COMMUNAUTÉ FRANÇAISE DE BELGIQUE
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MARIE DUFRASNE

Essai présenté en vue de l'obtention du grade de docteur
en sciences agronomiques et ingénierie biologique

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ABSTRACT

Crossbreeding is widely used in pig breeding to benefit from advantages of heterosis effects and breed complementarity. Breeding programs are specialized between sire and dam lines, with different selection objectives. Sire lines are mainly selected for production traits (e.g., growth, carcass quality, feed efficiency). Moreover, selection is often in purebred lines while the goal of selection is to improve crossbred performances. Hence, genetic selection of purebred parents involved in crossbreeding requires models accounting for crossbreeding effects, and able to combine data from different genetic types (purebreds and crossbreds) and different environmental conditions. Therefore, the objective of this thesis was to develop genetic models to estimate genetic parameters and breeding values for production traits in crossbred populations of pigs. A genetic model was developed to estimate the genetic potential of Walloon purebred Piétrain boars for growth performances in crossbreeding based on test station and on-farm data from purebred and crossbred pigs. Weight records from both systems were considered as different traits. Results showed that weights recorded in test station and on-farm were different traits but genetically correlated. Moreover, combining both sources of data allowed to increase reliability of estimated breeding values and Genotype x Environment interactions were detected for growth in the Walloon breeding program. The introduction of dominance effects, linked to crossbreeding, into the genetic model for growth in the crossbred population showed that dominance effects existed on growth of crossbred pigs. Moreover, the total and the additive genetic merits were better estimated than with a strictly additive model. Research conducted on commercial crossbred data from US Duroc sires displayed that the sire genetic effects were not negligible on traits like piglet birth weight, preweaning mortality, mortality at different stages of the grow-finishing period and hot carcass weight. Furthermore, sire genetic effects increased with age. Genetic studies of mortality in the population from US Duroc sires showed that mortality traits had a low heritability, increasing with age and that mortality was not antagonistic with market weight. Besides, genetic parameters estimated for birth weight and its relation with other production traits in crossbred populations from Piétrain and Duroc sires showed that birth weight could be used as an early indicator trait to improve latter performances. Finally, production traits were genetically correlated and should be selected simultaneously to reach the breeding goal.

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RÉSUMÉ

Le croisement est largement utilisé pour produire les porcs de production afin de bénéficier des avantages liés à l'effet d'hétérosis et à la complémentarité entre races. Les programmes de sélection sont spécialisés entre les lignées paternelles et maternelles, avec des objectifs de sélection différents. Les lignées paternelles sont principalement sélectionnées pour les caractères de production (ex: croissance, qualité de carcasse, efficacité alimentaire). De plus, la sélection se fait souvent en race pure alors que le but est d'améliorer les performances en croisement. Par conséquent, la sélection des parents de races pures impliqués dans les croisements nécessite des modèles prenant en compte les effets de croisement et capables de combiner des données mesurées sur des animaux de différents types génétiques (pures et croisés) et dans différents environnements. L'objectif de cette thèse était donc de développer des modèles pour estimer les paramètres génétiques et les valeurs d'élevage pour des caractères de production dans des populations de porcs croisés. Un modèle a été développé pour estimer le potentiel génétique des verrats Piétrain wallons en croisement pour la croissance, à partir de données mesurées en station de testage et en fermes, sur des porcs de race pure et croisés. Les poids mesurés dans les deux systèmes ont été considérés comme des caractères différents mais corrélés génétiquement. De plus, combiner les deux sources de données a permis d'augmenter la précision des valeurs d'élevage estimées et des interactions Génotype x Environnement sont apparues pour la croissance dans le programme de sélection wallon. L'introduction d'effets de dominance, qui sont liés au croisement, dans le modèle pour la croissance des porcs croisés a montré que les effets de dominance existaient sur la croissance. De plus, les potentiels génétiques total et additif étaient mieux estimés qu'avec un modèle purement additif. Les recherches menées sur des données venant de porcs croisés, issus de pères de race Duroc, ont montré que les effets génétiques paternels étaient non négligeables sur des caractères tels que le poids à la naissance, la mortalité avant sevrage, la mortalité à différents moments de la période engraissement-finition et le poids des carcasses. De plus, les effets génétiques paternels augmentaient avec l'âge. L'étude génétique de la mortalité dans la population croisée issue de verrats Duroc a montré que les caractères de mortalité avaient une faible héritabilité, qui augmentait avec l'âge, et que la mortalité n'était pas en opposition avec le poids final. Les paramètres génétiques estimés pour le poids à la naissance et ses relations avec d'autres caractères de production dans les populations croisées de pères Piétrain et Duroc ont montré que ce caractère pourrait être utilisé comme indicateur précoce pour l'amélioration des performances futures. Finalement, il est apparu que les caractères de production étaient génétiquement corrélés entre eux et devraient donc être sélectionnés simultanément pour atteindre l'objectif de sélection.

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Marie Dufrasne, November 2014

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CHAPTER I. GENERAL INTRODUCTION

CONTEXT

To improve the efficiency and the profitability of their production, commercial pork producers should rely on genetic improvement programs for pigs. Genetic improvement programs in the pig industry are typically organized as follows. Purebred parental lines are raised and selected in nucleus herds owned by breeding companies or breeding farms. They are kept in very controlled environmental conditions with high hygienic status and superior management practices. Parental lines are selected in these herds and then multiplied to compose parental stock used by pork producers to produce crossbred commercial pigs (Dekkers, 2007).

Pork producers widely use crossbreeding because of advantages coming from heterosis effects and breed complementarity, that lead to better performances in the crossbred population compared to parental purebred populations (Bidanel, 1992; Dekkers, 2007). Heterosis effects are related to crossbreeding and are responsible of better performances in the crossbred population compared to the average performance between both parental lines. Breed complementarity exploits crossbreeding by bringing together traits specifically selected in purebred parental lines but difficult to improve simultaneously in one breed because of antagonistic genetic relationships. As a consequence of using crossbreeding, genetic selection programs of parental lines can be different between sire and dam lines. Indeed, selection objectives are different: production traits for sire lines vs. reproduction and production traits for dam lines.

Genetic selection of parents involved in crossbreeding requires models taking into account genetic additive and non-additive effects related to crossbreeding. Additive effects represent the genetic part of a phenotype that is directly transmitted from parents to offspring. Conversely, non-additive effects represent the genetic part of a phenotype caused by interactions among alleles at the same gene locus (dominance) or at different gene loci (epistasis), not directly transmitted from parents to offspring because recreated at each generation. Effects linked to crossbreeding are difficult to model correctly because of additional parameters required to model crossbreeding effects among different breeds. As a consequence, across herd genetic evaluations are not easy to implement. Traditionally, genetic evaluations were often run separately for different breeds (VanRaden, 1992). Therefore, crossbred data were ignored and genetic selection of purebred parental lines was performed within breed and only based on purebred performances (Bijma and van Arendonk, 1998; Lutaaya et al., 2001; Lutaaya et al., 2002). However, genetic evaluations using data from crossbred animals are of great interest although they require the estimation of additive and non-additive effects related to crossbreeding.

Additive effects linked to crossbreeding depend on genetic differences between breeds or lines. These genetic differences explain partly why genetic correlations between purebred and crossbred performances are usually different than 1, ranging between 0.4 and 0.7 depending on the traits for pigs. For example, Habier et al. (2007) found genetic correlations between purebreds and crossbreds as low as 0.88 for average daily gain (ADG), 0.92 for backfat thickness (BF), 0.90 for lean meat content (LMC), and 0.74 for feed conversion ratio (FCR). Therefore, the additive genetic value estimated on purebred performances is not a good predictor of performances in crossbreeding (Dekkers, 2007). As pointed out before, purebred genetic evaluations ignore data recorded on crossbred animals, even if these data are becoming available and bring additional information that would allow improvement of reliabilities of estimated breeding values (Lutaaya et al., 2001; Ibáñez-Escriche et al., 2011). As a consequence, genetic evaluation models combining purebred and crossbred data are required to improve selection of purebred parents for crossbred performances (Wei and van der Werf, 1993; Lutaaya et al., 2002).

Non-additive genetic effects related to crossbreeding are caused by interaction of alleles inherited from each parents at the same locus or at different loci, at the individual level (Hoeschele and VanRaden, 1991). Currently, estimation of genetic effects often ignores non-additive genetic effects, like dominance. However, dominance might be important on production traits (Culbertson et al., 1998). The joint estimation of additive genetic and dominance effects allows for a more accurate estimate of the additive genetic merit of an animal transmitted to its progeny. Moreover, the knowledge of the dominance effects may be useful for mate selection program to maximize the genetic merit of the progeny (Henderson, 1989). The main reason for ignoring dominance effects was that these effects were difficult to model correctly and because the inverse of the dominance relationship matrix was computationally difficult to set up (Henderson, 1985). Hoeschele and VanRaden (1991) solved this issue by replacing the inverse of the dominance relationship matrix with the inverse of the sire-dam subclass relationship matrix, which corresponds to the covariance structure among sire-dam subclasses and represents the average dominance effects of many full-sibs.

Another specificity of pig breeding programs is the origin of the data. Data can come from nucleus farms or from test stations with very high hygienic status and controlled environmental conditions, and where performance recording systems are standardized. In contrast, data can also come from commercial farms where pigs are raised in a lower quality environment concerning hygiene, with less space per pig. Therefore, the low genetic correlations between purebred and crossbred performances pointed out by Dekkers (2007) may also be due to Genotype x Environment (GxE) interactions (Zumbach et al., 2007). Peškovičová et al. (2002) estimated genetic correlations between traits recorded on-farm and in test station. They found that the correlations were between 0.48 and 0.57 for ADG, and 0.75 for BF. Consequently, genetic models able to jointly consider different sources of data are needed to estimate correlations between traits recorded in different environments and GxE interactions (Bidanel and Ducos, 1996).

To sum up, useful genetic models for pig production would 1) combine data from purebred and crossbred animals, 2) include additive and non-additive (i.e., dominance) genetic effects, and 3) jointly consider different sources of data (i.e., station vs. farm data). These genetic models are used to estimate genetic parameters and breeding values for different traits, depending on selection objectives. The estimated breeding values (EBV) are used in breeding programs to define selection decision.

Breeding programs in terminal sire lines focused on genetic improvement of production traits, like growth rate, carcass composition or feed efficiency. These traits are of economic importance and expressed in market animals (Kanis et al., 2005). The objective is to produce fast growing pigs with high meat percentage and high feed efficiency. Breeding objectives in maternal lines are traits related to reproduction and fertility, like farrowing mortality, preweaning mortality (PWM) or litter size. However, production performances (i.e., growth, carcass quality) are also significant because dams transmit half of their genes to their production progeny (Cassidy et al., 2004).

Traditional production traits (growth, carcass quality, feed efficiency) have a moderate to high heritability. Heritability is a genetic paremeter defined as the ratio between the additive genetic and the phenotypic variances and quantifying the part of a performance that will be transmitted to the next generation through genes. Heritability ranges between 0 and 1 and the higher is the heritability, the more the differences among animals in a population are due to additive genetic effects. Moreover, traits need to be genetically variable to realize genetic progress. Production traits in pigs fulfill these conditions (e.g., Hermesch et al., 2000a; van Wijk et al., 2005); therefore, direct genetic selection to improve these traits is feasible. Furthermore, production traits are genetically correlated; selection to improve one trait may cause changes in the others. Genetic correlations between traits of interest are not always favorable (e.g., Hermesch et al., 2000b; van Wijk et al., 2005). Hence, genetic selection should be balanced between them to reach the breeding goal and to improve all traits in a desirable way.

An additional and unusual trait of interest in pig breeding programs is the survival of pigs during the grow-finishing period. Many studies focused on survival of production pigs between farrowing and weaning (e.g., Arango et al., 2005; Arango et al., 2006; Roehe et al., 2010). However, losses of pigs at higher age are more expensive because of increasing rearing costs with age, depending on feed, time and money invested (Hermesch et al., 2014). Moreover, if growing pigs do not survive, they will not produce. It would also be important to know the genetic relationships between survival traits and classical production traits to implement an efficient selection program.

Finally, to speed up genetic improvement, it could be interesting to find early indicator traits of future performances. A good early indicator trait is a trait recorded early in life, heritable and genetically correlated in a favorable way with the traits of interest. If genetic selection is possible early, on young animals, genetic progress would be faster and economical investments would be reduced on pigs that are not good selection candidates. The earliest trait recorded on pigs is the birth weight (BWT). This trait is often studied from the maternal side, because traits related to reproduction, like BWT, are strongly affected by maternal genetic effects (Arango et al., 2006). However, to improve sire lines, it is necessary to know the sire genetic effect on this trait to determine if piglet BWT could be genetically improved from the paternal side. As BWT is related to performances, like survival, growth rate, carcass composition (Fix et al., 2010), it could be a good candidate to be an early indicator trait.

AIM OF THE THESIS

The aim of this thesis is to present genetic evaluation models developed to improve genetic selection of terminal sire lines for production traits in commercial crossbred populations. These models are developed using purebred and crossbred data coming from diverse breeds, populations and environments. Genetic parameters for different populations and traits (growth, body weight, and survival traits) are estimated using these models.

OUTLINE

This thesis is a compilation of scientific papers organized in four parts (Chapter II to V), followed by a general discussion (Chapter VI), and general conclusions and perspectives (Chapter VII).

First of all, Chapter II presents a literature review covering 1) genetic evaluation methods of purebred pigs for crossbred performances and 2) estimates of genetic parameters for classical economically important traits in pig sire lines.

Then, Chapter III presents the development of the genetic evaluation system to improve growth performances of Piétrain boars in the Walloon Region of Belgium. Two aspects are investigated: multitrait and multi-environment models combining purebred and crossbred data (Chapter III.1), and the estimation of non-additive genetic effects on growth traits (Chapter III.2).

Chapter III.1 presents the genetic evaluation model developed to estimate the genetic potential of purebred Piétrain boars for crossbred performances in the Walloon Region of Belgium. This model is a multitrait and multi-environment model. Weight records are provided by two performance recording systems. The first one is the on-farm performance recording system where data are recorded on purebred and crossbred pigs. The second one is the progeny-test performed at the Walloon test station where data are recorded on crossbred pigs only. Weights recorded on-farm and at the test station are considered as different but genetically correlated traits. Genetic parameters are estimated for these traits to support the hypothesis of different but correlated traits between both recording systems. The gain in the reliability of EBV for the Walloon Piétrain boars when combining both sources of data is also checked.

Chapter III.2 presents the estimation of dominance effects for weights recorded in a crossbred population of pigs from Piétrain boars. The initial model is the one presented in Chapter III.1, considering only weights recorded on crossbred pigs at the test station. Genetic parameters estimated with a strictly additive model and with a model in which dominance effects are included are compared. The aim is to determine if dominance effects exist on growth traits in pigs and if additive effects are better estimated when dominance is introduced in the model.

Chapter IV focuses on the estimation of the sire genetic effects on different production traits to improve genetic selection of purebred sires for crossbreeding performances in a commercial population of pigs from US Duroc sires. This chapter is organized in two parts (Chapter IV.1 and IV.2).

Chapter IV.1 presents the estimation of sire genetic effects on traits recorded on crossbred piglets (BWT and PWM) and their relations with hot carcass weight (HCW). The aim is to assess the sire genetic effects on traits recorded on piglets. Moreover, if BWT is genetically variable and favorably correlated with PWM and HCW, this trait could be used as an early indicator of subsequent performances.

Chapter IV.2 focuses on the estimation of sire genetic effects on survival traits recorded through the life of production pigs and their relations with HCW. Most of the previous genetic studies focused on mortality of production pigs between birth and weaning. Few studies focused on mortality during grow-finishing period. Genetic parameters for survival of production pigs at different stages of their life are estimated to determine if a genetic selection is possible to improve survival of pigs during grow-finishing period. Moreover, genetic correlations between survival traits and HCW are estimated to assess the effect of genetic selection for survival on market weight.

Chapter V presents the estimation of genetic parameters for piglet BWT, weaning weight (WWT) and final live body weight (BW) in a crossbred population of pigs from Walloon Piétrain boars. The purpose of this chapter is to confront results obtained in Chapter IV.1 in a large population with results obtained in a small population from different purebred sire lines but similar traits. Moreover, the aim is to determine if BWT could be considered as an early indicator trait of future performances like growth rate and final weight.

Chapter VI is a general discussion regarding the obtained results. Several aspects are discussed in a larger perspective: 1) the advantages of combining purebred and crossbred data in genetic evaluations of purebred parents, 2) the utilization of genetic models considering data from diverse environments and the existence of GxE interactions in the Walloon breeding system, 3) the effects linked to the introduction of dominance effects into genetic evaluation models, 4) the opportunity of developing mate allocation programs based on the estimation of individual dominance effects, 5) the interest to estimate sire genetic effects on crossbred performances, 6) the soundness of using BWT as an indicator trait of subsequent performances, and 7) the interest of developing an economic multiple trait selection index combining EBV for different traits.

Finally, Chapter VII draws general conclusions of this thesis and addresses future perspectives of research.

FRAMEWORK

This thesis started in October 2009 and was initiated in the context of the development of the genetic evaluation program of Piétrain boars for crossbred performances under the framework of the *'Convention de collaboration technique et scientifique dans le cadre des évaluations génétiques (indexations) porcines de l'AWEP'*, jointly conducted by the Animal Science Unit of Gembloux Agro-Bio Tech, University of Liège (ULg-GxABT; Gembloux, Belgium), the Walloon Pig Breeders Association (AWEP; Ciney, Belgium) and the Animal Breeding, Quality Production and Welfare Unit of the Walloon Agricultural Research Center (CRA-W; Gembloux, Belgium), and partially funded by the Public Service of Wallonia (*Service Public de Wallonie – Direction Générale Opérationnelle Agriculture, Ressources naturelles et Environnement (DGARNE)*). Since October 2011, this thesis was fully supported by a scholarship grant provided by the *'Fonds pour la formation à la Recherche dans l'Industrie et dans l'Agriculture'* (FRIA; Brussels, Belgium). The research project was entitled 'Development of advanced genetic methods to estimate breed- and individual- specific combining abilities and Genotype X Environment effects: application to pig breeding'.

The aim of the project was to develop comprehensive models for the estimation of the genetic merit of purebred parental lines of pigs involved in crossbreeding, based on different sources of data recorded in diverse environments. Three aspects were considered in the initial project: 1) the development of multi-environment models, 2) the modeling of crossbreeding effects, and 3) the use of genomic information. Due to the unavailability of genomic information, the doctoral research focused on multitrait and multi-environment models including crossbreeding effects based on phenotypic and genealogical data. The main part of the research was undertaken at Gembloux Agro-Bio Tech, under the supervision of Prof. N. Gengler, on data from the progeny-testing scheme of Piétrain boars in the Walloon Region of Belgium, provided by the AWEP. A part of the research was realized at the Animal and Dairy Science Department of the University of Georgia (Athens, GA, USA), under the supervision of Dr. I. Misztal, on data provided by Smithfield Premium Genetics (Rose Hill, NC, USA).

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CHAPTER II. GENETIC SELECTION OF TERMINAL SIRE LINES FOR CROSSBREEDING PERFORMANCES AND GENETICS OF PRODUCTION TRAITS IN PIGS: A REVIEW

CHAPTER II

Crossbreeding is widely used in pig production. As a consequence, the genetic evaluation for crossbred performances of purebred pigs requires models allowing combination of purebred and crossbred data. The proper consideration of crossbreeding effects in the models is also of importance. Moreover, parental lines can be very specialized; i.e., paternal pig lines are mainly selected for production traits: growth, carcass composition and feed efficiency. Therefore, the objectives of this chapter were to review the genetic evaluation methods of purebred pigs for crossbred performances and to give an overview of genetic parameters for production traits in pigs.

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ABSTRACT

Genetic selection of terminal sire lines for crossbreeding performances and genetics of production traits in pigs: a review

Genetic improvement of pig terminal lines is economically important for pork producers. Crossbreeding is widely used in pig production to benefit from favorable effects of heterosis and complementarity between breeds or lines. Therefore, parental lines could be very specialized. Terminal sire lines are mainly selected for production traits. Classical production traits in pigs are growth, carcass composition and feed efficiency. To improve purebred lines for crossbred performances, selection objectives must be defined at the crossbred level. Genetic evaluation models combining purebred and crossbred data have been developed and allow to use data collected on crossbred animals in addition to purebred data. Crossbreeding also allows to exploit non-additive genetic effects like dominance, not negligible on production traits. Genetic parameters for production traits have been estimated for different populations, with different models. Regarding the literature, many results pointed out that production traits are heritable and genetically variable. Heritabilities ranged between: 0.13 and 0.52 for growth traits, 0.12 and 0.89 for carcass traits, and 0.13 and 0.40 for feed efficiency. Therefore, direct genetic selection is possible and efficient to improve these traits. However, production traits are also genetically correlated with each other, sometimes unfavorably. Hence, genetic improvement programs must balance them within comprehensive indexes in order to avoid the deterioration of one trait in favor of another one.

Keywords: Carcass composition, Feed efficiency, Genetic parameters, Growth, Pigs, Sire lines

RÉSUMÉ

Sélection génétique des lignées paternelles terminales pour les performances en croisement et génétique des caractères de production chez le porc: synthèse bibliographique

L’amélioration génétique des lignées terminales de porcs est économiquement importante pour les producteurs. Le croisement est largement utilisé en production porcine pour bénéficier des effets favorables de l’hétérosis et de la complémentarité entre races ou lignées. En conséquence, les lignées parentales peuvent être très spécialisées. Les lignées paternelles terminales sont sélectionnées principalement pour les caractères de production. Les caractères de production classiques chez le porc sont la croissance, la composition de la carcasse et l’efficacité alimentaire. Afin d’améliorer les lignées pures pour les performances en croisement, les objectifs de sélection doivent être définis au niveau des animaux croisés. Des modèles d’évaluations génétiques permettant d’utiliser conjointement des données pures et croisées ont été développés et permettent d’utiliser les données mesurées sur les animaux croisés ainsi que celles provenant d’animaux de races pures. Le croisement permet aussi d’exploiter les effets génétiques non-additifs, tel que la dominance, qui est non négligeable sur les caractères de production. Les paramètres génétiques des caractères de production ont été estimés pour différentes populations et avec différents modèles. Les résultats présentés dans diverses études montrent que ces caractères sont héritables et variables génétiquement. L'amélioration des caractères de production par la sélection génétique est donc possible et efficace. Cependant, ces caractères sont corrélés génétiquement entre eux, et parfois de manière non favorable. C'est pourquoi les programmes d'amélioration génétique doivent pondérer ces caractères au sein d'index de sélection globaux afin d'éviter la déterioration de l'un des caractères au profit de l'amélioration d'un autre.

Mots-clés: Composition de la carcasse, Efficacité alimentaire, Paramètres génétiques, Croissance, Porcs, Lignées paternelles

INTRODUCTION

In order to ensure the competitiveness of their sector, pork producers should rely on the genetic improvement of terminal sire lines. Currently, commercial pigs are mostly crossbred in order to take advantage of crossbreeding effects that lead to better performances in the crossbred population compared to performances of the purebred parents. Therefore, parental lines could be very specialized. In this context it is important to distinguish traits in the selection objective and index traits (selection criteria) between parental lines. The selection objectives for terminal sire lines are mainly determined by production traits (growth, carcass quality, feed efficiency) leading to pigs of full market value. However, the most important production trait to reach these objectives is the number of pigs reaching market value, which depends on traits related to reproduction (e.g., number of piglets per litter, number of piglets born alive, born dead, survival at weaning), but also survival during the grow-finishing period. Traits related to reproduction are often studied from the maternal side because it is well known that they are strongly affected by dam effects (Arango et al., 2006). However, a genetic influence of the sire may also exist (Hamann et al., 2004) and needs to be estimated to improve terminal sire lines. Hence, genetic selection of parental lines is different because of distinct selection objectives: production traits for sire lines, reproduction and production traits for dam lines.

The efficiency of selection of purebred lines for crossbreeding performances is function of the genetic correlation between crossbred and purebred performances, which is different than 1 and variable according to the trait (Dekkers, 2007). In a crossbreeding setting, as alleles from different breeds are present, non-additive genetic effects, in particular dominance effects, might be important (e.g., Culbertson et al., 1998) and should be introduced into genetic evaluation models for crossbred performances. The estimation of dominance effects improves the estimation of additive genetic values, transmitted across generation. Estimations of dominance effects are also useful for mate allocation programs to optimize the performances of the crossbred pigs (Henderson, 1989). However, dominance effects are currently ignored in genetic improvement programs, mostly because of two major issues. First, extracting dominance relationships from the pedigree information is difficult as no direct information of the alleles present in a given animal is available; therefore dominance effects are reduced to sire-dam effects

(Gengler et al., 1997). Second, the inversion of the dominance relationship matrix (Henderson, 1985) is an additional challenge. Nevertheless, under the hypothesis that sire-dam relationships reflect perfectly dominance relationships, Hoeschele and VanRaden (1991) addressed this issue by creating rules for the direct construction of the inverse of the dominance relationship matrix.

Therefore, this literature review will cover the genetic evaluation methods of purebred pigs for crossbred performances. Furthermore, it will provide an overview of estimates of genetic parameters for economically important traits in pig sire lines.

GENETIC EVALUATION IN CROSSBREEDING

Crossbreeding is widely used in pig production to take advantage of heterosis effects and complementarity between breeds or lines. It is also used in beef, poultry and plant species as corn. Heterosis effects are responsible of better performances in the crossbred population compared to mean performances of parental populations. Importance of heterosis effects depends on the genetic distance between the parental breeds (Bidanel, 1992). Complementarity between breeds or lines allows to bring together specific aptitudes coming from different breeds or lines, that are difficult to select together because of genetic antagonisms (Bidanel, 1992). For example, to produce valuable market pigs, it is favorable to cross sows having good reproduction and maternal aptitudes with boars selected for growth and meat content. Therefore, to optimize the use of crossbreeding, pure parental breeds or lines of high potential are needed. Hence, selection and selection objectives are different between maternal and paternal lines. Paternal lines, used as terminal lines for meat production, could be very specialized and selected for growth, carcass and meat quality.

Genetic evaluations of pigs are often performed within breed, based on purebred performances, therefore ignoring information coming from crossbred animals (Bijma and van Arendonk, 1998; Lutaaya et al., 2001; Lutaaya et al., 2002). However, the final goal of an organized breeding program is to improve the quality of animals intended for market, therefore to improve performances of crossbred animals (Ibáñez-Escriche et al., 2009). Based on these facts, breeding goals should be defined at the crossbred level to produce high quality market pigs. Moreover, performances of purebred animals can be poor predictors of crossbred performances because of genetic differences between purebreds and crossbreds. Indeed, the genetic correlations between purebred and crossbred performances could be as low as 0.4 to 0.7 in pigs, as pointed out by Dekkers (2007). Therefore, crossbred and purebred performances should be treated as genetically different traits. Furthermore, environmental differences exist between purebred and crossbred animals. Purebred pigs are usually housed under nucleus conditions in high-health environments; crossbred pigs are mostly raised under field conditions. Management, density of pigs, or health status are very different between nucleus and field herds. Therefore, differences between purebred and crossbred performances can also be explained by Genotype x Environment (GxE) interactions (Zumbach et al., 2007).

To improve selection of purebred animals for performances in crossbreeding, a solution is to perform combined crossbred-purebred selection (Wei and Van der Werf, 1993). As information from crossbred animals is becoming available, the interest of utilizing joint evaluation of purebreds and crossbreds arose. Therefore, data collected only on crossbred relatives can be used for the selection of purebred parents. The combined crossbred-purebred models improve the reliabilities of estimated purebred breeding values compared to strictly purebred models because it uses all available progeny information (Lutaaya et al., 2001; Ibáñez-Escriche et al., 2011). Therefore, it affects the ranking of purebred candidates to selection and it increases the response to selection (Bijma and van Arendonk, 1998; Ibáñez-Escriche et al., 2011). Also, it requires accurate recording of performances and pedigrees at the crossbred level. This information is not necessarily available given the fact that crossbred animals are raised under industrial environment where data recording is less organized than in nucleus herds.

Crossbreeding also allows to exploit non-additive genetic variability, like dominance. As it is now recognized that dominance effects are not negligible on the genetic variability of production traits, like growth (Culbertson et al., 1998), it would worth using them. Dominance effects are caused by interactions of alleles at the same locus and are not directly transmitted to the next generation (Hoeschele and VanRaden, 1991) but are recreated each generation by alleles inherited from each parents. As the genetic correlation between purebred and crossbred performances is also influenced by gene frequency and dominance level, it is useful to take into account additive and dominance (co)variances in genetic evaluation models of purebred for crossbred performances (Wei et al., 1991a, 1991b). The joint prediction of additive and dominance effects should allow for a more accurate estimation of the total genetic merit (additive or not) of an animal and therefore improve the estimation of additive effects.

Currently, estimation of genetic effect is often limited to additive effect because setting up the inverted dominance relationship matrix ($\mathbf{D^{-1}}$) is difficult from a computational point of view with large data sets (Henderson, 1985). Hoeschele and VanRaden (1991) replaced $\mathbf{D^{-1}}$ by the inverted sire-dam subclass relationship matrix $\mathbf{F^{-1}}$, postulating that subclasses for each pair of parents will catch the major part of the estimable variation (Gengler et al., 1997). Lo et al. (1997) developed a model for genetic evaluation in a two-breed terminal crossbreeding system that account for additive and dominance variances. This model is very useful if genetic correlations between purebred and crossbred performances are low, if both purebred and crossbred evaluations are of interest and if large amount of crossbred information is available. It is also very interesting to use this model when some traits are recorded on purebreds and others are only recorded on crossbreds (Lutaaya et al., 2002).

To conclude, selection objectives must be defined at the crossbred level to improve genetic selection of purebred pigs involved in crossbreeding programs. Furthermore, genetic evaluation models should take into account crossbreeding effects, additive as well as non-additive effects. Moreover, these models should allow to combine purebred and crossbred data coming from diverse environmental conditions.

GENETIC PARAMETERS FOR PRODUCTION TRAITS

As explained above, terminal lines could be very specialized regarding the breeding goals. Terminal sires give a random half of their genes to market progeny and genes influencing reproduction traits transmitted by these boars are never expressed in their progeny. Therefore, terminal sire lines used in crossbreeding to produce high quality market pigs are mainly selected for production traits of economic importance, i.e., growth, carcass composition, as well as feed efficiency because of the large part of feeding costs in production costs. Production traits are expressed in market animals, but also in animals selected to contribute to the improvement of the breeding herd. To implement a genetic selection for production traits, the estimated heritability in the population, quantifying the part of a performance depending on additive gene actions and transmitted to the next generation, should be sufficient. Genetic parameters for these traits are different between breeds or lines. Moreover, estimates rely on the structure of the studied population and the genetic model used for the estimation. Therefore, the following section will attempt to summarize estimates of heritability for the main production traits and genetic correlations among these traits.

Heritability

Different studies provided estimations of heritability for production traits in pigs. These studies differ in the origin of the data (test station or field data), breed and breed composition of the population (purebred or crossbred), model used to estimate genetic parameters, or definition of the trait. Therefore, the circumstances of data recording and trait definition will be mentioned.

Growth traits

Genetic potential of pigs for growth can be evaluated based on different traits. Common traits are average daily gain (ADG) between particular weights or ages, live body weight (BW) at different ages (usually at the end of the fattening period), hot carcass weight (HCW), or number of days from birth (DAYS) to reach a target weight. Target ages or weights depend on the market and the selection program implemented. Even if the traits may be different, there is a general consensus about the need of pigs to show reasonable growth. Table 1 provides an overview of heritability estimates for ADG in different breeds, and genetic evaluation systems. Estimates of heritability varied between 0.13 and 0.52 for ADG of purebred pigs and between 0.16 and 0.34 for crossbred pigs. The lowest heritability of 0.13 for ADG in a purebred population corresponds to heritability of ADG between 18 and 22 weeks. Authors of the study pointed out that a testing period of 4 weeks was probably too short to get reliable records of ADG and it explained the low heritability estimates (Hermesch et al., 2000a). Heritability estimates seemed to be lower in crossbred populations than in purebred populations. An explanation could be that purebred pigs are usually raised in nucleus farm with very controlled environment, high hygienic status and very accurate recording system. However, crossbred pigs are usually kept in environment of lower quality, with less space per pigs and lower hygienic status (Zumbach et al., 2007). Moreover, recording systems in crossbred populations are also less framed and precise, closer to actual environmental production conditions. Therefore, the environmental variations are higher in crossbred populations and lead to a lower heritability.

Table 1. Estimates of heritability for average daily gain (ADG) from various studies.

Age/weight range	Breed	Place	N	Model	Heritability	Reference
35 - 90 kg	LW	St	3,671	A+L	0.30	Ducos et al., 1993
	LD	St	3,630	A+L	0.34	
35 - 100 kg	LW	St	3,039	A+L	0.52	
	LD	St	2,695	A+L	0.46	
35 - 90 kg	PI	St	4,638	A+L	0.33	Bidanel and Ducos, 1995
35 - 100 kg	PI	St	1,575	A+L	0.38	
13 - 18 wk	LW/LD	St	3,227	A+L	0.27	Hermesch et al., 2000a
18 - 22 wk	LW/LD	St	3,227	A+L	0.13	
0 - 102 kg	LD	Fa	6,022	A+D+L	0.26	Lutaaya et al., 2001
	LW	Fa	24,170	A+D+L	0.28 – 0.30	
	LD x LW	Fa	3,135	A+D+L	0.23 – 0.27	
1.36 - 118 kg	(PI x LW) x C	Fa	1,818	A+L	0.19	van Wijk et al., 2005
30 - 105 kg	PI	St	4,276	A+CG	0.28 – 0.45	Habier et al., 2007
	PI x LD	St	13,980	A+CG	0.22 – 0.33	
0 - 172 d	DU	Fa	34,940	A+L	0.22 – 0.31	Zumbach et al., 2007
0 - 196 d	DU x (LD x LW)	Fa	29,154	S+M+L	0.16 – 0.19	
30 - 105 kg	PI x LD	St	3,454	S+CG	0.19 – 0.34	Habier et al., 2009

N: Number of records; LW: Large White; LD: Landrace; PI: Piétrain; DU: Duroc; C: Commercial line; Fa: Farm; St: Station; A: Animal; S: Sire; L: Litter; M: Maternal; D: Dominance; CG: Contemporary group.

Table 2 shows estimates of heritability for DAYS to reach a target weight from various studies. Estimates of heritability ranged between 0.26 and 0.44, depending on the breed, model and target weight. Heritabilities seem to be consistent across breeds for a same final live BW. Moreover, it appears that heritability of growth traits increased with age. Indeed, heritabilities were higher for DAYS to 113.5 kg than for DAYS to 100 kg. Heritabilities are also depending on underlying models used for parameters estimation. The increasing heritability of growth traits was in agreement with results reported in studies of BW with random regression models (e.g., Edwards et al., 2006; Köhn et al., 2007; Haraldsen et al., 2009).

According to these results, it appears that growth traits in pigs are reasonably highly heritable. Therefore, the performance of the animal will be a good predictor of its breeding value and genetic improvement of growth would be efficient trough direct genetic selection.

Table 2. Estimates of heritability for age to particular weight (DAYS) from various studies.

DAYS to	Breed	Place	N	Model	Heritability	Reference
100 kg	PI	St	5,464	A+L	0.30	Bidanel et al., 1994
100 kg	YO	Fa	47,360	A+L	0.31	Li and Kennedy, 1994
	LD	Fa	28,762	A+L	0.30	
	DU	Fa	14,020	A+L	0.26	
	HA	Fa	9,983	A+L	0.32	
104.5 kg	YO	Fa	239,354	A+D+EP	0.33	Culbertson et al., 1998
113.5 kg	YO	Fa	361,300	A+L	0.35	Chen et al., 2002
	YO	Fa	361,300	A+L+M	0.36	
	DU	Fa	154,833	A+L	0.40	
	DU	Fa	154,833	A+L+M	0.38	
	HA	Fa	99,311	A+L	0.44	
	HA	Fa	99,311	A+L+M	0.43	
	LD	Fa	71,097	A+L	0.40	
	LD	Fa	71,097	A+L+M	0.38	

N: Number of records; LD: Landrace; PI: Piétrain; DU: Duroc; YO: Yorkshire; HA: Hampshire; Fa: Farm; St: Station; A: Animal; L: Litter; M: Maternal; D: Dominance; EP: permanent environment.

Carcass quality traits

Carcass quality in pigs can be evaluated based on different traits. The most common traits are backfat thickness (BF), loin muscle depth (LMD) or lean meat content (LMC). Definition of traits can be very different as carcass quality can be estimated on alive pigs or measured on carcasses after slaughter. Selection objectives for carcass quality are also very different depending on the market. The Belgian pork market is traditionally looking for very lean carcasses with high LMC (Hanset and Van Snick, 1972, Youssao et al., 2002). This has had a very important impact on the selection of Belgian pig breeds, like Belgian Landrace or Piétrain, which highly focused on LMC improvement and decreasing of BF. However, the pork market can be different in other countries. Selection objectives are different in France compared to Belgium. French pig breeds are fatter, with less lean meat (Dumont and Roy, 1975). Such particularity is also partially mirrored in beef cattle in Belgium where the Belgian Blue Breed also benefits from a specific market with very specialized selection objectives, i.e., high meat content on carcasses and leanness of the meat. In dairy cattle however there is a large uniformity of breeding goals across country and production systems. A direct consequence is that traditional Belgian pig breeds (and to a certain extend beef cattle breeds) were developed and selected to achieve these specific breeding goals and would not necessarily perform well in another context and reach the breeding goals of a different market.

Table 3 presents estimates of heritability for BF from various studies. Estimates of heritability for BF ranged between 0.35 and 0.65 for purebred pigs, depending on the breeds and models. For crossbred pigs, heritabilities ranged between 0.24 and 0.45. Table 4 shows an overview of estimates of heritability for LMC from different studies. Lean meat content is predicted from BF and LMD measurements and therefore, behaves similarly to these traits. Estimates of heritability for LMC ranged between 0.12 and 0.89 for purebred pigs, and between 0.30 and 0.59 for crossbred pigs, depending on the breeds and models used for the estimation.

Table 3. Estimates of heritability for backfat thickness (BF) from various studies.

Breed	Place	Status	N	Model	Heritability	Reference
LW	St	Alive	3,671	A+L	0.64	Ducos et al., 1993
LD	St	Alive	3,671	A+L	0.56	
PI	St	Alive	5,464	A+L	0.45	Bidanel et al., 1994
YO	Fa	Alive	47,360	A+L	0.51	Li and Kennedy, 1994
LD	Fa	Alive	28,762	A+L	0.53	
DU	Fa	Alive	14,020	A+L	0.55	
HA	Fa	Alive	9,983	A+L	0.50	
PI	St	Alive	4,638	A+L	0.65	Bidanel and Ducos, 1995
YO	Fa	Dead	239,354	A+D+EP	0.44	Culbertson et al., 1998
LW/LD	St	Alive	3,223	A	0.60	Hermesch et al., 2000a
	St	Dead	2,303	A	0.46	
LD	Fa	Dead	6,022	A+D+L	0.51 – 0.52	Lutaaya et al., 2001
LW	Fa	Dead	6,135	A+D+L	0.35 – 0.38	
LD x LW	Fa	Dead	6,135	A+D+L	0.29	
YO	Fa	Alive	361,300	A+L	0.48	Chen et al., 2002
DU	Fa	Alive	154,833	A+L	0.48	
HA	Fa	Alive	99,311	A+L	0.49	
LD	Fa	Alive	71,097	A+L	0.48	
(PI x LW) x C	Fa	Dead	1,645	A+L	0.45	van Wijk et al., 2005
PI	St	Dead	4,276	A+CG	0.45 – 0.46	Habier et al., 2007
PI x LD	St	Dead	13,980	A+CG	0.24 – 0.41	
DU	Fa	Alive	33,888	A+L	0.38 – 0.46	Zumbach et al., 2007
DU x (LD x LW)	Fa	Dead	29,154	S+M+L	0.31 – 0.33	
PI x LD	St	Dead	3,454	S+CG	0.42 – 0.43	Habier et al., 2009

N: Number of records; LW: Large White; LD: Landrace; PI: Piétrain; DU: Duroc; YO: Yorkshire; HA: Hampshire; C: Commercial line; Fa: Farm; St: Station; A: Animal; S: Sire; L: Litter; M: Maternal; D: Dominance; CG: Contemporary group; EP: permanent environment.

Table 4. Estimates of heritability for lean meat content (LMC) from various studies.

Breed	Place	Status	N	Model	Heritability	Reference
LW	St	Dead	3,039	A+L	0.60	Ducos et al., 1993
LD	St	Dead	2,695	A+L	0.68	
PI	St	Dead	1,675	A+L	0.89	Bidanel and Ducos, 1995
LW	St	Dead	5,921	A+L	0.53	Knapp et al., 1997
LD	St	Dead	3,143	A+L	0.43	
PI	St	Dead	6,533	A+L	0.40	
(PI x LW) x C	Fa	Dead	1,645	A+L	0.43	van Wijk et al., 2005
PI	St	Dead	4,276	A+CG	0.55 – 0.64	Habier et al., 2007
PI x LD	St	Dead	13,980	A+CG	0.34 – 0.51	
PI x LD	St	Dead	3,454	S+CG	0.30 – 0.41	Habier et al., 2009
DU	Fa	Dead	7,916	A	0.47 – 0.58	Ibáñez-Escriche et al., 2011
LD	Fa	Dead	1,615	A	0.60 – 0.71	
PI	Fa	Dead	4,661	A	0.12 – 0.27	
DU x LD	Fa	Dead	1,907	A	0.55 – 0.59	
(DU x LD) x PI	Fa	Dead	8,555	A	0.37 – 0.50	

N: Number of records; LW: Large White; LD: Landrace; PI: Piétrain; DU: Duroc; C: Commercial line; Fa: Farm; St: Station; A: Animal; S: Sire; L: Litter; CG: Contemporary group.

For carcass quality traits, it appeared that, as for ADG, heritability in crossbred populations seems to be lower than in purebred populations. This is probably due to higher environmental variations in commercial crossbred herds than in nucleus purebred herds, reared in high quality environment. Another source of variations is the status (dead or alive) of the pig when the trait was recorded. Measurements on crossbred pigs are usually performed on carcasses because they are intended for meat production. Measurements on purebred animals are often made on live animals because they are potential selection candidates that cannot be slaughtered. Hermesch et al. (2000a) found that BF measured on live animals had a higher heritability than BF recorded on carcasses. These results also support the fact that heritabilities were higher for purebred than for crossbred and should potentially be considered as different but genetically correlated traits (recorded on alive pig vs. recorded on carcass). As these traits are highly correlated, the use of both in a genetic evaluation program would considerably increase the accuracy of breeding values for both traits. Regarding to these results, literature indicated that carcass traits were found to be highly heritable, even more than growth traits. Therefore, direct genetic selection to improve carcass quality of pigs is totally doable and should be very efficient.

Feed efficiency

Improvement of feed efficiency is of particular interest in animal production mainly because of the increasing costs of food. Different methods exist to appreciate feed efficiency. In pig production, feed efficiency is classically estimated either by the ratio between the weight gain and the feed intake of an animal, or by the feed conversion ratio (FCR), defined as the feed intake divided by the weight gain (Kennedy et al., 1993). The aim of the selection is to decrease feed intake while keeping weight gain at least constant.

Feed intake is usually only recorded in test station because equipment to accurately record feed intake are expensive and normally not available in production herds. Table 5 shows estimations of heritability for FCR from different studies. Feed conversion ratio appeared to have a low to moderate heritability, ranging between 0.13 and 0.30 depending on the breed and model used. The low heritability estimated by Hermesch et al. (2000a) for FCR between 18 and 22 weeks was also probably due to the too short testing period to get reliable records of FCR, as for ADG between the same ages reported before.

Table 5. Estimates of heritability for feed conversion ratio (FCR) from various studies.

Range	Breed	N	Model	Heritability	Reference
35 – 90 kg	LW	2,374	A+L	0.22	Ducos et al., 1993
	LD	3,671	A+L	0.25	
35 – 90 kg	PI	4,638	A+L	0.27	Bidanel and Ducos, 1995
18 – 22 wk	LW/LD	3,221	A	0.15	Hermesch et al., 2000a
30 – 105 kg	PI	4,276	A+CG	0.23 – 0.24	Habier et al., 2007
	PI x LD	13,980	A+CG	0.28 – 0.30	
30 – 105 kg	PI x LD	3,454	S+CG	0.13 – 0.23	Habier et al., 2009

N: Number of records; LW: Large White; LD: Landrace; PI: Piétrain; A: Animal; S: Sire; L: Litter; CG: Contemporary group.

Direct selection to improve feed efficiency is difficult because it is expressed as a ratio. An alternative currently widely used in different species as well as in pigs is to improve feed efficiency by selection on residual feed intake (RFI). Residual feed intake is defined as the difference between the actual feed intake of an animal and its expected feed intake predicted based on its maintenance and production (usually growth and BF in pigs) requirements (Kennedy et al., 1993). It allows to identify animals deviating from their expected feed intake. The objective of selection on RFI is to reduce RFI (Hoque and Suzuki, 2009). Table 6 shows estimations of heritability for RFI from different studies.

Residual feed intake appeared to have a moderate heritability, ranging between 0.14 and 0.40 depending on the studied population. According to these estimates, it seems that genetic variations exist for RFI. Therefore, direct selection on RFI to improve feed efficiency seems to be possible (Hoque and Suzuki, 2009).

Table 6. Estimates of heritability for residual feed intake (RFI) from various studies.

Breed	N	Model	Heritability	Reference
LD	793	A	0.14	Gilbert et al., 2007
	657	A	0.24	
YO	756	A	0.29	Cai et al., 2008
PI	2,312	A	0.40	Saintilan et al., 2010
DU	7,388	A+P	0.34 - 0.39	Do et al., 2013
LD	4,773	A+P	0.34 - 0.36	
YO	4,751	A+P	0.34 - 0.40	

N: Number of records; LD: Landrace; YO: Yorkshire; PI: Piétrain; DU: Duroc; A: Animal; P: Pen.

In conclusion, it appeared that production traits are heritable and have a genetic variability. Therefore, direct genetic selection to improve level of production traits should be efficient. However, traits of interest are genetically correlated with each other and selection for one trait has the potential to change another one.

Genetic correlations between production traits

The knowledge of genetic correlations between traits involved in the selection objective is necessary to implement an efficient selection program. Economically important traits might be unfavorably correlated with each other and should be balanced in the selection program in order to not deteriorate one trait while trying to improve another one. An overview of several studies presenting genetic correlations between production traits is shown in Table 7.

Estimates of genetic correlations between ADG and BF are unfavorable, low to moderate and ranged from 0.14 to 0.42, averaging 0.30 across studies. As LMC is predicted based on BF measurements, ADG and LMC are also unfavorably correlated. Estimates of genetic correlations ranged from -0.42 to -0.06, averaging -0.20. Estimates of genetic correlation between DAYS and BF are also unfavorable, low to moderate and ranged from -0.44 to -0.04, averaging -0.13. Changes in fat and lean tissue development during growth, and their relationships with growth rate are very important in pig production. Indeed, proportions of fat and lean meat of carcass are used to determine the economic value of the animal at slaughter (Wagner et al., 1999), which depends on the market where the carcass will be sold. Biological antagonisms have to be considered, e.g., growth and carcass quality seemed to be unfavorably related because it appeared that carcass fat content increased as BW increased (Gu et al., 1992). Therefore, fast growing pigs produce fatter carcasses that are not searched in the traditional pork production sector, especially in Belgium. However, according to Hermesch et al. (2000b), ADG at the beginning of the fattening period and at the end behave differently. Fast growing pig at the beginning is associated with leaner carcass than fast growing pig at later stages of the fattening period.

Table 7. Estimates of genetic correlations between production traits (ADG, DAYS, BF, LMC, FCR, RFI) from various studies.

Trait	BF	LMC	FCR	RFI	References*
ADG	0.30 (0.14 to 0.42)	-0.20 (-0.42 to -0.06)	-0.53 (-0.76 to -0.40)	0.04 (-0.35 to 0.25)	1, 4, 5, 7, 8, 9, 10, 11, 12
DAYS	-0.13 (-0.44 to -0.04)				2, 3, 6
BF		-0.71 (-0.98 to -0.54)	0.24 (-0.04 to 0.39)	0.06 (-0.19 to 0.44)	1, 4, 7, 8, 9, 10, 11, 12
LMC			-0.35 (-0.38 to -0.32)	-0.36 (-0.55 to -0.16)	8, 9, 11

* 1: Ducos et al., 1993; 2: Bidanel et al., 1994; 3: Li and Kennedy, 1994; 4: Bidanel and Ducos, 1995; 5: Hermesch et al., 2000b; 6: Chen et al., 2002; 7: van Wijk et al., 2005; 8: Gilbert et al., 2007; 9: Habier et al., 2007; 10: Cai et al., 2008; 11: Saintilan et al., 2010; 12: Do et al., 2013.

Estimates of genetic correlations between ADG and FCR appeared to be favorable and ranged from -0.76 to -0.40, averaging -0.53. Therefore, fast growing pigs tend to be more feed efficient. It is expected since FCR is the ratio between feed intake and ADG. It is advantageous because one of the objectives in selection to improve feed efficiency is the reduction of FCR. The ultimate objective is to reduce feed intake because of the cost of food and to keep ADG at least constant. Therefore, if the increasing ADG is related to increasing feed intake, it might not be really interesting. It depends on the difference between the additional profit related to the increasing ADG and the additional cost of food. This shows the difficulty to define efficiency traits and to perform genetic selection for these traits.

Estimates of genetic correlation between BF and LMC ranged from -0.98 to -0.54, averaging -0.71. Prediction of LMC is usually derived from BF and muscle depth.

Therefore the strong genetic correlation between BF and LMC is expected. Carcass with high BF will contain less lean meat.

Estimates of genetic correlations between BF and FCR ranged from -0.04 to 0.39, averaging 0.24; estimates of genetic correlations between LMC and FCR ranged from -0.38 to -0.32, averaging -0.35. Therefore, fatter pigs at slaughter tend to have higher feed intake.

Estimates of genetic correlation between RFI and ADG ranged from -0.35 to 0.25, averaging 0.04. The range of these estimations is large but it suggests that RFI and feed intake are likely to be independent of ADG. Therefore, selection to reduce RFI would also reduce feed intake, without affecting ADG, hence improving FCR (Gilbert et al., 2007; Hoque and Suzuki, 2009). Estimates of genetic correlation between RFI and BF ranged from -0.19 to 0.44, averaging 0.06; estimates of genetic correlation between RFI and LMC ranged from -0.55 to -0.16, averaging -0.36. As for ADG, selection for lower RFI does not seem to have an impact on BF. Nevertheless, the favorable genetic correlation between RFI and LMC suggests that improving feed efficiency (lower RFI) would also improve LMC.

As genetic correlations between traits imply a correlated response to selection, selection decision when several traits are considered will depend on the relative importance of these traits in the breeding goal. Optimal selection decisions can be achieved by using selection indexes combining different traits properly weighted by their economic importance.

CONCLUSION

Production pigs are mostly crossbreds. Crossbreeding allows to take advantage of heterosis effects and complementarity between breeds or lines to improve performances of market products, and therefore, their economic value. Currently, methods have been developed to perform genetic evaluations of purebred parents for crossbreeding performances and to combine purebred and crossbred data. Nevertheless, crossbred records, i.e., information close to what the commercial market is looking for, is seldom used directly in purebred selection. Combined crossbred-purebred models would also lead to improve reliabilities of estimated breeding values (EBV) because they use all available information related to an animal. Moreover, availability of crossbred data would allow to estimate and to exploit non-additive genetic variability, like dominance, that is not negligible on production traits. Inclusion of dominance effects leads to more accurate estimation of the total genetic merit of an animal, and therefore, to a better estimation of additive effects. Based on these theoretical considerations, a consequence of crossbred production pigs is that terminal parental lines could be very specialized. Terminal sire lines are selected almost exclusively for production traits expressed in their market progeny.

Also, all results showed that the main production traits, i.e., growth, carcass composition and feed efficiency, are heritable and genetically variable. Therefore, genetic improvement of these traits would be efficient through direct genetic selection. Production traits are also genetically correlated, but not always favorably. Hence, comprehensive selection programs should be undertaken to avoid deterioration of a trait because of the genetic improvement of another one.

To improve number of pigs reaching full market value, knowledge of the genetic of traits like birth weight (BWT) and survival at different stages of the life until slaughter are also important. Moreover, to improve the classical production traits, it is necessary to know the link between survival and traits determining the economic value of an animal. In the context of the selection of purebred terminal sire lines for crossbred performances, it is interesting to estimate the sire effects on traits mostly influenced by dams (e.g., BWT, survival in early life). Moreover, survival at later stages of the fattening period, until slaughter, is also very important from an economic point of view. Indeed, the loss of older pigs means the loss of higher value animals. To our knowledge, the genetic of survival after weaning and relationships with traditional production traits has not been studied in commercial crossbred populations.

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CHAPTER III. DEVELOPMENT OF THE GENETIC EVALUATION OF PUREBRED PIÉTRAIN BOARS FOR CROSSBRED PERFORMANCE

CHAPTER III

In the Walloon Region of Belgium, commercial pigs are traditionally produced from the matings of purebred Piétrain boars with purebred or crossbred dams from typical maternal lines, like Landrace. The use of Piétrain boars is historical considering that the Piétrain pig breed is originated from the Walloon part of Belgium, but currently widely used worldwide. The most important quality of Piétrain breed is its high dressing percentage, one of the highest among the main recognized pig breeds. Therefore, Piétrain boars are extensively used as terminal sires in crossbreeding settings to improve carcass quality of commercial pigs. However, as pointed out in Chapter II, purebred data are poor predictor of crossbred performances. Therefore, starting in 2007, a new breeding program for purebred Piétrain boars was implemented in the Walloon Region of Belgium. Since then, Piétrain boars have been progeny-tested in test station in crossbreeding instead of the former purebred progeny-test. Correlations between purebred and crossbred performances also reflect Genotype x Environment (GxE) interactions because purebreds and crossbreds are often kept in different environments. In the Walloon Region of Belgium, in addition to the progeny-test in test station, purebred and some crossbred pigs are performance-tested on-farm. Furthermore, Chapter II stated that, in crossbreeding, non-additive genetic effects, like dominance, might be not negligible on growth traits. Therefore, the objective of this chapter was to explore these aspects by 1) developing a multitrait and multi-environment model for the genetic evaluation of Piétrain boars for growth (Chapter III.1) and 2) exploring the introduction of dominance effects into genetic evaluation models for growth (Chapter III.2).

CHAPTER III.1 USING TEST STATION AND ON-FARM DATA FOR THE GENETIC EVALUATION OF PIÉTRAIN BOARS USED ON LANDRACE SOWS FOR GROWTH PERFORMANCE

CHAPTER III.1

Previous chapters stated that crossbred performances could be badly predicted based on purebred information only. Hence, the genetic selection of purebred parents for crossbred performances should combine purebred and crossbred data. Moreover, similar or identical traits recorded in different environmental conditions should be treated as genetically different traits due to potential Genotype x Environment (GxE) interactions. Therefore, the objective of this chapter was to present the genetic evaluation model for growth traits, using data from both purebred and crossbred pigs, developed for Walloon Piétrain boars. This model combined on-farm and test station data treated as different traits. The potential heterosis effect coming from the use of crossbreeding was included in the model. Another issue addressed in this chapter was the modeling of longitudinal data using a random regression model (RRM) and the consideration of variance heterogeneity related to growth data. Finally, in order to demonstrate the interest of combining various sources of data, the potential gain of reliability for estimated breeding values (EBV) of boars between using only test station data or combining test station and on-farm data was explored.

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ABSTRACT

The aim of this study was to develop a new genetic evaluation model to estimate the genetic merit of boars for growth based on 1) performance of their crossbred progeny fattened in the test station and 2) their own performance or those of relatives from the on-farm testing system. The model was a bivariate random regression animal model with linear splines and was applied to Piétrain boars from the Walloon Region of Belgium mated with Landrace sows. Data contained 1) 12,610 BW records from the test station collected on 1,435 crossbred pigs from Piétrain boars and Landrace sows, and 2) 52,993 BW records from the on-farm testing system collected on 50,670 pigs with a breed composition of at least 40% Piétrain or Landrace. Since 2007, 56 Piétrain boars have been tested in the station. Data used to estimate variance components and breeding values were standardized for the age to take into account heterogeneity of variances and then pre-adjusted at 210 d of age to put all records on the same scale. Body weight records from the test station and from the on-farm testing system were considered as 2 different traits. The heterosis effect was modeled as fixed regression on the heterozygosity coefficient. As all test station animals were similarly crossbred, smaller variation in heterozygosity caused the sampling error of the regression estimate at 210 d to be larger in the test station than in on-farm data with estimates of 28.35 ± 14.55 kg and 9.02 ± 0.67 kg, respectively. Therefore, the most likely reason for the large differences in estimates was sampling. Heritability estimates ranged from 0.37 to 0.60 at 210 and 75 d, respectively, for test station BW and from 0.42 to 0.60 at 210 d and 175 d, respectively, for on-farm BW. Genetic correlation decreased when the age interval between records increased, and were greater between ages for test station than for on-farm data. Genetic correlations between test station and on-farm BW at the same age were high: 0.90 at 175 d and 0.85 at 210 d. For the 56 boars tested in the station, the average reliability of their EBV for ADG between 100 and 210 d was improved from 0.60 using only test station data to 0.69 using jointly test station and on-farm data. Based on these results, the new model developed was considered as a good method of detection of differences in growth potential of Piétrain boars based on-test station and on-farm data.

Keywords: Crossbred progeny, Genetic parameter, Growth potential, Piétrain boar, Reliability, Variance heterogeneity

INTRODUCTION

Until recently, Piétrain boars in the Walloon Region of Belgium were selected based on performance recorded on their purebred progeny in the test station. However, Piétrain boars are mostly used in crossbreeding systems. In such breeding systems, among other variables, the efficiency of selection is a function of the genetic correlation between crossbred and purebred performance (Zumbach et al., 2007). However, the genetic correlation could be as low as 0.4 to 0.7 between purebred and crossbred performances due to genetic differences between purebred and crossbred animals and also due to environmental differences between selective and commercial conditions. Therefore, purebred performance can be considered as a poor predictor of crossbred genetic merit for some traits (Dekkers, 2007). Moreover, combining purebred and crossbred data to estimate genetic merit of purebred animals for crossbred performance increases the accuracy of EBV (Lutaaya et al., 2001; Habier et al., 2007). Several authors (Bidanel and Ducos, 1996; Peškovičová et al., 2002) proposed the joint use of test station and on-farm data if available; that is the case in the Walloon Region of Belgium.

Growth data, represented by repeated body weight (BW) records, are longitudinal data by nature and can often be modeled using random regression models (RRM; Huisman et al., 2002; Schaeffer, 2004; Bohmanova et al., 2005). With growth data, residual variances often increase with age and change similarly to phenotypic variance (Schaeffer, 2004).

The aim of this study was to develop a genetic evaluation model to estimate growth potential of boars based on BW records of their crossbred progeny in a test station. In addition, BW data of boars themselves and of some of their relatives from the on-farm testing system were used. The model developed was a bivariate RRM with linear splines, taking into account heterogeneity of variance.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were provided through the regular animal recording schemes managed by the Walloon Pig Breeding Association (AWEP; Ciney, Belgium).

Data

Since 2007 a new test station performance recording system for crossbred performance of Piétrain boars has been under development in the Walloon Region of Belgium. In Belgium, commercial pigs were mainly crossbred animals from Piétrain boars mated with Landrace sows. Additional records from test station data collected on boars themselves and on relatives were provided by the on-farm performance recording system. Both systems are managed by the AWEP.

Test Station Progeny Testing Scheme

Data were collected at the Walloon central test station between 2007 and 2010. Data were recorded on crossbred progeny of Piétrain boars mated with Landrace sows. Piglets were produced using synchronized sows and were, therefore, grouped in batches. Boars were provided by Walloon Piétrain breeders and by a regional artificial insemination (AI) center. Boars from the AI center were used as connection sires, linking batches. Connectedness of the new data was evaluated after each batch and then connection boars were chosen in the appropriate manner. In the data set, 56 different boars were progeny tested in the station. Sows were of the hyperprolific Landrace K+ line selection program (http://www.ciap-belgium.eu) and were provided by the Walloon Agricultural Research Centre (CRA-W; Gembloux, Belgium). These sows had known pedigrees and were sired by boars from the K+ program. Every 10 wk, selected Piétrain boars were mated to 5 randomly chosen sows. The majority of sows were mated in successive batches to different boars. For each boar, the aim was to have a minimum of 16 and a maximum of 25 piglets from 5 different sows per batch. When a boar did not reach 16 piglets in a batch, efforts were made to use him again in latter batches. At 4 wk of age, piglets from these matings were weighed and then selected simulating a commercial setting, to create batches of about 100 animals that entered the test station.

The progeny test began when piglets weighed about 20 kg. In the test station, pigs were randomly assigned in groups of 4. Data were recorded on castrated male and female animals. They were weighed every 15 d and between approximately 20 and 110 kg of BW.

On-Farm Performance Testing Scheme

Data were provided by the on-farm performance recording system between 1996 and 2010. The aim of this system was to potentially allow the estimation of the genetic value of pigs for recorded traits without having to slaughter them. In the Walloon Region of Belgium the on-farm performance recording system is not mandatory. Pig breeders choose to participate and also choose which animals to test. The majority of on-farm data were recorded on entire males but also on females and castrated males of various breed types. Entire males represented 78% of the on-farm data set, of which 60% were Piétrain purebreds, 15% were Landrace purebreds, and 25% were crossbreds. Females represented 21% of the on-farm data set, of which 41% were Landrace purebreds, 39% were Piétrain purebreds, and the remaining 20% were crossbreds. Only 1% of the on-farm data set was castrated males, which were mainly crossbreds.

This on-farm performance testing system was also applied to pigs from the test station that were measured the week before slaughtering, the test station being considered as a farm. Therefore, the 56 boars tested in station had crossbred progeny both at the test station and on farm. Furthermore, 34 of the 56 boars had additional progeny only tested on farm, 51 had own records, 51 had sires, and 17 had dams that were recorded in the on-farm system.

Ideally, on-farm data should be recorded on animals between 100 and 120 kg of BW before 220 d of age. Few animals were weighed more than once, with only about 5% of data having repeated records. The small number of repeated records could be explained due to the on-farm performance recording system; the genetic merit of animals around slaughter age is of greatest importance; therefore, one record per animal is typically sufficient.

Total Data Set. The total data set contained edited BW data of pigs from the test station and from the on-farm performance recording system. Body weight records collected in the 2 performance recording systems were considered as 2 different traits. Data from the test station were BW recorded on pigs between 50 and 210 d of age; and data from the on-farm recording system were BW recorded on pigs between 175 and 250 d of age. Breed types were Piétrain and Landrace purebreds from the on-farm testing scheme, and crossbred Piétrain with Landrace pigs from the test station and on-farm testing schemes. During the data editing process, only Piétrain × Landrace-type crossbred pigs that had a breed composition of at least 40% Piétrain or Landrace and at least 80% Piétrain and Landrace were retained to keep crossbred pigs with similar breed compositions to those from the test station.

A total of 56 Piétrain boars and 108 Landrace K+ sows sired by 35 K+ boars were used to produce the 1,435 test station crossbred animals. The total data set contained 12,610 BW records from these animals and 52,993 BW records observed on 50,670 animals from the on-farm performance recording system. As mentioned above, all animals recorded at the test station were crossbreds and 15,682 crossbred animals were also recorded on an on-farm level. Up to 10 generations of ancestors were recursively extracted from the pedigree database; 95% of animals had maximum 10 generations of known ancestors. The total number of animals in the extracted pedigree file was 80,969. Figures 1 and 2 show the distribution of BW records over age for test station and on-farm data, respectively.

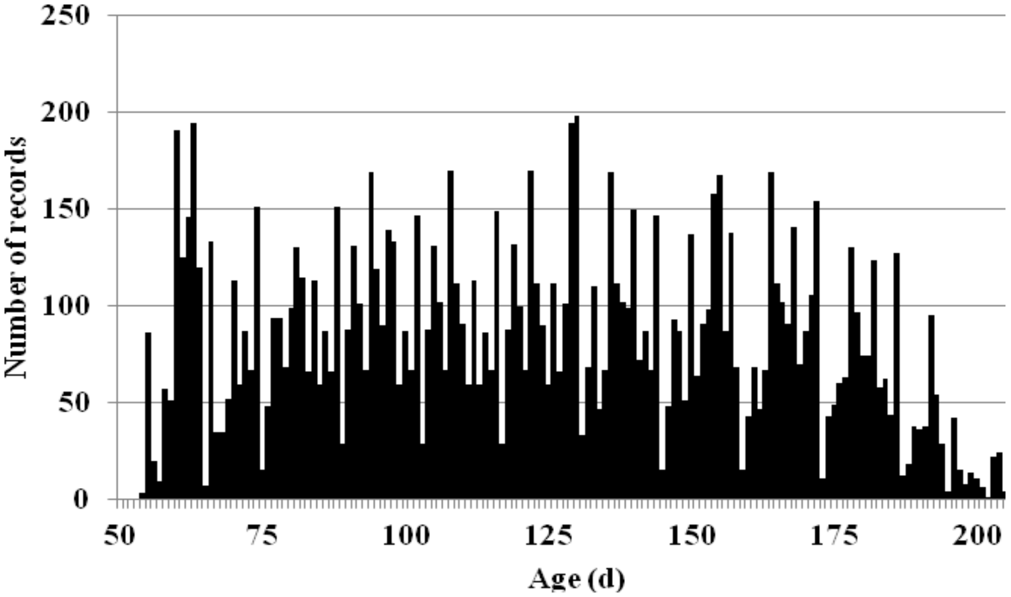

Figure 1. Distribution of test station BW records over the ages.

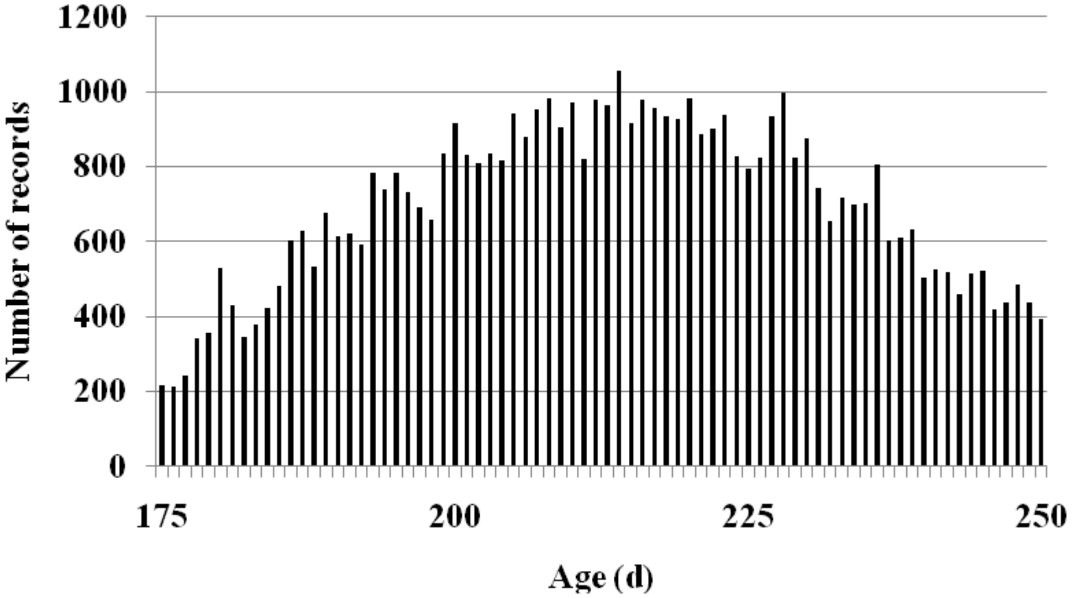

Figure 2. Distribution of on-farm BW records over the ages.

Standardization of Data

Growth data shows increasing variance over time (Huisman et al., 2002). Changes in variance could be partially modeled by RRM, but part of variance heterogeneity remains potentially in the residual variance (Jaffrezic et al., 2000). With growth data, residual variances are often considered increasing with age and changing similarly to phenotypic variance (Schaeffer, 2004). There are various methods of considering the heterogeneity of variances. Data could be adjusted before the analysis as proposed by Wiggans and VanRaden (1991). Another method is to integrate adjustment for heterogeneity of variances into the analyses as proposed by Meuwissen et al. (1996). This allows joint estimation of breeding values and heterogeneous variances.

In this study, a simpler robust pre-adjustment method was used, while retaining the feature of modeling variance differences a priori. Data for each day of age was considered homogeneous for its variance, and adjustment for variance heterogeneity between days of age was done using the following standardization procedure: standardized BW were calculated for both traits separately by subtracting an estimated trait mean and dividing by a SD, both defined as functions of age in days; estimated phenotypic mean and SD were computed based on the equation of smoothing curves of the evolution of phenotypic mean and SD of BW with age for each trait. Equations of the smoothing curves were obtained with PROC GLM (SAS Inst. Inc., Cary, NC) testing different order polynomials. Standardized records were then pre-adjusted to 210 d of age. The equation to obtain standardized and pre-adjusted records y_{ij}^{*} was

$$y_{ij}^{*} = \frac{y_{ij}-m_i}{\sigma_i}\sigma_{210} + m_{210},$$

where y_{ij} is the phenotypic value of animal j at age i, m_i is the estimated phenotypic mean at age i, σ_i is the estimated phenotypic SD at age i, σ_{210} is the estimated phenotypic SD at 210 d of age, and m_{210} is the estimated phenotypic mean at 210 d of age.

Models

The model developed in this study was a random regression animal model with linear splines. A linear spline is a smooth curve over an interval formed by linked segments of linear polynomials at knot points. In this study, RRM with splines was chosen, as it is a straightforward extension on a multitrait model, where BW are recorded at ages corresponding to knots. However, multitrait models require age pre-adjustment of data and restrictive age ranges must be established (Robbins et al., 2005). This could lead to elimination of records taken outside of these age ranges, resulting in a loss of a large amount of data.

In matrix notation, the bivariate model could be represented as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Q}(\mathbf{Za} + \mathbf{Zp}) + \mathbf{e},$$

where $\mathbf{y}$ is the vector of standardized and adjusted observations, $\mathbf{b}$ is the vector of fixed effects, $\mathbf{a}$ is the vector of random additive genetic effects, $\mathbf{p}$ is the vector of random permanent environment effects, $\mathbf{e}$ is the vector of random residuals, $\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices relating observations to various effects, and $\mathbf{Q}$ is the matrix of linear spline coefficients.

Fixed effects were sex, contemporary groups, and heterosis effect. Sex of animal was defined as fixed effect in the model because BW are measured on females, entire males, and castrated males. This effect is important in reflecting the difference of growth patterns based on sex. Contemporary groups were created using a clustering algorithm to contain at least 3 animals measured at the same location within an interval with a maximum of 75 d. This effect was important because data from on-farm testing system are recorded on a heterogeneous environment, at different times. Contemporary groups allow a comparison of animals raised in diverse environments. Groups of 3 animals over 75 d were a minimalistic compromise, as on-farm animals were not measured at the same date, but in function of ages. Therefore, it is possible to have only 1 animal tested per farm in a long period of time. Heterosis was modeled as regression on an overall heterozygosity coefficient. This effect was required because the data set contained crossbred animals.

Random effects were additive genetic, permanent environment, and residual effects. Additive genetic and permanent environment effects were modeled by random regressions using linear splines with the same number and location of knots for these 2 effects. According to Jamrozik et al. (2010), position and number of knots should not be identical for different traits but reflect trait-specific patterns. Therefore, in this study, number and position of knots were different between the 2 traits analyzed. For both traits, extreme knots were located at extreme ages in the data set used. Additional knots were added to have good representation of BW evolution with age of animal. Test station BW were modeled with 4 knots at 50, 100, 175, and 210 d. On-farm BW were modeled with 3 knots at 175, 210, and 250 d. Model fitness was tested by computing residuals from a BLUP (Best linear unbiased prediction) evaluation. The Student’s t-test was used to test whether the means of mean residual distributions in function of age in day were significantly different from zero.

A consequence of the standardization was that all fixed and random effects were defined on a transformed scale. Solutions on original scales were obtained by back-transformation as the model used can be considered as an approximate multiplicative mixed model (Kachman and Everett, 1993).

Variance Components Estimation

The variance components were estimated by the restricted maximum likelihood (REML) method using the REMLF90 program (Misztal, 2011) on a sample of the total data set due to computing limitations. Animals in the sample were selected to maximize genetic and environmental links between both traits through the use of data from related animals and environmental conditions. Therefore, this sample contained all standardized

BW records of pigs fattened in test station and also standardized BW recorded on pigs from the farms of origin of the 56 boars tested in the station. Body weight records of the sample were standardized with the same estimated means and SD than those for the total data set. This sample contained all 12,610 BW records from test station and 10,559 BW records observed on 9,906 different animals from the on-farm performance recording system.

Estimation of Breeding Values and Reliabilities

The EBV for BW at the age corresponding to knots was directly obtained from the solutions of the mixed model fit to the total data set using standardized records. Estimated breeding values EBV_{ij}^* were de-standardized as follows:

$$EBV_{\boldsymbol{ij}}^* = \frac{EBV_{ij}}{\sigma_{210}}\sigma_i,$$

where EBV_{ij} is the standardized EBV of animal j at age i, σ_{210} is the estimated phenotypic SD at 210 d of age, and σ_i is the estimated phenotypic SD at age i.

The most interesting growth information is growth rate linked to the fattening period. In the Walloon Region of Belgium, the period between 100 and 210 d of age was chosen for the computation of average daily gain (ADG) and boars were ranked according to this trait. Average daily gain of boars between 100 and 210 d was computed as follows:

$$ADG(g/d) = \frac{(EBV_{210}^* + m_{210}) - (EBV_{100}^* + m_{100})}{210 - 100} 1{,}000,$$

where m_{100} and m_{210} are estimated phenotypic means of the population at 100 and 210 d of age, respectively.

Reliabilities were defined as the squared correlation between true breeding value and EBV and were a direct function of the prediction error variance (PEV; Jamrozik et al., 2000). They were computed for each EBV as follows:

$$r^2 = 1 - \frac{P}{\sigma_g^2},$$

where P is the PEV and σ_g^2 is the estimated genetic variance. The values of PEV depended mainly on number of progeny tested per boar but depended also on direct connections [i.e., number of other sires with progeny in the same batch (Tosh and Wilton, 1994)] or on the number of batch where the sire had progeny tested and the availability of on-farm correlated data. Reliability for ADG between 100 and 210 d was computed using reliabilities of EBV at 100 and 210 d and genetic correlation between BW at 100 and 210 d. The computations used the same selection index based on the approach applied by Cole and VanRaden (2010). A multitrait reliability (MTREL) for ADG between 100 and 210 d was computed based on the MTREL for both BW at 100 and 210 d. Using additional on-farm data should improve reliabilities. Therefore, additional single-trait reliabilities (STREL) were computed using an equivalent single-trait model where all on-farm data were considered missing. Differences between MTREL and STREL expressed the impact of additional information from the on-farm recording system to increase reliability of EBV of boars tested in the station.

RESULTS AND DISCUSSION

Data

Figure 3 shows the evolution of mean BW and SD over age for test station data and the equation of smoothing curves used to obtain values used to standardize BW records. Different orders of polynomial functions were tested to find the appropriate smoothing curves.

The mean BW of pigs from the test station increased between 50 and 210 d with a slight inflection at about 175 d of age. Based on coefficients of determination, the best smoothing curve for evolution of mean BW was a cubic polynomial curve. Evolution of SD was very similar and increased until 175 d. This should be due to scale effect because SD followed the BW increasing with age. However, SD decreased after 175 d and values were less stable, probably due to fewer pigs measured after this age. Again, the best smoothing curve was cubic polynomial. Coefficients of determination of the smoothing curves were high: 0.98 for mean and 0.85 for SD observed on test station BW.

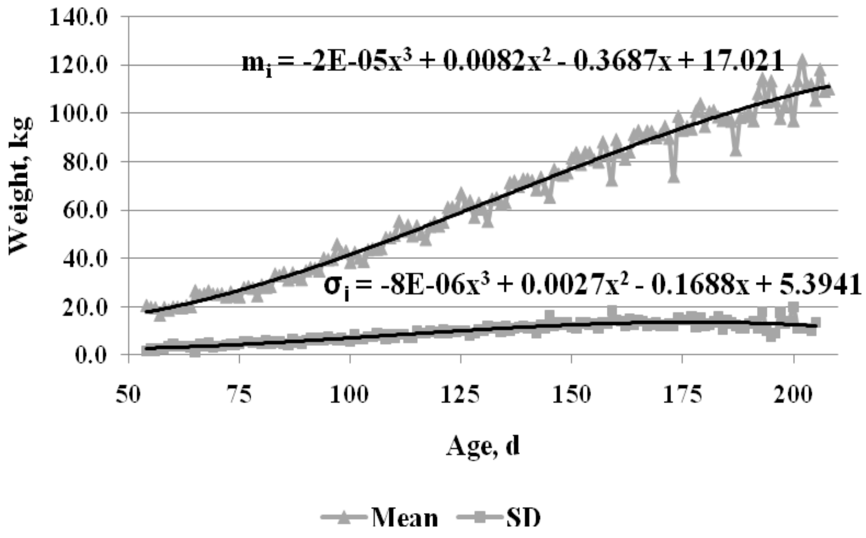

Figure 3. Evolution of mean BW and SD of BW with ages between 50 and 210 d for test station records and equation of smoothing curves.

Figure 4 shows the evolution of mean BW and SD over age for on-farm data. Equations of smoothing curves used to standardize data are also presented in Figure 4. The mean BW of pigs measured on farm increased regularly from 175 to 250 d of age. Based on this, the best smoothing curve was linear for the mean. However, SD had a quadratic evolution over this period with a minimum at about 200 d. The smallest SD at about 200 d was probably due to a large amount of data around this age. Coefficients of determination were again high with values for on-farm BW of 0.99 for mean and 0.78 for SD.

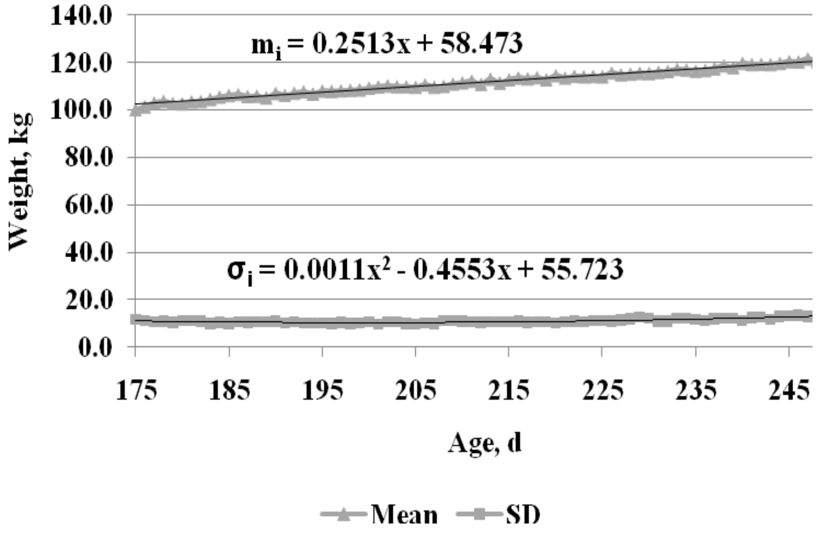

Figure 4. Evolution of mean BW and SD of BW with ages between 175 and 250 d for on-farm records and equation of smoothing curves.

In general, systematic age effect tended to disappear with standardization and pre-adjustment of data in function of age. This led to a less variable mean and SD of BW with age for both traits analyzed. Moreover, as a RRM was used, small remaining differences in means and SD could be modeled.

Models

As explained previously, fixed effects included in the model were sex, contemporary groups and heterozygosity coefficient as a linear covariable. According to a preliminary variance analysis with PROC GLM using a linear model while including fixed effects, all effects were highly significant for test station and on-farm BW, with P-values <0.0001.

Solution for heterosis effect showed that crossbred animals had better growth than purebred animals. Estimates for heterosis were 28.35 ± 14.55 kg and 9.02 ± 0.67 kg for the test station and on-farm BW, respectively at a standard age of 210 d. Obtaining reliable estimations for heterosis effect is always very difficult. The difference observed between estimates for test station and on-farm BW could be attributed to sampling errors as all test station pigs were crossbreds and they had similar heterozygosity. The small amount of variation in heterozygosity causes the SE of the regression to be large. For test station BW, the heterosis effect explained 24.4% of the mean BW at 210 d of age. This estimate shows that a part of the mean is most likely confounded with this larger heterosis effect. As all test station animals have a very similar degree of heterozygosity, the effect of this potentially inflated estimation should remain limited as it affects animals similarly. However, the relative estimate on an on-farm basis was around 8.1% of the mean BW at 210 d, which should have been expected. This agrees with results reported by Schneider et al. (1982) who found that percentage heterosis ranged from 3.7 to 10.5% for BW records. Also, given the multiplicative nature of this model, fixed effects on the original scale are affected by multiplicative factors for each heterogeneity class (i.e., for each day of age in this study; Kachman and Everett, 1993). Therefore, the heterosis effect estimate depended on age. Figures 5 and 6 show changes of heterosis effect with age for test station and on-farm BW, respectively.

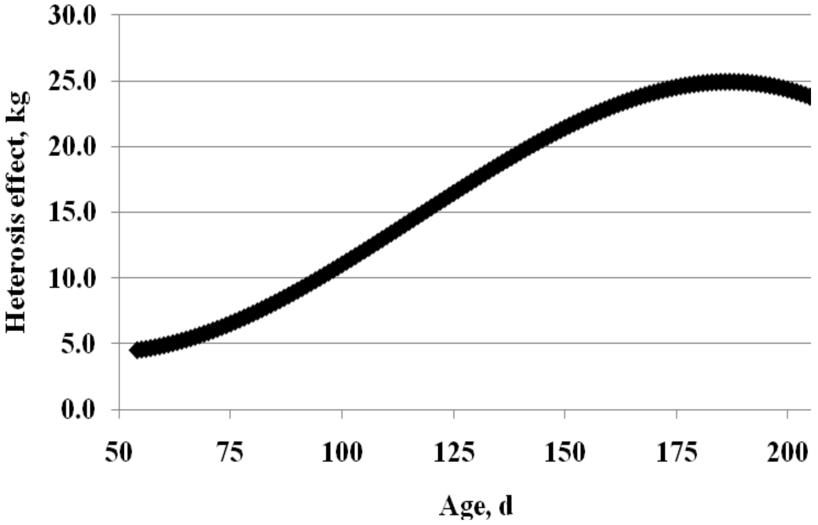

Figure 5. Evolution of heterosis effect with ages between 50 and 210 d for test station BW.

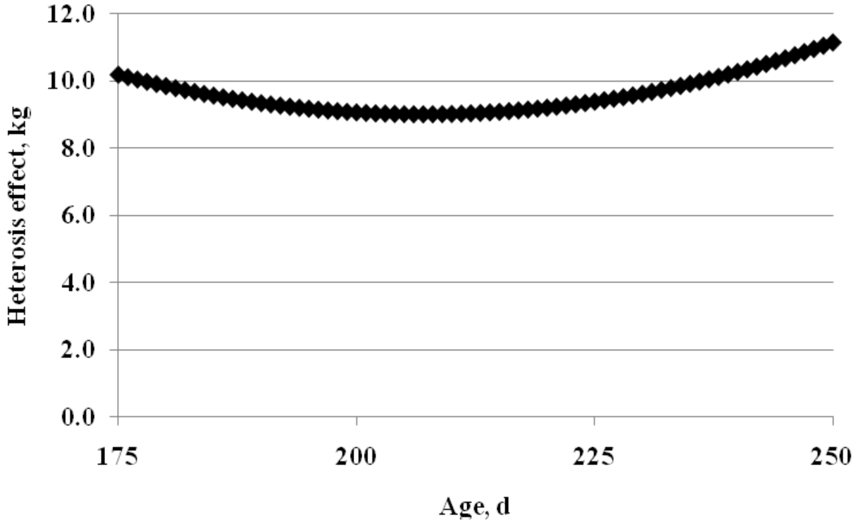

Figure 6. Evolution of heterosis effect with ages between 175 and 250 d for on-farm BW.

Genetic Parameters

Variance Components and Heritability

Table 8 shows relative variance components and total variance on the original scale for test station BW calculated every 25 d and for each knot between 50 and 210 d. Heritability ranged from 0.37 at 210 d of age to 0.60 at 75 d of age and tended to decrease with age. These results were somewhat different than estimates from the literature: Edwards et al. (2006) or Haraldsen et al. (2009) presented increasing heritability of BW data of pigs with age. However, Huisman et al. (2002) found that heritability of BW had a tendency to decrease as pigs became older with a RRM spline model. Permanent environment variance explained between 32 and 52% of the total variance and its importance tended to increase with age and became weaker than additive genetic variance at about 200 d of age. Residual variance represented 5 to 12% of the total variance as a function of age. As expected, total variance tended to increase with age, probably due to scale effects (Iwaisaki et al., 2005).

Table 8. Relative variance components and total variance on the original scale for test station BW in function of age between 50 and 210 d.

	Relative variance component			Variance, kg²
Age, d	**Genetic**	**Permanent environment**	**Residual**	**Total**
50	0.59	0.36	0.05	10.13
75	0.60	0.32	0.08	14.87
100	0.53	0.39	0.08	38.78
125	0.53	0.37	0.10	68.93
150	0.51	0.38	0.11	103.27
175	0.46	0.43	0.11	138.93
200	0.40	0.48	0.12	132.53
210	0.37	0.52	0.11	129.30

Based on variance components estimated at 100 and 210 d of age, heritability was computed for ADG in test station between 100 and 210 d, giving an estimate of 0.41. This was in agreement with values of heritability found in the literature for ADG of Piétrain pigs. Bidanel and Ducos (1995) obtained heritability estimates of 0.33 for ADG from 35 to 90 kg, measured on candidate selection Piétrain boars in the test station, and 0.38 for ADG between 35 and 100 kg, measured on Piétrain pigs in the test station slaughtered at the end of the testing period. Habier et al. (2007) reported estimates of 0.45 for purebred progeny and 0.22 for crossbred progeny of Piétrain boars tested in the test station for ADG between 30 and 105 kg.

Table 9 shows relative variance components and total variance on the original scale for on-farm BW calculated every 25 d and for each knot between 175 and 250 d. Heritability varied between 0.42 at 200 d to 0.60 at 175 d and decreased from 175 to 200 d and then increased until 250 d. Mean heritability over the considered period of age was 0.50. The importance of permanent environment variance increased from 175 to 210 d of age, where permanent environment variance was greater than additive genetic variance, and then decreased until 250 d of age. Permanent environment variance explained 35 to 52% of the total variance. Estimated residual variance was relatively low and represented about 5% of the total variance. Total variance was greater at ages corresponding to knots.

Table 9. Relative variance components and total variance on the original scale for on-farm BW in function of age between 175 and 250 d.

	Relative variance component			**Variance, kg²**
Age, d	**Genetic**	**Permanent environment**	**Residual**	**Total**
175	0.60	0.35	0.05	127.03
200	0.42	0.52	0.06	93.16
210	0.43	0.52	0.05	114.20
225	0.46	0.48	0.06	95.29
250	0.59	0.37	0.04	192.33

Additive genetic and permanent environment variances were modeled using the same number of knots for each trait separately. According to Pool et al. (2000), in a RRM it is better to fit the same number of parameters for the genetic and the permanent environmental part. If permanent environment were modeled with only 1 parameter, estimated genetic variance could be overestimated at the beginning and at the end of the growth curve. As a consequence, estimated heritability also fluctuated with age.

Some variations are also observed in the evolution of estimated total variances, especially for on-farm BW. These variations were greater at ages corresponding to knots. This is most likely an artifact due to modeling by RRM with linear splines. However an advantage of spline RRM is that there are no poor fits at the extreme of the trajectory and the model is not affected by sparse data (Misztal, 2006). Huisman et al. (2002) used different RRM to describe BW data of pigs and compared them with a multitrait model. In a multitrait model, records taken at different ages are treated as different traits. So, variance components and EBV are estimated for these target ages. With RRM, it is possible to compute variance components and EBV at any age and also between age of recording (Huisman et al., 2002; Legarra et al., 2004; Iwaisaki et al., 2005). Moreover, according to Huisman et al. (2002), variance components estimated with RRM using linear splines are comparable with variance components estimated with multitrait model where BW at age corresponding to knots are considered as different traits. However, between knots, expected evolution of variance functions will not be smooth. This is especially the case when correlations between adjacent knots are not very high. Evolution of variances could be smoother; however, this would imply a large number of knots and then potential computation problems (Misztal, 2006).

Correlations

Table 10 presents genetic (above diagonal) and phenotypic (below diagonal) correlations between BW at 50, 75, 100, 125, 150, 175, 200, and 210 d of age for test station data. Genetic correlations between adjacent ages were high (>0.90). As expected, genetic correlations between BW decreased as intervals between ages became greater. Moreover, genetic correlations between adjacent ages tended to be greater when age increased. Phenotypic correlations between adjacent ages were less than genetic correlations. They also decreased when age interval became greater, with some exceptions. Again, phenotypic correlations between adjacent ages were greater at greater ages.

Table 10. Genetic (above diagonal) and phenotypic (below diagonal) correlations for test station BW.

Age, d	**50**	**75**	**100**	**125**	**150**	**175**	**200**	**210**
50	-	0.96	0.79	0.76	0.70	0.59	0.55	0.53
75	0.87	-	0.92	0.90	0.84	0.72	0.67	0.63
100	0.60	0.81	-	0.99	0.93	0.82	0.74	0.70
125	0.56	0.77	0.88	-	0.98	0.91	0.84	0.79
150	0.48	0.67	0.79	0.85	-	0.97	0.92	0.88
175	0.37	0.52	0.63	0.75	0.85	-	0.97	0.94
200	0.41	0.53	0.58	0.69	0.78	0.82	-	0.99
210	0.39	0.53	0.53	0.68	0.80	0.81	0.99	-

Table 11 presents genetic (above diagonal) and phenotypic (below diagonal) correlations between BW at 175, 200, 210, 225, and 250 d of age for on-farm data. Genetic correlations between adjacent ages were high (>0.70), although less than for test station data and decreased rapidly when interval between ages increased. They became negative between BW at 175 and 250 d. As explained earlier, these relatively low correlations between knots could explain that evolution of estimated variances was not smooth for the considered period. Phenotypic correlations were greater than genetic correlations but also decreased with increasing age interval. The decreasing correlations when interval between ages increased were in agreement with results for RRM presented by Huisman et al. (2002). As splines were used, negative correlations between BW at different ages should not be considered as an artifact as observed in RRM with polynomials (Kettunen et al., 2000). A potential reason could be that BW recorded much later from optimal age express a different trait than early BW records.

Table 11. Genetic (above diagonal) and phenotypic (below diagonal) correlations for on-farm BW.

Age, d	**175**	**200**	**210**	**225**	**250**
175	-	0.70	0.43	0.12	-0.35
200	0.73	-	0.95	0.74	0.18
210	0.80	0.99		0.88	0.38
225	0.31	0.77	0.94	-	0.77
250	-0.20	0.26	0.50	0.72	-

Table 12 shows genetic correlation between test station and on-farm BW at ages corresponding to knots. Genetic correlations decreased when age interval increased. The genetic correlations between on-farm BW at 175 d of age and test station BW increased with age until 175 d where correlation was maximum, then decreased until 210 d of age. The genetic correlation between on-farm BW at 210 d of age and test station BW increased with test station age and was the greatest between both BW at 210 d of age. As expected, the genetic correlation between on-farm BW at 250 d of age was negatively to approximately uncorrelated with test station BW between 50 and 210 d of age. Genetic correlation between test station BW and on-farm BW at 210 d of age was 0.85. As this age can be considered as reference point, the observed correlation reflects the genetic correlations between both environments and recording systems. It should be stressed that genetic correlations between BW at 175 d of age were even larger with an estimate of 0.90. Still, both results justified the initial hypothesis that test station and on-farm BW should be considered as different traits. These results also suggested that there are not only genetic factors which influence performance but there were also GxE interactions (Bidanel and Ducos, 1996; Zumbach et al., 2007). Relatively high genetic correlations between test station and on-farm BW at the same ages indicate potentially decreased GxE interactions. Therefore, EBV for growth from test station data should be good predictors for what happens at the on-farm commercial level where selection must be effective. Also, based on the still rather high correlation, as suggested by Peškovičová et al. (2002), joint evaluation of test station and on-farm data should still increase accuracy of EBV for both traits.

Table 12. Genetic correlations between test station (subscript S) and on-farm (subscript F) BW at ages corresponding to knots.

Age, d	**50_S**	**100_S**	**175_S**	**210_S**
175_F	0.65	0.86	0.90	0.79
210_F	0.26	0.42	0.73	0.85
250_F	-0.57	-0.44	-0.06	0.05

Fit of the Model

Fit of the model was tested by computing mean residuals across ages for each trait based on the model developed. The aim was to ensure that the model developed fitted well the expected age trend. Checking this was also required, as data were pre-adjusted. According to results from the Student's t-test, the means of mean residual distributions were not significantly different from zero, with P = 0.7417 for test station BW and P = 0.6885 for on-farm BW. Therefore, it seemed that the model developed fitted well the data.

Estimation of Breeding Values and Reliabilities

Table 13 shows descriptive statistics of reliabilities (MTREL and STREL) associated with EBV for the 56 boars tested in the test station, number of progeny tested per boar, and number of batches in which the boar had progeny tested.

The mean reliability of EBV of boars for ADG was quite high, so it allowed having relatively accurate selection of boars. The mean STREL was 0.61 when only test station data were used and the mean MTREL was 0.69 with the multitrait model combining test station and on-farm data. Therefore, the use of data recorded on boars themselves and on relatives on farm in addition to data recorded on crossbred progeny of tested boars allowed an average relative increase of reliability of about 8%, which confirms results obtained in other studies (e.g., Habier et al., 2007). These results were obtained despite the fact that boars had few progeny tested, on average (26), in few batches (1.6, on average).

Table 13. Descriptive statistics of single-trait reliability (STREL) from test station data without on-farm data, and multitrait reliability (MTREL) of EBV for ADG and distribution of numbers of progeny and batches for boars tested in the test station.

	Mean	SD	Minimum	Maximum
STREL	0.61	0.11	0.33	0.83
MTREL	0.69	0.10	0.39	0.86
Number of progeny	26.4	14.9	5	94
Number of batches	1.6	1.1	1	6

Conclusions

The aim of this study was to develop a new genetic evaluation model to estimate genetic merit of boars for growth using a bivariate random regression animal model with linear splines. The data set used contained test station BW recorded on crossbred progeny of boars fattened in the test station and BW recorded on boars themselves and on other relatives from the on-farm testing system. The model was applied to the genetic evaluation of Piétrain boars mated with Landrace sows in the Walloon Region of Belgium. Results obtained for the estimation of variance components, breeding values, and their associated reliabilities showed that the model was able to identify genetic differences for growth potential with adequate reliabilities. Relatively high genetic correlations between test station and on-farm data suggested that correlated response to the use of test station results at a commercial level would be possible to select Piétrain boars.

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CHAPTER III.2 ESTIMATION OF DOMINANCE VARIANCE FOR LIVE BODY WEIGHT IN A CROSSBRED POPULATION OF PIGS

CHAPTER III.2

Chapter II stated that non-additive genetic effects, such as dominance, are involved in crossbreeding settings, and that they are not negligible on production traits like growth. Moreover, it seems that the joint prediction of additive and dominance effects in genetic evaluation models of purebred animals for crossbred performances should improve the estimation of additive genetic effects. Therefore, the objective of this chapter was to explore the estimation of dominance variance for growth traits in a crossbred population of pigs. The additive (transmissible) genetic effects estimated either with a strictly additive genetic model or with a model including also dominance were then compared. Finally, as a random regression model (RRM) was used to model the longitudinal weight data, the evolution of the magnitude of dominance effects with age was assessed.

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ABSTRACT

The objective of this study was to estimate the dominance variance for repeated live BW records in a crossbred population of pigs. Data were provided by the Walloon Pig Breeding Association and included 22,197 BW records of 2,999 crossbred Piétrain × Landrace K+ pigs from 50 to 210 d of age. The BW records were standardized and adjusted to 210 d of age for analysis. Three single-trait random regression animal models were used: Model 1 without parental subclass effect, Model 2 with parental subclasses considered unrelated, and Model 3 with the complete parental dominance relationship matrix. Each model included sex, contemporary group, and heterosis as fixed effects as well as additive genetic, permanent environment, and residual as random effects. Variance components and their SE were estimated using a Gibbs sampling algorithm. Heritability tended to increase with age: from 0.50 to 0.64 for Model 1, from 0.19 to 0.42 for Model 2, and from 0.31 to 0.53 for Model 3. Permanent environmental variance tended to decrease with age and accounted for 29 to 44% of total variance for Model 1, 29 to 37% of total variance for Model 2, and 34 to 51% of total variance for Model 3. Residual variance explained <10% of total variance for the 3 models. Dominance variance was computed as 4 times the estimated parental subclass variance. Dominance variance accounted for 22 to 40% of total variance for Model 2 and 5 to 11% of total variance for Model 3, with a decrease with age for both models. Results showed that dominance effects exist for growth traits in pigs and may be reasonably large. The use of the complete dominance relationship matrix may improve the estimation of additive genetic variances and breeding values. Moreover, a dominance effect could be especially useful in selection programs for individual matings through the use of specific combining ability to maximize growth potential of crossbred progeny.

Key words: Body weight, Dominance, Genetic parameter, Growth, Pig, Random regression

INTRODUCTION

Currently, estimation of genetic effect is often limited to additive effect in across-herd genetic evaluation systems for pigs and dominance effect is ignored. However, the dominance effect may not be negligible for growth traits (Culbertson et al., 1998). Dominance effects are caused by interactions of alleles at the same locus and are not directly transmitted from an animal to its progeny (Hoeschele and VanRaden, 1991) but are recreated each generation by alleles inherited from each parent. The joint prediction of additive and individual dominance effects should allow for more accurate estimate of the total genetic merit (additive or not) of an animal and, therefore, improve the estimation of additive effects. Moreover, knowledge of the dominance effect may be beneficial for mate selection programs so that the genetic merit of the progeny can be maximized (Henderson, 1989). This is potentially very useful for populations with large numbers of full-sibs and those with specialized sire and dam lines, such as pigs.

Setting up the inverted dominance relationship matrix ($\mathbf{D^{-1}}$) is difficult from a computational point of view with large data sets (Henderson, 1985). Hoeschele and VanRaden (1991) replaced $\mathbf{D^{-1}}$ by the inverted sire–dam subclass relationship matrix ($\mathbf{F^{-1}}$), postulating that subclasses for each pair of parents will capture the major part of the estimable variation (Gengler et al., 1997). Although this does not correspond to the actual dominance covariance structure, it provides the covariances among sire–dam subclasses that represent the average dominance effect of many full-sibs and make dominance models feasible with large data sets. Variance associated with sire–dam subclass effects represents a quarter of the dominance variance.

The objective of this study was to estimate dominance variance for body weight (BW) records in crossbred Piétrain × Landrace pigs and to assess the effect of using parental dominance subclass relationships on the estimation of dominance variance.

MATERIALS AND METHODS

Data

Animal Care and Use Committee approval was not obtained for this study because data were obtained from an existing database. Data were provided by the

Walloon Pig Breeding Association (AWEP; Ciney, Belgium) and were collected through the system for genetic evaluation of Piétrain boars for crossbred performance in the Walloon region of Belgium as described by Dufrasne et al. (2011). Data were from the same data set used for November 2013 routine genetic evaluations.

The edited data set consisted of 22,197 repeated BW records from 2,999 crossbred pigs at the Walloon test station from 2007 through 2013. Pigs were separated into 29 different groups of approximately 100 animals that were tested together. Body weights were recorded every 15 d during the progeny test between 50 and 210 d of age. To account for variance heterogeneity associated with growth data (Huisman et al., 2002), raw BW records were standardized for each day of age and then pre-adjusted to 210 d of age as described by Dufrasne et al. (2011). Standardized and pre-adjusted records (y_{ij}^{*}) were computed as

$$y_{ij}^{*} = \left[\left(y_{ij} - m_i\right) / \sigma_i\right]\sigma_{210} + m_{210},$$

in which y_{ij} is the phenotypic value of animal j at age i, m_i is the estimated phenotypic mean at age i, σ_i is the estimated phenotypic SD at age i, σ_{210} is the estimated phenotypic SD at 210 d of age, and m_{210} is the estimated phenotypic mean at 210 d of age. Estimated phenotypic mean and SD were based on smoothed curves for BW over time. Equations for the smoothed curves and their R^2 (Figure 7) were obtained by testing different order polynomials with PROC GLM (SAS Inst. Inc., Cary, NC).

Crossbred animals were produced from the mating of purebred Piétrain boars with hyperprolific Landrace sows. Dams were from the hyperprolific Landrace K+ line selection program (www.ciap-belgium.org/) and were provided by the Walloon Agricultural Research Centre (CRA-W; Gembloux, Belgium). A total of 111 Piétrain boars and 201 Landrace K+ sows were used to produce the 2,999 crossbred pigs. Pedigrees were traced back 10 generations, and a total of 8,989 animals were included in the pedigree file. A total of 749 parental dominance subclasses were formed by discarding subclasses that did not affect variance component estimation (i.e., that did not bring ties to other subclasses).

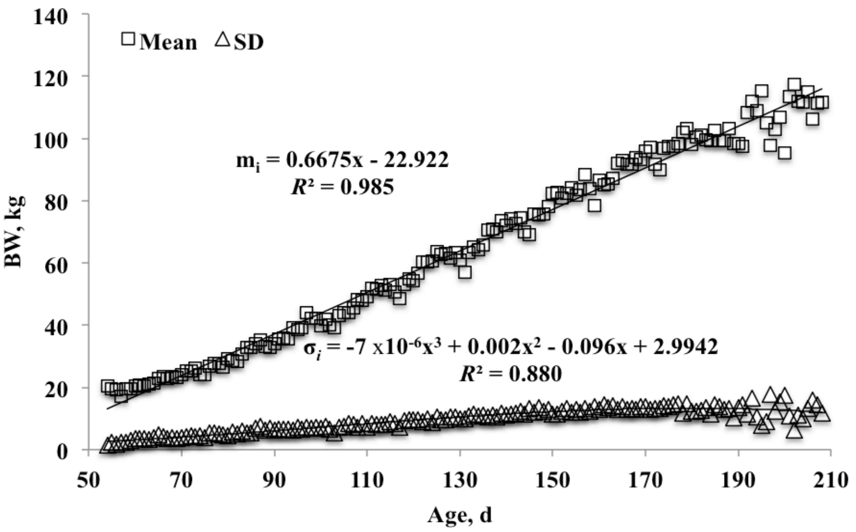

Figure 7. Observed mean and SD of BW between 50 and 210 d of age and their respective smoothed curves with equations and R^2 for crossbred Piétrain × Landrace K+ pigs.

Methods

A random regression animal model with linear splines was used to account for the longitudinal nature of the data. To assess the effect of using a parental dominance subclass relationship matrix on the estimation of dominance variance, variance components were estimated with 3 different models: Model 1 without parental dominance subclass effects, Model 2 with parental subclasses assumed unrelated, and Model 3 with the complete parental dominance subclass relationship matrix.

The general equation for Model 1 was

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Q}(\mathbf{Z_a a} + \mathbf{Z_p p}) + \mathbf{e},$$

in which $\mathbf{y}$ is a vector of standardized and pre-adjusted BW records; $\mathbf{b}$ is a vector of fixed effects; $\mathbf{a}$ is a vector of random additive genetic effects; $\mathbf{p}$ is a vector of random permanent environmental effects; $\mathbf{e}$ is a vector of random residuals; $\mathbf{X}$, $\mathbf{Z_a}$, and $\mathbf{Z_p}$ are incidence matrices that relate $\mathbf{y}$ to $\mathbf{b}$, $\mathbf{a}$, and $\mathbf{p}$, respectively; $\mathbf{Q}$ is a matrix of linear splines coefficients.

The general equation for Models 2 and 3 was

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Q}(\mathbf{Z_a a} + \mathbf{Z_p p} + \mathbf{Wf}) + \mathbf{e},$$

in which $\mathbf{f}$ is a vector of random parental (dominance) subclass effects and $\mathbf{W}$ is an incidence matrix linking $\mathbf{y}$ with $\mathbf{f}$. For Model 2, parental subclasses were considered to be unrelated; therefore, var($\mathbf{f}$) was assumed to be $\mathbf{I}\sigma_f^2$. For Model 3, the parental dominance subclass relationship matrix, $\mathbf{F}$, as defined by Hoeschele and VanRaden (1991) was used, and var($\mathbf{f}$) was assumed to be $\mathbf{F}\sigma_f^2$. The algorithm presented by Hoeschele and VanRaden (1991) allows efficient computation of the inverse of $\mathbf{F}$ with large numbers of parental subclasses. For this study, with 749 parental subclasses, $\mathbf{F}$ was computed explicitly (after parental subclasses that provide ties were listed) and then inverted for use in the mixed model equations. Total dominance variance (σ_d^2) was estimated as $4\sigma_f^2$, because parental dominance variance (σ_f^2) is a quarter of total dominance variance.

For each model, fixed effects were sex (female or castrated male), contemporary group assigned by recording date, and heterosis. Heterosis effect was modeled as a regression on an overall heterozygosity coefficient. Covariates for heterozygosity were included to account for heterosis occurring with crossbred animals from different parental breeds. Heterozygosity coefficients were computed as $1-\mathbf{c}_\mathbf{s}'\mathbf{c}_\mathbf{d}$, in which $\mathbf{c}_\mathbf{s}$ and $\mathbf{c}_\mathbf{d}$ are vectors of fractions of breed composition for the sire and the dam of the animal, respectively (Gengler et al., 1997). By including a heterosis effect in the model, the average allele interaction was separated from the dominance effect. As crossbred animals were all very similar, the heterosis effect was similar but not completely equal for all animals; heterozygosity varied between 88 and 100%. In contrast with other dominance studies (e.g., Gengler et al., 1997, 1998; Culbertson et al., 1998), inbreeding was not included because the animals were all crossbreds.

Additive genetic, permanent environmental, and parental dominance effects were modeled by random regressions using linear splines with 4 knots. Extreme knots were located at 50 and 210 d of age. Additional knots were added at 100 and 175 d for a better representation of BW associated with animal age.

Estimates of variance components and their SE were obtained with a Gibbs sampling algorithm; the GIBBS2F90 program (Misztal et al., 2002) was used with flat priors for variances and covariances. Priors were computed using the REMLF90 program (Misztal et al., 2002). The program POSTGIBBSF90 (Misztal et al., 2002) was used for post-Gibbs analyses. A single chain of 100,000 cycles with a burn-in period of the first 20,000 iterations was run. The stationary stage was confirmed by graphical inspection of plots of sampled values vs. iterations. Every sample after the burn-in period was retained to compute mean and SE, which was SD of the posterior distribution.

RESULTS

Estimates of variance components relative to total variance are shown in Figure 8 for Model 1. This model is the type used in the current genetic evaluation system in the Walloon region of Belgium. Estimates of heritability were high; they increased from 0.50 at 50 d of age to 0.64 at 150 d of age and then gradually decreased to 0.60 at 210 d. The SE for estimated heritability averaged 0.072 and ranged from 0.060 to 0.086. Permanent environmental variance accounted for about 35% of total variance. Relative permanent environmental variance ranged from 0.29 (125 d of age) to 0.44 (50 d of age); it decreased from 50 to 125 d of age and then tended to increase until 210 d of age. The SE for relative permanent environmental variance averaged 0.069 and ranged from 0.057 to 0.085. Residual variance represented 2 to 9% of total variance as a function of age, with a mean SE of 0.004 for relative residual variance.

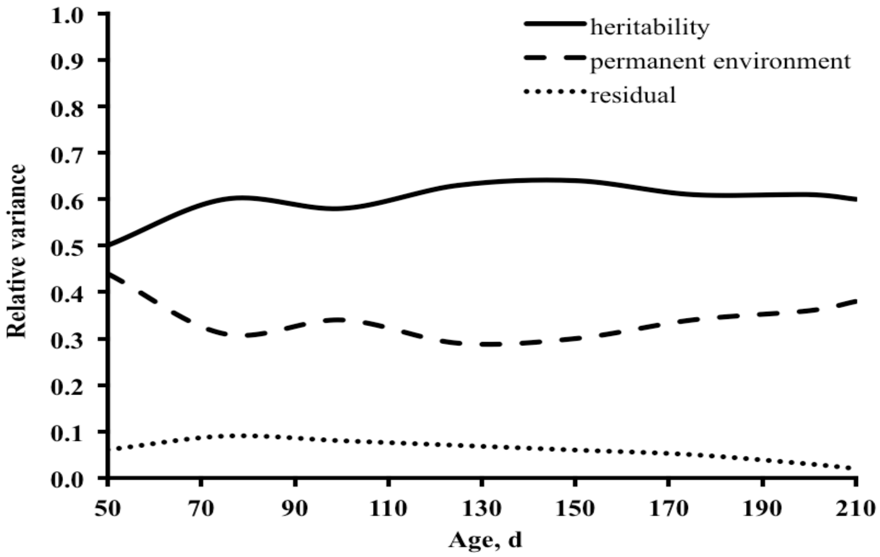

Figure 8. Variance of additive genetic (heritability), permanent environmental, and residual effects relative to total variance for BW by animal age between 50 and 210 d for model without parental subclasses (Model 1).

Estimates of variance components relative to total variance are shown in Figure 9 for Model 2. Heritability was lower than for Model 1; it increased from 0.19 at 50 d of age to 0.42 at 150 d of age and then decreased gradually to 0.39 at 210 d of age. The SE for estimated heritability averaged 0.062 and ranged from 0.047 to 0.070. Relative permanent environmental variance for Model 2 was similar to that for Model 1 and ranged from 0.29 to 0.37 with a mean of 0.31 between 50 and 210 d of age. The SE for relative permanent environmental variance averaged 0.043 and ranged from 0.036 to 0.048. Estimates of dominance variance were high and represented from 22 to 40% of total variance with a maximum at 50 d of age and a minimum at 175 d of age. Dominance variance tended to decrease over time. The SE for relative dominance variance averaged 0.052 and ranged from 0.044 to 0.066. Residual variance represented 2 to 7% of total variance, with a mean SE of 0.004.

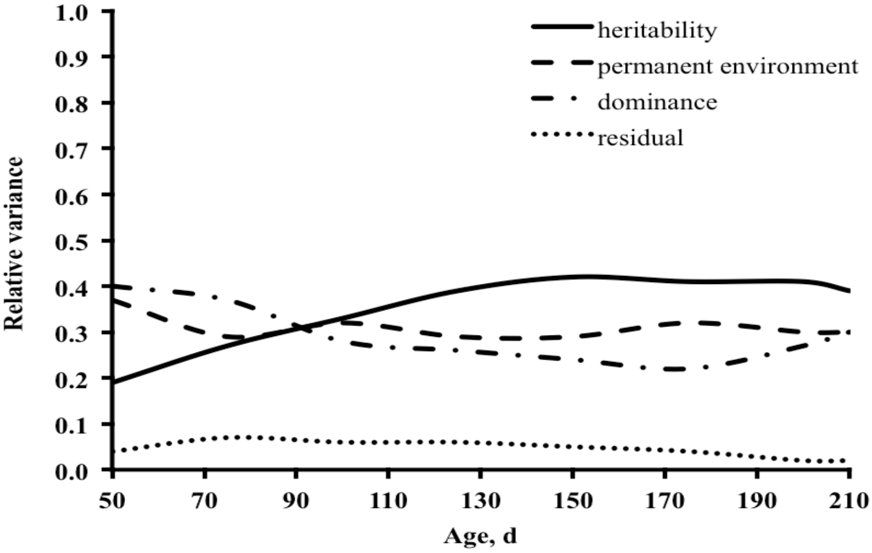

Figure 9. Variance of additive genetic (heritability), dominance, permanent environmental, and residual effects relative to total variance for BW by animal age between 50 and 210 d for model with unrelated parental subclasses (Model 2).

Estimates of variance components relative to total variance are shown in Figure 10 for Model 3. Estimated heritability was intermediate to that of Models 1 and 2; it increased over time from 0.31 at 50 d of age to 0.53 at 150 d of age and then decreased gradually to 0.51 at 210 d of age. The SE for estimated heritability averaged 0.065 and ranged from 0.056 to 0.077. Permanent environmental variance for Model 3 tended to be higher than for Models 1 and 2; it accounted for 34 to 51% of total variance. The SE for relative permanent environmental variance averaged 0.058 and ranged from 0.049 to 0.073. Estimates of dominance variance were lower than for Model 2; they represented 11% of total variance at 50 d of age, which gradually decreased to 5% at 175 d of age and then increased slightly to 7% at 210 d. The SE for relative dominance variance averaged 0.016 and ranged from 0.013 to 0.021. Residual variance accounted for 2 to 9% of total variance, with a mean SE of 0.003.

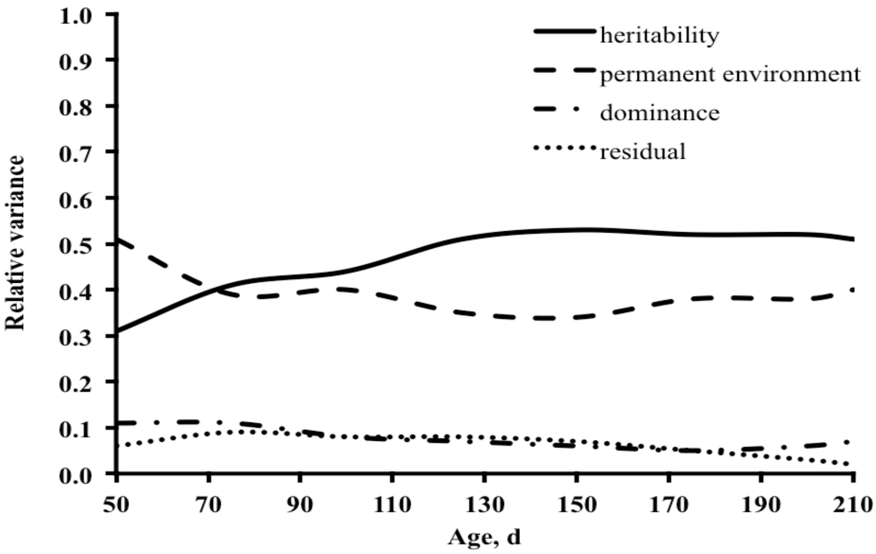

Figure 10. Variance of additive genetic (heritability), dominance, permanent environmental, and residual effects relative to total variance for BW by animal age between 50 and 210 d for model with the complete parental dominance relationship matrix (Model 3).

Heritability, relative permanent environmental variance, and relative residual variance for the 3 models followed the same patterns, but the values for each were different among the models. Estimated heritabilities were highest for Model 1 and lowest for Model 2. Relative permanent environmental variance was highest for Model 3 and lowest for Model 2. Relative residual variance was very similar for Models 1 and 3 but lower for Model 2. Estimates of dominance variance were larger for Model 2 than for Model 3.

DISCUSSION

The increasing heritability of BW with age agreed with findings of other studies. Edwards et al. (2006), Köhn et al. (2007), and Haraldsen et al. (2009) also found increasing heritability for pig BW with random regression analyses. Lewis and Brotherstone (2002) also reported increasing heritability of BW over time in sheep using random regression techniques, as did Baldi et al. (2010a,b) in cattle. Heritabilities, especially from Model 1, were higher than those reported in other studies (e.g., Huisman et al., 2002; Edwards et al., 2006) for pig BW. However, the high heritabilities in this study agreed with results of Dufrasne et al. (2011) for the same population and the same model with a smaller data set. An explanation for the high heritabilities of BW could be that data were collected in a unique test station by trained technicians and, therefore, with less risk of measurement bias. In addition, genetic selection of Belgian Piétrain boars has not been organized or intense. Therefore, genetic variability in the studied population remains quite large and could explain the large heritability estimates for this population.

Estimated heritability was lower when a dominance effect was included in the model (Models 2 and 3), which agrees with results of Wei and van der Werf (1993) and Rodriguez-Almeida et al. (1995). Additive variance appeared to be overestimated in Model 1. Dominance effects are partly responsible for resemblance between relatives, and dominance variance was part of the additive variance in Model 1. Therefore, including dominance variance in the model should allow better estimation of additive variance. Estimates of BW heritability over time from models that included dominance effects were closer to results reported in the literature (Huisman et al., 2002; Edwards et al., 2006; Haraldsen et al., 2009). Heritabilities also appeared to be lower when parental subclasses were considered unrelated (Model 2) compared with heritabilities estimated using the complete dominance relationships (Model 3), which is an indirect indication that neglecting parental subclass covariances could lead to confounding additive and sire–dam subclass effects.

Estimates of dominance variance decreased with age for both Models 2 and 3. With Model 2, dominance variance was between 22 and 40% of phenotypic variance. Estimated dominance variance appeared to be higher than additive variance until 100 d of age. Between 100 and 210 d of age, dominance variance represented 54 to 85% of additive variance. Dominance variance estimated with Model 3 was lower than dominance variance estimated with Model 2: about 5 to 11% of phenotypic variance and 10 to 35% of additive variance depending on age, with dominance variance highest before 100 d of age.

The high absolute dominance variances as well as the large dominance variances compared with additive variances agreed with previous results for growth trait in different species. Culbertson et al. (1998) found that dominance variance for days to BW of 104.5 kg in pigs was about 10% of phenotypic variance and 30% of additive variance.

In beef cattle, for postweaning gain between 205 and 365 d of age, Gengler et al. (1998) reported an absolute dominance variance of 10 or 18% depending on contemporary group definition and a dominance variance that represented about 50 or 94% of additive variance. Misztal et al. (1997) found that dominance variances were almost 10% of phenotypic variance and almost 30% of additive variances for strength and body depth in dairy cattle.

As mentioned by Gengler et al. (1997), the changes in estimates of dominance variance between Models 2 and 3 may be because for Model 2, dominance variance included variances other than dominance only. For Model 3, dominance variance was reduced and redistributed to other variances. Additive, permanent environmental, and, to a lesser extent, residual variances were higher with Model 3 than with Model 2. By using the complete parental subclass relationship matrix as in Model 3, the amount of dominance information was increased and that influenced the dominance genetic effect (Gengler et al., 1997).

For each parameter, the estimation range (estimate plus or minus SE) did not include 0. Moreover, the SE of the relative additive genetic and permanent environmental variances were smaller with models that included dominance effects (Models 2 and 3) compared with an additive model (Model 1). Therefore, the introduction of a dominance genetic effect in addition to an additive genetic effect allowed better parameter estimations. In addition, SE for relative dominance variance were lower when the complete parental subclass relationship matrix was used.

Additive genetic, permanent environmental, and dominance variances were modeled using a RRM with linear splines, which was more complex than models usually used in dominance studies (e.g., Culbertson et al., 1998). As a consequence, variance components varied with age, which allowed estimation of dominance effects at different ages. However, plots for variance functions were not smooth, and variations were observed and more important at ages corresponding to knots. This is probably an artifact from modeling by RRM with linear splines. According to Huisman et al. (2002), variance components estimated with RRM using linear splines are comparable with variance components estimated with a multitrait model in which BW at ages corresponding to knots are considered as different traits. However, between knots, plots for variance functions are not expected to be smooth, especially when correlations between adjacent knots are not very high. Even so, RRM with splines has some major advantages, such as no poor fit at the extreme of the trajectory and no influence of sparse data (Misztal, 2006). In addition, RRM models allow estimation of variance components and genetic parameters at any age and not only at recording age (Huisman et al., 2002; Legarra et al., 2004; Iwaisaki et al., 2005). Variance plots could be smoother if more knots were used, but potential computation problems may appear (Misztal, 2006).

Implications

Estimation of dominance variance with a RRM allowed the estimation of a dominance effect for pig BW between 50 and 210 d of age. The results indicated that dominance effects exist for growth traits in pigs, may be large, and tend to decrease with age. In addition, estimates of genetic parameters from models that included dominance effects were closer to literature values and also had lower SE than estimates from the model with only an additive effect. Another interesting result is that the model using the full parental dominance relationship matrix had more reliable results. Therefore, the use of unrelated parental subclasses might not be a good option.

Results of this study also showed that dominance variance exists for pig growth traits and that inclusion of dominance effects in genetic evaluation models is possible and will improve estimation of additive breeding values. In this study's situation, where crossbred animals were from few sire–dam pairs, the inclusion of related sire–dam subclass effects seemed to improve the estimation of additive effects by removing nonadditive effects. Moreover, according to DeStefano and Hoeschele (1992), the dominance effect could be used to determine individual matings through the prediction of specific combining ability (interaction at the same locus between sire and dam alleles) for each possible pair of parents in the population. Selection index procedures have been proposed to estimate the required unknown sire–dam subclass effects from already known sire–dam subclass effects of related animals (e.g., Misztal et al., 1998; Varona and Misztal, 1999). Now, several years after many studies focused on dominance (e.g., Misztal et al., 1998), interest in the estimation and use of dominance effects is growing again (e.g., Su et al., 2012; Sun et al., 2013; Vitezica et al., 2013), particularly in a genomic setting. As shown in this study, knowledge of dominance relationships is critical, and that knowledge could be improved through genomics.

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CHAPTER IV. ESTIMATION OF THE SIRE GENETIC EFFECTS ON PRODUCTION TRAITS TO IMPROVE CROSSBRED PERFORMANCES

CHAPTER IV

As pointed out in Chapter II, the genetic improvement of terminal sire lines for production traits is of importance for pork producers because of genetic progress expected at the commercial level. Therefore, the genetic influence of the sire on production traits needs to be assessed. To speed up the genetic progress, genetic selection should be done as early as possible during the lifetime of animals. Hence, if early indicator traits of subsequent performances can be identified, sires candidate to selection could be identified at an earlier age. Besides, survival of production pigs is of importance, mainly from the economic point of view, because of the increase of rearing costs with age. Therefore, the objective of this chapter was to assess the sire genetic influence on production traits in a commercial crossbred population of pigs, exploring these aspects by 1) the estimation of genetic parameters for traits recorded on piglets and their relationships with final market weight, and 2) the estimation of genetic parameters for survival traits from birth to slaughter and their relationships with final market weight. Data used in this chapter were provided by Smithfield Premium Genetics (Rose Hill, NC, USA), a large multinational breeding company involved in the swine sector. Performances were recorded on commercial crossbred pigs from US Duroc sires. The access to these data allowed to work on larger datasets and new traits, like survival traits.

CHAPTER IV.1 ESTIMATION OF GENETIC PARAMETERS FOR BIRTH WEIGHT, PREWEANING MORTALITY, AND HOT CARCASS WEIGHT OF CROSSBRED PIGS

CHAPTER IV.1

The use of crossbreeding in pig production allows having separate sire and dam lines, for which selection objectives are different. Terminal sire lines are mainly selected for production traits that optimize the economic value of their progeny. Besides, the number of pigs reaching full market value depends on traits usually selected from the maternal side, like piglet birth weight (BWT) or preweaning mortality (PWM). However, the genetic influence of the sire on these traits, recorded on young animals, should also be known to improve early selection of purebred sires. Moreover, BWT is related to production performances. Therefore, the objective of this chapter was to estimate genetic parameters for BWT, PWM and hot carcass weight (HCW) in a crossbred population. An animal model splitting the animal additive genetic effect into sire and dam components was used to assess the sire genetic effects on the studied traits. The estimation of genetic parameters was done with a linear-threshold mixed model that allowed combinations of continuous (BWT and HCW) and categorical (PWM) traits. Heritability, sire genetic, dam and litter effects were estimated, as well as correlations between traits.

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ABSTRACT

Genetic parameters for birth weight (BWT), preweaning mortality (PWM), and hot carcass weight (HCW) were estimated for a crossbred pig population to determine if BWT could be used as an early predictor for later performances. Sire genetic effects for those traits were estimated to determine if early selection of purebred sires used in crossbreeding could be improved. Data were recorded from 1 commercial farm between 2008 and 2010. Data were from 24,376 crossbred pigs from Duroc sires and crossbred Large White × Landrace dams and included 24,376 BWT and PWM records and 13,029 HCW records. For the analysis, PWM was considered as a binary trait (0 for live or 1 for dead piglet at weaning). A multitrait threshold-linear animal model was used, with animal effect divided into sire genetic and dam effects; the dam effects included both genetic and environmental variation due to the absence of pedigree information for crossbred dams. Fixed effects were sex and parity for all traits, contemporary groups for BWT and HCW, and age at slaughter as a linear covariable for HCW. Random effects were sire additive genetic, dam, litter, and residual effects for all traits and contemporary group for PWM. Heritability estimates were 0.04 for BWT, 0.02 for PWM, and 0.12 for HCW. The ratio between sire genetic and total estimated variances was 0.01 for BWT and PWM and 0.03 for HCW. Dam and litter variances explained, respectively, 14% and 15% of total variance for BWT, 2% and 10% for PWM, and 3% and 8% for HCW. Genetic correlations were -0.52 between BWT and PWM, 0.55 between BWT and HCW, and -0.13 between PWM and HCW. Selection of purebred sires for higher BWT of crossbreds may slightly improve survival until weaning and final market weight at the commercial level.

Key words: Birth weight, Crossbred, Genetic parameter, Performance, Pig, Threshold

INTRODUCTION

Economic gain in commercial swine production results mainly from the sale of pigs reaching full market value. Sow prolificacy has been emphasized in many breeding programs with the intent of increasing the number of pigs reaching full market value while maintaining the same number of sows within the herd. This selection objective has resulted in a significant increase in the number of pigs born alive per litter. As a result of increased litter size, there has been a decrease in individual pig birth weight (BWT; Quiniou et al., 2002). Several studies have reported that piglet BWT is related to performances (e.g., piglet survival, growth rate, carcass composition, meat quality) and therefore is an important economic trait in pig production. Low BWT is related to a higher preweaning mortality (PWM), reduced weight gain from weaning to the finishing period, and a fatter carcass (Fix et al., 2010). Therefore, pigs with low BWT require more days on feed to reach market weight and potentially produce a lower-quality carcass (Gondret et al., 2005; Bérard et al., 2008; Rehfeldt et al., 2008; Fix et al., 2010). Economic loss associated with low BWT may be attributed to inefficient subsequent performance throughout the fattening period. However, selection for higher piglet BWT should be implemented carefully because of the negative relationship between BWT and litter size, which results in the necessity to select both traits simultaneously (Fix et al., 2010).

The ability to make genetic improvement at the commercial level depends heavily on selection programs implemented on purebred lines at the nucleus level. Therefore, the genetic influence of both purebred parents on the commercial performance of crossbred progeny must be determined. Piglet BWT and PWM are strongly influenced by maternal effects (Arango et al., 2006); therefore, genetic parameters for these traits have historically been estimated from dam components, although a genetic effect of the sire is possible (Knol et al., 2002; Hamann et al., 2004). Knowledge of paternal genetic effects and heritabilities for BWT and survival could have a large economic impact if the inclusion of a paternal component is beneficial to implement within a commercial pig breeding program (Hamann et al., 2004). Moreover, a better understanding of the paternal genetic effect on piglet traits may lead to the ability to identify sires at an earlier age.

The objective of this study was to estimate genetic parameters for BWT, PWM, and HCW for commercial crossbred pigs to assess the influence of paternal effects and to determine if BWT could be a good early predictor for subsequent performances.

MATERIALS AND METHODS

Data

Animal Care and Use Committee approval was not obtained for this study because data were obtained from an existing database.

Data were provided by Smithfield Premium Genetics (Rose Hill, NC, USA). After discarding records with incomplete or inconsistent data, information recorded from 2008 through 2010 on 1 commercial farm was available for 24,376 crossbred pigs. Crossbred animals were produced from the mating of purebred Duroc boars with crossbred Large White × Landrace sows. Pedigree data were not available for crossbred dams.

A description of the data is shown in Table 14. Piglet BWT and PWM status (dead or alive) were available for the 24,376 animals. The piglet BWT was recorded within 24 h of birth on the commercial farm. Of those pigs, 13,029 had subsequent HCW records. Mean age at slaughter was 192 ± 12 d. Pedigrees were traced back 2 generations, and a total of 26,136 animals and 2,016 litters were included. A total of 193 different sires and 1,671 dams had progeny with a recorded BWT and PWM status, and 191 sires and 1,639 dams had progeny with HCW. Distributions of records by sire and dam family are shown in Tables 15 and 16, respectively. On average, each sire was mated with 8.7 dams, and each dam had 1.2 litters. Sows had records for ≤ 10 parities, but records for parities 7 through 10 ($<7\%$ of records) were grouped together. The mean number of parity was 3.5 ± 1.9. Among the 1671 dams, 1413 had pigs recorded in parity >1. Contemporary groups (15) were defined on the basis of piglets born during the same year and month.

Table 14. Description of data.

Item	Value
No. of records	24,376
No. of animals in pedigree	26,136
No. of litters	2,016
No. of dams	1,671
No. of sires	193
No. of contemporary groups	15
Parity	
Mean	3.54
SD	1.90
Age at slaughter, d	
Mean	188.78
SD	28.70

Table 15. Distribution of records by sire family for birth weight (BWT), preweaning mortality (PWM), and HCW.

Trait	Mean	SD	Minimum	Maximum
BWT (n = 193)	126.30	118.72	6	741
PWM (n = 193)	126.30	118.72	6	741
HCW (n = 191)	68.21	67.49	2	398

Table 16. Distribution of records by dam family for birth weight (BWT), preweaning mortality (PWM), and HCW.

Trait	Mean	SD	Minimum	Maximum
BWT (n = 1,671)	14.59	7.19	1	61
PWM (n = 1,671)	14.59	7.19	1	61
HCW (n = 1,639)	7.95	4.63	1	36

Statistical Analysis

An animal model was used to estimate genetic parameters. To separate the animal additive genetic effects into sire and dam components as in Zumbach et al. (2007), a model with sire additive genetic effects and dam effects was considered. This allowed the estimation of sire genetic covariance based on their crossbred progeny. Moreover, this model was better adapted as the dam effect had to include both genetic and environmental variations due to the lack of pedigree information for the crossbred dams. The equation for the general multipletrait model was

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Zs} + \mathbf{Ud} + \mathbf{Wl} + \mathbf{Qc} + \mathbf{e},$$

where **y** is a vector of observations (BWT, PWM status, or HCW), β is a vector of fixed effects, **s** is a vector of additive genetic effects of the sire, **d** is a vector of dam effects composed of dam additive genetic effects and dam environmental effects, **l** is a vector of common litter effects assigned by litter of the dam and assumed to be uncorrelated, **c** is a vector of random contemporary group effect, **X**, **Z**, **U**, **Q**, and **W** are incidence matrices that relate observations to effects, and **e** is a vector of residual effects. For the observed traits, BWT and HCW were continuous, but PWM status was a binary trait (0 if the piglet was still alive at weaning or 1 if the piglet died before weaning).

Fixed effects were sex and parity number for all traits. Contemporary groups were fitted as a fixed effect for BWT and HCW but as a random effect for PWM status to avoid the "extreme category problem" that would occur with contemporary groups with no dead piglets at weaning (Misztal et al., 1989). Age at slaughter was included as linear covariable for HCW only.

For all traits, sire additive genetic, dam, common litter, and residual effects were included as random effects. In this model, the animal additive effect is partitioned into sire additive genetic effect, dam additive genetic effect included in the dam effect, and Mendelian sampling included in the residuals. The variance of the sire genetic effects describes 1/4 of the total additive genetic variance and represents the genetic component of the model. The residual variance for the binary trait was fixed to 1. The (co)variance matrices were assumed to be

$$\mathbf{Var}\begin{bmatrix}\mathbf{s_1}\\ \mathbf{s_2}\\ \mathbf{s_3}\end{bmatrix} = \mathbf{A} \otimes \begin{bmatrix}\sigma^2_{s_1} & \sigma_{s_1,s_2} & \sigma_{s_1,s_3}\\ & \sigma^2_{s_2} & \sigma_{s_2,s_3}\\ & \mathbf{Symm} & \sigma^2_{s_3}\end{bmatrix}, \mathbf{Var}\begin{bmatrix}\mathbf{d_1}\\ \mathbf{d_2}\\ \mathbf{d_3}\end{bmatrix} = \mathbf{I} \otimes \begin{bmatrix}\sigma^2_{d_1} & \sigma_{d_1,d_2} & \sigma_{d_1,d_3}\\ & \sigma^2_{d_2} & \sigma_{d_2,d_3}\\ & \mathbf{Symm} & \sigma^2_{d_3}\end{bmatrix},$$

$$\mathbf{Var}\begin{bmatrix}\mathbf{l_1}\\ \mathbf{l_2}\\ \mathbf{l_3}\end{bmatrix} = \mathbf{I} \otimes \begin{bmatrix}\sigma^2_{l_1} & 0 & 0\\ & \sigma^2_{l_2} & 0\\ & \mathbf{Symm} & \sigma^2_{l_3}\end{bmatrix}, \mathbf{Var}\begin{bmatrix}\mathbf{e_1}\\ \mathbf{e_2}\\ \mathbf{e_3}\end{bmatrix} = \mathbf{I} \otimes \begin{bmatrix}\sigma^2_{e_1} & 0 & 0\\ & \sigma^2_{e_2} & 0\\ & \mathbf{Symm} & \sigma^2_{e_3}\end{bmatrix},$$

$$\mathbf{Var}\,[\mathbf{c_2}] = \mathbf{I} \otimes \sigma^2_{c_2},$$

where **A** is the additive relationship matrix and **I** is an identity matrix; traits 1, 2, and 3 refer to BWT, PWM, and HCW, respectively.

Estimations of (co)variance components were obtained with a Gibbs sampling algorithm, using the THRGIBBSF90 program (Misztal et al., 2002; Montpellier, France) with flat priors for (co)variances. This program allows the estimation of (co)variance components and genetic parameters in threshold mixed models with combinations of categorical and continuous traits (Lee et al., 2002). The program POSTGIBBSF90 (Misztal et al., 2002; Montpellier, France) was used for post-Gibbs analysis. A single chain of 250,000 cycles with a burn-in of the first 50,000 iterations was run for the analysis. The stationary stage was confirmed by graphical inspection of plots of sampled values vs. iterations. Every 10th sample was retained to compute mean and SE, obtained as SD of the posterior distribution. Starting values for (co)variance components were obtained from preliminary analyses using linear models implemented with restricted maximum likelihood and bivariate threshold-linear analyses.

RESULTS AND DISCUSSION

The mean BWT of 1.40 kg with SD = 0.32 kg was similar to mean BWT reported in other studies (Grandinson et al., 2002; Knol et al., 2002; Arango et al., 2006; Fix et al., 2010). The mean HCW of 93.37 kg with a SD = 8.60 kg is in agreement with HCW reported by Fix et al. (2010) but is somewhat higher than the final weight reported by Zumbach et al. (2007) in similar crossbred populations. On average, litter had 12.1 ± 3.8 piglets born alive. The PWM rate for all piglets was 16.99%, rising from 15.26% in parity 1 to 19.58% in parity 7 or later. The PWM rate of 16.99% is higher than the rate of 11.8% reported by Arango et al. (2006) for piglets that were alive after birth but is similar to PWM rates in other studies (e.g., Knol et al., 2002; Quiniou et al., 2002; Cecchinato et al., 2010). In this study, piglets from parities up to 10 were included, with 20% of piglets from parities higher than 5, whereas Arango et al. (2006) reported only 4% of piglets were represented for parities of ≥5. Moreover, they found that PWM rate increased only for parities of ≥7. Therefore, the higher PWM rate in this study could be the result of the larger proportion of piglets from later parities. Phenotypic correlations were -0.25 between BWT and PWM, 0.20 between BWT and HCW, and -0.48 between PWM and HCW. As expected, PWM rate decreased as BWT increased, as shown in Figure 11.

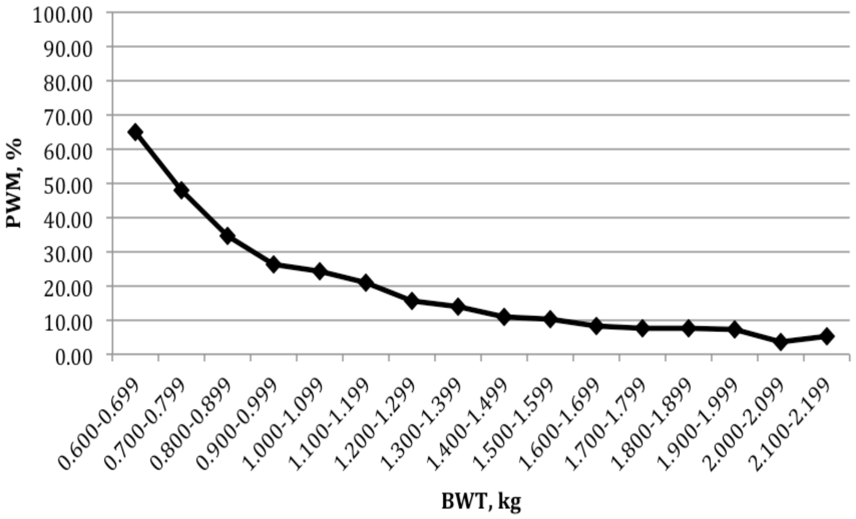

Figure 11. Relationship of preweaning mortality (PWM) rate with birth weight (BWT).

Estimates of variance components for BWT, PWM, and HCW are in Table 17. Histograms of posterior distributions of estimated (co)variance components (figure not shown) were quasi-normal for all traits, and the Geweke test did not detect any lack of convergence. Estimated sire genetic variance was small for each trait (0.001 for BWT, 0.006 for PWM, and 2.028 for HCW). Estimated sire covariances were negative between BWT and PWM (-0.001) and between PWM and HCW (-0.014). Estimated sire covariance was positive between BWT and HCW (0.025). Estimated dam and litter variances were similar for BWT (0.015) and were higher than estimated sire variance. For PWM, estimated litter variance was higher than estimated sire variance; moreover, both were higher than estimated dam variance. For HCW, estimated dam variance was on the same order as sire variance but lower than estimated litter variance. Estimated dam covariances had the same sign than estimated sire covariances. Estimated residual variances were high compared to other variance components for each trait (0.070 for BWT, 1.000 for PWM, and 56.228 for HCW). The relatively high residual variances could be due to the variation of the Mendelian sampling, which is not included directly in the model (Zumbach et al., 2007). Therefore, the Mendelian sampling becomes part of the residual and contributes to the increasing of the estimated residual variance.

Table 17. Estimates (SE) of (co)variances for sire genetic, contemporary group, dam, litter, and residual effects for birth weight (BWT), preweaning mortality (PWM), and HCW of crossbred pigs[1].

Effect	Trait	BWT	PWM	HCW
Sire genetic	BWT	0.001 (0.0004)	-0.001 (0.0009)	0.025 (0.0091)
	PWM		0.064 (0.0039)	-0.014 (0.0275)
	HCW			2.028 (0.4518)
Contemporary group	BWT			
	PWM		0.028 (0.0278)	
	HCW			
Dam	BWT	0.015 (0.0017)	-0.015 (0.0056)	0.081 (0.0346)
	PWM		0.039 (0.0143)	-0.077 (0.0502)
	HCW			2.209 (0.7247)
Litter	BWT	0.015 (0.0015)		
	PWM		0.102 (0.0165)	
	HCW			4.914 (0.7987)
Residual	BWT	0.070 (0.0007)		
	PWM		1.000 (0.0080)	
	HCW			56.228 (0.7522)

[1] Variances on diagonal; covariances above diagonal

Estimated heritability was 0.042 for BWT, 0.022 for PWM, and 0.124 for HCW (Table 18). For each trait, the estimated heritability was at the lower range of literature estimates, especially for HCW (e.g., Grandinson et al., 2002; Knol et al., 2002; Lund et al., 2002; Arango et al., 2006; Zumbach et al., 2007; Cecchinato et al., 2010). Comparison with literature estimates is difficult because of the different structures of data sets and different models. In many studies, mortality traits were modeled with linear models (van Arendonk et al., 1996; Knol et al., 2002; Mesa et al., 2006), which ignore the categorical nature of those traits. Also, animals in this study were crossbreds, and some traits in crossbred populations have lower heritabilities than in purebred populations (Lutaaya et al., 2001).

To determine if the sire component of each trait was useful for sire selection in a breeding program, the sire genetic effect was calculated as the ratio of estimated sire variance to total variance. Because the estimated sire genetic variance was small compared with total variance for each trait, the sire genetic effect (Table 18) was small (0.011 for BWT, 0.005 for PWM, and 0.031 for HCW). The larger effect of sire on HCW compared with BWT and PWM could be the result of declining maternal effect over time. Because piglet traits such as BWT and PWM are strongly influenced by maternal effects, most studies have usually included only maternal effects in analyses. However, Hamann et al. (2004) estimated genetic parameters for litter size, which is a trait strongly affected by maternal effects, as both sow and boar traits. They found that the sire had a small but significant effect on that trait.

The estimated dam effect was defined as the ratio between the estimated dam variance and the total variance (Table 18). Because of the lack of pedigree information for the crossbred dams, the dam effect is composed of genetic and environmental components. Estimated dam effects were higher than direct heritabilities for BWT (0.146) and for PWM (0.033) but lower for HCW (0.034). Also, estimated dam effects were higher than sire genetic effects for BWT and PWM but on the same order of values for HCW. As expected, the dam effect is more important than the sire genetic effect on early recorded traits, especially on BWT compared to PWM (van Arendonk et al., 1996; Grandinson et al., 2002; Knol et al., 2002; Lund et al., 2002; Arango et al., 2006). Moreover, when the dam effects for BWT and HCW are compared, it appears that the maternal influence is attenuated with age. For HCW, the dam effect is of the same magnitude as the sire genetic effect. However, the dam effect contains a genetic part and an environmental part. Therefore, either the sire genetic effect is higher than the dam genetic effect, or the dam effect is mainly genetic rather than environmental in later performances (Zumbach et al., 2007).

The common litter effect was defined as the ratio of estimated litter variance to total variance. The litter effect (Table 18) explained a large portion of total variance for piglet traits (0.143 for BWT, 0.086 for PWM). However, the common litter effect is lower for HCW (0.075) compared to heritability. Cecchinato et al. (2010) found that the litter variance was larger than the sire variance for preweaning survival of piglets, which confirms that piglet survival is mainly affected by the litter effects. The smaller common litter effect for HCW compared with BWT indicates that effects common to littermates dissipate with age, like the dam effects. In the literature, the proportion of total variance explained by the litter effect at market age was 4% to 6% for backfat and 5% to 12% for weight per day of age and HCW (Lutaaya et al., 2001; Zumbach et al., 2007). Moreover, the birth litter explained a larger part of the total variance than the dam did for HCW, as found by Zumbach et al. (2007) with a similar model.

Table 18. Estimates (SE) of heritability, sire genetic, dam, and litter effects for birth weight (BWT), preweaning mortality (PWM), and HCW of crossbred pigs.

Effect	BWT	PWM	HCW
Heritability	0.04 (0.015)	0.02 (0.013)	0.12 (0.024)
Sire genetic	0.01 (0.004)	0.01 (0.003)	0.03 (0.007)
Dam	0.15 (0.016)	0.03 (0.012)	0.03 (0.011)
Common litter	0.14 (0.015)	0.09 (0.014)	0.08 (0.012)

A common issue with the dam effect is cross-fostering and possible confounding of maternal and permanent environmental effects. For cross-fostered piglets, the maternal genetic effect is different before and after crossfostering, BWT vs. PWM, for example. One strategy to deal with that is to include in the model the effect of the adoptive dam. However, in this study, the sow that raised the piglet is assumed to be the real mother of the piglet because of the lack of information available about the adoptive dam. In this case, the effect of the nurse dam for PWM and, to a smaller extent, for HCW is assumed to be part of the common litter effect. Knol et al. (2002) studied piglet survival with the genetic effect of the adoptive dam. They had issues with the estimation of genetic parameters (i.e., negative heritabilities) and convergence.

Piglet BWT was genetically correlated with PWM (-0.52 ± 0.33) and HCW (0.55 ± 0.15). The SE of these correlations were lower than their corresponding estimates and did not include zero, supporting the genetic association between traits. The genetic correlation between PWM and HCW was lower (-0.13 ± 0.24). The SE was greater than its corresponding correlation and did include zero. This indicates no genetic association between PWM and HCW. The greater SE may also be because fewer data were considered. Moreover, such a low correlation might partly be the result of the data structure because dead piglets at weaning had no HCW record. Phenotypic correlations had the same sign than genetic correlations but were lower between BWT and PWM (-0.25) and between BWT and HCW (0.20) and higher between PWM and HCW (-0.48). The dam correlations were also favorable between BWT and PWM (-0.62 ± 0.23) and between BWT and HCW (0.45 ± 0.19). These correlations indicate that piglets from a dam providing favorable genes and environment have a greater chance to survive until weaning and to reach a high final market weight. The dam correlation between PWM and HCW was low (-0.26 ± 0.17) but stronger than the sire genetic correlation.

The negative genetic correlation between BWT and PWM is in agreement with other studies (Grandinson et al., 2002; Arango et al., 2006; Roehe et al., 2010) and indicates a favorable genetic link between BWT and piglet survival until weaning. However, selection for higher BWT should be carefully undertaken; very high BWT may increase farrowing mortality because of other problems such as dystocia or prolonged parturition (Grandinson et al., 2002). As reported by Herring et al. (2010), BWT is positively correlated with final weight. Thus, BWT may be a good indicator of final market weight, as BWT is heritable and genetically correlated with HCW. Moreover, BWT is expressed earlier in life and is recorded earlier. Therefore, selection on BWT as a way to improve HCW may provide an opportunity to accelerate genetic progress.

The favorable genetic correlations of BWT with PWM and HCW indicate that selection for high BWT can improve survival until weaning and final market weight for crossbred pigs. Therefore, BWT could be used as an early predictor of subsequent performances. However, such selection should not be extreme because of the association between high BWT and higher farrowing mortality (Grandinson et al., 2002; Arango et al., 2006), which is not economically advantageous. Moreover, this situation is more common in sire lines with lower prolificacies, as was evident in this study. Indeed, fewer piglets per litter leads to heavier piglets and a higher frequency of dystocia, and that affects the survival for the whole litter (Ibáñez-Escriche et al., 2009). Therefore, a profitable selection on survival rate needs to balance survival and birth weight. A restricted selection index (Kempthorne and Nordskog, 1959) is often used in such situations where changes in 1 particular trait, such as BWT, are restricted to zero while selecting for correlated traits of direct interest, such as PWM and HCW.

Litter size at weaning is an important economic trait. Many breeding programs focus on selection to increase the number of piglets born per litter as a way to improve litter size at weaning (Grandinson et al., 2002). Selection index often puts large economic values on litter size and PWM (De Vries, 1989). However, selection to increase litter size at birth does not guarantee survival until weaning and larger litter at weaning. Indeed, litter size has a negative impact on preweaning survival and is linked to an increasing number of light piglets per litter and higher variations of piglet BWT within litter (van Arendonk et al., 1996; Milligan et al., 2002). High BWT variations within litter lead to competitive exclusion of light piglets from access to productive teats. Therefore, differences in BWT between light and heavy piglets are often maintained or even increased until weaning, and smaller piglets at birth have lower survival rates, which has a negative economic impact for producers (Milligan et al., 2002). Therefore, litter size must not be forgotten in the selection goal because it has indirect influence on survival rate (Lund et al., 2002; Arango et al., 2005). However, selection for litter size should be coupled with maintaining a minimum threshold for BWT to avoid too light piglets with more risks of PWM.

Approximate reliabilities of sire breeding values for the 3 traits were computed with the following formula:

$$\mathrm{REL} = \frac{\mathrm{ns}^2}{(\mathrm{n}-1)\mathrm{s}^2 + 4}$$

where n is the total number of progeny of the sire and s^2 is the ratio between the sire genetic variance and the total variance. The mean approximate reliabilities of sire breeding values were 0.21 (0.14) for BWT and PWM and 0.29 (0.18) for HCW. These mean approximate reliabilities are low because of low sire genetic variance. Also, reliability depends on the number of progeny of the sire. Therefore, sires with a large number of progeny will have breeding values with higher reliability. However, the number of progeny per sire is variable (Table 15), which leads to a low mean approximate reliability. Theoretically, reliabilities should be higher with an animal model because of the use of the genetic relationships among all animals instead of only relationships among sires. However, because this is a crossbred population, an animal model would be suboptimal.

The genetic effect of the sire on BWT, PWM, and HCW was low. Thus, on the basis of these results, direct selection of purebred sires may not be very efficient to improve those traits in crossbred populations. Subsequently, it may be easier to improve BWT from the maternal side than from the paternal side. However, BWT was genetically correlated with PWM and HCW. Therefore, selection on BWT could be a way to improve survival of piglets until weaning and final market weight. It could also improve the genetic progress as BWT is recorded earlier in the life of the animal. However, selection should be focused not only on improvement of BWT but also on an optimum combination of BWT, survival, and litter size.

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CHAPTER IV.2 GENETIC ANALYSIS OF PIG SURVIVAL UP TO COMMERCIAL WEIGHT IN A CROSSBRED POPULATION

CHAPTER IV.2

An unusual, but also economically important selection objective in pig production is survival during the grow-finishing period. Indeed, if pigs die during this period, it represents investment losses for pig producers. Commonly, genetic studies of pig survival focused on farrowing and preweaning survival, or on sow survival. However, to our knowledge, survival of growing pigs after weaning and correlations with subsequent performances have rarely been studied, although it represents an economically important trait due to the increase of rearing costs with age. Therefore, the objective of this chapter was to estimate genetic parameters for survival traits recorded at different stages of the fattening period and their relations with final market weight. Mortality definition included natural death, but also pigs culled because of low body conditions and health issues. Survival was studied from the paternal side with a sire model. The aim was to estimate the sire genetic effects on these traits to explore the opportunity of a genetic selection of terminal sire lines for survival. The genetic models used to estimate genetic parameters were linear-threshold mixed models to consider simultaneously categorical (survival traits) and continuous (market weight) traits according to their natural distributions.

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ABSTRACT

Records from 99,384 crossbred pigs from Duroc sires and LargeWhite × Landrace dams were used to estimate genetic parameters for survival traits at different stages of the fattening period, and their relations with final weight. Traits analyzed were preweaning mortality (PWM), culling between weaning and harvesting (C_{all}), culling during the farrowing period (C_{far}), in the nursery site (C_{nur}), during the finishing phase (C_{fin}), and hot carcass weight (HCW). Because of the binary nature of PWM and culling traits, threshold-linear models were used: Model 1, including PWM, C_{all}, and HCW; Model 2, including PWM, C_{far}, C_{nur}, C_{fin}, and HCW. Both models included sex and parity number as fixed effects for all traits. Contemporary groups were considered as fixed effect for HCW and as random effects for the binary traits. Random effects were sire additive genetic, common litter, and residual effects for all traits and models. Heritability estimates were 0.03 for PWM, and 0.15 for HCW with both models, 0.06 for C_{all} with Model 1, and 0.06 for C_{far}, 0.14 for C_{nur}, and 0.10 for C_{fin} with Model 2. Litter variance explained a large part of the total variance and its influence declined slightly with age. For Model 1, genetic correlations were -0.36 between PWM and C_{all}, -0.02 between PWM and HCW, and -0.25 between C_{all} and HCW; correlations for litter effect were -0.15 between PWM and C_{all}, -0.19 between PWM and HCW, and -0.21 between C_{all} and HCW. For Model 2, genetic correlations were all positive between PWM and culling traits, except between PWM and C_{nur} (-0.61). Genetic correlations between HCW and the other traits were moderate and negative to null. Correlations for common litter effect were all negative between traits, except between C_{far} and C_{fin}, and between C_{nur} and C_{fin}. Heritability of PWM and culling traits increased with age period. Therefore, selection for survival after weaning may be more efficient. The low genetic correlations between PWM and culling traits suggest that different genes influence pre and postweaning mortality. The HCW was not correlated with the other traits. However, relationships are not strongly unfavorable, therefore selection for survival and high final weight is possible.

Keywords: Crossbred, Commercial weight, Fattening stage, Genetic analysis, Pig, Survival

INTRODUCTION

Parameters used to measure performance in grow-finish pigs include mortality rate, growth and feed conversion. Increased mortality rates within the finishing period can result in a significant loss of investment and is an indication of poor animal health and/or animal welfare practices. Many studies have focused on farrowing and preweaning piglet mortality (e.g., Arango et al., 2005, 2006; Ibáñez-Escriche et al., 2009) or sow mortality (e.g., Chagnon et al., 1991; Sasaki and Koketsu, 2008). However, losses at higher age are even more economically important because of increasing rearing costs with age (Fuerst-Waltl and Sørensen, 2010) and to our knowledge, no genetic studies have investigated pig mortality between weaning and final market weight. Growing pig mortality includes pigs that die naturally as well as pigs that are euthanized. Pigs are usually euthanized to relieve the animal from pain or poor living conditions due to low body condition, poor health and hernia ruptures. These pigs are not only considered economically unprofitable but are also considered to be at risk of spreading disease to the rest of the herd and are discarded before the next phase of growth.

Environmental factors (i.e., management, housing, and hygienic status) also play a major role in growth and survival but may not be consistent over time. In contrast, genetic progress is permanent and cumulative across generations. However, additive genetic variation for survival must exist for improvement to occur (Henderson et al., 2011). Genetic analyses of survival until production age has been done in dairy cows and sheep (e.g., Fuerst-Waltl and Sørensen, 2010; Hatcher et al., 2010; Henderson et al., 2011). Those studies revealed that estimated direct heritabilities of survival traits during different periods are low. However, a sufficient genetic variability could still allow developing selection strategies for overall better survival (Henderson et al., 2011).

The objective of this study was to estimate genetic parameters for survival traits at different stages of the fattening period, from weaning to harvesting, and their genetic relations with the final market weight in a commercial crossbred population of pigs.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because data were obtained from an existing database.

Data

Data were provided by Smithfield Premium Genetics (Rose Hill, NC, USA). The final dataset consisted of 99,384 records after discarding animals with incomplete or inconsistent information; the pedigree file included information for 103,980 animals. Data were recorded in a crossbred population of pigs between 2008 and 2010 on 1 commercial farm. Crossbred pigs were produced from the mating of purebred Duroc boars with crossbred LargeWhite × Landrace sows. Pedigree data were not available for crossbred dams. Sows had records for ≤ 10 parities, but records for parities 7-10 were grouped together; percentages of records available by parity number are shown in Table 19.

Table 19. Percentages of records by parity number.

Parity number	Percentage of records
1	17.0
2	18.5
3	17.5
4	15.0
5	12.0
6	10.0
7-10	10.0

Five survival traits were analyzed: preweaning mortality (PWM), which was the mortality of live born piglets before weaning at <21 d of age; culled during the farrowing phase (C_{far}), which were piglets that survived until weaning but could not be moved to the nursery site at <30 d of age because of low weaning weight (<2.7 kg), poor body condition, or poor health; culled during the nursery phase (C_{nur}), which were pigs that survived past 60 d of age but could not be moved to the finishing site because of poor body condition or poor health; culled during the finishing phase (C_{fin}), which were pigs that survived past 150 d of age but had poor body condition or poor health that required removal from the herd by euthanasia or had some other defect that resulted in the animal being sold to a discount market from the finishing site rather than being sent to the packing plant; and hot carcass weight (HCW). All culling traits were also grouped together and considered as 1 trait (C_{all}). Mortality and culling (PWM, C_{far}, C_{nur}, C_{fin}, and C_{all}) were considered to be binary traits (0 if the pig was still alive or not culled and 1 if the pig died or was censored at weaning or moving time); HCW was a continuous trait.

A description of the data is shown in Table 20. The PWM status (dead or alive) was available for 99,384 animals. Of those pigs, 58,989 had C_{far} records, 58,856 had C_{nur} records, and 58,691 had C_{fin} records. The HCW was available for 51,933 of the pigs still in the system after the finishing phase. Mean age at slaughter was 194 ± 13 d. A total of 302 different purebred Duroc sires had progeny with PWM status recorded, and 229 of those sires had progeny with the other traits recorded. Mean parity number was 3.5 ± 1.9. Among the 1,671 dams, 1,413 had pigs recorded in parity >1. Contemporary groups were defined on the basis of piglets born during the same year and month because all animals at the commercial farm were managed similarly.

Table 20. Description of data by survival trait.

Trait	**Preweaning mortality**	**Culling phase**			**Hot carcass weight**
		Farrowing	**Nursery**	**Finishing**	
No. of records	99,384	58,989	58,856	58,691	51,933
No. of litters	11,144	8,225	8,225	8,224	8,186
No. of dams	4,388	3,556	3,556	3,556	3,549
No. of sires	302	229	229	229	229
No. of contemporary groups	31	24	24	24	24

Statistical analysis

Single- and multiple-trait analyses with a sire model were used to estimate variance components. Only results from multiple-trait analyses are presented. The equation for the general multiple-trait model was

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}\mathbf{s} + \mathbf{W}\mathbf{l} + \mathbf{Q}\mathbf{c} + \mathbf{e},$$

where $\mathbf{y}$ is a vector of observations (PWM, culling status, or HCW), β is a vector of fixed effects, $\mathbf{s}$ is a vector of additive genetic effects of the sire; $\mathbf{l}$ is a vector of common litter effects assigned by litter of the dam, $\mathbf{c}$ is a vector of random contemporary group effects; $\mathbf{X}$, $\mathbf{Z}$, $\mathbf{W}$, and $\mathbf{Q}$ are incidence matrices that relate observations to effects, and $\mathbf{e}$ is a vector of residual effects. Sire genetic effect was defined as the ratio of estimated sire genetic variance to total variance; common litter was defined as the ratio of estimated litter variance to total variance.

Two multiple-trait models were used to investigate differences between considering mortality or culling between weaning and slaughter as 1 unique trait or as different traits in each phase of the grow-finishing period. Model 1 included PWM, C_{all}, and HCW; Model 2 included PWM, C_{far}, C_{nur}, C_{fin}, and HCW. Fixed effects were sex and parity number for all traits. Contemporary groups were fitted as a fixed effect for HCW but as a random effect for all categorical traits (PWM, C_{far}, C_{nur}, C_{fin}, and C_{all}) to avoid the "extreme category problem" that occurs with contemporary groups with no dead piglets at weaning or with no culled pigs at the different culling phases (Misztal et al., 1989). For both models, sire additive genetic, common litter, and residual effects were included as random effects. Dam effect was not considered in either model because of the absence of pedigree information for crossbred dams, which would cause the dam effect to include genetic and environmental dam variations. In addition, common litter and dam effects would have been confounded. The variance of the sire genetic effects describes 1/4 of the total additive genetic variance and represents the genetic component of the models. The residual variance for categorical traits was fixed to 1. Covariances for contemporary groups and residual effects were fixed to 0, whereas covariances of litter and sire genetic effects were included in the model.

Estimation of (co)variance components were obtained by a Bayesian approach via Gibbs sampling using the THRGIBBSF90 program (Misztal et al., 2002) with flat priors for (co)variances. This program allows the estimation of (co)variance components and genetic parameters in linear-threshold mixed models with combinations of categorical and continuous traits (Lee et al., 2002). The program POSTGIBBSF90 (Misztal et al., 2002) was used for post-Gibbs analysis. A single chain of 250,000 cycles with a burn-in of the first 50,000 iterations was run for the analyses. The stationary stage was confirmed by graphical inspection of plots of sampled values vs. iterations. Every 10th sample was retained to compute mean and SE, obtained as SD of the posterior distribution.

RESULTS AND DISCUSSION

Descriptive statistics

The numbers of records and mean PWM and culling rates are shown in Table 21. Mean PWM rate for all piglets was 24.5%, which is high compared with values reported in the literature: 17.1% by van Arendonk et al. (1996), 18.0% (including stillbirth) by Grandinson et al. (2002), 11.7% in dam lines and 15.0% in a sire line by Knol et al. (2002), and 11.8% by Arango et al. (2006). An explanation for the high PWM rate in this study could be that the pigs were crossbred and raised in a commercial setting; the other studies included only purebred piglets in nucleus herds, which have better hygiene and more space per pig than found commercially. Moreover, piglets in this study were from parities up to 10, with 20% from parities higher than 5. Arango et al. (2006) reported only 4% of piglets were from parities of ≥ 5; they found that PWM rate increased with increasing parity number, especially for parities ≥ 7. Therefore, the higher PWM rate in this study could result from the larger proportion of piglets from later parities.

Table 21. Numbers of records and survival rates by trait.

Trait	No. of observations	Frequency (%)
Preweaning mortality rate	99,384	24.5
Culled overall	58,989	0.8
Culled during farrowing phase	58,989	0.2
Culled during nursery phase	58,856	0.3
Culled during finishing phase	58,691	0.3

The C_{all} rate, which corresponds to pigs dead or culled during the entire grow-finisher period, was 0.8%; that rate is low but agrees somewhat with other studies. Le Foll et al. (1988) observed 0.7% mortality in the grow-finisher phase in a study of farrow-to-finish operations. That rate can be considered as excellent according to Clermont and Désilets (1982). Culling rates tended to increase with age (0.2% for C_{far} to 0.3% for C_{fin}), which agrees with the finding of Maes et al. (2001) that mortality rates increased for older finishing pigs.

Mean HCW was 92.3 ± 9.1 kg, which agrees with HCW reported by Zumbach et al. (2007) and Fix et al. (2010) in similar crossbred populations. Minimum and maximum HCW were 60.3 and 122.9 kg, respectively.

Estimates of genetic parameters

Estimates of genetic parameters for Models 1 and 2 are shown in Table 22. For mortality and culling traits, estimated heritability was lower in early life and slightly increased as pigs grew older. In Model 1, heritability increased from 0.03 for PWM to 0.06 for C_{all}. In Model 2, heritability increased from PWM to C_{nur} (0.03 for PWM, 0.06 for C_{far}, and 0.14 for C_{nur}) and then decreased slightly for C_{fin} (0.10). With both models, the heritability estimate was 0.15 for HCW. For PWM and HCW, estimated heritabilities agreed with literature estimates (e.g., Grandinson et al., 2002; Arango et al., 2006;

Zumbach et al., 2007; Cecchinato et al., 2010; Dufrasne et al., 2013). Heritability for C_{all} is difficult to compare with literature estimates because it is not commonly analyzed in pig production. However, it could be compared with mortality at various stages of life in other species. Heritabilities of mortality traits for dairy cattle and sheep are low and tend to increase with age (e.g., Cloete et al., 2009; Fuerst-Waltl and Sørensen, 2010; Hatcher et al., 2010; Henderson et al., 2011; van Pelt et al., 2012).

The sire genetic effect followed the same pattern as heritability because of its definition. Estimated sire genetic effect was 0.01 for PWM, 0.02 for C_{all}, and 0.04 for HCW with Model 1; 0.01 for PWM, 0.02 for C_{far}, 0.03 for C_{nur} and C_{fin}, and 0.04 for HCW with Model 2. Dufrasne et al. (2013) presented similar estimates of sire genetic effect for PWM and HCW in the same population. They also found that the genetic effect of sire tended to increase with animal age (from 0.01 for PWM to 0.04 for HCW). Traits recorded on piglets and young animals are strongly influenced by maternal effect (e.g., Grandinson et al., 2002; Knol et al., 2002; Hamann et al., 2004; Arango et al., 2006). Therefore, the increasing effect of the sire could result from decreasing maternal effect overtime. Usually genetic studies of traits that are greatly influenced by the dam have included only maternal effects in analyses and did not account for sire effects. However, Hamann et al. (2004) estimated genetic parameters for litter size, which is a trait strongly affected by maternal effects, and considered it as both a dam and sire trait. They found that the sire had a small but not negligible effect on that trait.

Litter variance explained a large part of total variance, especially for piglets (0.16 for PWM). Common litter effect seemed to decline slightly with age (0.13 for C_{all} and 0.14 for HCW in Model 1; 0.18 for C_{far}, 0.19 for C_{nur}, 0.10 for C_{fin}, and 0.14 for HCW in Model 2). Dufrasne et al. (2013) estimated common litter effects for PWM and HCW in the same population and reported effects of 0.09 for PWM and 0.08 for HCW, which is approximately half the size of estimations in this study. However, the model used by Dufrasne et al. (2013) also included a dam effect, because it influences the development of pigs, especially at early age. As only the sire side of the pedigree was available, only the sire genetic effect was included in the model because the dam effect would include the genetic and the environmental variations, and each part could not be disentangle. Therefore, the dam effect may have inflated the common litter effect in this study. Cecchinato et al. (2010) found that litter variance was larger than sire variance for preweaning survival of piglets, which confirms that piglet survival is mainly affected by litter. Results for culling traits also indicated that the common environment of litter has a large influence on survival during the grow-finisher phase. In the literature, the proportion of total variance explained by litter at market age was 4-6% for backfat and 5-12% for weight per day of age and HCW (Lutaaya et al., 2001; Zumbach et al., 2007). However, the common litter effects found in this study were higher than those reported for similar traits in other studies (Zumbach et al., 2007; Roehe et al., 2010), also probably because maternal effect was part of litter effect.

Estimates of genetic and common litter correlations between traits are shown in Table 23. For Model 1, PWM was negatively correlated genetically with C_{all} (-0.36 ± 0.26) and uncorrelated with HCW (-0.02 ± 0.15); C_{all} was unfavorably correlated with HCW (-0.25 ± 0.20). However, SE were large compared with their corresponding estimations. In a previous study with the same population, Dufrasne et al. (2013) also found no genetic association between PWM and HCW. Genetic improvement of survival before weaning may not favor survival at later ages. Moreover, survival traits were not correlated with HCW. Therefore, different genes seem to influence survival and growth traits. Selection for both would require an index combining these traits to improve one without deteriorate the other one.

For Model 2, genetic correlations between survival periods were positive (0.13 to 0.59), except between PWM and C_{nur} (-0.61). The genetic correlation of PWM was low with C_{far} (0.13 ± 0.32) and C_{fin} (0.17 ± 0.14). Genetic analysis of calf and heifer losses in dairy cows indicated that potentially different genes are responsible for pre- and post-weaning mortality (e.g., Fuerst-Waltl and Sørensen, 2010; Henderson et al., 2011). The SE of the correlation between PWM and C_{far} was greater than the corresponding correlation and did include 0, which may indicate no genetic association between the traits. The strong negative genetic correlation between PWM and C_{nur} with low SE (-0.61 ± 0.09) indicated that the 2 traits were antagonistic as high PWM was associated with low C_{nur}. Among the culling phases, genetic correlations of C_{far} with later phases were positive (0.36 ± 0.30 with C_{nur} and 0.44 ± 0.19 with C_{fin}). The high positive correlation between C_{nur} and C_{fin} (0.59 ± 0.12) indicated that pigs transferred to the finishing site have more chance to stay until full market value. Genetic correlations of HCW were moderate and negative with C_{far} (-0.37 ± 0.19) and C_{fin} (-0.34 ± 0.17); HCW was uncorrelated with PWM (0.01 ± 0.13) and C_{nur} (0.00 ± 0.17).

Correlations for common litter effect were all negative for Model 1 (-0.15 between PWM and C_{all}, -0.19 between PWM and HCW, and -0.21 between C_{all} and HCW); all SE were small, which indicated that the estimate were accurate. The correlations suggest that piglets born in an unfavorable environment for survival until weaning have more chance to survive until slaughter and that a favorable environment for survival until slaughter is related with a low final weight.

Correlations for common litter effect were all negative (-0.04 to -0.26) for Model 2, with the exception of correlations of C_{fin} with C_{far} (0.27) and C_{nur} (0.16). These results indicate that a favorable environment for survival during 1 growing period is not necessarily favorable for survival in another growing period or for pigs to reach a high final weight.

One of the primary reasons that 2 models were investigated was the low mortality and culling rates in the different post-weaning phases. The culling traits were grouped together to raise the frequency and thereby obtain better estimates of genetic parameters. However, based on SE, better estimations were obtained with Model 2, which included culling in each phase as a different trait. In addition, mortality or culling risk did not seem uniform throughout the fattening period. Indeed, death or culling could be more prevalent during 1 phase compared with another (Maes et al., 2004). Therefore, Model 2 appears to be more appropriate for studying pig survival during the fattening period and developing an appropriate index to select for survival during the different phase of fattening and high final weight.

Table 22. Estimates (SE) of heritability, sire genetic, and litter effects for survival traits by statistical model.

Model	Effect	Preweaning mortality	Culling Phase				Hot carcass weight
			Farrowing	Nursery	Finishing	Overall	
1	Heritability	0.03 (0.007)				0.06 (0.025)	0.15 (0.017)
	Sire genetic	0.01 (0.002)				0.02 (0.006)	0.04 (0.005)
	Common litter	0.16 (0.005)				0.13 (0.029)	0.14 (0.004)
2	Heritability	0.03 (0.005)	0.06 (0.034)	0.14 (0.045)	0.10 (0.044)		0.15 (0.016)
	Sire genetic	0.01 (0.001)	0.02 (0.009)	0.03 (0.012)	0.03 (0.012)		0.04 (0.005)
	Common litter	0.16 (0.005)	0.18 (0.047)	0.19 (0.057)	0.10 (0.042)		0.14 (0.004)

Table 23. Estimates (SE) of genetic (above diagonal) and common litter (below diagonal) correlations for survival traits by statistical model.

Model	Trait[a]	PWM	C_{far}	C_{nur}	C_{fin}	C_{all}	HCW
1	PWM					-0.36 (0.26)	-0.02 (0.15)
	C_{all}	-0.15 (0.06)					-0.25 (0.20)
	HCW	-0.19 (0.03)				-0.21 (0.06)	
2	PWM		0.13 (0.32)	-0.61 (0.11)	0.17 (0.14)		0.01 (0.13)
	C_{far}	-0.04 (0.08)		0.36 (0.30)	0.44 (0.19)		-0.37 (0.19)
	C_{nur}	-0.11 (0.09)	-0.16 (0.21)		0.59 (0.12)		0.00 (0.17)
	C_{fin}	-0.19 (0.10)	0.27 (0.16)	0.19 (0.15)			-0.34 (0.17)
	HCW	-0.19 (0.03)	-0.11 (0.09)	-0.14 (0.08)	-0.26 (0.09)		

[a] PWM: preweaning mortality; C_{far}: culled during farrowing phase; C_{nur}: culled during nursery phase; C_{fin}: culled during finishing phase; C_{all}: culled overall; and HCW: hot carcass weight.

CONCLUSION

Genetic selection for survival during the grow-finishing period is often neglected. However, losses of pigs at later ages have high economic impact because of increased rearing costs. Selection programs usually focus only on preweaning survival and do not consider survival after weaning. Preweaning mortality had a low heritability and was only slightly correlated genetically with post-weaning mortality, which suggests that mortality before and after weaning are controlled by different genes. Heritability of mortality traits increased with age periods, which implies that selection for survival after weaning could be more effective than selection only for survival before weaning, especially for sire lines. The sire genetic effect on PWM was small but increased on mortality in the following periods. Moreover, survival traits appear to be uncorrelated with growth traits. Therefore, selection for survival until slaughter does not guarantee a higher final market weight. However, because these traits are not highly antagonistic, selecting for both should be possible and could be implemented by breeding companies.

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CHAPTER V. GENETIC PARAMETERS FOR INDIVIDUAL BIRTH WEIGHT, WEANING WEIGHT AND FINAL WEIGHT OF CROSSBRED PIGS FROM PIÉTRAIN BOARS

CHAPTER V

Chapter IV.1 indicated that piglet birth weight (BWT) was genetically correlated in a favorable way with latter performances in the population from US Duroc sires. Hence, genetic selection on BWT could accelerate genetic progress because of early selection opportunity. Chapter II showed that estimates of genetic parameters might be different between breeds, populations, or models used. Therefore, the objective of this chapter was to estimate genetic parameters for BWT, weaning weight (WWT), and final live body weight (BW) in a crossbred population of pigs from Walloon Piétrain boars. As BWT and WWT are known to be influenced by maternal effects, the model used was an animal model with direct and maternal genetic effects correlated. This study was also of interest for pig producers in the Walloon Region of Belgium. Indeed, they widely use hyperprolific sows on Piétrain boars to produce commercial pigs. Since sow prolificacy appears to be unfavorably linked with BWT, the consequences of large litter size on BWT and subsequent performances are of great interest.

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ABSTRACT

Genetic parameters for birth weight (BWT), weaning weight (WWT), and final weight (BW) were estimated for crossbred pigs from Piétrain boars raised in test station. Estimates of direct heritability were moderate (0.25 to 0.42), suggesting that genetic improvement of growth would be possible. Estimates of maternal heritability were 0.24 for BWT and WWT, and 0.05 for BW, indicating that the genetic influence of the dam on growth was not negligible until weaning. Genetic correlations between direct and maternal effects for BWT and WWT were moderate and unfavorable (-0.52 and -0.57 respectively). Direct genetic correlations were high and favorable between traits (0.40 to 0.75), suggesting that a high BWT is a good predictor to produce pigs with high final weight. Maternal genetic correlations between traits were low (0.01 to 0.03). Selection for higher BWT would increase final market weight but should be balanced with survival traits.

Keywords: Genetic parameters, Pig, Weight

INTRODUCTION

Genetic selection and breeding programs are a good way to improve the efficiency of pork production. In addition to production traits (growth, carcass and meat quality), many breeding programs focused on reproduction traits like sow prolificacy or birth weight (BWT) to increase the number of pigs reaching full market value. The result was that selection to improve sow prolificacy led to an increase of litter size at birth. However, an issue was the negative relationship between litter size and BWT. Indeed, larger litter is related to lighter piglets at birth and larger BWT variations within litters. Moreover, differences in weight between light and heavy piglets at birth are often maintained and even increased during growth (Milligan et al., 2002).

Several studies have reported that piglet BWT is an important economic trait in pig production because of its relation with later performances like piglet survival, growth rate, carcass composition, and meat quality. Indeed, a low BWT is related to more risk of preweaning mortality, a reduced weight gain during the production period and fatter carcass. Therefore, those pigs would require more days to reach market weight and produce lower quality carcass at market weight (Gondret et al., 2005; Arango et al., 2006; Bérard et al., 2008; Rehfeldt et al., 2008; Fix et al., 2010). As economic gain in commercial swine production mainly results from pigs reaching full market value, selection programs implemented to improve production traits should not forget weight recorded in early life, like BWT and weaning weights (WWT).

Since 2007, a new genetic evaluation system of Piétrain boars for crossbred performances has been developed in the Walloon Region of Belgium. Piétrain boars are now progeny tested in test station in crossbreeding with hyperprolific Landrace sows. As Walloon pig producers widely use hyperprolific sows to produce commercial pigs, they are concerned about the loss of BWT and its consequences coming from larger litters. Therefore, the objective of this study was to estimate variance components and genetic parameters for individual piglet BWT, WWT, and live body weight (BW) at the end of the fattening period in a crossbred population of pigs selected to enter the progeny-test in test station in the Walloon Region of Belgium.

MATERIALS AND METHODS

Progeny testing scheme

Boars are provided by Walloon Piétrain breeders and by the artificial insemination center. Sows are from the hyperprolific Landrace K+ selection program (www.ciap-belgium.org) and provided by the Walloon Agricultural Research Centre (CRA-W; Gembloux, Belgium). Every 10 weeks, 6 selected Piétrain boars are randomly mated to sows. Piglets are weighed within about 4 days of age. Piglets are weaned at 4 weeks of age, weighed and then selected to create batches of about 100 animals that entered the test station. The aim is to have between 16 and 25 piglets per tested boar from 5 different sows. Boars from the artificial insemination center are used to connect different batches. The progeny-test in test station starts when piglets weigh about 20 kg at maximum 6 weeks of age and ends when pigs weigh about 110 kg. Data are recorded on castrated males and females. In the test station, piglets are randomly assigned in groups of 4 per pen. Every 15 days, pigs are weighed and the total pen feed intake is recorded. The week before slaughter, backfat thickness, loin muscle depth and meat percentage are recorded on live animals by ultrasound using the Piglog 105 apparatus. Additional carcass quality traits (e.g., backfat thickness, meat percentage, carcass weight, conformation index) are recorded at the slaughterhouse on carcasses.

Data

Data used in this study were recorded on piglets selected to enter the progeny-test, between 2007 and 2013. After discarding records with incomplete or inconsistent information, individual piglet BWT records (recorded within about 4 days of age) were available for 2,270 piglets from 91 different sires and 190 different dams. Of those pigs, 2,071 had WWT records and 2,192 had live BW recorded at the end of the fattening period. Mean age at BW measurement was 192 ± 11 days. Pedigrees were traced back 10 generations, and a total of 8,148 animals and 395 litters were included. Contemporary groups were defined on the basis of piglets born during the same year and month for BWT and WWT, and on the basis of year and month of recording for BW.

Statistical analyses

Models used to estimate genetic parameters were bivariate animal models with the genetic effect composed of a direct genetic effect and a maternal genetic effect. The general equation of the model developed was

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wm} + \mathbf{Uc} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of observations, $\mathbf{b}$ is the vector of fixed effects, $\mathbf{a}$ is the vector of random direct animal genetic effect, $\mathbf{m}$ is the vector of random maternal genetic effect, $\mathbf{c}$ is the vector of random common litter effect, $\mathbf{e}$ is the vector of random residuals, and $\mathbf{X}$, $\mathbf{Z}$, $\mathbf{W}$, and $\mathbf{U}$ are incidence matrices that relate observations to various effects.

For each model, fixed effects were sex (female or castrated male), and contemporary groups, different according to traits as defined above. Ages at recording were defined as linear covariables for each trait to take into account the variability in age at measurement. Covariance of litter effects was included, as well as covariances for direct genetic effects, maternal genetic effects, and covariances between direct and maternal genetic effects for BWT and WWT.

Estimation of (co)variance components and their SE, obtained as SD of the posterior distribution, were obtained with a Gibbs sampling algorithm, using the GIBBS2F90 program. The program POSTGIBBSF90 was used for post-Gibbs analysis (Misztal et al., 2002). Single chains of 150,000 cycles with a burn-in of the first 20,000 iterations were run. Every sample was retained to compute mean and SE of the posterior distributions.

RESULTS AND DISCUSSION

The mean BWT was 2.35 kg with SD = 0.41 kg. Because BWT was not recorded within 24 hours of birth as usual, but within about 4 days of age, what we considered as BWT was higher than values commonly reported in literature. The mean weight at weaning was 7.85 kg with a SD = 1.01 kg at a mean age of 26 days. The mean live BW at the end of the growing period was 113.07 kg with a SD = 10.85 kg at a mean age of 192 days. Phenotypic correlations were 0.10 between BWT and WWT, 0.16 between BWT and BW, and 0.11 between WWT and BW.

Estimates of direct heritability, maternal heritability, and common litter effect with their SE for traits are presented in Table 24. Estimates of direct heritability were 0.25 for BWT, 0.42 for WWT, and 0.27 for BW. Estimated heritability for BWT was higher than values usually reported in literature. Indeed, the majority of study reported direct heritability of BWT lower than 0.10 (e.g., Grandinson et al., 2002; Arango et al., 2006). However, another study reported a higher value of heritability for BWT (0.36) for crossbred pigs under outdoor conditions (Roehe et al., 2010). A possible reason that might explain this high heritability of BWT could be the fact that it is not exactly the BWT recorded within 24 hours of birth as usual, but weight recorded around 4 days of age. Because heritability of weight increases with age (Edwards et al., 2006; Haraldsen et al., 2009), estimated heritability of BW at 4 days of age was somewhat higher than heritability for weight recorded the day of birth. As for BWT, estimated heritability for WWT was high (0.42) compared to other studies (e.g., Kaufmann et al., 2000). The estimated heritability for BW (0.27) was in agreement with literature estimates (e.g., Bidanel et al., 1994; Edwards et al., 2006; Zumbach et al., 2007). An explanation for the high heritabilities of weight records we obtained could be the fact that data were collected in a unique test station by a trained technician. Therefore, there could be less risk of measurement bias. Nevertheless, these relatively high estimates of heritability for weight at different ages supported the fact that growth traits are heritable. Maternal genetic heritability was 0.24 for BWT, which is in agreement with results in other studies (e.g., Grandinson et al., 2002; Knol et al., 2002; Arango et al., 2006). Estimated maternal heritability of WWT was 0.24 and in agreement with results presented by Kaufmann et al. (2000). It appeared that genetic influence of the dam was important on weight until weaning, but decreased as the direct influence of the piglet genotype increased. Estimate of maternal heritability was low (0.05) for BW, due to the decreasing influence of maternal genes on growth with age. The genetic correlation between the direct and the maternal effect was -0.52 for BWT and -0.57 for WWT. These moderate and unfavorable values were in agreement with results reported in literature (e.g., Arango et al., 2006; Roehe et al., 2010). This indicated that the genetic control of growth of piglets was different between the direct and the maternal genetic effect. The common litter effect explained 19% of the total variance for BWT, 9% for WWT, and 3% for BW. As expected, the effect common to littermates on live weight dissipated with age.

Table 24. Estimates (SE) of direct heritability, maternal heritability and common litter effect for birth weight (BWT), weaning weight (WWT), and final weight (BW) of crossbred pigs.

Effect	BWT	WWT	BW
Direct heritability	0.25 (0.07)	0.42 (0.08)	0.27 (0.05)
Maternal heritability	0.24 (0.07)	0.24 (0.06)	0.05 (0.02)
Common litter effect	0.19 (0.04)	0.09 (0.03)	0.03 (0.02)

Estimates of direct genetic correlations and maternal genetic correlations between traits with their SE are presented in Table 25. Direct genetic correlations between BWT, WWT, and BW were high and favorable. Moreover, as expected, correlations decreased as interval between ages became greater. Genetic correlations were the highest between BWT and the 2 other traits. Therefore, it seemed that BWT was a good predictor of later growth performances and it supported the influence of BWT on latter performances. This result strengthens the importance of taking into account BWT when selecting for higher prolificacy. Maternal genetic correlations between traits were very low. Therefore, it seems that dam providing favorable genes for high BWT did not necessarily provide favorable genes for growth. However, the SE of these estimations were large and did include zero, therefore these results should be considered very carefully. These high SE of estimations were probably due the small dataset used to estimate variance components and genetic parameters. These results should be confirmed with a larger dataset. The correlations due to common litter effects were 0.21 ± 0.05 between BWT and WWT, -0.04 ± 0.22 between BWT and BW, and -0.16 ± 0.28 between WWT and BW. Therefore, the environment provided by littermates affected BWT and WWT in the same way. However, it was less obvious for correlations between BW and the other traits because of the large SE of the estimations.

Table 25. Estimates (SE) of direct genetic correlations (above diagonal), and maternal correlations (under diagonal) between traits[1].

	BWT	WWT	BW
BWT	-	0.75 (0.08)	0.59 (0.11)
WWT	0.02 (0.02)	-	0.40 (0.28)
BW	0.01 (0.21)	0.03 (0.21)	-

[1] BWT: birth weight; WWT: weaning weight; BW: final weight

CONCLUSION

Given that BWT, WWT, and BW were heritable, genetic improvement of these traits appeared to be possible through genetic selection based on these traits. Because of the high and favorable genetic correlations between BWT and the other traits, selection for a high BWT could improve growth rate and consequently the final market weight. But, higher BWT is also associated with reduced litter size at birth and at weaning, and more risks of farrowing and preweaning mortality, which are not advantageous economically for producers. Current selection programs for higher prolificacy will reduce BWT and therefore influence BW negatively. As BWT is an early recorded trait, selection to improve final weight could be done early, which is economically interesting. Therefore, given the economic importance and the complex relationships between all these traits, selection programs should combine them carefully, using appropriate selection index, to take into account these genetic relationships and to allow improvement of one trait without deteriorating another, and to optimize economic gain for producers.

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CHAPTER VI. GENERAL DISCUSSION

CHAPTER VI

Chapters II to V presented genetic evaluation procedures for the genetic improvement of purebred sire lines of pigs for performances in crossbreeding at the commercial level for various production traits. Therefore, the objective of this chapter was to discuss results obtained in a wider perspective. The following aspects will be addressed: combined crossbred-purebred and multi-environment models, the estimation of dominance effects and sire genetic effects, the interest of selection on piglet birth weight (BWT), and the genetic improvement of several production traits simultaneously.

COMBINED CROSSBRED-PUREBRED SELECTION

In pig production, as in many species, crossbreeding is used to take advantages of heterosis and breed complementarity. Genetic selection was usually performed in purebred parental lines while the aim of the selection was to improve crossbred performances (Ibáñez-Escriche et al., 2009). The genetic correlations between purebred and crossbred performances set the efficiency of this selection. Due to genetic differences between purebreds and crossbreds, and due to non-additive genetic effects related to crossbreeding, the correlations between purebred and crossbred performances are lower than 1. Therefore, purebred performances would badly predict crossbred performances (Dekkers, 2007). Hence, combined purebred and crossbred selection has been proposed by several authors (Wei and van der Steen, 1991; Lo et al., 1993; Bijma and van Arendonk, 1998).

Combined crossbred-purebred selection method requires collecting data from both crossbreds and purebreds. Data collection differs for both. Actually, crossbred animals are generally not individually identified, and individual performances are often not available, except in some experimental herds. It is the case in the Walloon Region of Belgium, with the progeny-test of Piétrain boars in crossbreeding. However, crossbred progeny are raised in test station. Therefore, environmental conditions are very standardized and controlled, and do not necessarily reflect what happens in field conditions. Consequently, data from production crossbred animals recorded in commercial herds would be very useful to improve the efficiency of selection. Smithfield Premium Genetics (Rose Hill, NC, USA), a large US breeding company, have large amount of crossbred data coming from their commercial farms, where pigs are raised in conditions very close to typical commercial production settings.

A significant advantage of combined crossbred-purebred selection is the increasing reliability of genetic evaluations. Additional information coming from crossbred pigs would improve reliability of purebred estimated breeding values (EBV), as pointed out in several studies (Lutaaya et al., 2002; Habier et al., 2007; Ibáñez-Escriche et al., 2011). In Chapter III.1, EBV for average daily gain (ADG) and their reliabilities were estimated for purebred Piétrain boars with a multitrait model combining data from test station (crossbred data) and data recorded on-farm (purebred and crossbred data). Reliabilities of these EBV were compared with reliabilities of EBV of ADG for the same boars, but using a single-trait model with only crossbred data from test station. Results showed that combining crossbred data from test station with crossbred and purebred data recorded on-farm allowed increasing by 8% the reliability of EBV of purebred Piétrain boars. Hence, combined crossbred-purebred selection has indeed not negligible advantages, especially in small populations with small datasets, as it is the case for the genetic evaluations of Piétrain boars in the Walloon Region of Belgium.

Another implication of the poor correlation between purebred and crossbred performances is the re-ranking of animals between strictly purebred and combined crossbred-purebred selection. An animal ranked as best in purebred breeding will not necessarily be the best in crossbreeding (Lutaaya et al., 2001; Habier et al., 2007; Ibáñez-Escriche et al., 2011). If the goal of the selection program is the highest genetic merit in crossbreeding, it would be better to use purebred and crossbred data to estimate the genetic merit of purebreds. However, if the number of crossbred animals is low compared to purebred, the use of crossbred data has a low impact for the genetic evaluation of purebreds (Lutaaya et al., 2001). Therefore, it would be interesting to promote data collection on crossbred animals in commercial herds.

The incomplete correlations between purebred and crossbred performances are not only due to genetic effects linked to crossbreeding. It could also be explained by Genotype x Environment (GxE) interactions. Therefore, genetic models accounting for data from diverse environment are necessary to quantify potential GxE interactions.

MULTI-ENVIRONMENT MODELS

In pig breeding, phenotypic data are provided by diverse testing scheme. Data can be recorded on animal candidate to selection or on relatives, in test station or on-farm (Kovac and Groeneveld, 1990). As described in Chapter III, in the Walloon Region of Belgium, purebred Piétrain boars are performance-tested on-farm. Traits measured are live body weight (BW), ultrasonic backfat thickness (BF), ultrasonic loin muscle depth (LMD), and lean meat content (LMC) predicted from ultrasonic BF and LMD measurements. Sows are also recorded on-farm, as well as some crossbred production pigs. Piétrain boars are also progeny-tested in test station, for crossbreeding performances. Traits recorded on crossbred progeny are BW throughout the testing period, feed intake, and carcass quality traits like, BF, LMC, or hot carcass weight (HCW). Therefore, models that allow carrying out genetic evaluations combining data from diverse environments are needed. Estimation of genetic parameters for on-farm and test station records are possible with these models, as well as the estimation of genetic correlations between traits recorded in both systems. The genetic correlations between identical or similar traits recorded in different environments allow to quantify the importance of GxE interactions. These interactions reveal differences in housing, feeding systems, health status, and other management practices (Bidanel and Ducos, 1996). This is interesting to know the importance of GxE interactions to set the efficiency of the breeding program. Indeed, a boar that performs well in an environment could have bad performances in other conditions.

Results presented in Chapter III.1 showed that the genetic correlations between BW recorded at identical ages in test station and on-farm were high: 0.90 at 175 days, and 0.85 at 210 days. However, these genetic correlations were different than 1, revealing GxE interactions in the Walloon breeding program. Nevertheless, the high genetic correlations between both systems suggested low GxE interactions for growth. Therefore, EBV for growth in test station would well correspond to the genetic potential for growth on-farm, reflecting conditions closer to commercial environment.

For the same population, genetic correlations have been estimated between similar carcass traits coming from test station and on-farm performance recording systems. The considered traits were BF and LMC. For pigs recorded on-farm and at the test station, measurements were taken on live animals with an ultrasonic apparatus, the Piglog 105. Pigs from the test station were slaughtered at the end of the testing period. Then, the same traits (BF and LMC) were recorded on carcasses at the slaughterhouse. Traits were obviously considered as different because of different methods of measurements and status (dead vs. alive) of pig at recording.

Table 26 shows the descriptive statistics for the dataset used to estimate the genetic correlations. The model used was a multitrait animal model. Fixed effects were sex and age at recording, defined as linear covariable, for all traits. Contemporary groups, as described in Chapter III.1, were defined as fixed effects for traits recorded on live animals. Slaughter date was defined as fixed effect for traits recorded on carcasses.

Heterosis effect was modeled as regression on an overall heterozygosity coefficient. Variance components were estimated with the REMLF90 program (Misztal et al., 2002).

Table 26. Descriptive statistics for backfat thickness (BF) and lean meat content (LMC) recorded on carcass at the slaughterhouse (sl) or on live pigs with the Piglog 105 (pl).

Trait	Number of records	Mean	SD
BF_{sl}, mm	2,974	13.13	3.26
LMC_{sl}, %	2,974	61.73	3.44
BF_{pl}, mm	8,469	7.85	3.60
LMC_{pl}, %	8,469	65.73	4.34

Table 26 shows large differences between mean BF_{sl} and BF_{pl}, and therefore between mean LMC_{sl} and LMC_{pl}, because LMC is computed based on BF and LMD records. These large differences supported the hypothesis that those traits should be considered as different because they originate from different systems. Estimates of genetic correlations between similar traits were low: 0.36 between BF records; 0.28 between LMC records. These low correlations between similar traits indicated that GxE interactions were important for these traits. Results could be explained by dissimilar recording conditions: status of the pig at measurement (dead or alive), recording methods (ultrasonic or optical). Moreover, measurements taken at the slaughterhouse are very standardized, because recorded with automatized devices, while records taken on live animals could contain more bias depending on the technician, or if the pig moves. However, the higher correlations between BW records compared to correlations between similar carcass traits were not in agreement with results presented in previous studies (Bidanel and Ducos, 1996; Peškovičová et al., 2002). Indeed, they found higher genetic correlations between BF measurements than between growth traits. They justified their results by the fact that growth traits differ according to the environment whereas BF measurements should stay the same (Bidanel and Ducos, 1996).

Genetic correlations between traits recorded in different environments depend not only on GxE interactions, but also on genetic correlations between purebred and crossbred performances, as explained before (Bidanel and Ducos, 1996; Zumbach et al., 2007) and on the amount of additive and non-additive effects (Esfandyari et al., 2014). Non-additive genetic effects, like dominance, are linked to crossbreeding. It appeared that ignoring dominance variance in genetic evaluations leads to overestimate additive genetic variance and underestimate genetic correlations (Wei and van der Werf, 1993).

ESTIMATION OF DOMINANCE EFFECTS

Chapter III.2 stated that the introduction of dominance effects in the genetic evaluation models allows for a better estimation of additive genetic variance. Additive variance and heritability appeared to be overestimated with a strictly additive model. Therefore, genetic models estimating additive and dominance effects simultaneously led to a better estimation of the additive genetic merit (i.e., transmissible to the next generation).

Dominance variance for growth traits in pigs seemed to be not negligible. With a model including dominance effects with the parental subclass relationship matrix (Hoeschele and VanRaden, 1991), estimated dominance variance accounted for 5 to 11% of the phenotypic variance and for 10 to 35% of the additive variance for BW, depending on age, in a crossbred population from Piétrain boars. These results were in agreement with other studies of the estimation of dominance for growth traits in pigs (Culbertson et al., 1998), in beef cattle (Gengler et al., 1998) or in dairy cattle (Misztal et al., 1997).

In order to estimate dominance effects on other production traits, a similar strategy than the one presented in Chapter III.2 was used for BF and LMC recorded on crossbred pigs in the Walloon Region of Belgium. The dataset was the same as described the previous section (Table 26). Traits were BF_{sl} and LMC_{sl} recorded on carcass at the slaughterhouse. Models were single-trait animal models, with random dominance effects. Fixed effects were sex, slaughter date and heterosis modeled as linear regression on an overall heterozygosity coefficient.

Results showed that estimates of dominance variances were close to zero and accounted for less than 1% of total variance for both traits. For BF_{sl}, dominance variance accounted for 1% of additive variance; for LMC_{sl}, dominance variance accounted for 2% of additive variance. Similar results for BF were found by Culbertson et al. (1998), and by Lutaaya et al. (2001) in preliminary analysis. It appeared that carcass quality traits have high heritability (in the narrow sense); this could justify the low dominance variance for these traits.

One of the main limitations in the inclusion of dominance effects into genetic evaluations is the size of datasets required to compute accurate estimates of dominance variance. Large datasets are needed, but it brought the problem of computing limitations that has been addressed by using iteration methods (Misztal et al., 1998). The use of small datasets leaded to inaccurate estimations with large standard error (SE; Gengler et al., 1997). Therefore, results obtained in Chapter III.2, with a small dataset, should be confirmed with a larger dataset. However, it was in line with literature and supported the existence of dominance variance for growth traits in pigs.

IMPLEMENTATION OF MATE ALLOCATION PROGRAMS

Introduction of dominance effects into genetic evaluation models is useful for unbiased estimation of additive genetic effects. Moreover, dominance effects could be used in mate allocation programs strategy. Dominance variance is due to interaction of alleles from the sire and the dam at the same locus and is not transmitted across generations (Hoeschele and VanRaden, 1991). This represents the specific combining ability of a particular sire with a particular dam. Prediction of the specific combining ability could be useful in mating programs to maximize the genetic merit of the progeny by choosing combinations of sire and dam to produce the best progeny. This is of particular interest in species with high reproductive rate and short generation intervals, as in pigs (DeStefano and Hoeschele, 1992). Genetic gain of selection on specific combining abilities depends, amongst other things, on the dominance variance. An optimized mate allocation program used for commercial production should result from planned mating maximizing the total (additive and dominance) genetic potential of progeny, even if only the estimated additive genetic value is transmitted to the progeny. Indeed, studies showed that selection including dominance effects increased the expected genetic merit of the progeny compared to programs including only additive effects (Toro and Varona, 2010; Sun et al., 2013).

However, specific combining ability has to be computed for each pair of parents. Therefore, each selection candidate will have multiple estimates of genetic merit, one for each possible mating and for each trait evaluated (Misztal et al., 1998), which leads to large computation requirements. Computing procedures have been developed to overcome these issues (Varona and Misztal, 1999). Also, to reduce the number of potential prediction of genetic value for one animal, estimation of combining abilities could be limited to the prediction of progeny merit for the mating of a particular sire with random dams from the maternal population. This strategy could be considered in the Walloon Region of Belgium. Formally, production pigs result from the mating of Piétrain sires with Landrace dams. Therefore, it would be interesting to favor Piétrain boars that maximize the progeny merit when they are mated with any Landrace dams.

ESTIMATION OF SIRE GENETIC EFFECTS

Genetic progress in crossbred commercial herds depends on selection performed at the nucleus level in purebred parental lines. In pigs, selection of purebred parental lines is very specialized. Selection objectives in sire lines are mainly production traits while traits relative to reproduction and piglet performances are traditionally studied from the dam side. However, genetic influence of the sire on these traits may exist and a better knowledge of the sire genetic effects on traits like piglet birth weight (BWT) or preweaning mortality (PWM) would allow early selection of sires. Hamann et al. (2004) studied the sire and dam additive genetic components on number of pigs born alive, a trait relative to fertility of the sow. The aim of their study was to determine whether the sire genetic effect on this trait would be usable for selection of sires. Their results showed that even if the sire additive genetic variance was small, it constitutes a significant part of the total variance. Therefore direct selection of sire can lead to genetic improvement of this trait.

In Chapter IV, genetic parameters were estimated for different traits, among which some related to sow fertility and recorded on piglets: BWT and PWM. Models developed were not animal models, but models with sire genetic effects. The main reason was the lack of pedigree information for the dams of the crossbred pigs with performance recorded. Another reason was that the aim of the study was the genetic selection of purebred sires in order to improve these traits. Therefore, the knowledge of the sire genetic effects was needed.

Chapter IV.1 described the estimation of genetic parameters for BWT, PWM and HCW. The aim was to develop a model for the genetic selection of purebred sires for crossbred performances. As expected, the dam effect, composed in that case of genetic and environmental components, was more important than the sire genetic effect on BWT and PWM. However, the dam effect seemed to decline with age as it was of the same magnitude than the sire genetic effect for HCW. For the three studied traits, the sire genetic effect was small, but significant.

Chapter IV.2 presented the estimation of genetic parameters for repeated mortality traits recorded between birth and slaughter, and their relationships with HCW. The genetic selection of sires with high genetic potential for survival is of great interest for pig producers. Losses of pigs have a large economic impact, which increases with the age of animal at death (Fuerst-Waltl and Sørensen, 2010). But there are also health and welfare concerns. To our knowledge, none or few studies have investigated pig mortality between weaning and harvesting. Mortality was recorded before weaning (PWM), during the farrowing phase (C_{far}), during the nursery phase (C_{nur}), and during the finishing phase (C_{fin}). Estimates of heritability for mortality traits were low and tended to increase with age, as it is the case in other livestock species. As a consequence, estimates of sire genetic effects, defined in this case as ¼ of the additive genetic variance, were also low but significant. These results showed the potential of implementing genetic selection programs of purebred sires for survival traits. Another interesting result was the low genetic correlation between PWM and post-weaning mortality, suggesting that different factors (e.g., direct genetic effects, parental genetic effects, environmental effects) influence mortality before and after weaning. Preweaning mortality is probably more influenced by maternal genes and environment and less by the own genes of the pig while the genetic influence of the dam decreases after weaning. Finally, mortality and HCW seemed to be uncorrelated. Therefore, genetic selection to improve survival would not affect negatively growth traits, which are traditional economically important traits and one of the final goals of pig selection programs.

According to results presented in Chapter IV, sire additive genetic effects existed on traits recorded on piglets and more related to fertility of the dam. Therefore, genetic evaluation of purebred sires for these traits with sire models is worth considering and direct genetic selection of sires would be possible. As traits are recorded early, genetic selection could be implemented earlier in life and the genetic progress would be accelerated. Moreover, mortality traits after weaning showed sufficient genetic variability to implement genetic selection to improve survival between weaning and harvesting.

PIGLET BIRTH WEIGHT AS INDICATOR TRAIT

Another aspect involved in Chapter IV, but also in Chapter V, was the potential of using BWT as an early indicator trait of subsequent performances. To be considered as an indicator, the trait should be easy to measure, have an important economic value, have a sufficient genetic variability and be heritable, and also be favorably genetically correlated with traits of interest (Shook, 1989).

It appeared that BWT fulfilled these conditions. This trait should be easy to measure, as it requires only to weight piglets as soon as possible after birth. Studies have reported that BWT is an important economic trait in pig production because market gives it an economical value (Knap, 2014). However, the economic importance of BWT comes mainly from its relationships with later performances of economic interest. Low BWT increases risks of PWM and mortality during the nursery phase, decreases ADG, and leads to fatter carcasses with reduced LMC (e.g., Quiniou et al., 2002; Schinckel et al., 2007; Rehefeldt et al., 2008; Fix et al., 2010; Schinckel et al., 2010). Genetic studies of BWT showed that it has a low to moderate heritability, as presented in Chapters IV.1 and V, but also in previous studies (e.g., Grandinson et al., 2002; Arango et al., 2006; Roehe et al., 2010). Finally, BWT has a favorable genetic correlation with economically important production traits, as explained before. Chapter IV.1 showed that high BWT is related to lower PWM and higher HCW; Chapter V presented high favorable genetic correlations between BWT and WWT or final BW. Therefore, BWT could be considered as an indicator trait of subsequent performances. Moreover, as BWT is recorded early in life, it could be used as an early indicator of performances. Selection on BWT to improve final performances would accelerate genetic progress.

MULTIPLE TRAIT SELECTION INDEX

Chapters III to V showed genetic models to estimate genetic parameters and EBV for different traits. It could be single-trait models, estimating EBV for a trait at once. Genetic models could also be multitrait, estimating EBV for several traits simultaneously by taking into account performances for other traits and relationships between them. The result is that for each trait, an EBV is computed, reflecting the genetic potential of an animal transmitted to its progeny. To improve efficiency and quality of animal production in commercial pig breeding, it could be necessary to improve several traits simultaneously. In pigs, animals combining favorable genetic potential for growth rate, feed efficiency and carcass quality are sought. A multiple trait selection index makes that feasible by combining phenotypic and pedigree information with economic weight in one index value. This is a two-step procedure: first, EBV are estimated for each trait included in the selection goal; then, EBV are combined, weighted by their economic importance, resulting in one index value representing the aggregate genetic value of an animal. Therefore, the development of selection index required the knowledge of phenotypic, genetic and economic parameters for each trait in the breeding goal. To compute economic weights, it is necessary to know the net profit, defining the efficiency of the production system. The net profit is the difference between the total income per slaughter animals and the total costs of production. Moreover, for each trait, the effect of the change in genetic merit by one unit on the net profit need to be calculated in order to derive marginal economic values. Then, EBV of traits in the breeding goal are combined into the index, weighted by their economic values derived from marginal economic values (Schneeberger et al., 1992). Economic weights are changing, depending on the market because they are related to local costs, prices and performance levels. They are also different over time because these parameters are always changing.

To develop a multiple trait selection index, it is necessary to decide which traits should be included in the index to reach the breeding goal. Breeding goal traits could be split into six categories (Knap, 2014). The first category brings together classical production traits easy to measure (e.g., growth). The second category consists in production traits with low heritability (e.g., litter size), or traits difficult to record (e.g., feed intake). The third category contains traits with an economic impact because of their relations with traditional production traits (e.g., mortality). The fourth category contains traits that become of economic importance because of new policies in the market (e.g., boar taint). The fifth category consists in traits that have not yet any economic impact admitted, but are expected to in the future (e.g., meat quality). The sixth category is constituted by traits with profitability difficult to quantify for producers, but with a value at the market level (e.g., muscle conformation). Currently, traits included in the index are traits adding information, easy to measure, and with an obvious economic value, usually growth, BF and FCR.

An issue is that traits are genetically linked and show a correlated response to selection. Genetic selection to improve one trait leads to genetic changes in other traits, not always in a favorable way. For example, fast growing pigs have better feed efficiency, but also produce fatter carcasses. This situation can be handled with different approaches (Knap, 2014). The first option is to accept unfavorable responses and leave it unchanged. The second option is to remove from the breeding goals traits with unwanted response. Of course, correlated response will stay, but with less impact because the weighting factor is set to zero. The third option is to use restricted selection index. A restricted selection index (Kempthorne and Nordskog, 1959) implies that changes for one particular trait are reduced to zero while selecting for correlated traits of interest. To reduce the selection response to zero, weighting factors on this trait are modified. For example, in Belgium, producers are looking for fast growing pigs with low FCR, mainly because of economic concerns. But at the same time, they want low fat carcasses, because payment of pigs at slaughter is based on LMC. Therefore, a solution would be to restrict change in BF to zero while selecting directly for growth and feed efficiency.

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CHAPTER VII. GENERAL CONCLUSIONS AND PERSPECTIVES

CHAPTER VII

Research conducted trough this thesis allowed to reach conclusions and opened further perspectives of research in the context of genetic selection of pigs used in crossbreeding. Therefore, the aim of this chapter was to summarize the main conclusions obtained from Chapters II to V and to expose future perspectives of research.

GENERAL CONCLUSIONS

The main conclusions that could be drawn from this thesis are:

- Genetic variability existed for growth traits in the Walloon Piétrain population. Therefore, genetic selection of Piétrain boars to improve growth of their crossbred progeny would be possible and efficient.
- Genetic models combining diverse sources of data (recorded on purebred and crossbred pigs, in test station and on-farm) led to increase reliability of estimated breeding values.
- Genotype x Environment interactions existed for weight records in the Walloon breeding program, but were low. Therefore, genetic selection of Piétrain boars based on test station data would improve growth on farm at the commercial level.
- Genotype x Environment interactions were high for carcass quality traits in the Walloon breeding program. Therefore, genetic selection of Piétrain boars to improve carcass quality based on ultrasonic measurements of traits recorded on live animals would not lead to the improvement of carcass quality as it is recorded and paid at the slaughterhouse (i.e., traits recorded on carcasses).
- The introduction of dominance effects into genetic evaluation models allowed for a better estimation of additive genetic effects, transmitted to the next generation.
- Dominance effects were found on growth traits in pigs and could be used to implement mate allocation programs through the prediction of specific combining abilities, in order to maximize the genetic merit of the commercial crossbred progeny.
- Piglet birth weight, preweaning mortality and carcass weight were heritable and genetically correlated in a favorable way. Therefore, these traits could be improved by genetic selection. Sire genetic effects on these traits were low but significant. Thus, direct selection of sire in an attempt to improve these traits might be efficient.
- Mortality traits recorded several times from weaning to harvesting showed low heritability, increasing with age at death. Therefore, genetic selection to reduce mortality of pigs throughout the life would be possible. Moreover, because mortality traits appeared to be uncorrelated with final weight, such selection should not affect economic value of production pigs.

- Piglet birth weight could be used as an early indicator of commercial performances as this trait is 1) easy to record early in life, 2) has an economic value, 3) is heritable and genetically variable, and 4) is genetically correlated with important economic traits in a favorable way. However, selection on this trait should be undertaken carefully because of deleterious effects on other important traits as farrowing mortality and litter size.

PERSPECTIVES

A part of the research carried out in this thesis were undertaken in the framework of the development of the genetic breeding program of Piétrain boars for crossbreeding performances in the Walloon Region of Belgium. The results obtained contributed largely to the development of genetic evaluation models currently used in routine genetic evaluations in Wallonia. Studies presented in the present thesis opened further opportunities of research in order to improve the genetic evaluation models and optimize the selection program of Piétrain boars.

Selection index

Pig producers are largely interested in commercial pigs with high growth rate, high meat percentage on carcass and high feed efficiency. Currently, the genetic evaluation program gives estimates of breeding values for each trait apart. Selection to improve these traits simultaneously is difficult because of antagonistic relationships between them. Therefore, it would be profitable to compute the economic values of the traits and to combine breeding values weighted by their economic values into a multiple trait selection index. Each purebred boar could therefore be selected on one value combining its estimated breeding values for traits of interest, weighted by the appropriate economic values for the local production system.

Expand data recording at the commercial level

Chapter III.1 and several previous studies showed significant advantages of joint evaluation of purebreds and crossbreds, especially for the genetic selection of purebred parents for crossbred performances (Lutaaya et al., 2002; Ibáñez-Escriche et al., 2011). However, it requires pedigrees and performances recorded at the commercial level, which is not common. Currently, data used in the genetic evaluations are provided by two sources. The first one is data from the test station, recorded on crossbred pigs. The second one is data collected on-farm at the nucleus level, mainly on purebred animals. Another large source of information for the genetic evaluations is data from the commercial herds using Piétrain boars from Walloon breeders as reproductive sires. The main issue is that commercial pigs are usually not individually identified and recorded. Thus, it would require investments to implement such performance recording system. However, it would be beneficial for the genetic selection efficiency by increasing the amount of data and therefore the reliability of genetic evaluations. Moreover, it would improve genetic progress.

Implementation of mate allocation program

The knowledge of dominance effects is useful to develop mate allocation programs (DeStefano and Hoeschele, 1992). This would help producers to choose the sire and the dam that maximize the genetic merit of the crossbred progeny, through the knowledge of the specific combining ability. The strategy would be to estimate the specific combining ability for each potential mating. Therefore, each boar would have several estimates of genetic merit. Based on these values, mating advices would be done to pig producers to help them in mating choices. This could be an additional way to take advantage of the current use of crossbreeding.

Genomic selection

As explained before, combined crossbred-purebred selection requires pedigree and performance data recorded at the commercial level, which is not easy to get. Dekkers (2007) suggested using genomic selection to select purebreds for crossbred performances. Genomic selection, also called genome-wide selection, consists in the prediction of breeding values using genome-wide dense markers, like Single Nucleotide Polymorphisms (SNP; Meuwissen et al., 2001). Genomic selection of purebreds for crossbred performances requires genotypes of purebred parents and those of a sample of their crossbred progeny, as well as their phenotypes. The estimation of SNP effects on crossbred performances can be realized and then applied on purebred genotypes to select purebred parents (Dekkers, 2007). Two main advantages of genomic selection for crossbred performances could overcome the issue of data collection at the commercial level: 1) pedigree information of crossbred are not needed, and 2) prediction of SNP effects are valid for several generations without requiring new phenotypes of crossbreds.

Genomic selection of purebreds for crossbred performances, as proposed by Dekkers (2007), still requires phenotypes and genotypes recorded on a sample of crossbred animals, which is a major issue in pig breeding program. Investigations have recently been done to assess the possibility of genomic selection of purebreds for crossbred performances only based on purebred data (Esfandyari et al., 2014). Results, based on simulation studies, showed that it would be possible to select purebreds for crossbred performances without crossbred information. Moreover, as dominance is involved in crossbreeding, inclusion of dominance effects in the genomic selection models may be beneficial for selection for crossbred performances and design of mate allocation programs. Interest in non-additive genetic effects as dominance became again fashionable thanks to advances realized in genomic studies (e.g., Su et al., 2012; Vitezica et al., 2013). Prediction of dominance effects with genomic models appeared to be easier because it makes possible to know, for each locus, the genotype of an animal. Moreover, the inclusion of dominance effects into genomic models increases the accuracy of the genomic breeding value predicted and it helps for the prediction of the genotypic value of a future mating (Toro and Varona, 2010).

Implementation of genomic selection program would be profitable for the breeding program of Walloon Piétrain boars. Genotyping could be limited to purebred sires and dams, and crossbred progeny involved in the progeny-test in test station. As all crossbred pigs at the test station are individually identified and recorded, they could represent the sample of crossbred animals needed for the prediction of SNP effects. Moreover, if results presented by Esfandyari et al. (2014) would be confirmed on real data, only purebred parents could be genotyped, with appropriate results in the selection of purebreds for crossbred performances. This will therefore reduce costs linked to genotyping analyses.

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LIST OF ABREVIATIONS

ADG	Average daily gain
AWEP	Walloon Pig Breeders Association
BF	Backfat thickness
BW	Body weight
BWT	Birth weight
C_{all}	Culling between weaning and harvesting
C_{far}	Culling during farrowing phase
C_{fin}	Cullinh during finishing phase
C_{nur}	Culling in the nursery site
DAYS	Age
EBV	Estimated breeding value
FCR	Feed conversion ratio
GxE	Genotype x Environment
HCW	Hot carcass weight
LMC	Lean meat content
LMD	Loin muscle depth
PWM	Preweaning mortality
RFI	Residual feed intake
RRM	Random regression model
WWT	Weaning weight

LIST OF ORAL PRESENTATIONS

Dufrasne, M., H. Hammami, V. Jaspart, J. Wavreille, and N. Gengler. 2010. Development of a new genetic evaluation model for carcass quality based on crossbred performances of Piétrain boars in the Walloon Region of Belgium. At: *9th World Congress on Genetics Applied to Livestock Production*. Leipzig, Germany.

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