-test of 4 paternal half sibs and 2 full sibs was completed, and thus 250 YS was selected at the 1st step based on the test results and parental EBVs. Then, YS was mated to herd book boars (HB) for YS>HB and YS>HS and for progeny testing on stations. YS had their 1st offspring at the age of 1 yr and continued their service for 1 yr (productive lifetime = 1 yr). The progeny performance for YS were available at 20 months (1.67 yr) old. Based on the progeny performance as well as the information for the 1st step selection, 210 ES were selected from 215 YS. Subsequently, ES farrowed the 1st offspring in HB and HS (i.e. ES>HB and ES>HS) at 2 yr old, and they were further used for 3 yr (productive lifetime = 3 yr). The survival rate after each reproduction cycle (survival rate) for each SG was the same as DL (Table 5). The pedigree matrix were constructed in analogy to DL (Table 3).

2.2.1.2 Genomic selection schemes

Two types of GS schemes were modelled for each line, both focusing on the modification to the selection strategy for the male path in ***Conv***: (1) a hybrid scheme that selected young and elite boars incorporating genomic information (***Hybrid***), and (2) an extreme scheme that selected genotyped male juveniles as young and elite boars before progeny information was available (***Juvenile***).

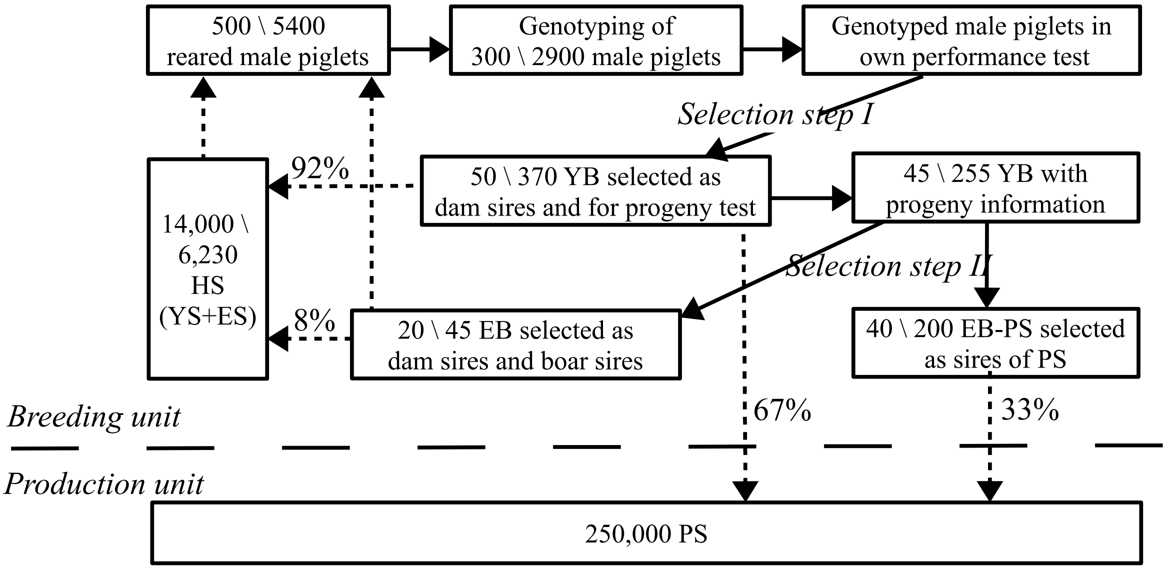


Figure 2 Selection steps for herd book boars in the genomic selection schemes ***Hybrid***. The figures prior to the "\" refer to German-Landrace, while the ones after that refer to Piétrain. The arrows with solid line refer to the selection steps and the arrows with dashed line refer to the selection paths. The proportions indicate the rates of gene contribution. YB = young boars; EB = elite boars; EB-PS = elite boars siring production sows; YS = young sows; ES = elite sows; PS = production sows.

Table 7 Breeding events for herd book boars in the modelled genomic scheme ***Hybrid*** **(a)** and ***Juvenile*** **(b)**.

(a)

Age	Breeding events for boars
0	Birth, genotyping of reference population completed
21 d	Genotyping of reared candidates Reared candidates entering the field test of own performances
8 m	Completion of field test, GEBV available, the 1st step selection for young boars (YB)
10 m	Completion of 2-month quarantine in artificial insemination (AI) stations, mating of YB
1.15 yr	Birth of the 1st offspring of YB assuming 114 days of gestation for sows
2 yr	Progeny information (on station-test-traits) is available, the 2nd-step selection for elite boars (EB) and elite boars siring production sows (EB-PS), mating of EB or PB-PS
2.3 yr	Birth of the 1st offspring of EB and EB-PS assuming 114 days of gestation for sows
4.3 yr	Use time of EB and EB-PS for 2 years

(b)

Age	Breeding events for boars
0	Birth, genotyping of reference population completed
21 d	Genotyping reared candidates Reared candidates entering the field test of own performances
8 m	Completion of field test, GEBV available, selection for young boars (YB), elite boars (EB) and elite boars siring production sows (EB-PS)
10 m	Completion of 2-month quarantine in AI stations, mating of YB, EB and EB-PS
1.15 yr	Birth of the 1st offspring of YB, EB and EB-PS assuming 114 days of gestation for sows
2 yr	Progeny information (on station-test-traits) for parental EBV estimation is available
3.15 yr	Use time and YB, EB and EB-PS for 2 years

Table 8 Definition of selection groups (SGs) in the modelled genomic schemes ***Hybrid*** **(a)** and ***Juvenile*** **(b)** in ZPLAN+. The figures prior to the "\" refer to German-Landrace, while the ones after that refer to Piétrain.

(a)

SG [1]	Size [2]	Candidates [3]	Selected [4]	Prod. Lifetime (yr) [5]	1st offs. (yr) [6]	Surv. Rate [7]
YB	500 \ 5,400	300 \ 2,900	50 \ 370	2.15 \ 1.15	1.15	0.9
EB	40 \ 255	45 \ 255	20 \ 45	2	3.3 \ 2.3	0.9
EB-PS	80 \ 255	45 \ 255	40 \ 200	2	3.3 \ 2.3	1
YS	12,000 \ 5,600	10,800 \ 430	3,500 \ 250	1	1	0.7
ES	2,000 \ 215	2,450 \ 215	666 \ 210	3	2	0.7
PS	250,000	50,000	50,000	5	1	1

(b)

SG [1]	Size [2]	Candidates [3]	Selected [4]	Prod. Lifetime [5]	Age (1st offspring) [6]	Surv. Rate [7]
YB	500 \ 5,400	300 \ 2,900	50 \ 370	2	1.15	0.9
EB	40 \ 90	300 \ 2,900	20 \ 45	2	1.15	0.9
EB-PS	80 \ 400	300 \ 2,900	40 \ 200	2	1.15	1
YS	12,000 \ 5,600	10,800 \ 430	3,500 \ 250	1	1	0.7
ES	2,000 \ 630	2,450 \ 215	666 \ 210	3	2	0.7
PS	250,000	50,000	50,000	5	1	1

[1] Five selection groups were classified in the breeding unit (i.e. YB, EB, EB-PS, YS and ES) and one selection group in the production unit (i.e. PS); YB = (genotyped) young boars; EB = (genotyped) elite boars; EB-PS = (genotyped) elite boars siring production sow; YS = young sows; ES = elite sows; PS = production sows.

[2] Population size of the selection group.

[3] Number of candidates.

[4] Number of selected animals for replacement per time unit.

[5] Productive lifetime: use time of a SG from the 1st reproduction to culling.

[6] Age of animals in a SG when producing the 1st offsprings.

[7] Survival rate: The proportion of animals remained in the SG after each reproduction.

The ***Hybrid*** scheme maintained the selection steps for herd book boars in the conventional selection scheme (***Conv***) (Figure 2). Compared to the breeding events in ***Conv***, a reference population was genotyped before the birth of the candidates. The YB candidates were genotyped before entering own performance test at 21 day (Table 7 **(a)**). Besides, daughter proofs on litter size traits (AGF and LGF) was abandoned for the 2nd step selection, which would lead to an earlier age for EB or EB-PS to generate the 1st offspring. In reference to several assays of GS in pigs (Bennewitz et al., 2011; Ramos et al., 2009; Wellmann et al., 2013), it was assumed for DL and PI the reference population was composed of 1000 progeny-tested boars. The costs for genotyping were assumed 150 € per genotyped animal. Male candidates were qualified by an examination of conformation and functional records as well as the family selection. Then they were genotyped at 21 day old just before sent to own performance test (of DG and SPECK) in fields. Until 8 months old, both own performances and GEBVs were available. The costs for own performance test were 40 €. Based on them, as well as the parental EBVs, the 1st step selection was conducted for YB (Table 9 **(a)**). YB was selected as dam sires for the selection paths YB>HS and YB>PS. At this point, 50 YB were selected from 300 candidates for DL, while for PI 370 YB were selected from 2900 candidates. After 2 months quarantine used in AI stations, YB served HS and PS. Following a gestation period of 114 days for sows, YB had the 1st offspring at ca. 1.15 years old. Then YB were continued to be used in the herd book for 1.15 years (productive lifetime = 1.15 yr) (Table 8 **(a)**). Progenies of YB were picked up for station-test (of ADG, FCR, IMF, LMP and pH_1) in forms of 9 full-sib groups with 2 full sibs in each. The costs for station-test (ST) was assumed 100 € per test animal. The progeny information was available for YB at the age of 2 yr. Without waiting for daughter performance on AGF and LGF, the 2nd step selection was conducted immediately. Elite boars were selected based on progeny performance in stations as well as the criteria for the 1st step selection. At this step, EB were selected for the selection paths EB>HB and EB>HS. EB-PS were selected as sires of production sows (PS) (i.e. EB-PS>PS). For DL, 20 EB and 40 EB-PS were selected from 45 YB survived in AI stations, while for PI 45 EB and 200 EB-PS were selected out of 255 survived YB. Then EB served HS and EB-PS served PS, and subsequently EB and EB-PS had their 1st offspring of EB and EB-PS at the age of 2.3 yr. After that, both EB and EB-PS were arranged to be used in AI stations for 2 years (productive lifetime =2 yr).The survival rate after each reproduction cycle (survival rate) for YB, EB and EB-PS was the same as ***Conv*** (Table 8 **(a)**). Also, the pedigree matrix was constructed in analogy to ***Conv*** (Table 3).

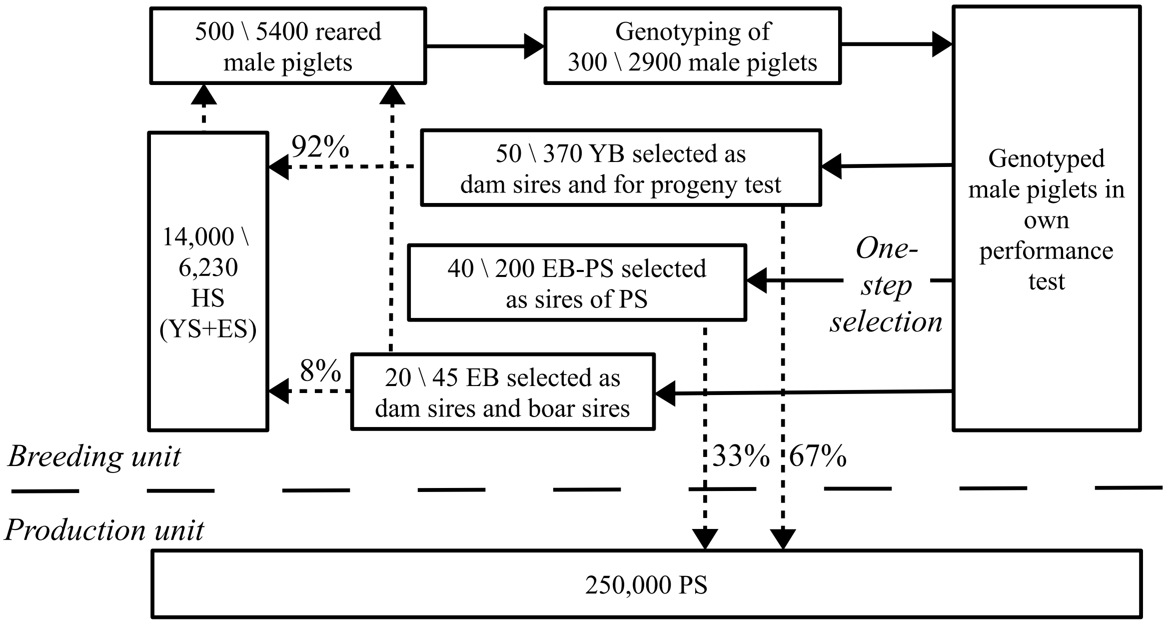


Figure 3 Selection steps for herd book boars in the genomic selection schemes *Juvenile*. The figures prior to the "\" refer to German-Landrace, while the ones after that refer to Piétrain. The arrows with solid line refer to the selection steps and the arrows with dashed line refer to the selection paths. The proportions indicate the rates of gene contribution. YB = young boars; EB = elite boars; EB-PS = elite boars siring production sows; YS = young sows; ES = elite sows; PS = production sows.

The ***Juvenile*** scheme applied a one-step selection for genotyped young boars to enter YB, EB and EB-PS (Figure 3). The male candidates were genotyped at 21 d and then entered the field-test for own performances (Table 7 **(b)**). Until the completion of the test (ca. 8 months old), a one-step selection was carried out based on GEBVs, parental EBVs and own performance of DG and SPECK (Table 9 **(b)**). For DL, 50 genotyped young boars were selected from 300 candidates to enter the selection group YB. The best 20 genotyped young boars were used for siring herd book boars and sows (EB) and the best 20 for siring production sows (EB-PS). For PI, 370, 45 and 200 best boars were selected out of 2900 candidates as YB, EB and EB-PS respectively. After 2 months quarantine in AI stations, YB, EB and EB-PS were mated for producing the next generation. Hence, YB, EB and EB-PS had their 1st offspring at 1.15 yr old. Following this, they were all used for 2 yr (productive lifetime = 2 yr) (Table 8 **(b)**). The progeny information was available at 2 yr old. The survival rates after each reproduction cycle (survival rate) for YB, EB and EB-PS was the same as rates in ***Conv*** (Table 8 **(b)**). The pedigree matrix was constructed similarly to ***Conv*** (Table 3).

Table 9 Cost parameters in terms of cost groups (or defined selection groups) in the genomic selection schemes ***Hybrid*** **(a)** and ***Juvenile*** **(b)**.

(a)

Cost group [1]	Cost parameters						
	Info. Source [2]	Test [3]	No. of tested groups	No. of ind. in tested groups	Relation between tested groups	Cost per ind. (€)	Mean age of cost group (yr) [4]
Ref. Pop.	-	Genotyping	1	1000	-	150	0
YB	Sire	EBVs	1	1	-	-	0
	Dam	EBVs	1	1	-	-	0
	Self	Genotyping	1	1	-	150	0
	Self	FT1	1	1	-	40	0.67
EB or EB-PS [5]	Progeny	ST	9	2	Half-sib	100	2

(b)

Cost group [1]	Cost parameters						
	Info. Source [2]	Test [3]	No. of tested groups	No. of ind. in tested groups	Relation between tested groups	Cost per ind. (€)	Mean age of cost group (yr) [4]
Ref. Pop.	-	Genotyping	1	1000	-	150	0
YB, EB or EB-PS [5]	Sire	EBVs	1	1	-	-	0
	Dam	EBVs	1	1	-	-	0
	Self	Genotyping	1	1	-	150	0
	Self	FT1	1	1	-	40	0.67

[1] Ref. Pop. = reference population. Five selection groups were classified in the breeding unit (i.e. YB, EB, EB-PS, YS and ES) and one selection group in the production unit (i.e. PS); YB = (genotyped) young boars; EB = (genotyped) elite boars; EB-PS = (genotyped) elite boars siring production sow; YS = young sows; ES = elite sows; PS = production sows.

[2] PHS = paternal half-sibs; FS = full-sibs.

[3] EBVs = BLUP estimated breeding values for breeding goal traits; ST = station-test of ADG, FCR, IMF, LMP and pH$_1$; FT1= field-test of DG and SPECK.

[4] Mean age of cost group when the information source is available.

[5] The information sources for the 1st step selection for YB were also included in the selection criteria for the 2nd step selection for EB or EB-PS, but were not repeatedly listed.

For each GS scheme, two parameters were varied as follows per purebred line. The reference population size (*N*) was varied between 1000 and 2500 per purebred line in steps of 500. The number of genotyped male candidates (N_{gmc}) was varied between 300 and 1200 for DL and between 2900 and 3800 for PI, both in steps of 300. These variations would incur increases of the genotyping costs and thus the discounted costs.

2.2.2 Modelling practices

Practical modelling of a selection scheme using ZPLAN+ needs to input parameters in four modules: “Economic factors”, “Selection group”, “Pedigree-matrix” and “Breed”. In the “Economic factors”, “time unit” was defined as 1 year , and “investment period” as 10 years in analogy to Wünsch et al. (1999). Annual interest rate was set as 3% for calculating discounted cost and 5% for calculating discounted return. In the module of “Selection group”, each selection group was defined using the parameters listed in Table 5 and 8. Costs parameters were also defined (Table 6 and 9). In the “Breed” module, all the considered traits, either in the breeding goal or in the selection index, were defined in terms of economic weight (w), heritability (h^2), phenotypic standard deviation (σ_p), and genetic and phenotypic correlations with other traits (Table 2). The BLUP EBVs of parents are not allowed to be defined directly within the current version ZPLAN+. An indirect definition was developed, treating an EBV for a trait of a parent as a “dummy” trait with null economic weight, heritability of 1 and phenotypic/genetic standard deviation equal to $r_{EBV,TBV} \times \sigma_{TBV}$, where $r_{EBV,TBV}$ is the correlation of EBV and true breeding value (TBV) (see Appendix). GEBV for each breeding goal trait was defined via specifying a number of parameters in the following equation. According to the Dekkers (2007), Haberland et al. (2011) and Daetwyler et al. (2008, 2010), the accuracy of GEBV (correlation between GEBV and true breeding value) were predicted as:

$$r_{mg,i} = q_i * r_{\hat{Q}} = q_i * \sqrt{\frac{N * r_i^2}{N * r_i^2 + M_e}} \quad \text{(Equ.2).}$$

$r_{\hat{Q}}$ denotes the accuracy of estimates of marker effects in the reference population size. r_i

refers to the accuracy of breeding values for the trait *i* in the reference population (Simianer, 2009). Herein the theoretical accuracy of the (BLUP) EBV for sires (See Table 2) was used, assuming that the reference population consisted of progeny-tested boars. The proportion of genetic variance explained by genome-wide markers (q^2) was assumed as 0.8 (i.e. $q = 0.9$) for all the breeding goal traits, reflecting a high LD pattern in the population that is comparable to an maximum level detected for the Illumina Bovine SNP50 BeadChip (Woolliams et al., 2010). N represents the reference population size, as mentioned above. The value for effective number of independent chromosome segments (M_e) was constant for all considered traits within each line, and was calculated by

$$M_e = \frac{2 N_e L}{\ln(4 N_e L)} \quad \text{(Equ.3) (Goddard, 2009),}$$

where N_e denotes the generation effective population size and L represents the genome length in Morgans (L=30, based on Tribout et al., (2012)). The generation effective population size (N_e) for DL or PI was estimated based on the average coefficient of inbreeding ($\bar{F}_t$) of the cohort born in the year t (Hill, 1979; Pérez-Enciso, 1995; VanRaden, 1992), wherein the real-world mean generation interval was specified as 2.15 years for either line according to Pausch (2009). To achieve this, pedigree data of totally 67,207 DL and 36,735 PI herd book animals, born between 1980 and 2007 in Bavaria, was analyzed. Meanwhile, in order to examine the reliability of the calculated $\bar{F}_t$, the average pedigree completeness ($C_{p,t}$) (Cassell et al., 2003) of the cohort born in the year t was also calculated considering a depth of 3 generations. The calculations of $\bar{F}_t$ and $C_{p,t}$ were performed using the PyPedal package (Cole, 2007).

3 Results

3.1 German-Landrace

3.1.1 Effective number of independent chromosome segments

For DL, the effective number of independent chromosome segments (M_e =1120) was determined by the generation effective population size (N_e = 187) via the Goddard's formula (2009). The estimation of N_e, adopted the considerably reliable average annual coefficients of inbreeding ($\bar{F}_t$) on the birth year *t* from 1989 to 2003. Herein the reliability of a $\bar{F}_t$ is judged by two criteria: 1) the $\bar{F}_t$ fits an increasing trend over the birth years; 2) the average pedigree completeness on the year *t* ($C_{p,t}$) is over 0.8. The $\bar{F}_t$ grows until 2003 and then declines in the following years (Figure 4). A possible reason for such decline is the introduction of herd book animals from outside of Bavaria. On the other hand, the tendency of $C_{p,t}$ since 1989 is over 0.8, suggesting that the individuals born after 1989 appear to have relatively sufficient pedigree data (Figure 5).

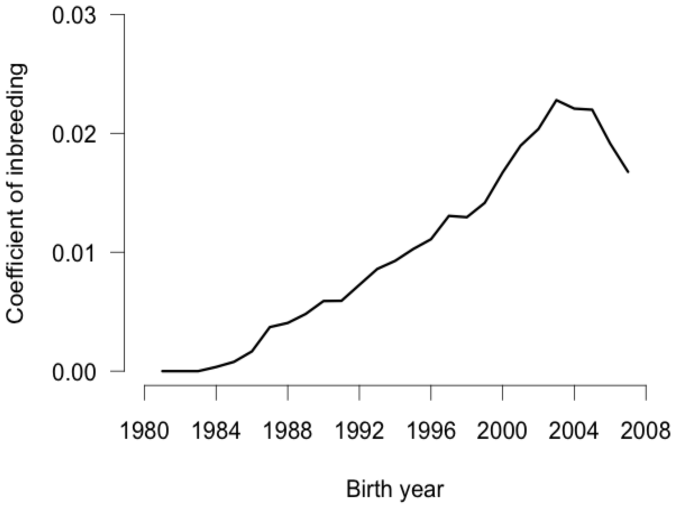


Figure 4 Trend of the average coefficient of inbreeding of the herd book animals for German-Landrace over the birth year from 1980 to 2007.

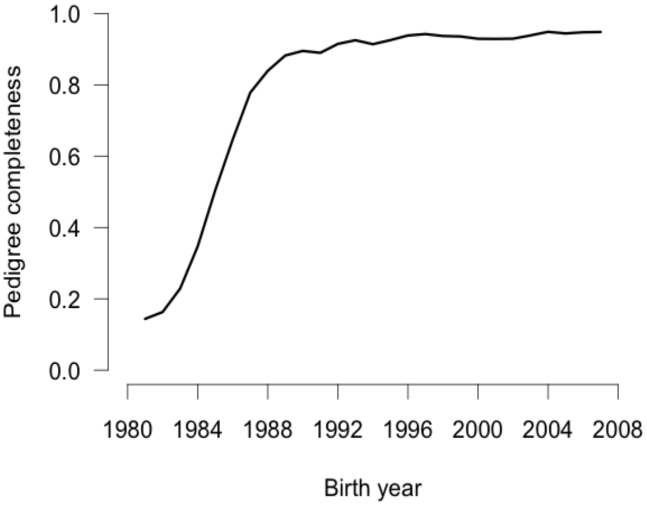


Figure 5 Trend of the average pedigree completeness of the herd book animals for German-Landrace over the birth year from 1980 to 2007.

3.1.2 Overall generation interval

The overall generation interval (ΔT) is expected to be 2.472 yr for the conventional selection scheme (***Conv***) (Table 10). Compared with the level for ***Conv***, the ΔT for the GS scheme ***Hybrid*** and ***Juvenile*** is 14% and 23% shorter, resulting in 2.116 yr and 1.892 yr respectively. The shortened ΔT for ***Hybrid*** is due to the skip of waiting for daughter information on litter size traits (Table 7 **(a)**), while the reduced ΔT for ***Juvenile*** owes to the early selection and use of young boars with genomic information for breeding (Table 7 **(b)**). The variation of reference population size or number of genotyped male candidates has no effect on the overall generation interval.

3.1.3 Accuracy of selection index for elite boars

Compared with reduced generation intervals, the major potential for GS in pig breeding mainly relies on increased accuracy of selection (Ibañez-Escriche and Gonzalez-Recio, 2011; Simianer, 2009). In this study, an economic breeding objective aggregating multiple traits was considered. Accuracy of selection index (r_{TI}) was investigated for elite boars, which are subject to the sharpest selection compared to the other selection paths. ***Conv*** can achieve a r_{TI} for elite boars as 0.7688

(Table 10). With the reference population size (*N*) of 1000, the GS scheme ***Hybrid*** can create a r_{TI} for elite boars as high as 0.7409, 96% of the level for ***Conv***. ***Juvenile*** is inferior to ***Hybrid*** in r_{TI} for elite boars, resulting in a level of 0.7063.

Table 10 Overview of evaluation parameters for the conventional selection scheme (***Conv***), the genomic selection schemes ***Hybrid*** and ***Juvenile*** for German-Landrace given the size of reference population of 1000 and the number genotyped male candidates of 2900. For abbreviations of traits, see footnote Table 2.

Parameter	Unit	***Conv***	***Hybrid***	***Juvenile***
Overall generation interval	year	2.47153	2.11556	1.89216
relative	%	100	86	77
r_{TI} for young boars †		0.49944	0.7063	0.7063
relative	%	100	141	141
r_{TI} for elite boars †		0.76881	0.74092	0.7063
relative	%	100	96	92
Annual natural genetic gain				
ADG	g/day	10.04431	13.21540	13.6244
relative	%	100	132	136
AGF	piglets	0.17979	0.23432	0.26799
relative	%	100	130	149
FCR	kg/kg	-0.01364	-0.01819	-0.01901
relative	%	100	133	139
LGF	piglets	0.18927	0.24755	0.28283
relative	%	100	131	149
STLP	%	1.07213	1.58717	1.40809
relative	%	100	148	131
Annual monetary genetic gain	€	7.11187	9.37953	10.37432
relative	%	100	132	146
Discounted return	€	32.92539	50.15094	58.26844
relative	%	100	152	177
Discounted costs	€	26.10326	26.84016	26.84016
relative	%	100	103	103
Profit	€	6.82214	23.31077	31.42828
Profit, relative	%	100	342	461

† r_{TI} = correlation between selection index and aggregate economic breeding value (accuracy of selection index).

For GS schemes, r_{TI} for elite boars can be affected by reference population size (N) via the accuracies of genomic estimated breeding values, as reflected by Equ.2. The theoretical background was illustrated by Dekkers (2007) and Daetwyler et al. (2008). Increasing N from the base scenario 1000 to 2500, one may observe an asymptotical growth trend for such r_{TI} for both ***Hybrid*** and ***Juvenile*** (Figure 6). Besides, the r_{TI} for ***Hybrid*** is higher than ***Juvenile*** given any scenario of N. This is owing to the additional progeny information integrated in the selection index for ***Hybrid***. Nevertheless, the superiority of ***Hybrid*** over ***Juvenile*** for the r_{TI} diminishes with the increase of N. With the base scenario of N (1000), ***Hybrid*** is 5% superior to ***Juvenile***, while 2% superior when N is increased to 2500. Increasing N can also arises comparative advantages of GS schemes over the conventional selection scheme (***Conv***) in r_{TI} for elite boars. Compared with ***Conv***, ***Hybrid*** shows 3% interior for the r_{TI} given $N = 1000$, and evolves to be 6.5% superior when N is increased to 2500. The superiority of ***Hybrid*** has become visible since $N = 1500$. Similarly, ***Juvenile*** presents 8% interiority for the r_{TI} compared with ***Conv*** with $N = 1000$, and 1.2% superior when N is increased to 2000. For the extreme case $N = 2500$, ***Juvenile*** turns out 4% superior to ***Conv***.

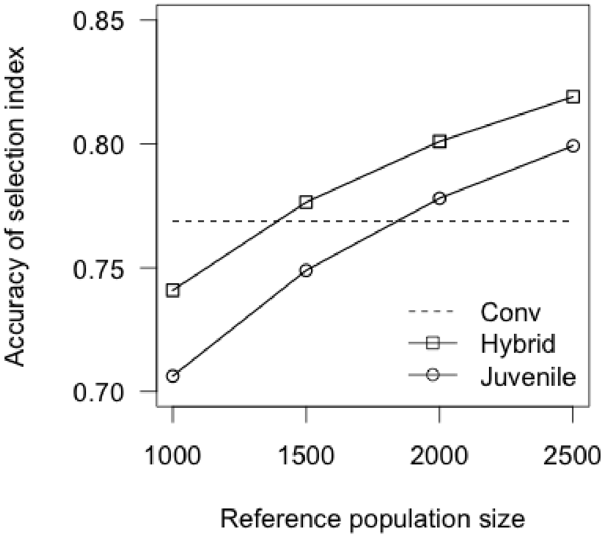


Figure 6 Trends for the accuracy of selection index for elite boars for the genomic selection schemes ***Hybrid*** and ***Juvenile*** for German-Landrace depending on reference population size, compared to the conventional selection scheme (***Conv***).

3.1.4 Annual natural and monetary genetic gain

Conv enables fatteners to obtain 10.044 g as the average daily gain (ADG) per year (Table 10). Implementing the GS scheme ***Hybrid*** can enhance such *ANGG* for ADG by 32%, while conducting the GS scheme ***Juvenile*** may improve it by 36%.

Since the trait weaned piglets per litter (AGF) has a high genetic relationship (0.884) with weaned piglets per litter (LGF) (Table 2), the *ANGG* for AGF and LGF are similar under each selection scheme. Under ***Conv***, sows are expected to farrow additional 0.1798 AGF and 0.1893 LGF per year. Carrying out ***Hybrid*** will increase the *ANGG* for AGF and LGF by 30%, while applying ***Juvenile*** will create an increase of 49% (Table 10).

The genetic trend for the trait feed conversion ratio (FCR) refers to feed intake in kg per kg body mass gain. Implementing ***Conv*** will result in an *ANGG* for FCR to be -0.01364, reflecting an annual reduction of 0.01364 kg in feed intake per kg body mass gain. The GS scheme ***Hybrid*** will increase the yearly reduction by 33%, and ***Juvenile*** is able to increase it by 39%

The genetic trend for the trait number of inverted teats (STLP) represents the percentage of progeny of a boar that has no inverted teats. Conducting ***Conv*** may yield a *ANGG* of 1.0721 percentage points (Table 10). Performing he GS scheme ***Hybrid*** may enhance the *ANGG* by 48%. While implementing ***Juvenile*** can create an increase in the *ANGG* by 31%.

Annual monetary genetic gain (*AMGG*) measures trends for aggregate economic breeding value in the context of economic selection index models. *AMGG* is calculated as the sum of the *ANGG* for individual breeding goal traits weighted by their economic weights (Table 2). As shown in Table 10, applying ***Conv*** is expected to achieve a *AMGG* as 7.1112 €. In contrast, adopting the GS schemes ***Hybrid*** and ***Juvenile*** is likely to gain the *AMGG* by 32% and 46% respectively.

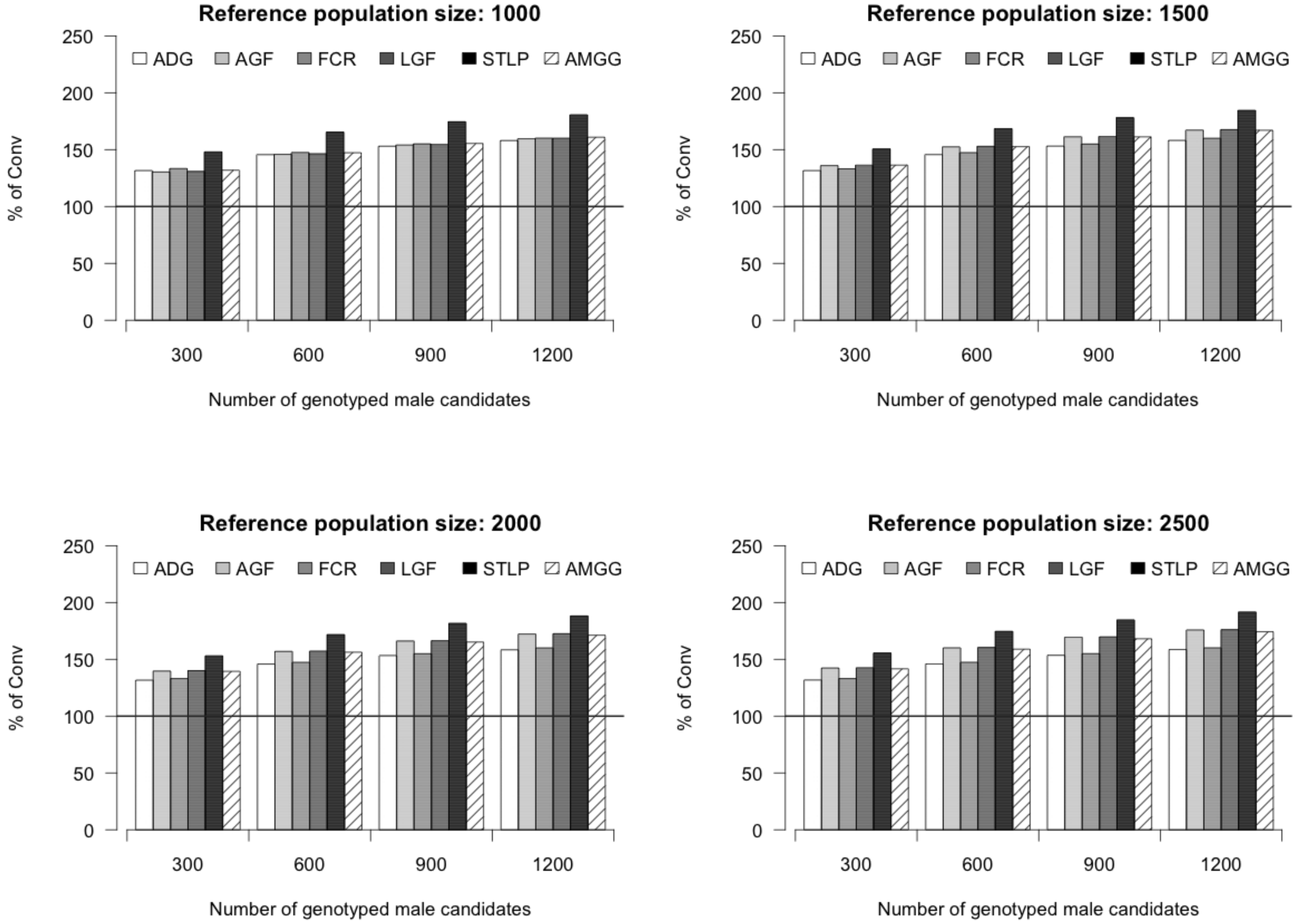


Figure 7 Annual natural genetic gain (*ANGG*) for breeding goal traits and annual monetary genetic gain (*AMGG*) relative to the conventional scheme (***Conv***) (set to 100%) under the genomic selection scheme ***Hybrid*** for German-Landrace depending on number of genotyped males and reference population size. For the abbreviations for traits, see footnote Table 2.

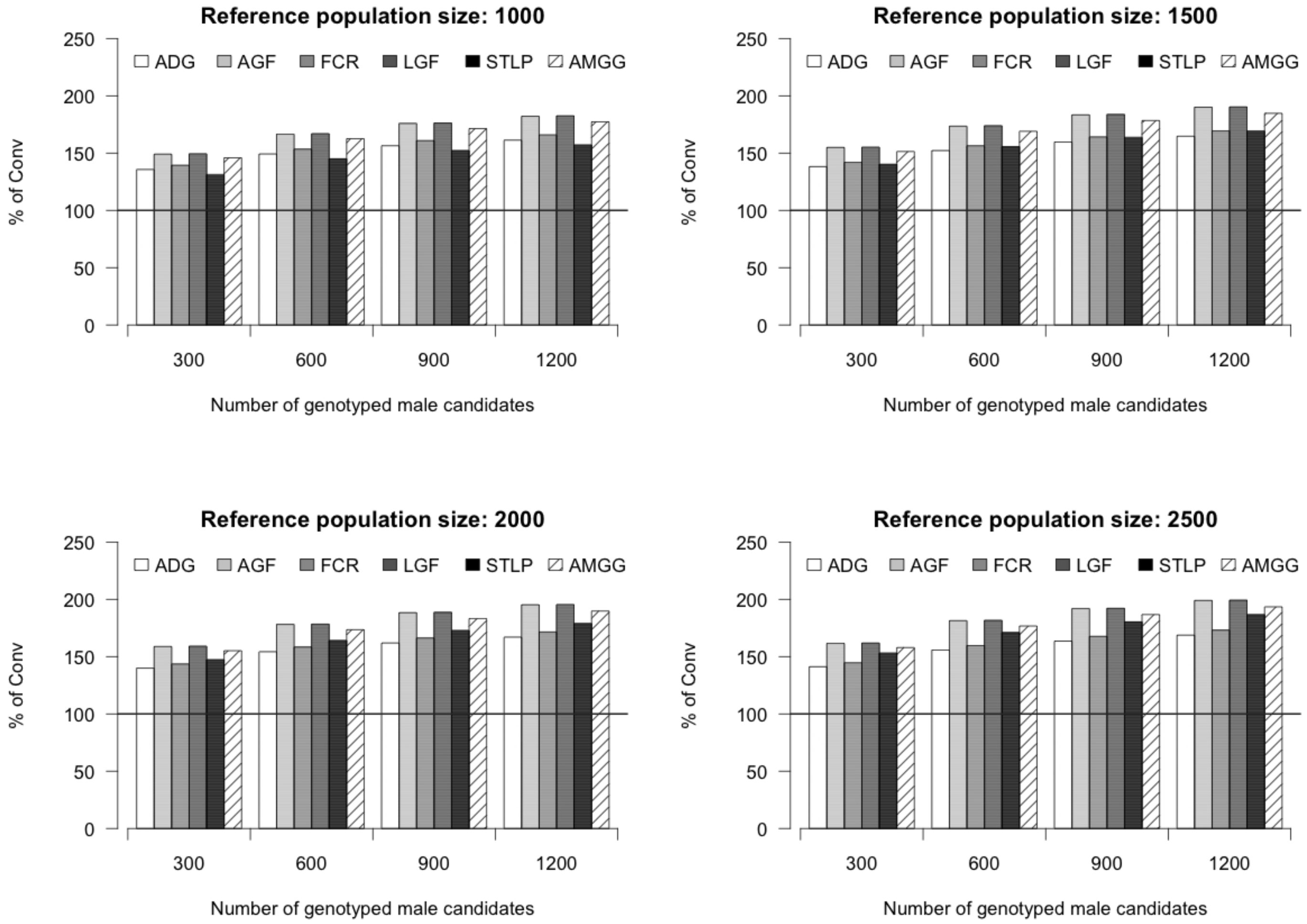


Figure 8 Annual natural genetic gain (*ANGG*) for breeding goal traits and annual monetary genetic gain (*AMGG*) relative to the conventional scheme (***Conv***) (set to 100%) under the genomic selection scheme ***Juvenile*** for German-Landrace depending on number of genotyped males and reference population size. For the abbreviations for traits, see footnote Table 2.

For the GS schemes, both *AMGG* and *ANGG* can be increased by enlarging the number of genotyped male candidates (N_{gmc}) and the reference population size (N). This is because that enlarging N_{gmc} may increase the replacement rate and thus the selection intensity for the male path, while enlarging N can enable the rises of the r_{TI} for the male path via Equ. 2. Figure 7 shows the *ANGG* as well as the *AMGG* for **Hybrid** relative to **Conv**, depending on N_{gmc} and N. In general, the relative *ANGG* for the breeding goal traits individually grow asymptotically with the enlargement of

N_{gmc} and N, and the relative *ANGG* for the trait STLP shows the highest level among the traits given any scenario of N_{gmc} and of N. Compared to fattening trait (ADG and FCR), enlarging N leads to higher growth rates for the relative *ANGG* for litter size traits (AGF and LGF). For example, for the basic scenario of N (1000), the relative *ANGG* for litter size traits are comparable to the levels for the fattening traits (ADG and FCR), while they rise to be the second highest level (only lower than the relative *ANGG* for STLP) when N is scaled to 2500. Similar to ***Hybrid***, asymptotical growths for the relative *ANGG* and *AMGG* were observed along with the enlargement of N_{gmc} and N in ***Juvenile*** (Figure 8). Litter size traits surpass any other breeding goal trait for each scenario of N_{gmc} and N. Compared to fattening traits, increasing N has larger effects on the growth of the relative *ANGG* for STLP. For the basic scenario of N (1000), the relative *ANGG* for STLP ranks the lowest. It exceeds the level for fattening traits when N is scaled to 2500.

3.1.5 Discounted return, costs and profit

Discounted returns are calculated as the monetary value of the annual monetary genetic gain expressed by improved animals in the whole population over the time of investment (10 yr). Applying ***Conv*** may bring a discounted return of 32.9554 € per animal (Table 10). Assuming $N = 1000$ and $N_{gmc} = 300$, investing in the GS scheme ***Hybrid*** may add the discounted return by 52%, and investing in ***Juvenile*** can achieve an add of 77%.

Discounted costs aggregate the costs for individual tests (Table 6 and 9), discounted with the interest rate for costs and the mean age of the cost group (VIT, 2011). One principle for modelling the GS schemes was to maintain the performance testing system in the conventional scheme. Based on that, genotyping reference and candidate population was integrated in the GS schemes. Running ***Conv*** requires a discounted costs of 26.1033 € per animal. For the base scenario of N (1000) and of N_{gmc} (300), the discounted costs per animal amounts to 26.8402 € for both ***Hybrid*** and ***Juvenile***.

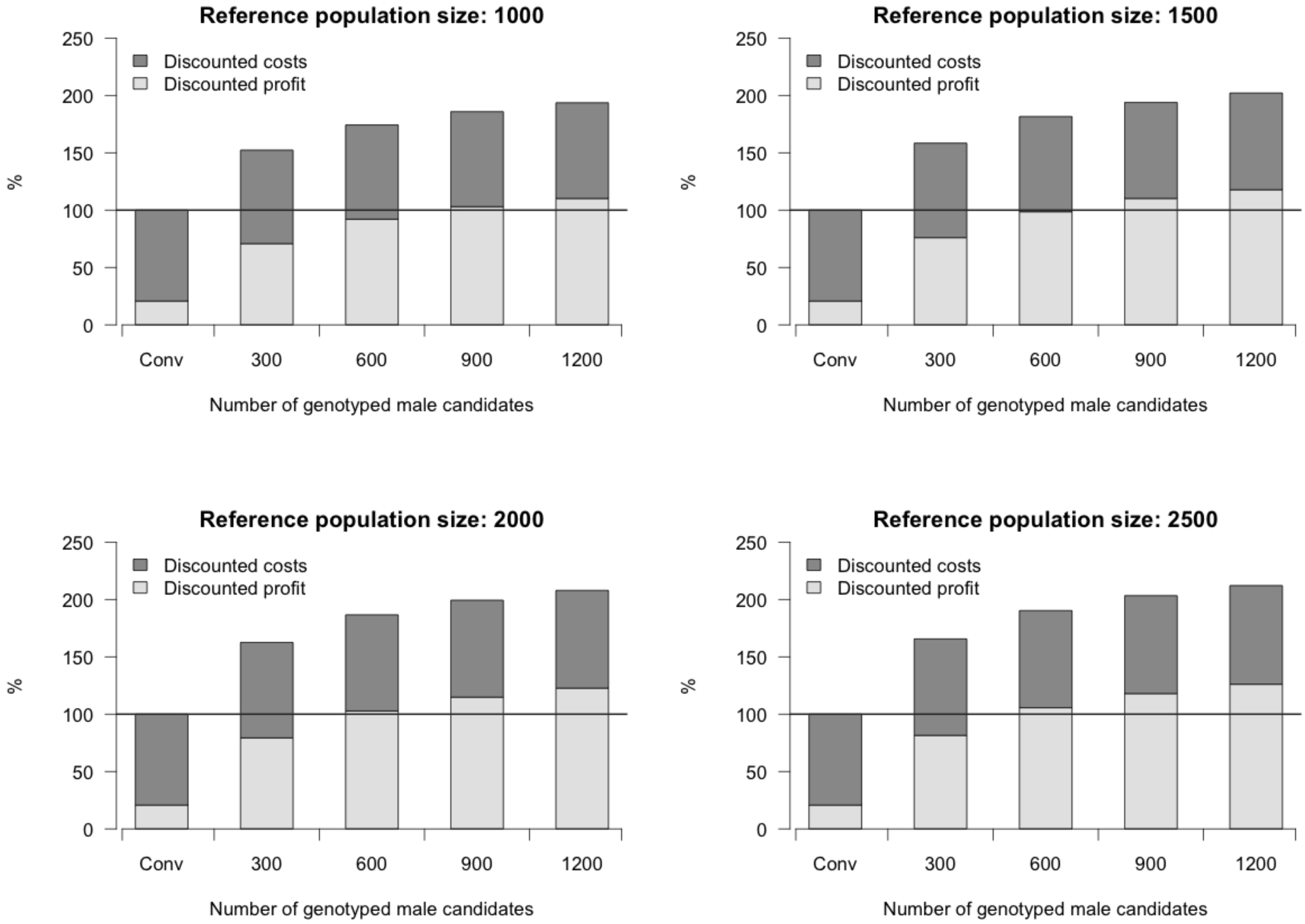


Figure 9 Discounted profit and discounted costs (sum = discounted return) for the genomic selection scheme ***Hybrid*** relative to the conventional scheme (***Conv***) for German-Landrace depending on the the number of genotyped males and reference population size. The discounted return for ***Conv*** is set to 100%.

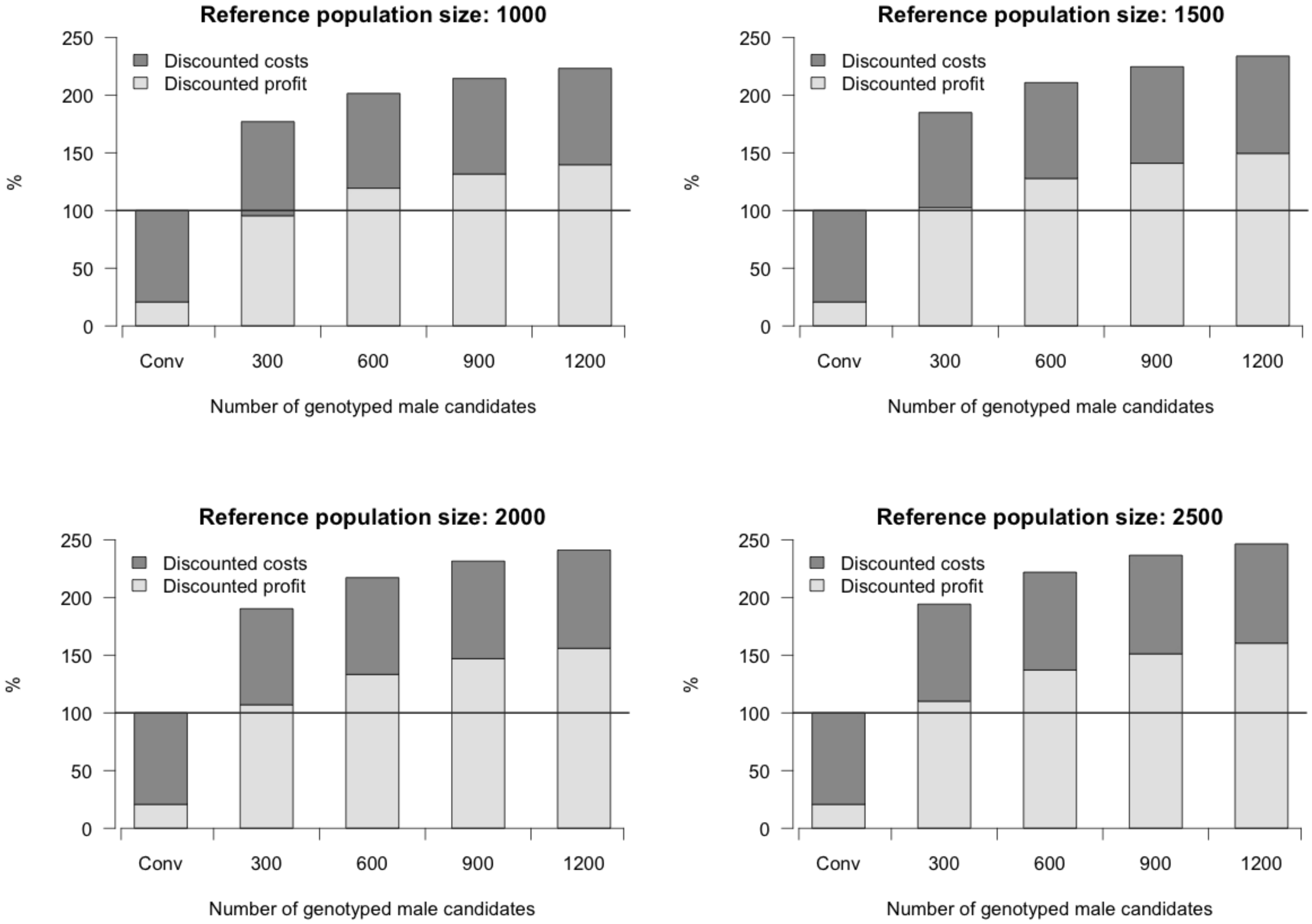


Figure 10 Discounted profit and discounted costs (sum = discounted return) for the genomic selection scheme ***Juvenile*** relative to the conventional scheme (***Conv***) for German-Landrace depending on the the number of genotyped males and reference population size. The discounted return for ***Conv*** is set to 100%.

By deducting the discounted costs from the discounted return, the discounted profit from investing in ***Conv*** may be 6.8221 € per animal. While the discounted profit can be 242% and 361% higher respectively by running the GS scheme ***Hybrid*** and ***Juvenile***. Discounted return as well as profit for the GS schemes can be raised with enlarging N_{gmc} and N. The discounted return and profit relative to the magnitude under ***Conv*** increases asymptotically as enlarging N_{gmc} from 300 to 1200 (Figure 9 and 8). Fixing on a particular N_{gmc}, discounted return and profit can also rise asymptotically while enlarging N from 1000 to 2500.

3.2 Piétrain

3.2.1 Effective number of independent chromosome segments

The effective number of independent chromosome segments (M_e) for PI is predicted as 957. The effective population size (N_e) is estimated to be 157 based on the average annual coefficients of inbreeding ($\bar{F}_t$) from the birth year 1989 to 2007. These coefficients are considered reliable for the estimation of N_e as they meet the criteria described in the section **3.1.1**. As shown in Figure 11, the $\bar{F}_t$ for PI rises steadily from the birth year 1980 until 2007. Besides, average pedigree completeness ($C_{p,t}$) from the birth year 1989 to 2007 is over 0.8 (Figure 12).

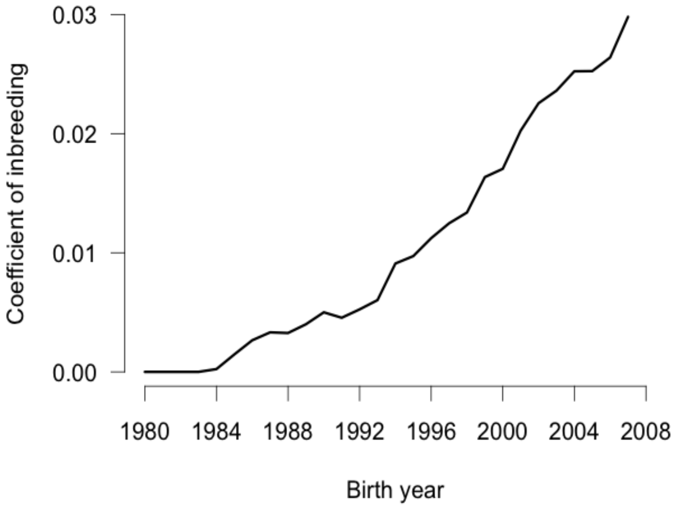


Figure 11 Trend of the average coefficient of inbreeding of the herd book animals for Piétrain over the birth year from 1980 to 2007.

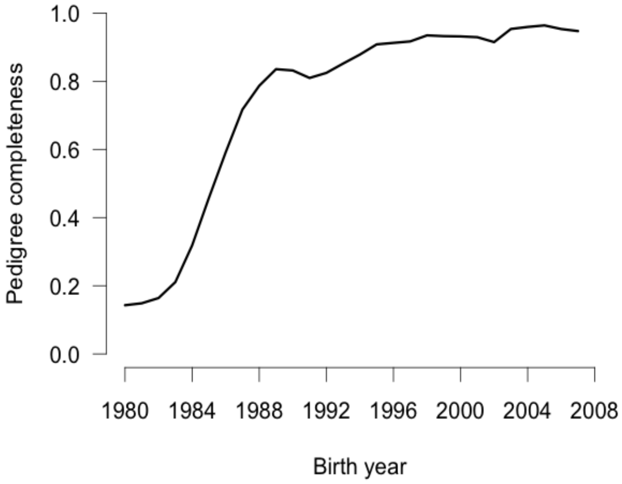


Figure 12 Trend of the average pedigree completeness of the herd book animals for Piétrain over the birth year from 1980 to 2007.

3.2.2 Overall generation interval

The overall generation interval (ΔT) is expected to be 2.1156 yr for the ***Conv*** for PI. Implementing the GS scheme ***Hybrid*** modelled for PI will not change the ΔT substantially (Table 11). This is because in ***Hybrid*** genotyping the male candidates was performed at an early stage of the life (e.g. at the weaning age) so that the age for the 1st reproduction for the sires as well as the production lifetime is consist with those in ***Conv*** (Table 7 **(a)**). For the GS scheme ***Juvenile***, the ΔT is reduced by 15% compared to ***Conv***, resulting in 1.7973 yr. The reduction is due to the early use of genotyped sires without waiting for progeny information (Table 7 **(a)**).

Table 11 Overview of evaluation parameters for the conventional selection scheme (***Conv***), the genomic selection schemes ***Hybrid*** and ***Juvenile*** for Piétrain given the size of reference population of 1000 and the number genotyped male candidates of 2900. For abbreviations of traits, see footnote Table 2.

Parameter	Unit	*Conv*	*Hybrid*	*Juvenile*
Overall generation interval	year	2.11556	2.11556	1.79726
relative	%	100	100	85
r_{TI} for young boars †		0.37739	0.65249	0.65249
relative	%	100	173	173
r_{TI} for elite boars †		0.76417	0.81585	0.65249
relative	%	100	107	85
Annual natural genetic gain				
ADG	g/day	7.52917	9.66292	10.73014
relative	%	100	128	143
FCR	kg/kg	-0.02141	-0.0276	-0.03068
relative	%	100	129	143
IMF	%	0.02587	0.03075	0.03219
relative	%	100	119	124
LMP	%	0.15569	0.1885	0.18453
relative	%	100	121	119
pH_1	-	-0.00058	-0.00119	-0.00304
relative	%	100	205	524
Annual monetary genetic gain	€	1.94721	2.45367	2.64337
relative	%	100	126	136
Discounted return	€	11.62898	15.46584	18.43046
relative	%	100	133	158
Discounted costs	€	3.20558	5.43738	5.43763
relative	%	100	170	170
Profit	€	8.4234	10.02846	12.99283
Profit, relative	%	100	119	154

† r_{TI} = correlation between selection index and aggregate economic breeding value (accuracy of selection index).

3.2.3 Accuracy of selection index for elite boars

By conducting ***Conv***, the accuracy of selection index (r_{TI}) for elite boars can reach as high as 0.7642 (Table 11). Assuming the reference population size (N) as 1000, the GS scheme ***Hybrid*** enables a r_{TI} as 0.8159 for elite boars, which can be 7% higher than the level of ***Conv***. In contrast, the GS scheme ***Juvenile*** can only achieve a moderate r_{TI} for elite boars as 0.6525. It turns out to be 15% lower than the level under ***Conv***.

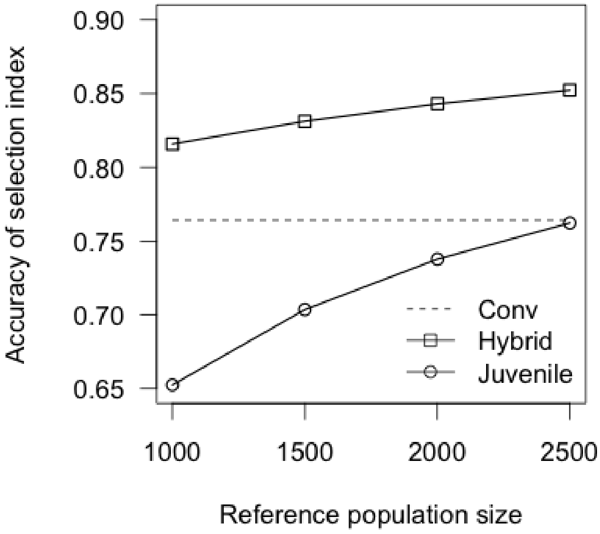


Figure 13 Trends for the accuracy of selection index for elite boars for the genomic selection schemes ***Hybrid*** and ***Juvenile*** for Piétrain depending on reference population size, compared to the conventional selection scheme (***Conv***).

Increasing the reference population size (*N*) from the base scenario 1000 to 2500 can enhance the r_{TI} for elite boars for the GS schemes (Figure 13). Similar to DL, the r_{TI} for both ***Hybrid*** and ***Juvenile*** grow asymptotically with the increase of *N*. The growth rates are considerably lower than the rates in DL respectively. Between the two GS schemes, ***Hybrid*** is superior to ***Juvenile*** in the r_{TI} with the increase of *N*. However, the r_{TI} for ***Hybrid*** grows much more slowly than ***Juvenile***, thus the superiority for ***Hybrid*** diminishes. The r_{TI} for ***Hybrid*** is more than 0.15 higher than ***Juvenile*** for the scenario N =1000, and it become 0.1 points above the magnitude of ***Juvenile*** when *N* is increased to 2500. Compared to ***Conv***, ***Hybrid*** shows a superiority in the r_{TI} for elite boars, while ***Hybrid*** presents a interiority with varying *N* between 1000 and 2500. The r_{TI} for ***Juvenile*** is likely to reach the level of ***Conv*** at the circumstance of $N = 2500$.

3.2.4 Annual natural and monetary genetic gain

Conv is able to improve the average daily gain (ADG) by 7.5292 g annually. The GS scheme ***Hybrid*** can increase this annual natural genetic gain (*ANGG*) by 28%, while ***Juvenile*** may enhance it by 43%.

By implementing ***Conv,*** an annual reduction of 0.02141 kg in the feed intake can be realized per kg body mass gain. Applying ***Hybrid*** can intensify such reduction by 28%, while using ***Juvenile*** can increase the reduction by 43%.

The intramuscular fat content (IMF) may be improved by 0.02587 percentage per year with the implementation of ***Conv***. This improvement can be enhanced by 19% when conducting ***Hybrid***. In contrast, conducting the GS scheme ***Juvenile*** is expected to raise the *ANGG* for ***Conv*** by 24%.

High lean meat percentage (LMP) is one of the advantageous characteristics for PI. When carrying out ***Conv***, LMP may be increased by 0.1557 percentages per year. Performing ***Hybrid*** can increase such *ANGG* by 21%, while adopting ***Juvenile*** may achieve an gaining by 19%.

In the present multiple-trait selection modelling study, the pH value in M. long dorsi measured 45 minutes post mortem (pH_1) is found the only trait showing unfavorable genetic trends for all the selection schemes. Conducting ***Conv*** would create an annual decrease of 5.8×10^{-4} units in pH value (Table 11). Operating the GS scheme ***Hybrid*** would enhance such decrease by 105%. With the implementation of ***Juvenile***, the annual decrease is expected to be 3.04×10^{-3}, 424% higher than the value under ***Conv***.

Running the conventional selection scheme for PI may achieve an annual monetary genetic gain (*AMGG*) of 1.9472 € (Table 11). When shifting to using GS scheme ***Hybrid*** and ***Juvenile***, the *AMGG* would be increased by 26% and 36% respectively.

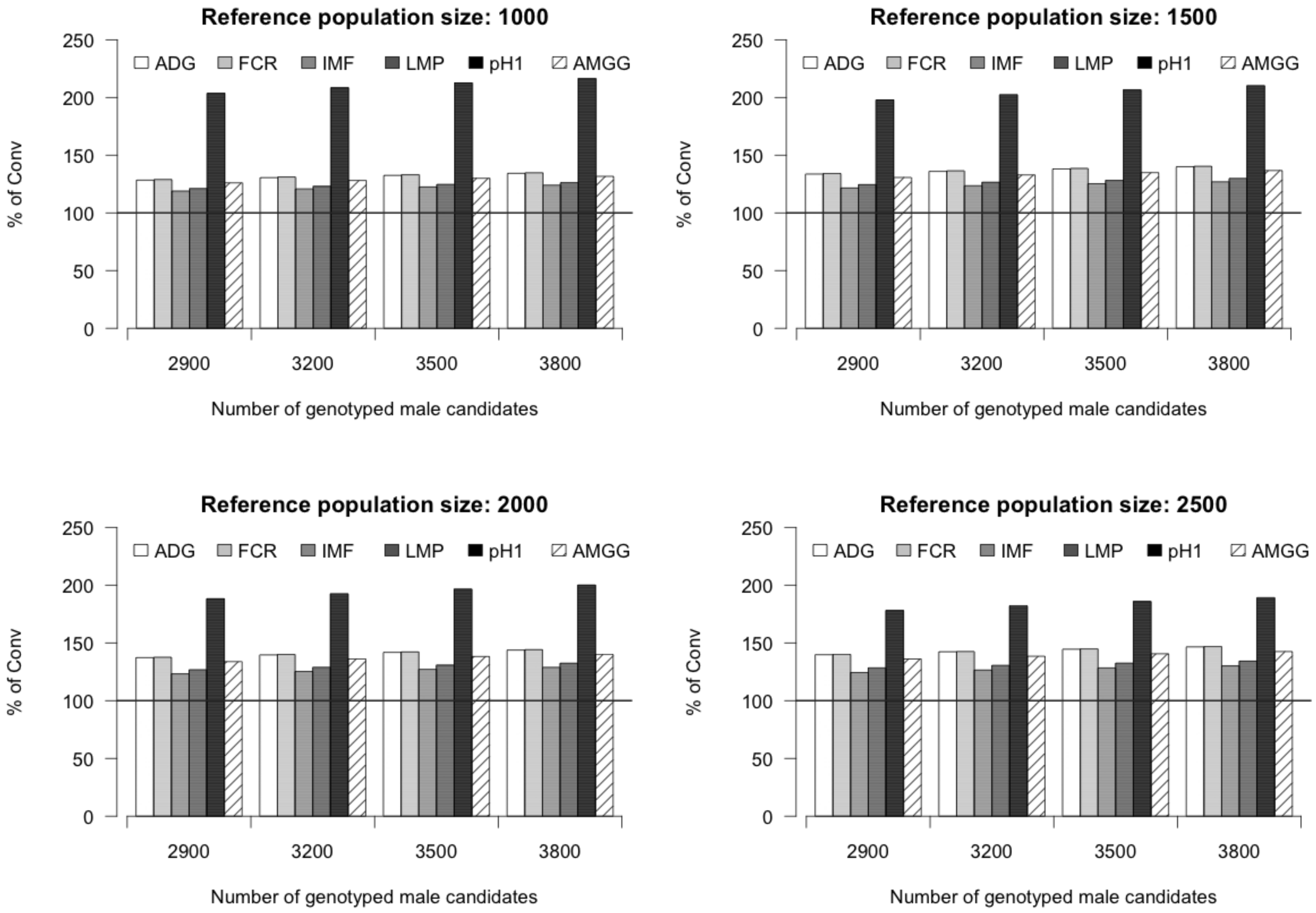
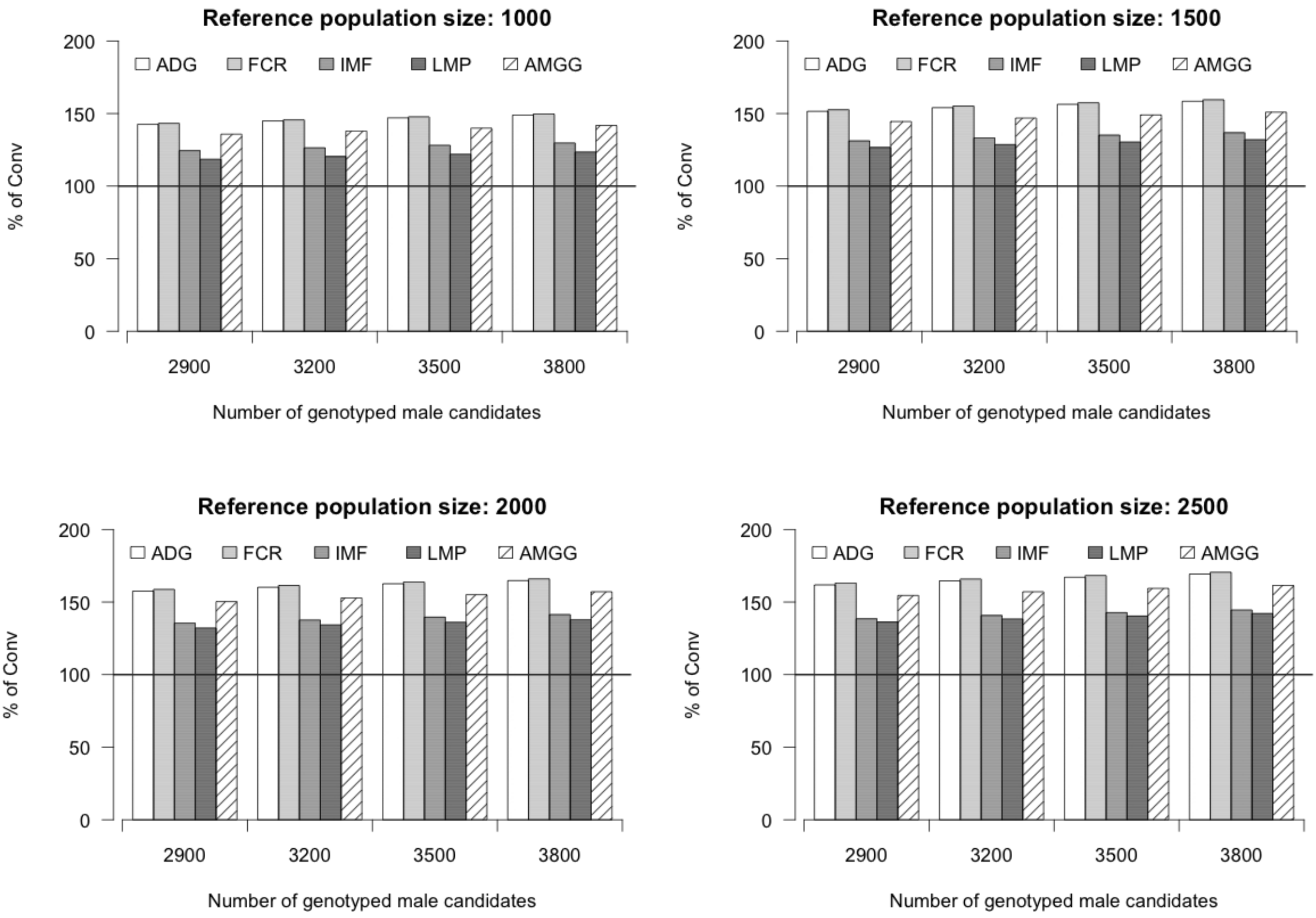


Figure 14 Annual natural genetic gain (*ANGG*) for breeding goal traits and annual monetary genetic gain (*AMGG*) relative to the conventional scheme (***Conv***) (set to 100%) under the genomic selection scheme ***Hybrid*** for Piétrain depending on number of genotyped males and reference population size. For the abbreviations for traits, see footnote Table 2.

(a)


Reference population size: 1000
Reference population size: 1500
Reference population size: 2000
Reference population size: 2500
ADG
FCR
IMF
LMP
AMGG
% of Conv
0
50
100
150
200
2900
3200
3500
3800
Number of genotyped male candidates

(b)

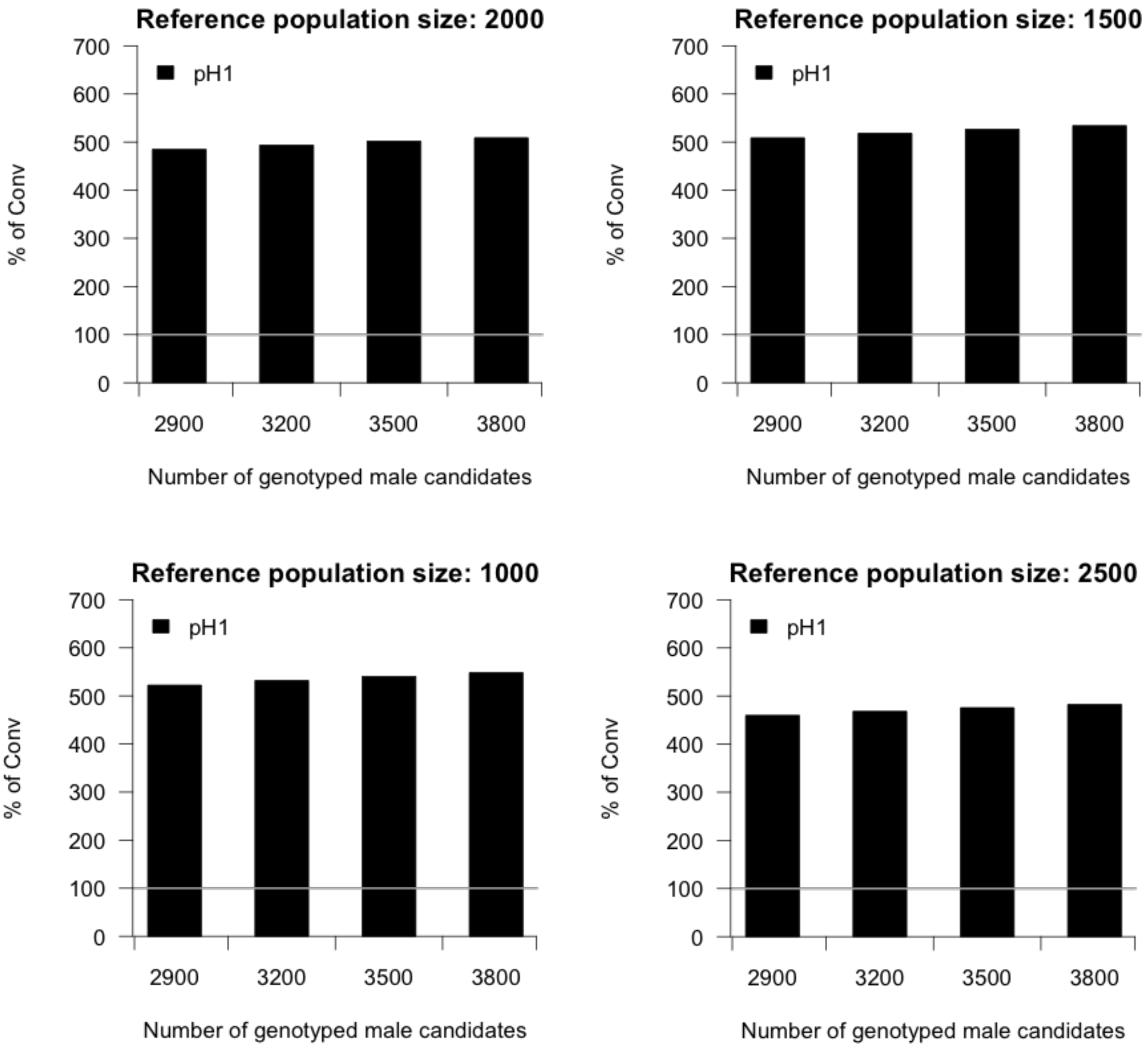


Figure 15 Annual natural genetic gain (*ANGG*) for breeding goal traits ADG, FCR, IMF, LMP and annual monetary genetic gain (*AMGG*) **(a)**, and annual natural genetic gain (*ANGG*) for the trait pH_1 **(b)**, relative to the conventional scheme (***Conv***) (set to 100%) under the genomic selection scheme ***Juvenile*** for Piétrain depending on number of genotyped males and reference population size. For the abbreviations for traits, see footnote Table 2.

During the implementation of the GS schemes, enlarging the number of genotyped male candidates (N_{gmc}) from 2900 to 3800 will lead to asymptotical increases for the *AMGG* and *ANGG*. However, the increments relative to ***Conv*** are not significant per 300 extra male candidates genotyped (Figure 14 and 15). For each scenario of *N*, in both ***Hybrid*** and ***Juvenile***, pH_1 obtains the highest magnitude among the five breeding goal traits for *ANGG* relative to ***Conv***. The relative magnitude for IMF is lower than that for LMP in ***Hybrid***, while in ***Juvenile*** this phenomena is reversed. On the other hand, enlarging the reference population size (*N*) also shows the opportunity to increase the *ANGG* and *AMGG*. The stimulus comes from the asymptotical growth of the r_{TI} for the male path via Equ. 2. With fixing N_{gmc}, the relative *ANGG* for the traits ADG, FCR, IMF and LMP grows asymptotically along with enlarging *N* from 1000 to 2500. On the contrary, the relative *ANGG* for pH_1 shows an asymptotical decreasing trend. This indicates there can be a compensation for the decrease of the pH value through enlarging *N*. Although the *ANGG* for pH_1 relative to ***Conv*** appears remarkably sensitive to the enlargement of N_{gmc} and *N*, this has no significant impact on the asymptotical increase tendency for the trend for the aggregate economic breeding value (*AMGG*). The explanation is the trait pH_1 has a small economic weight and absolute genetic change compared to other traits, and thus generating a small contribution to the monetary genetic gain.

3.2.5 Discounted return, costs and profit

Over an investment period of 10 years, conducting ***Conv*** may result in 11.628 € as the discounted return per animal (Table 11). Such return can be increased by 33% and by 58% respectively if adopting the GS scheme ***Hybrid*** and ***Juvenile***, assuming 2900 genotyped male candidates (N_{gmc} = 2900) and a reference population sized 1000 (N = 1000). The discounted costs amount to 3.2059 € per animal with the implementation of ***Conv***. In comparison, running ***Hybrid*** or ***Juvenile*** adds on the discounted costs by 70% particular for genotyping the candidate and the reference populations. The discounted profit from conducting ***Conv*** is 8.4234 € per animal. Breeders would benefit 19% and 54% more profit from applying ***Hybrid*** or ***Juvenile***. Similar to the GS schemes for DL, asymptotical increases for the discounted return and profit relative to ***Conv*** can be observed with the enlargement of N_{gmc} and *N* (Figure 16 and 17). The background is the asymptotical increases in the selection intensity and the accuracy of selection index (r_{TI}) for the male path. Besides, the discounted costs relative to ***Conv*** are added linearly. The marginal increases for the relative discounted return and profit is much thiner compared to DL, and is further narrowed while enlarging N_{gmc} and N.

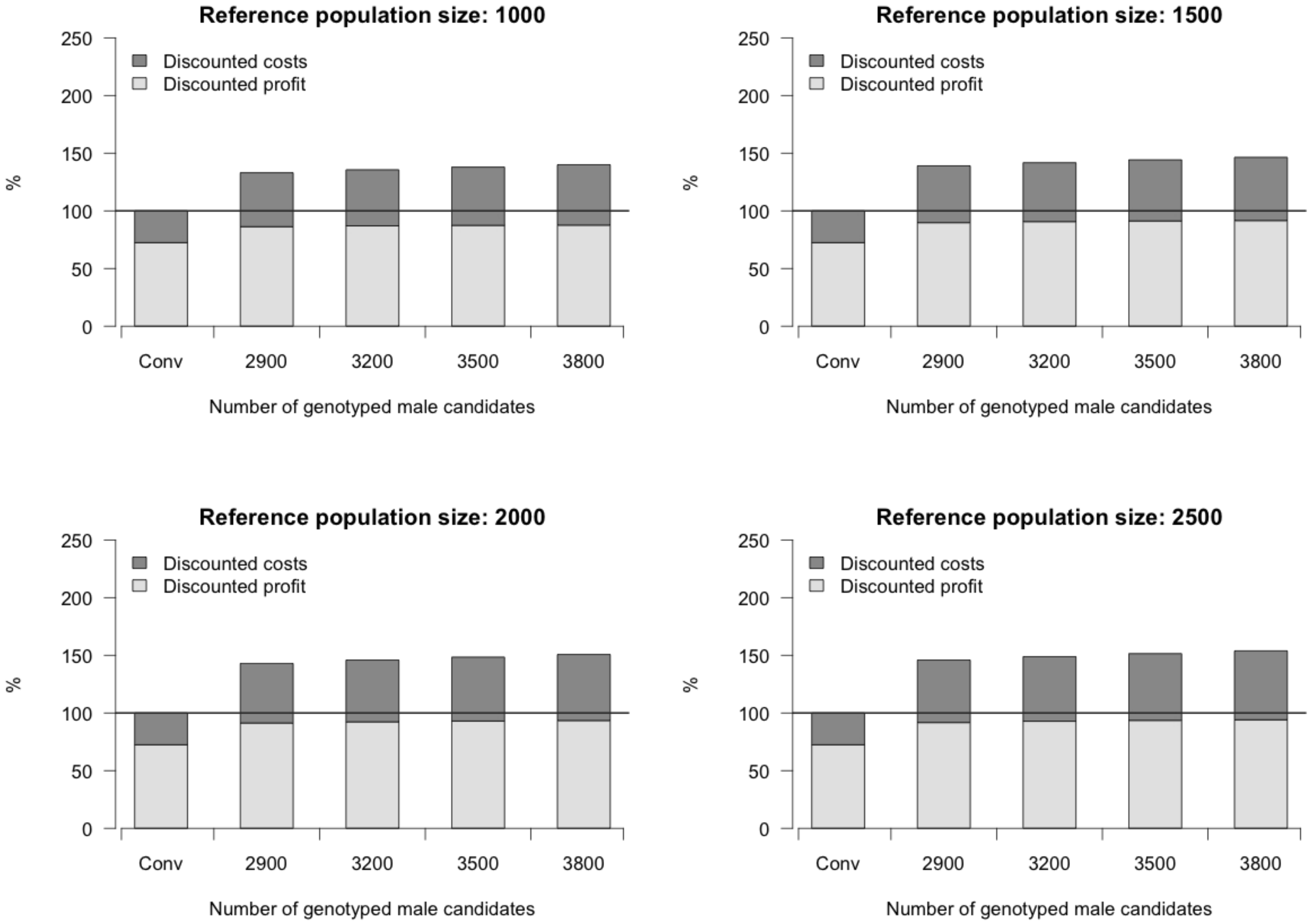


Figure 16 Discounted profit and discounted costs (sum = discounted return) for the genomic selection scheme ***Hybrid*** relative to the conventional scheme (***Conv***) for Piétrain depending on the the number of genotyped males and reference population size. The discounted return for ***Conv*** is set to 100%.

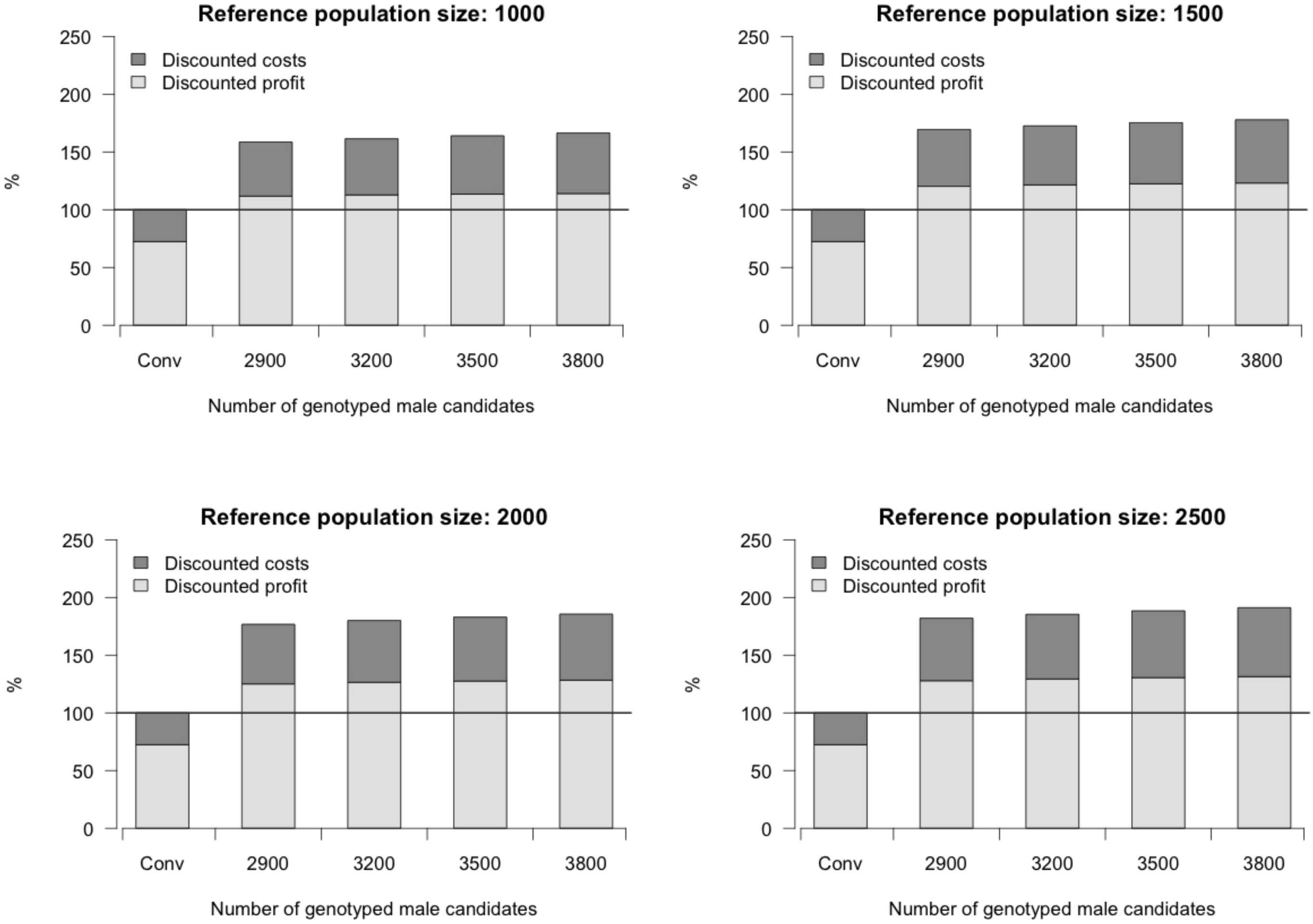


Figure 17 Discounted profit and discounted costs (sum = discounted return) for the genomic selection scheme ***Juvenile*** relative to the conventional scheme (***Conv***) for Piétrain depending on the number of genotyped males and reference population size. The discounted return for ***Conv*** is set to 100%.

4 Discussion

Estimation of genome-wide marker effects within a reference population, and transferring the estimates to animals in the whole population, is the key feature of genomic selection methodology (Haberland et al., 2012). The availability of 60k SNP chips for *Sus Scrofa* (Ramos et al., 2009) provides an opportunity to achieve highly accurate GEBVs for pigs that are comparative to those for dairy cattle (Cleveland et al., 2010). Dekkers (2007) illustrated that accuracy of GEBV (r_{mg}) depends on the proportion of genetic variance explained by markers (q^2) and the accuracy of estimates of marker effects ($r_{\hat{Q}}$) that are in linkage disequilibrium (LD) with QTL. Parameter q^2 is essentially based on the marker density and the extent of LD existing in the population. High values of r^2 as reported by Uimari and Tapio (2011) and Badke et al. (2012) in the US and Finnish pig breeds respectively are comparative with those in North American Holstein cattle. These findings corroborate the potential of applying GS in DL and PI breeding programs. Erbe et al. (2011) empirically determined $q = 0.9$ using a sample of Holstein Friesian bulls. To the best of my knowledge such empirical estimate are not available for pigs so far. Thus, $q = 0.9$ was referenced in this study assuming that a comparably dense SNP chip was exploited and sufficient LD exists in the observed populations. Deterministic calculations were used to predict $r_{\hat{Q}}$ (see Equ. 2) in the present study. This prediction method was fairly validated by the observation data from the US and Australian Holstein Friesian and Jersey dairy cattle populations (Hayes et al., 2009b). Although ZPLAN+ dose not model Bulmer effects (Bulmer, 1971), the reduction in genetic variance was implicitly considered because the genetic parameters were estimated based on the ongoing breeding programs. A limiting factor for a practical implementation of GS in pig breeding programs will be the availability of enough progeny tested boars as the reference population members (Simianer, 2009). Small reference population sizes may lead to insufficient reliabilities of GEBVs, especially for the low heritability traits, such as litter size. Ibánẽz-Escriche et al. (2009) stated that genomic selection could use crossbred pigs as a training population in order to select purebreds. This solution might be applied to the Bavarian pig populations, because since 2005 there has been a breeding value estimation utilizing purebred and crossbred information simultaneously (Habier et al., 2009a). Simianer (2009) and Haberland et al. (2010) both demonstrated significant advantages of genomic selection for pigs with an assumption of a reference population sized 1000 (i.e. N = 1000). This assumption for N was repeated and extended to 1500, 2000 and 2500 in the present modelling study. In order to determine the effective number of independent chromosome segments (M_e) (Equ.3), the effective population size (N_e) was estimated as 187 for DL and 157 for PI. All the output economic evaluation parameters are based on one single round of selection. Fixed costs for maintaining the ongoing breeding framework (e.g. the costs for housing, feed and labor force) are not included due to the challenge to quantify them per animal. The discounted costs for a modelled GS scheme aggregates the variable costs for genotyping the reference population and the male candidate population, in addition to the costs for the performance tests used in the conventional scheme (Table 9). The costs of genotyping per animal was assumed 150 € with a high-density SNP chip. This amount can possibly be reduced by using a low-density chip in combination with genotype-imputation technique (Cleveland and Hickey, 2013; Habier et al., 2009b; Wellmann et al., 2013). One of advantages for applying the technique is there can be more selection candidates genotyped due to the reduced genotyping costs. As Sitzenstock et al. (2013a) stressed, the discounted costs are realistic whereas the discounted return is a theoretically predicted value. The discounted return will only be realized when the improved breeding products are sold, or if the overall genetic superiority increases the market share. The continuous investment in progeny testing for the turnover of the reference population and in the re-calibration of SNP effects are required in practice in order to avoid dramatic declines in accuracies of GEBV over generations. The influences of dynamic population sizes (e.g. the reference population size, the number of progeny-tested boars per generation) on the economic evaluation parameters due to multi-round selections are beyond the scope of this study. In the era of genomic selection in pigs, a reference population is routinely genotyped prior to selection practices. A candidate population is likely genotyped at birth for pre-selection (Akanno et al., 2013), or following a pre-selection based on pedigree information and own performance (Henryon et al., 2012). The latter was evidenced more economically efficient for the case along with large candidate population sizes and high genotyping costs. Herein, an intermediate strategy is designed. That is to genotype the male candidates after a pre-selection based on the pedigree information (i.e. the parental EBVs) but before entering own performance tests (Figure 2). This design may preserve the contribution of pedigree information to the selection response, and also avoid genotyping all the reared male piglets which usually constitute a large candidate population size.

Based on ***Conv***, two types of GS schemes were modelled for DL or PI: (1) a hybrid scheme incorporating genomic information in the conventional selection strategy (***Hybrid***), and (2) a simplified scheme that selected genotyped male juveniles for breeding before progeny information was available (***Juvenile***). An additional modification to the ***Hybrid*** for DL was the abdication of the daughter proofs regarding litter size.

4.1 German-Landrace

4.1.1 The GS scheme *Hybrid*

The GS scheme ***Hybrid*** for DL especially selected genotyped young boars as well as genotyped elite boars without daughters' litter size records. This idea is based on a hypothesis that the potential of GS in pigs is especially of interest for traits with low heritability such as litter size (Ibañez-Escriche and Gonzalez-Recio, 2011). In ***Hybrid***, EB or EB-PS can be selected and used for service 1 yr earlier without waiting for the daughter proofs (Table 7 **(a)** vs. Table 4 **(a)**). Subsequently, the overall generation interval averaging all the selection paths is shortened by 14% considering an investment horizon of 10 years (Table 10).

Given $N = 1000$, additionally including the GEBVs in the conventional selection index for YB significantly increases the accuracy of selection index (r_{TI}) from 0.4994 to 0.7063 (Table 10). Thus, a considerable gain in the selection response can be expected within the selection group YB. The increase in r_{TI} for YB corresponds to an increase from 0.56 to 0.78 (Haberland et al., 2010), when a same reference population size (1000) was used to model GS strategies for *SUISAG* terminal sire-line PREMO®. Similar trends were also observed in two stochastic modelling studies: from 0.44 to 0.62 (Akanno et al., 2013) and from 0.44 to 0.52 (Lillehammer et al., 2013), where different sizes and compositions of reference population were considered. For the case with one trait in the index and the same trait in the aggregate genotype, there were more reports on the increase of r_{TI} for young boars (Cleveland et al., 2010; Lillehammer et al., 2011; Simianer, 2009; Tribout et al., 2012). Increases of r_{TI} for young bulls are often presented in genomic breeding programs for dairy cattle. Täubert et al. (2011) observed a substantial increase in the r_{TI} from 0.54 to 0.73 when incorporating GEBVs for serval economic traits. Thomasen et al. (2014) showed a maximum improvement for the reliability of selection index for young bulls from 25 to 64% (i.e. from 0.50 to 0.80 for r_{TI}), which was reported quite close to the reliability for the proven bulls (67%) (i.e. $r_{TI} = 0.82$). In this study, the increased r_{TI} for YB (0.7063) is not competitive with the r_{TI} for the conventionally selected elite boars (EB or EB-PS) (0.7688), which have the progeny proofs from station as well as the daughter proofs regarding litter size. Nevertheless, the gap is much smaller than the one between the r_{TI} for genotyped young boars (0.78) and the traditional old boars (~0.90) as reported by Haberland et al. (2010). This is due to the different breeding goal traits and amount of included genomic information. Because the two-step selection strategy for the male path was maintained in ***Hybrid***, the GEBVs were also included in the index of selection for EB and EB-PS. Preconditioned by the skip of the daughter performance on litter size, the inclusion of GEBVs led to a r_{TI} for EB and EB-PS as high as 0.7409 which was 4% lower than the level in ***Conv*** (0.7688) (Table 10). The r_{TI} for YB, EB and EB-PS can be improved by enlarging *N* (Figure 6). The theoretical background of this phenomenon is the increase of accuracy of GEBV (r_{mg}) for individual breeding goal traits (Table 12). The r_{TI} for YB starts to be competitive with the level for the conventionally selected elite boars (EB or EB-PS) when *N* is scaled to 2000 (data not shown), while the r_{TI} for EB and EB-PS is superior to that when *N* is enlarged to 1500.

Table 12 Predicted accuracy of genomic breeding value (r_{mg}) for breeding goal traits depending on the reference population size (*N*) for the genomic selection schemes for German-Landrace. For abbreviations of traits, see footnote Table 2.

Trait	r_{mg}†			
	N=1000	N=1500	N=2000	N=2500
ADG	0.5639	0.6314	0.6758	0.7074
AGF	0.5288	0.5980	0.6447	0.6786
FCR	0.5407	0.6095	0.6555	0.6886
LGF	0.5329	0.6020	0.6485	0.6821
STLP	0.5026	0.5726	0.6206	0.6560

† Predicted via Equ.2., according to Dekkers (2007) , Haberland et al. (2011) and Daetwyler et al. (2008, 2010).

Given the base scenario for the reference population size (i.e. $N = 1000$) and for the number of genotyped male candidates (i.e. $N_{gmc} = 300$), the annual monetary genetic gain (*AMGG*) for ***Hybrid*** was increased by 32% relative to ***Conv***. This expected increase is higher than the 14% increase in the monetary genetic gain per pig per year (from 94 for a pedigree-based strategy to 110 $ for a GS strategy) reported by Akanno et al. (2013) where a stochastic approach was applied to evaluate GS. In quantity, *AMGG* is the sum of the economically weighted annual natural genetic gain (*ANGG*) for individual breeding goal traits. In parallel to the increase of *AMGG* relative to ***Conv***, the *ANGG* for ***Hybrid*** was observed to increase in a desired direction for all the breeding goal traits. The trait STLP had a highest *ANGG* relative to ***Conv*** of 148%, while the other four traits ADG, AGF, FCR and LGF obtained a level of ca. 130% individually (Table 10). Therefore, ***Hybrid*** is particularly effective to genetic improvements of STLP. The similar relative increase for the litter size traits (AGF and LGF) and the fattening traits (ADG and FCR) indicates ***Hybrid*** is applicable to a special breeding aim where the both types of traits need to be balanced. However, from an economic perspective, STLP is not competitive to the other traits in creating benefit, due to the relatively lowest economic weight.

Within ***Hybrid***, the *AMGG* and *ANGG* for individual breeding traits can be further increased by enlarging N (Figure 7). The main reason is an asymptotical increasing tendency for accuracy of GEBV (r_{mg}) for individual breeding goal traits (Table 12). Among the traits, STLP remains the highest magnitude of *ANGG* relative to ***Conv*** for each scenario of N and N_{gmc}. Litter size traits (AGF and LGF) may outperform fattening traits (ADG and FCR) in the relative *ANGG* as long as N is enlarged more than 1000, and this comparative advantage will be strengthened with the enlargement. For example, with fixing N_{gmc} as 1200, the ratio of AGF to ADG in *ANGG* per genetic standard deviation ($\boldsymbol{\sigma_p}$) amounts to 1.69 given $N = 1000$, and extends to 1.85 when $N = 2500$. The increasing gap with adding genotype information confirms the hypothesis that GS is especially potential for low heritability traits such as litter size (Ibañez-Escriche and Gonzalez-Recio, 2011). Of more practical relevance for such observation is that litter size is predominantly emphasized compared to fattening traits in the next 5-yr breeding objective for DL. A gap of selection response was observed in a modelled GS for layers between egg weight and laying performance (Sitzenstock et al., 2013a), and between 350-day milk yield and calving to first service for dairy cattle (König and Swalve, 2009). The substantial reason for the gap in the either case was the negative genetic correlation between the two traits in comparison. In this study, the mechanism behind the increasing gap between the litter size and fattening traits is distinct. The litter size traits have extremely small genetic correlations with the fattening traits (see Table 2), so that the inclusion of GEBVs enables higher gaining in the accuracies of selection for the litter size traits. The greater effect of genomic information on the accuracy of selection for the trait LGF corresponds to the observations from Akanno et al. (2013) with stochastically simulated data. On the other hand, enlarging N_{gmc} can also increase the *ANGG* and *AMGG* via increasing the selection intensity on the genotyped male candidates (Figure 7). The superiority of the litter size to the fattening traits in the *ANGG* relative to ***Conv*** can also be enhanced, however, the increase rate appears much smaller compared to that when enlarging *N*. Hitherto, the expected results in *ANGG* from modelling ***Hybrid*** confirms the presumption from Simianer (2009) that the major potential for genomic selection can be realized through higher accuracy and increased selection intensity.

Economic efficiency of GS is of much interest for the Bavarian breeders, especially when facing extensive market competition of stock animals. Due to substantial differences from dairy cattle regarding breeding structure and biological condition, the comparative benefits from GS need to be evaluated for pigs. Bavarian pig breeds have unique breeding objectives and testing systems, thus there may be specific economic implications when attempting to integrate GS in the existing breeding programs. For the modelling with ZPLAN+, discounted return for a selection scheme is the sum of the monetary genetic gain weighted with the corresponding Standardized Discounted Expression (SDE) value realized in individual selection paths. 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 genetic gain of the parental selection group (Sitzenstock et al., 2013b). Only variable costs were considered aggregating the discounted costs for individual performance tests as well as genotyping, since fixed costs such as housing, labor and utilities have not yet clearly quantified. In contrast to return, the costs for a particular test is realized, and thus discounted only once at the time of occurrence within the investment horizon (Table 9). ***Hybrid*** was designed to take into account two extra cost groups based on ***Conv***: genotyping the reference and the male candidate populations. For a 10-year investment period, they were presumed to occur at the age of 0 yr. Thus, no discounting was applied to the genotyping costs. Confined to the above cost condition, ***Hybrid*** for DL shows a significant economic efficiency. For the base scenario of N (1000) and of N_{gmc} (300), the discounted return for ***Hybrid*** is 52% higher relative to ***Conv***, while the discounted costs are only added by 3% due to including the genomic information, leading to a gain of 242% in the discounted profit. There are few reports on economic efficiency analyses for GS schemes designed for pigs. The expected increase in discounted return of 52% is higher than the increases of 17% observed by Akanno et al. (2013) when using a stochastic approach to compare a GS and a pedigree-based scheme. The expected increase of 52% is also higher than the 37% increase reported by Simianer (2009), where GS for a single-trait breeding goal (litter size) was investigated. Enlarging N and N_{gmc} can raise the discounted return as well as profit asymptotically (Figure 9). The expected trend for discounted return corresponds to a demonstration from Henryon et al. (2012), where marginal returns from genomic selection diminish as the proportion of genotyped selection candidates increases. With increasing N and N_{gmc}, marginal increases of the discounted costs are observed as the total added costs are allocated to the whole population individuals (262,620). The asymptotical increase for discounted profit is because, the marginal costs increase linearly due to genotyping of additional animals in the reference or the male candidate population, while the extra returns result from the asymptotical increases in the accuracy of the genomic information or the selection intensity, respectively, through the enlargement of N or N_{gmc}. The observed developments in this study for discounted return, costs and profit are also similar to the trends with the increase of reference and candidate population sizes for the GS schemes in a layer breeding program (Sitzenstock et al., 2013a).

4.1.2 The GS scheme *Juvenile*

In the GS scheme ***Juvenile***, only genotyped young males without any progeny and daughter proofs were selected for entering AI, which allows a substantial reduction of generation interval. Without waiting for the progeny and daughter information, EB and EB-PS can be selected and used for service in parallel to YB at a 10 months age (Table 7 **(b)**). Thus, EB and EB-PS were at 1.15 yr old when the 1st offspring were born. Considering an investment period of 10 years, the overall generation interval was reduced by 23% from 2.47 to 1.89 yr in ***Juvenile*** (Table 10). For the layer breeding, the age at selection in cocks and hens relies on the age when the performance of the hens is recorded, and genomic selection can reduce the generation interval from e.g. 14.5

months to the biological limit of ca. 8 months (Sitzenstock et al., 2013a). In such case, breeding animals of both sexes are particularly 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 are available. For ***Juvenile***, the generation interval can not be expected to be reduced to the biological limit. YB, EB and EB-PS were not used until an age of 10 months, about 4 months later than the earliest age for biological maturity. This arrangement has two practical implications. Firstly, the own performances on the traits DG and FCR are necessary for selling boars on the farm level, and they are available as early as 8 months age. Secondly, the selected AI boars require a 2-month quarantine before semen production. The 23% of reduction in generation interval in ***Juvenile*** can contribute to annual natural and monetary genetic gain, however, compared to dairy cattle the impact is much smaller. In diary cattle genomic breeding programs, AI bulls are usually selected by using GEBVs among young genotyped males capable of producing semen at e.g. 15 months old, which is versus 5 to 6 yr in the conventional program (Täubert et al., 2011). Although GEBVs of young bulls are less accurate than conventional breeding values estimated for progeny-tested bulls, the loss in accuracy of selection is compensated by a huge reduction in generation intervals (Bouquet and Juga, 2013). Schaeffer (2006) presented a reduction from 6.5 to 1.75 yr. Therefore, genetic gain can be rapidly cumulated over a substantially shortened generation. Due to the biological condition of relatively short generation interval for pigs (ca. 2 to 2.5 yr), substantial reductions of generation interval is hardly expected through abandoning progeny performance. To evaluate the impact of the reduced generation interval on the *ANGG* and *AMGG*, the natural and monetary genetic gains per generation (i.e. *ANGG* × the overall generation interval and *AMGG* × the overall generation interval) can be compared to ***Conv***. The results show that ***Juvenile*** is superior to ***Conv*** in the both gains per generation under the base scenario of N (1000) and of N_{gmc} (300). It indicates that for ***Juvenile*** the higher annual genetic gains are more affected by the increased accuracy of selection (i.e. r_{TI} for the selection group YB) than the reduction of generation interval. This considerably confirms the perspective from Ibañez-Escriche and Gonzalez-Recio (2011) that the genetic gain of GS for pigs is mainly improved by increasing the accuracy of selection. Another remarkable advantage of shortening generation interval for dairy cattle is the substantial reduction of breeding costs. In the traditional breeding programs, waiting ca. 5 yr for the performances of daughters is required in order to identify elite bulls with accurate breeding values. Assuming a waiting time of 4.5 yr and feeding and keeping costs of 5 € per bull per day, Leisen (1999) reported that 32% of the costs for progeny testing are related to unproductive waiting period of bulls from insemination completion to breeding value estimation. Although the feeding and housing costs per test boar were not yet clearly quantified and not considered in the present modelling, it is believed that such costs incurred during the wait for the complete daughter information are much less compared to diary cattle. One explanation for this is the relatively shorter waiting time. The other explanation might be that the mixture of a half sib- and a progeny testing design for selections of herd book boars (Habier et al., 2009a) reduced the average waiting time per test boar. The latter means that considerable poorly-proven boars with few daughter information are used for breeding the next generation of herd book animals. Sitzenstock et al. (2013a) pointed out there are considerable economic losses due to the matings of a substantial proportion of cows to test bulls with an inferior average breeding value compared to progeny tested bulls. These economic losses, together with the housing costs, add up to ca. €25 000 per tested bull. The comparative economic losses also exist in the current Bavarian breeding framework, because in some important breeding herds poorly-proven natural service sires are mated to the purebred breeding sows, whereas the well-proven AI-boars are kept in AI stations for the only purpose of producing semen for the piglet production (Habier et al., 2009a). Nevertheless, cumulative genetic progress is only achieved in the breeding unit not in the production unit.

Juvenile was modelled to select the YB, EB and EB-SP based on the same information sources (pedigree, own and genomic information). Thus, the r_{TI} for YB, EB and EB-SP is expected to be equivalent. Compared to ***Conv***, the r_{TI} for YB is increased from 0.4994 to 0.7063 provided N = 1000, as the case under ***Hybrid***. While the r_{TI} for EB or EB-PS is decreased from 0.7688 to 0.7063 (Table 10) due to skipping all the progeny and daughter proofs. Equivalent to the r_{TI} for YB under ***Hybrid***, the r_{TI} for all selected males (YB, EB and EB-PS) can be superior to the conventionally selected males when N is upsized to 2000 (Figure 6).

Given the base scenario of N (1000) and of N_{gmc} (300), the *AMGG* for ***Juvenile*** was observed 46% higher relative to ***Conv*** (Table 10). Higher *ANGG* was also observed for all the breeding goal traits. The relative *ANGG* to ***Conv*** for STLP was 17 percentages lower than that under

Hybrid, whereas for the rest of the traits higher relative *ANGG* was resulted. Enlarging *N* and N_{gmc} leads to an asymptotical increase of *AMGG* in ***Juvenile*** as well as of *ANGG* for individual breeding goal traits. For each scenario of *N* and N_{gmc}, the litter size traits (AGF and LGF) have the highest increases relative to ***Conv*** (Figure 8). With the enlargement of *N* and N_{gmc}, the *ANGG* for the fattening traits (ADG and FCR) relative to ***Conv*** increases more slowly than the litter size traits, resulting in an expanding gap between the two types of traits. The explanation might be that there is an extremely small genetic correlation of litter size with fattening traits (see Table 2), and the combination of genomic information entails a higher accuracy of selection on litter size. The trait STLP shows a higher increase rate than the fattening traits. For example, the lowest ranking for the *ANGG* relative to ***Conv*** given *N* = 1000 ascends to the third place when *N* is enlarged over 2000.

By implementing ***Juvenile***, economic advantage is remarkable over ***Conv***. For the base scenario of *N* (1000) and of N_{gmc} (300), the discounted return and profit is observed 77% and 361% higher relative to ***Conv***, which turns out to be 15 and 119 percentages higher than the relative level under ***Hybrid***, respectively (Table 10). In spite of lacking progeny information compared to ***Hybrid***, the observed higher magnitude in discounted return resulted from the earlier selection and use of the elite boars. Because of that, the genetic superiority due to the selection round of elite boars (EB and EB-PS) could be transmitted to the successive generations earlier, so that within a defined investment period (10 years) extra proportions of the genetic gain could be accumulated in the realization selection groups HS and PS. In the context of the gene flow method (Hill, 1979), the extent of the accumulation is measured by Standardized Discounted Expression (SDE) in terms of selection paths. 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 genetic gain (Sitzenstock et al., 2013b). In a short word, the reason for the observed higher magnitude in discounted return under ***Juvenile*** vs. ***Hybrid***, can be explained by the resulted higher Standardized Discounted Expression (SDE) for the selection paths EB>HS and EB-PS>PS respectively. In addition to the introduction of the genotyping with high-density SNP chips, the conventional performance tests in fields and on stations was kept in order to re-calibrate SNP effects and to estimate parental EBVs**.** Thus, the discounted costs were resulted to be equal to the amount under ***Hybrid***, which was only added by 3% based on ***Conv***. Discounted return and profit can also be increased with enlarging N and N_{gmc} (Figure 10). The asymptotical increasing trend are similar to the decreasing marginal increases in return and profit in a layer GS breeding program (Sitzenstock et al., 2013a). The theoretical background is the asymptotical increase of $AMGG$ with enlarging N and N_{gmc}, and on the other hand, the linear increase of the discounted costs.

4.2 Piétrain

4.2.1 The GS scheme *Hybrid*

Piétrain is characterized with high flesh and ham proportion and the low fat proportion (Sambraus, 1994), and used as the only terminal sire-line in the production segment of the Bavarian breeding pyramid. In the modelled GS scheme ***Hybrid*** for PI, genomic information was additionally incorporated at the time of the first-step selection based on the conventional scheme (Table 7 **(a)**). Thus, the resulting generation interval will not be changed (Table 11).

Given $N = 1000$, and additionally involving the genomic information may increase the accuracy of the selection index (r_{TI}) for YB from 0.3774 to 0.6525 (Table 11). Such trend is analogous to several reports on the substantial increase of r_{TI} for the genotyped young boars (Akanno et al., 2013; Haberland et al., 2010; Lillehammer et al., 2013), and for genotyped young bulls (Täubert et al., 2011; Thomasen et al., 2014). Although the reported increases differed in magnitudes, commonly these increased r_{TI} for the genotyped young males were still not comparable to the levels for the conventionally selected elite males which are based on the sufficient progeny information. In ***Hybrid*** for PI, the elite boars were selected based on the GEBVs in addition to all the conventional information (parental EBVs, own performances in fields and progeny performances on station). As a consequence, the r_{TI} for elite boars was increased by 7% based on ***Conv***, from 0.7642 to 0.8159 (Table 11). Further increases for young and elite boars are possible, and asymptotical when enlarging N (Figure 13). The threshold of N for the genotyped young boars exceeding the conventionally selected elite boars in the r_{TI} may be 2500, resulting in an increase by 17% from 0.6525 to 0.7623 (data not shown). The r_{TI} for the genotyped elite boars grew more steadily when N is enlarged from 1000 to 2500, creating an increase of only 4% from 0.8159 to 0.8523.

With the base scenario of *N* (1000) and of N_{gmc} (2900), the genetic trend for all the breeding goal traits was observed to develop in the favored direction under ***Hybrid***, expect for the meat quality trait pH_1. Under ***Conv***, a decrease of 0.00058 units in pH value (i.e. *ANGG* = -0.00058) may occur. It can be further enhanced by 105% due to the integration of genomic information (Table 11). In spite of this, the *AMGG*, which aggregates the economically weighted *ANGG* for all the traits, was still increased by 26% based on ***Conv***. It suggests the economic loss due to the negative *ANGG* for pH_1 can be offset by the benefits from the increases of *ANGG* for the rest of the traits. The fattening trait FCR was improved with a decline in *ANGG* by 29%, while the *ANGG* for ADG was increased by a similar percentage (28%). The carcass trait LMP and the meat quality trait IMF was improved by ca. 20% in *ANGG*, individually. Since PI is distinguished for high flesh proportion, the observed increases of *ANGG* for IMF and LMP emphasize the position of PI as a sire line.

Similar to DL, enlarging *N* can increase the magnitude of *AMGG* relative to ***Conv***, as well as the relative magnitude of *ANGG* for all the traits except the trait pH_1 (Figure 14). For the trait pH_1, the reduction in the relative *ANGG* was observed, indicating that the unfavored decrease in the pH value under ***Conv*** will be reduced by enlarging *N*. The trait pH_1 was superior to other traits in the relative *ANGG*, however, this superiority becomes narrow with enlargement of *N*. On the other hand, enlarging N_{gmc} from 2900 to 3800 analogously increases the *AMGG* and *ANGG* for all the breeding goal traits, as was the case for DL. Nevertheless, all of these increases are slower compared to DL. The major reason might be the larger base number of genotyped male candidates (2900) compared to 300 on the side of DL, so that the increment of 300 on the base number allowed for smaller change in selection intensity. The increase of the relative *ANGG* for pH_1 represented an enhancement of the decrease of the pH value achieved under ***Conv***, and thus is unfavorable for breeders. A increasing gap between the fattening traits (ADG, FCR) and the trait LMP in relative *ANGG* was also observed, although it may not be particularly clear with a background of the genetic changes for the trait pH_1. This gap may be the consequence of the unfavorable genetic correlations of LMP with ADG (-0.350) and with FCR (-0.380) (Table 2).

For the modelling of ***Hybrid***, genotype information was additionally combined in the conventional scheme. Thus, the increase of the operational costs will source from genotyping the reference and the male candidate populations. Given the base scenario of N (1000) and of N_{gmc} (2900) discounted costs were increased by 70% relative to ***Conv*** (Table 11), in contrast to the 3% increase for DL (Table 10). This is because there was a greater number of male candidates that need to be genotyped in PI (2900), compared 300 on the side of DL. For discounted return, the expected increase of 33% is smaller than that in DL (52%). However, it is higher than the 17% increase reported by Akanno et al. (2013) when using a stochastic approach to compare a GS with a pedigree-based scheme. The larger increase percentage in discounted costs, and the smaller increase percentage in return lead to a lower increase (19%) in discounted profit compared to the DL side (242%). Enlarging N and N_{gmc} will bring about further increases in the discounted return, costs as well as profit, although these increases are not substantial (Figure 17). The explanation for this is the total increase is apportioned to the whole population individuals (261,725), respectively. The increase in the relative discounted return is asymptotical and complies with Henryon et al. (2012), where diminishing marginal returns from genomic selection is reasoned as the proportion of genotyped selection candidates increases in a stochastically simulated population. The asymptotical increase for discounted profit was also observed. That is because the marginal costs increase linearly due to genotyping extra animals in the reference or male candidate population, while the benefits resulting from grow asymptotically with the enlargement of N or N_{gmc}.

4.2.2 The GS scheme *Juvenile*

Based on the conventional scheme, the GS scheme ***Juvenile*** skipped the wait of progeny performances and selected juvenile males with genomic information for breeding. Compared to ***Conv***, the elite boars (EB and EB-PS) can be selected earlier, at the same time as the young boars (Table 7 **(b)**). Thus, the overall generation interval can effectively be shortened by 15% over an investment period of 10 years (Table 11). The theoretical comparison with other species and practical relevances for the reduction of the generation interval are similar to the case under ***Juvenile*** for DL (see section **4.1.2**).

As the design in DL, ***Juvenile*** carried out a one-step selection for elite boars (EB and EB-PS) in parallel to young boars (YB), based on the same number of selection candidates and the same information source: pedigree, own and genomic information (Table 8). As a result, an equivalent accuracy of selection index (r_{TI}) (0.6525) was observed for young and elite boars with the base scenario of N (1000) and of N_{gmc} (2900), which is 73% higher and 15% lower than the r_{TI} under ***Conv***, respectively (Table 11). The increase of r_{TI} for young boars originates from the additional combination of GEBVs, while the decline for elite boars is ascribe to the loss of the informativeness due to the substitution of GEBVs for the progeny performances in the index. Along with the enlargement of N, accuracy of genomic breeding value (r_{mg}) for each trait grows asymptotically (Table 13). This contributes to the increasing r_{TI} for all selected males (YB, EB and EB-PS). Equal to the r_{TI} for YB under ***Hybrid***, the r_{TI} for YB, EB and EB-PS is superior to the conventionally selected males when N is scaled up to 2500.

Table 13 Predicted accuracy of genomic breeding value (r_{mg}) for breeding goal traits depending on the reference population size (N) for the genomic selection schemes for Piétrain. For abbreviations of traits, see footnote Table 2.

Trait	r_{mg} †			
	N=1000	N=1500	N=2000	N=2500
ADG	0.5548	0.6229	0.6679	0.7001
FCR	0.5462	0.6148	0.6604	0.6931
IMF	0.5837	0.6498	0.6925	0.7226
LMP	0.5815	0.6478	0.6907	0.7210
pH_1	0.5862	0.6521	0.6947	0.7246

† Predicted via Equ.2., according to Dekkers (2007) , Haberland et al. (2011) and Daetwyler et al. (2008, 2010).

By applying the base scenario of N (1000) and of N_{gmc} (2900) to ***Juvenile***, the substitution of genomic information for progeny performances will advance the *AMGG* for ***Hybrid***, leading to a 36% increase relative to ***Conv*** (Table 11). The annual genetic gain for the breeding goal traits were enhanced in the desired direction, with the exception of pH_1. The decrease in the pH value under ***Conv*** was by strengthened by 424%. This markedly decrease was resulted based on mathematical modelling and seems impossible in practice. However, it may remind breeders to pay special attention to balanced breeding when applying genomic selection schemes. Implementing ***Juvenile*** can create a higher relative *ANGG* than ***Hybrid*** for all the traits except for LMP (Table 11). The fattening traits ADG and FCR obtained 143% with 15 percentage larger than the level under ***Hybrid***, and the relative *ANGG* for carcass trait IMF was 5 percentage larger. The relative *ANGG* for LMP was 2 percentage lower than the level under ***Hybrid***. Nevertheless, such relative *ANGG* was 19% higher compared to ***Conv*** also consolidate PI as a sire line in Bavaria.

Enlarging N_{gmc} and N can accelerate the annual natural genetic gain for the breeding goal traits and the annual monetary genetic gain. An exceptional case may be the annual genetic gain for the trait pH_1 when particularly enlarging N. With fixing N_{gmc}, the magnitude for the *ANGG* relative to ***Conv*** was reduced (Figure 15 **(b)**). This indicates that, the decline in the pH value observed under the base scenario of N (1000), can be compensated, which is favored for meat quality. Despite of these changes, the relative *ANGG* for pH_1 was superior to the rest of the traits for each scenario of N_{gmc} from 2900 to 3800 and of N from 1000 to 2500. Figure 15 also illustrated the asymptotical increases for the rest of the traits in *ANGG* relative to ***Conv*** with enlarging N_{gmc} and N, and there was an increasing gap between fattening traits (ADG and FCR) and the carcass trait LMP. This may be due to the negative genetic correlations of LMP with ADG (-0.350), and with FCR (-0.380) (see Table 2).

Although the progeny information was not taken into account at the stages of selection for the breeding males, the progeny testing were necessary anyway for the re-calibration of additive genetic effects for SNPs and for the traditional breeding value estimation in practice. Hence, the discounted costs for ***Juvenile*** should be equal to those for ***Conv*** and ***Hybrid***. Given the base scenario of N (1000) and of N_{gmc} (2900) discounted costs were 70% higher relative to ***Conv*** (Table 11). Discounted return and profit were further increased based on ***Hybrid***. The amount relative to ***Conv*** was 58% and 54% respectively, with an increase of 25% and 35% based on the relative amount under ***Hybrid*** (Table 11). The reason for such increase was that the early selection and use of elite boars allowed early transmission of the genes of elite boars (EB, EB-PS) to the successive generations, so that within a defined investment period (10 years) extra proportions of the genetic gain originating from elite boars could be accumulated in the realization selection groups HS and PS. Ultimately, higher Standardized Discounted Expression (SDE) for the selection paths EB>HS and EB-PS>PS can be resulted during the mathematical modelling within ZPLAN+. Enlarging N and N_{gmc} has positive effect on discounted return, costs, as well as profit. The magnitudes relative to ***Conv*** were observed to increase with the enlargements, however, the marginal increases diminish These trends were similar to the observations in GS schemes modelled for a commercial layer breeding (Sitzenstock et al., 2013a). The substantial drive for the increases of discounted return is the asymptotical growths of accuracy of genomic breeding value (r_{mg}) for individual breeding goal traits (Table 13). The asymptotical increase when enlarging N_{gmc} corresponds to a conclusion from Henryon et al. (2012), where marginal returns from genomic selection diminish as the proportion of genotyped selection candidates increases. The theoretical reason for this was the asymptotical increase of selection intensity. As the marginal costs increase linearly due to adding the individuals in the reference and male candidate populations, hence the discounted profit presented an asymptotical increase in accordance with the trend for the discounted return.

5 Conclusions

Increases in the annual genetic gain for breeding goal traits and in the investment revenue are possible in the Bavarian German-Landrace and Piétrain breeding programs by transforming the conventional selection scheme into the two modelled genomic selection schemes. In the conventional scheme, young boars were selected at the first step based on the pedigree information and the own performance, and elite boars were selected at the second step when the progeny performances were available. In the genomic selection scheme ***Hybrid***, genotypic information was additionally included in the selection criteria for young boars. Exclusively for German-Landrace, waiting for daughter litter size performances was skipped for the selection for elite boars. In addition to the inclusion of genomic information, the genomic selection scheme ***Juvenile*** was modelled to select elite boars at an earlier age without waiting for the progeny performances. The increased annual genetic gain is mainly due to the integration of genomic information in the selection criteria for young boars. The shortened generation interval can also contribute to the increased annual genetic gain when applying the scheme modelled to use the elite boars without waiting for the progeny performance. This scheme is expected to be superior to the scheme that only integrates the genotypes in the annual genetic gain for the overall breeding goal and investment efficiency. Adding genotypic information through enlarging the sizes of the reference population and the genotyped male candidates can increase the annual genetic gain and the benefit for both genomic selection schemes. The limiting factor of insufficient reference population size can be addressed through recruiting the boars with crossbred progeny performances. Under both genomic selection schemes, a substantial increase in the annual genetic gain is particularly evident for the litter size traits in the German-Landrace breeding population, which is the major dam line in Bavaria. The increased annual genetic gain for the carcass trait, lean meat percentage of carcass (LMP), emphasizes Piétrain as the sire line in Bavaria. However, the unfavorable genetic trend for the meat quality trait, pH value in M. long dorsi measured 45 minutes post mortem (pH$_1$), may be further decreased.

6 Summary

Genomic selection shows advantages in cattle breeding compared to traditional selection strategies. Adoption of this technique in pig breeding was reported promising for economically relevant traits, e.g. litter size, fattening and meat quality traits. The availability of 60K Single-Nucleotide-Polymorphism (SNP) chip for *Sus Scrofa* and decreasing genotyping costs offer an opportunity to implement genomic selection strategies in the Bavarian pig breeding programs. In this study, a progeny-testing-based conventional selection scheme and two genomic selection schemes were modelled for the German-Landrace (DL) and Piétrain (PI) nuclear breeding, respectively. In the conventional scheme, young boars were selected at the first step based on the pedigree information and the own performance, and elite boars were selected at the second step when the progeny performances were available. In the genomic selection scheme ***Hybrid***, genotypic information was additionally included in the selection criteria for young boars. Specifically for German-Landrace, daughter litter size performances was not included into the selection criteria for elite boars. In addition to the above-mentioned inclusion of genomic information, the genomic selection scheme ***Juvenile*** was designed to select elite boars without waiting for the progeny performances, and to use elite boars at an early age as young boars.

In the scheme ***Hybrid*** for German-Landrace, the overall generation interval was shortened by 14% compared to the conventional scheme. This is because there is no need of waiting for daughter litter size performances. Provided a reference population sized 1000 and 300 genotyped male candidates, the genetic trend in terms of annual natural genetic gain was increased by 32%, 30%, 33%, 31% and 48% for the traits average daily gain (ADG), feed conversion ratio between 30 and 105 kg live weight (FCR), number of live born piglets per litter (LGF), number of weaned piglets per litter (AGF) and number of inverted teats (STLP), respectively. The trend for aggregate economic breeding value in terms of annual monetary genetic gain was increased by 32%. These increases were essentially attributed to a substantial gain of 41% in the accuracy of selection index for young boars due to the combination of genomic information. The scheme ***Hybrid*** was shown to be economically efficient. In this study, the return, costs and profit accumulated in the investment period of 10 years was discounted to the present value. Compared to the conventional scheme, the scheme ***Hybrid*** may raise the discounted return, costs and profit

by 52%, 3% and 242%, respectively.

On the side of Piétrain, the overall generation interval was expected to be equivalent to that under the conventional scheme. With a reference population sized 1000 and 300 genotyped male candidates, applying the scheme ***Hybrid*** strengthens the genetic trend for the traits ADG, FCR, intramuscular fat content (IMF), lean meat percentage of carcass (LMP) and pH value in M. long dorsi measured 45 minutes post mortem (pH_1) by 28%, 29%, 19%, 21% and 105%, respectively. The application also allow an increase of 26% in the trend for aggregate economic breeding value. These increases were mainly due to the increase of 73% in the accuracy of selection index for young boars through the inclusion of genomic information. By investing in the scheme ***Hybrid*** instead of the conventional scheme, the discounted return, costs and profit may be boosted by 33%, 70% and 19%, respectively.

In the scheme ***Juvenile*** for German-Landrace, the overall generation interval was shortened by 23% compared to the conventional scheme. Given a reference population sized 1000 and 300 genotyped male candidates, the accuracy of selection index for young boars was increased by 41%. As the progeny information were excluded, elite boars were observed to obtain an equal accuracy, resulting in an decrease of 8% compared to the conventional scheme. Owing to the increased accuracy for young boars in addition to the reduced generation interval, the genetic trend was increased by 36%, 49%, 39%, 49% and 31% for the breeding goal traits ADG, AGF, FCR, LGF and STLP, respectively, and the trend for aggregate economic breeding value was increased by 46%. Investing in the scheme ***Juvenile*** may lead to an increase in discounted return and profits by 77% and 361% respectively, while the discounted costs were observed to be consistent with the level under the ***Hybrid***. This was explained by the fact that the progeny tests can not be eliminated in the scheme ***Juvenile*** for re-calibrating the SNP genetic effects in case of linkage-disequilibrium decay over generations.

On the side of Piétrain, the overall generation was shortened by 15%. The accuracy of selection index for young boars was increased by 73%, while the accuracy for elite boars was reduced by 15%. The genetic trend for the traits ADG, FCR, IMF, LMP and pH_1 was enhanced by 43%, 43%, 24%, 19% and 424%, respectively. An increase of 36% in the trend for aggregate economic breeding value was also observed. Discounted return, costs and profit were increased by 58%, 70% and 54%, respectively.

For both modelled genomic selection schemes, enlarging the sizes of the reference population and the genotyped male candidates theoretically increases the accuracy of estimated genomic breeding value and the selection intensity, respectively, and hence will strengthen the observed annual genetic gains, discounted returns and discounted profits. The marginal increase in the magnitudes for discounted return and profit diminishes along with the enlargements. In Piétrain, an exceptional case was observed for the trait pH_1. When particularly enlarging the size of reference population, there can be compensations for the unfavorable genetic gain.

In conclusion, genomic selection can substantially increase the efficiency of breeding programs for the Bavarian German-Landrace and Piétrain populations. Increases in the annual genetic gain for the breeding goal traits are mainly due to the integration of genomic information under the modelled genomic selection scheme ***Hybrid***. The shortened generation interval can additionally contribute to the increased annual genetic gain under the scheme ***Juvenile***. Although the breeding structures for both lines do not allow for a cost reduction, the latter scheme was shown more profitable. In the future, adding reference population members and genotyped male candidates can be applied to increase annual genetic gain and benefit. For former strategy, the insufficiency of purebred progeny tested boars can be addressed through including the boars with crossbred progeny performances.

7 Zusammenfassung

Beim Rind ist die genomische Selektion vorteilhaft gegenüber traditionellen Selektionsstrategien. Für wirtschaftlich relevante Merkmale in Schweinezuchtprogrammen, wie beispielweise Wurfgröße, Mastleistungs- und Fleischqualitätsmerkmale, scheint die Einführung der genomischen Selektion ebenfalls vielversprechend zu sein. Die Verfügbarkeit eines 60K SNP-Array für *Sus Scrofa* und sinkende Genotypisierungskosten ermöglichen die Implementierung der genomischen Selektion im bayerischen Schweinezuchtprogramm. In der vorliegenden Arbeit wurde für die Deutsche Landrasse (DL) und Piétrain (PI) Herdbuchpopulationen jeweils ein konventionelles mit zwei genomischen Selektionsszenarien verglichen. Im konventionellen Szenario werden die Jungeber in einer ersten Selektionsstufe aufgrund von Pedigreeinformation und Eigenleistungsprüfung selektiert; nach abgeschlossener Nachkommenprüfung werden in einer zweiten Selektionsstufe die Eliteeber selektiert. Im genomischen Szenario ***Hybrid*** wurde für die Jungeberselektion neben Pedigreeinformation und Eigenleistungsprüfung zusätzlich Genotypinformation verwendet. In der deutschen Landrasse wurde die Wurfgröße nicht als Selektionskriterium für die Eliteeber ausgewählt. Zusätzlich zu der oben genannten Einbeziehung der genomischen Information, wurde im genomischen Selektionsszenario ***Juvenile*** auf die Nachkommenprüfung verzichtet, sodass Eliteeber bereits im jungen Alter eingesetzt werden können.

Im Szenario ***Hybrid*** kann im Vergleich zum konventionellen Szenario das Generationsintervall in der DL Population um 14% gesenkt werden, da nicht mehr auf das Merkmal Wurfgröße gewartet werden muss. Bei einer Referenzpopulation von 1000 Ebern und 300 genotypisierten Selektionskandidaten erhöht sich der jährliche Zuchtfortschritt je nach Merkmal um 30 (Futterverwertung) bis 48% (Stülpzitzen) (32% tägliche Zunahme; 33% Anzahl lebendgeborener Ferkel. 31% Anzahl abgesetzter Ferkel). Im Gesamtzuchtwert, dargestellt als finanzieller Gewinn, konnte eine 32%-ige Steigerung erreicht werden. Der höhere Zuchtfortschritt beruht hauptsächlich auf einer 41% höheren Genauigkeit des Selektionsindex der Selektionskandidaten durch Berücksichtigung von Genotypinformation. Hinsichtlich der Kosten für die Eigenleistungsprüfung war das Szenario ***Hybrid*** ökonomisch äußerst effizient. In der

vorliegenden Studie wurden die akkumulierten Erträge, Kosten und Gewinne für eine Investitionsperiode von 10 Jahren zum aktuellen Wert diskontiert. Im Vergleich zum konventionellen Programm können im Szenario ***Hybrid*** 52% höhere Erträge erzielt werden, während nur um 3% höhere Kosten anfallen. Dadurch kann ein um 242% höherer Gewinn erzielt werden.

In der Piétrain Population muss im Szenario ***Hybrid*** mit einem unveränderten Generationsintervall gerechnet werden. Bei einer Referenzpopulation von 1000 Ebern und 300 jährlich genotypisierten Selektionskandidaten erhöht sich im Szenario ***Hybrid*** der Zuchtfortschritt je nach Merkmal um 19 (Intramuskulärer Fettgehalt) bis 105% (pH-Wert 45 min nach Schlachtung im M. Long dorsi; pH_1) (28% tägliche Zunahme; 29% Futterverwertung und 19 intramuskulärer Fettgehalt), wobei sich der Zuchtfortschritt im Gesamtzuchtwert um 26% erhöht. Wie in der DL Population beruht der höhere Zuchtfortschritt hauptsächlich auf einer deutlichen Steigerung (73%) der Genauigkeit des Selektionsindex der Selektionskandidaten durch Berücksichtigung von Genotypinformation. Im Szenario ***Hybrid*** können die diskontierten Erträge um 33% gesteigert werden, die diskontierten anfallenden Kosten erhöhen sich um 70%. Letztendlich kann ein um 19% höherer Gewinn nach Diskontierung erzielt werden.

Im Szenario ***Juvenile*** reduziert sich das Generationsintervall in der DL Population um 23%. Bei einer Referenzpopulation von 1000 Ebern und 300 jährlich genotypisierten Selektionskandidaten erhöht sich die Genauigkeit des Selektionsindex bei den Selektionskandidaten um 41%. Da auf die aufwendige Nachkommenprüfung verzichtet wird, sinkt jedoch die Genauigkeit des Selektionsindex der geprüften Eber um 8%. Aufgrund der deutlich höheren Genauigkeit bei den Jungebern und des niedrigeren Generationsintervalls, kann der Zuchtfortschritt um 31 (Stülpzitzen) bis 49% (abgesetzte Ferkel und lebend geborene Ferkel) gesteigert werden (36 % tägliche Zunahme; 39% Futterverwertung). Im Gesamtzuchtwert ist ein um 46% höherer Zuchtfortschritt möglich. Gegenüber dem konventionellen Szenario kann der diskontierte Ertrag um 77% und der diskontierte Gewinn um 361% gesteigert werden. Die Kosten sind identisch wie im Szenario ***Hybrid***, da für die Rekalibrierung der SNP-Effekte nicht auf die Nachkommenprüfung verzichtet werden kann.

In der Piétrain Population kann das Generationsintervall um 15% reduziert werden. Die Genauigkeit des Selektionsindex der Jungeber erhöht sich um 73%, während die Genauigkeit bei den Altebern um 15% abnimmt. Daraus ergibt sich ein höherer Zuchtfortschritt von 19% (Magerfleischanteil) bis zu 424% (pH_1) (43% für tägliche Zunahme und Futterverwertung; 24% für intramuskulären Fettgehalt). Der Zuchtfortschritt im Gesamtzuchtwert erhöht sich um 36%. Nach Diskontierung kann mit 58% höheren Erträgen, 70% höheren Kosten und einem um 54% höheren Gewinn gerechnet werden.

Eine größere Referenzpopulation und die Typisierung mehrerer Selektionskandidaten erhöht die Genauigkeit der genomischen Zuchtwerte und die Selektionsintensität beider Selektionsszenarien. Dadurch kann der Zuchtfortschritt, der monetäre Ertrag und der monetäre Gewinn erhöht werden. Jedoch reduziert sich mit einer steigenden Zahl an Genotypisierungen deren Grenznutzen. In der Piétrain Population konnte beim Merkmal pH_1 eine Besonderheit beobachtet werden. Während eine Vergrößerung der Referenzpopulation einen deutlich höheren Zuchtfortschritt im Merkmal pH_1 erlaubt, hat eine größere Anzahl genotypisierter Selektionskandidaten keinen Effekt.

Die Implementierung der genomischen Selektion kann zu einer deutlichen Steigerung der Effizienz in den bayerischen DL und Piétrain Populationen führen. Der höhere Zuchtfortschritt im Szenario ***Hybrid*** in allen Merkmalen des Zuchtziels resultiert hauptsächlich von der Einbeziehung der Genotypinformationen in der ersten Selektionsstufe. Durch ein deutlich reduziertes Generationsintervall (***Juvenile***) kann der Zuchtfortschritt noch weiter gesteigert werden. Obwohl strukturbedingt keine Kostenreduktion möglich ist, war das Szenario ***Juvenile*** am profitabelsten. Zukünftig kann durch größer werdende Referenzpopulationen und die Ausdehnung der Genotypisierung der Selektionskandidaten der zu erwartende Zuchtfortschritt weiter gesteigert werden. Die Referenzpopulation kann durch die Aufnahme von Ebern, die ausschließlich in der Kreuzungszucht getestet wurden, weiter vergrößert werden.

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Appendix

Method for calculations of the (co)variances in ***P***, ***C*** and ***G*** matrices when constructing a selection index that combines pedigree information (parental EBVs), genomic information (GEBVs) and phenotypic observations into a selection index.

ZPLAN+ allows combining genomic information (or GEBVs) into a selection index by treating the GEBVs as "genomic" traits in parallel to normal traits (Dekkers, 2007). This combination can be carried out directly in ZPLAN+ by defining "genomic" traits in terms of the parameters q, N, r_i, M_e (see Equ.2). The genotypic and phenotypic correlation coefficients of "genomic" traits among each other, and with normal traits are automatically calculated. Then these correlation coefficients are used for calculation of the covariances in ***P***, ***C***, and ***G*** matrices.

On the other hand, the combination of parental EBVs (using BLUP) is a routine in practical breeding programs. However, there is no direct options in the latest version of ZPLAN+ for combining parental EBVs into a index in analogy to GEBVs. In order to address this problem, Dekkers's method (2007) was extended to calculate the (co)variances in ***P***, ***C***, and ***G*** matrices when constructing a selection index that combines pedigree information (parental EBVs), in addition to genomic information (GEBVs) and phenotypic observations. In this method, an EBV for a trait of a parent was treated as a "dummy" trait with heritability of 1, null economic weight and phenotypic/genetic standard deviation of $r_{EBV,TBV}\ \sigma_{TBV}$, where $r_{EBV,TBV}$ is the correlation of EBV and true breeding value (TBV). The core of this method is to deduce the following parameters: phenotypic/genetic standard deviation of EBVs of each parent, as well as the correlation coefficients of EBVs of a parent among each other, with EBVs of the other parent, GEBVs, and normal traits (see the following Formula 1-6). In ZPLAN+, above (co)variances in ***P***, ***G*** and ***C*** can be calculated automatically when "dummy" traits were defined in terms of heritability of 1, economic weight of null and the above deduced parameters.

One considers an overall breeding goal (H) for an animal:

$$H = \boldsymbol{w}'\boldsymbol{TBV} \quad ,$$

where the vector $\boldsymbol{TBV}$ contains the true breeding values for m traits and $\boldsymbol{w}'$ is a vector for the economic weights, i.e.,

$$\boldsymbol{TBV}' = [TBV_1, TBV_2, ..., TBV_m] \text{ and } \boldsymbol{w}' = [w_1, w_2, ..., w_m].$$

It is also considered that, the selection index (T) for the animal is composed of four sources of information:1) BLUP EBVs of the sire ($SEBV$), 2) BLUP EBVs of the dam ($DEBV$), 3) own GEBVs ($GEBV$), and 4) phenotypic observations (y). For each of the former three sources, there are m records (i.e. estimated breeding values) for m breeding goal traits correspondingly. For the source of y, there are t records (or individuals) with each accounting for n traits. T can be expressed as

$$T = \boldsymbol{b}'\boldsymbol{x}$$

where $\boldsymbol{x}$ is the vector of records from the above-mentioned sources and $\boldsymbol{b}$ is the index coefficients. According to selection index theory, $\boldsymbol{b}$ are calculated as

$$\boldsymbol{b} = \boldsymbol{P}^{-1}\boldsymbol{G}\boldsymbol{w}$$

and the accuracy of T is

$$r_{T\hat{T}} = \sqrt{\frac{\boldsymbol{b}'\boldsymbol{P}\boldsymbol{b}}{\boldsymbol{w}'\boldsymbol{C}\boldsymbol{w}}}$$

with matrices $\boldsymbol{P}$, $\boldsymbol{C}$, and $\boldsymbol{G}$ as explained below.

P matrix:

$$\boldsymbol{P}=\begin{bmatrix} \boldsymbol{P}_{SEBV:SEBV} & \boldsymbol{P}_{SEBV:DEBV} & \boldsymbol{P}_{SEBV:GEBV} & \boldsymbol{P}_{SEBV:y} \\ \boldsymbol{P}^T_{SEBV:DEBV} & \boldsymbol{P}_{DEBV:DEBV} & \boldsymbol{P}_{DEBV:GEBV} & \boldsymbol{P}_{DEBV:y} \\ \boldsymbol{P}^T_{SEBV:GEBV} & \boldsymbol{P}^T_{DEBV:GEBV} & \boldsymbol{P}_{GEBV:GEBV} & \boldsymbol{P}_{GEBV:y} \\ \boldsymbol{P}^T_{SEBV:y} & \boldsymbol{P}^T_{DEBV:y} & \boldsymbol{P}^T_{GEBV:y} & \boldsymbol{P}_{y:y} \end{bmatrix}$$

The matrix $\boldsymbol{P}$ can be denoted by the sub-matrix of $\boldsymbol{P}_{k:l}$ denoting the covariance between the records from the source of k and the records from the source of l (k, l = $SEBV$, $DEBV$, $GEBV$ or y). The notation for the sub-matrix $\boldsymbol{P}_{k:l}$ is the following with the traits i and j,

$$\boldsymbol{P}_{k:l}=\begin{bmatrix} \sigma_{k_1l_1} & \sigma_{k_1l_2} & \cdots & \sigma_{k_1l_i} & \cdots & \sigma_{k_1l_j} & \cdots & \sigma_{k_1l_m} \\ & \sigma_{k_2l_2} & \cdots & \sigma_{k_2l_i} & \cdots & \sigma_{k_2l_j} & \cdots & \sigma_{k_2l_m} \\ & & \cdots & \cdots & \cdots & \cdots & \cdots & \vdots \\ & & & \sigma_{k_il_i} & \cdots & \sigma_{k_il_j} & \cdots & \sigma_{k_il_m} \\ & & & & \cdots & \cdots & \cdots & \vdots \\ & & & & & \sigma_{k_jl_j} & \cdots & \sigma_{k_jl_m} \\ & & & & & & \cdots & \vdots \\ sym. & & & & & & & \sigma_{k_zl_m} \end{bmatrix},$$

where z denotes the number of traits in k and

$$z=\begin{cases} m & (k = SEBV,\ DEBV \text{ or } GEBV) \\ n & (k = y) \end{cases}$$

Elements in $\boldsymbol{P}_{k:l}$ can be illustrate as below.

Diagonal (when $k = l$, $i = j$):

- Variance of records of a given source k: $\sigma^2_{k_i}$ with

$$\sigma_{k_i} = r_{k_i,TBV_i}\sigma_{TBV_i} = r_{k_i,TBV_i} h_i \sigma_{p_i} \quad (k = SEBV, DEBV \text{ or } GEBV) \qquad \text{<Formula 1>}$$

and

$$\sigma_{k_i} = \sigma_{y_i} = r_{y_i,TBV_i} h_i \sigma_{p_i} \quad (k = y), \text{ where}$$

$$r_{y_i,TBV_i} = \sqrt{\frac{1+(t-1)ah_i^2}{t h_i^2}}$$

where r_{k_i,TBV_i} is the correlation between k and TBV for the trait i, and it refers to r_{AI_i} in this thesis (see Table 2); h_i is the squared root of heritability for the trait i; σ_{p_i} is the phenotypic standard deviation for the trait i; a is the additive genetic relationship among t individuals within y.

Off-diagonal:

- Covariance between records on different traits (i and j) from the same source (i.e. $k = l$ and $i \neq j$):

$$\sigma_{k_i k_j} = r_{k_i,k_j}\sigma_{k_i}\sigma_{k_j} \quad \text{with}$$

$$r_{k_i,k_j} = r_{k_i,TBV_i} r_{k_j,TBV_j} r_{TBV_i,TBV_j} \quad (k = SEBV, DEBV \text{ or } GEBV) \qquad \text{<Formula 2>}$$

and

$$\sigma_{k_i k_j} = \sigma_{y_i y_j} = \frac{r_{p_{ij}}\sigma_{p_i}\sigma_{p_j} + (t-1)a\, r_{TBV_i,TBV_j}\sigma_{TBV_i}\sigma_{TBV_j}}{t} \quad (k = y)$$

- Covariance between records on same trait i from different sources (k and l) (i.e. $k \neq l$ and $i = j$):

$$\sigma_{k_i l_i} = a_{k,l} r_{k_i,l_i}\sigma_{k_i}\sigma_{l_i} \quad \text{with}$$

$$r_{k_i,l_i} = r_{k_i,TBV_i} r_{l_i,TBV_i} \quad (k = SEBV, DEBV, GEBV) \qquad \text{<Formula 3>}$$

and

$\sigma_{k_i l_i} = \sigma_{y_i l_i} = a_{y,l} r_{y_i, l_i} \sigma_{y_i} \sigma_{l_i}$ ($k = y$; $l = SEBV$, $DEBV$ or $GEBV$), where

$r_{y_i, l_i} = r_{y_i, TBV_i} r_{l_i, TBV_i}$ <Formula 4>

where $a_{k,l}$ is the additive genetic relationship between records in *k* and *l*.

- Covariance between records on different traits (*i* and *j*) from different sources (*k* and *l*) (i.e. $k \neq l$ and $i \neq j$):

$\sigma_{k_i l_j} = a_{k,l} r_{k_i, l_j} \sigma_{k_i} \sigma_{l_j}$ with

$r_{k_i, l_j} = r_{k_i, TBV_i} r_{l_j, TBV_j} r_{TBV_i, TBV_j}$ (k=$SEBV$, $DEBV$, $GEBV$) <Formula 5>

and

$\sigma_{k_i, l_j} = \sigma_{y_i l_j} = a_{yl} r_{y_i, l_j} \sigma_{y_i} \sigma_{l_j}$ ($k = y$; $l = SEBV$, $DEBV$ or $GEBV$), where

$r_{y_i, l_j} = r_{y_i, TBV_i} r_{l_j, TBV_j} r_{TBV_i, TBV_j}$ <Formula 6>

G matrix:

$$\boldsymbol{G}' = \left[\boldsymbol{G}_{SEBV:TBV} \quad \boldsymbol{G}_{DEBV:TBV} \quad \boldsymbol{G}_{GEBV:TBV} \quad \boldsymbol{G}_{y:TBV}\right]$$

The matrix ***G*** can be denoted by the sub-matrix of $\boldsymbol{G}_{k:TBV}$ denoting the covariance between *y* records from the source of *k* (k = $SEBV$, $DEBV$, $GEBV$ or y) and ***TBV***, where *z* denotes the number of traits in *k* and

$$z = \begin{cases} m & (k = SEBV,\ DEBV \text{ or } GEBV) \\ n & (k = y) \end{cases}$$

Thus, the notation for $\boldsymbol{G}_{k:TBV}$ is

$$\boldsymbol{G}_{k:TBV}=\begin{bmatrix} \sigma_{k_1TBV_1} & \sigma_{k_1TBV_2} & \cdots & \sigma_{k_1TBV_i} & \cdots & \sigma_{k_1TBV_j} & \cdots & \sigma_{k_1k_m} \\ & \sigma_{k_2TBV_2} & \cdots & \sigma_{k_2TBV_i} & \cdots & \sigma_{k_2TBV_j} & \cdots & \sigma_{k_2TBV_m} \\ & & \cdots & \cdots & \cdots & \cdots & \cdots & \vdots \\ & & & \sigma_{k_iTBV_i} & \cdots & \sigma_{k_iTBV_j} & \cdots & \sigma_{k_iTBV_m} \\ & & & & \cdots & \cdots & \cdots & \vdots \\ & & & & & \sigma_{k_jTBV_j} & \cdots & \sigma_{k_jTBV_m} \\ & & & & & & \cdots & \vdots \\ sym. & & & & & & & \sigma_{k_zTBV_m} \end{bmatrix} .$$

$\sigma_{k_iTBV_j}$ represents the covariance between the record from the source of *k* for breeding goal trait *i* and the TBV for the breeding goal trait *j*, and is calculated by using the formula:

$$\sigma_{k_iTBV_j}=a_{k,TBV}r_{k_i,TBV_j}\sigma_{k_i}\sigma_{TBV_j}=a_{k,TBV}r_{k_i,TBV_i}r_{TBV_i,TBV_j}\sigma_{k_i}\sigma_{TBV_j} ,$$

where $a_{k,TBV}$ is the additive genetic relationship between the individual in the breeding goal and individuals in the index source of *k*.

C matrix:

$$\boldsymbol{C}=\begin{bmatrix} \sigma_{TBV_1TBV_1} & \sigma_{TBV_1TBV_2} & \cdots & \sigma_{TBV_1TBV_i} & \cdots & \sigma_{TBV_1TBV_j} & \cdots & \sigma_{TBV_1TBV_m} \\ & \sigma_{TBV_2TBV_2} & \cdots & \sigma_{TBV_2TBV_i} & \cdots & \sigma_{TBV_2TBV_j} & \cdots & \sigma_{TBV_2TBV_m} \\ & & \cdots & \cdots & \cdots & \cdots & \cdots & \vdots \\ & & & \sigma_{TBV_iTBV_i} & \cdots & \sigma_{TBV_iTBV_j} & \cdots & \sigma_{TBV_iTBV_m} \\ & & & & \cdots & \cdots & \cdots & \vdots \\ & & & & & \sigma_{TBV_jTBV_j} & \cdots & \sigma_{TBV_jTBV_m} \\ & & & & & & \cdots & \vdots \\ sym. & & & & & & & \sigma_{TBV_mTBV_m} \end{bmatrix}$$

Covariances between TBV_i and TBV_j were calculated by using the following formula:

$$\sigma_{TBV_iTBV_j}=r_{TBV_i,TBV_j}\sigma_{TBV_i}\sigma_{TBV_j} .$$