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BOARD INVITED REVIEW: The purebred-crossbred correlation in pigs: A review of theory, estimates, and implications[1]

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ABSTRACT: Pig and poultry production relies on crossbreeding of purebred populations to produce production animals. In those breeding schemes, selection takes place within the purebred population to improve crossbred performance (CB performance). The genetic correlation between purebred performance (PB performance) and CB performance (r_{pc}) is, however, lower than unity for many traits. When r_{pc} is low, the use of CB performance in selection is required to achieve sizable genetic progress. The objectives of this paper were to describe the different components and importance of r_{pc}, and to review existing literature that report r_{pc} estimates in pigs. The r_{pc} has 3 components: 1) genotype by genotype interactions, 2) genotype by environment interactions, and 3) differences in trait measurements. We theoretically showed that direct selection for CB performance reduces the response to selection in purebreds for PB performance by a factor $\frac{1}{r_{PC}^2}$, when achieving the same crossbred response as obtained with indirect selection based on PB performance. This implies that direct selection for CB performance leads to less extreme PB performances and thus potentially easier management in the nucleus, especially for traits with low r_{pc}. In the review, 201 r_{pc} estimates from 27 studies were considered, published between 1964 and 2017. The average r_{pc} estimate was 0.63, with 50% of the estimates between 0.45 and 0.87. Standard errors of the estimates were on average 0.16, with 50% of the standard errors between 0.06 and 0.19. For all different trait categories, e.g., Growth, Meat amount, Meat quality, Feed, and Fertility, the average r_{pc} was around 0.6. Genotype by environment interactions appeared to have a smaller contribution to r_{pc} than genotype by genotype interactions. More research regarding the impact of the different components on the r_{pc} can help to improve breeding programs. Future studies are advised to report characteristics of the herd environments in detail, to report estimated h^2 and additive genetic variances for purebreds and crossbreds, to report the estimated r_{pc} with standard errors or confidence intervals, to estimate separate r_{pc} for different pure lines, and to genotype the animals under study.

Key words: crossbreeding, genotype by environment interaction, pigs, purebred-crossbred correlation

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INTRODUCTION

Pig and poultry production uses crossbreeding of pure lines or breeds to produce production animals. This enables us 1) to capitalize on heterosis, the phenomenon that crossbreds outperform the average of the purebred parents; 2) to benefit from breed complementarity (Sellier, 1976), e.g., to cross lines specialized for different traits (Smith, 1964); and 3) to be flexible in creating different products for different

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markets, by changing line composition of the crossbred animals (Dickerson, 1973).

The breeding goal of those systems is to improve crossbred performance, while selection commonly takes place in purebred animals based on purebred performance. Thus, selection is indirect, and the accuracy of selection depends on the genetic correlation between purebred (**PB**) and crossbred (**CB**) performance (r_{pc}). This selection approach may be suboptimal, depending on the magnitude of r_{pc} (Bijma and van Arendonk, 1998). An r_{pc} lower than 0.8 may indicate an advantage of combined purebred and crossbred selection over purebred selection (Wei and Van der Werf, 1994; van Grevenhof and van der Werf, 2015). More generally, genetic correlations lower than 0.8 may suggest agriculturally and biologically relevant differences (Robertson, 1959), possibly warranting a specific breeding program for each environment, instead of having one joint breeding program across those environments (Mulder et al., 2006). A general belief that the r_{pc} often may be (considerably) smaller than unity has motivated the development of combined purebred and crossbred selection (**CCPS**) strategies that jointly consider purebred and crossbred information (Wei and Van der Werf, 1994) and can increase the response to selection (Ibáñez-Escriche et al., 2011).

The first objective of this paper is to describe the different components and importance of r_{pc}. The r_{pc} is mainly relevant in pigs and chickens. As a second objective of this paper, we focus on reviewing existing literature that report estimates of the r_{pc} in pigs.

THEORETICAL BACKGROUND

This paper is organized as follows. We start with some theoretical background of r_{pc}; what are the components of r_{pc} and what is the importance of r_{pc} in selection schemes? This theory is followed by an overall description and classification of the existing literature reporting r_{pc} values in pigs, thereby summarizing and discussing r_{pc} estimates per trait category or investigating the effect of each of the different components of r_{pc}. Finally, we give recommendations and guidelines for future studies estimating and reporting r_{pc} values.

As explained before, the r_{pc} is the genetic correlation between PB and CB performance, which can be regarded as 2 different traits. The genetic correlation is generally defined as the correlation between breeding values for 2 traits of the same individuals (Bohren et al., 1966; Falconer and Mackay, 1996). The concept of breeding values is based on allele substitution effects of the causal variants. It can theoretically be shown that the genetic correlation between 2 traits is equal to the correlation between allele substitution effects of the causal variants for those traits (Wientjes et al., 2017). The genetic correlation can also be interpreted in terms of variance explained, where the genetic correlation represents the square root of the proportion of genetic variance in 1 trait that could be explained by the genetic variation in the other trait. Altogether, it indicates that a high r_{pc} means that PB and CB performance are highly likely influenced by the same causal variants with the same effects and a low r_{pc} means that PB and CB performance are influenced by different causal variants and/or that the causal variants have different effects.

Components of the r_{pc}

The r_{pc} is a combination of 3 main components, each of the components can reduce the r_{pc}. The first component is due to genotype by genotype interactions (**GxG**) as a result of differences in genetic background of purebred versus crossbred animals. Allele frequencies at causal variants in purebreds are likely to differ from allele frequencies in crossbreds. Those differences in allele frequencies can result in differences in allele substitution effects of causal variants under dominant gene action (Fisher, 1918; Fisher, 1930; Falconer and Mackay, 1996). Moreover, due to epistatic interactions, the allele substitution effect of 1 locus can differ when the allele frequencies at another locus, with which the first locus interacts, are different (Fisher, 1918; Fisher, 1930). Therefore, differences in allele frequencies between populations can result in differences in effects of causal variants in purebred versus crossbred animals (Wei et al., 1991b), especially for traits with large dominance variation (Wei et al., 1991b; Wei and van der Werf, 1995), thereby resulting in an r_{pc} below 1.

Second, deviations of the r_{pc} from 1 can be due to genotype by environment interactions (**GxE**), indicating that the effects of the causal variants depend on the environment in which the animal is housed. GxE can have 2 different components: 1) heterogeneity of genetic variance in different environments, and 2) differences in ranking of individuals based on their breeding values in different environments. Effectively, only the effect leading to re-ranking of individuals based on their breeding value for PB versus CB performance affects the r_{pc}. For the r_{pc}, the contrasting environments are the nucleus versus the commercial herd environment. Nucleus environments tend to have high biosecurity levels, resulting in the absence or low presence of pathogens, while group size tends to be small and feeding is often ad libitum or semirestricted (Rothschild and Ruvinsky, 2011). In commercial environments, biosecurity levels are typically less strict, herd environment may be more variable, group size tends to be larger, and restricted feeding is more commonly applied (Rothschild and Ruvinsky, 2011). Moreover, on-farm cooling systems might be bet-

ter in the nucleus environment, resulting in a larger effect of heat stress in crossbred animals on commercial farms (Fragomeni et al., 2016). Therefore, the genes affecting traits like disease tolerance and response to heat stress may have a larger effect on performance in the commercial compared to the nucleus environment (Dekkers, 2007). Thus, the set of causal variants and their effects related to performance can differ for purebreds housed in nucleus environments compared to crossbreds housed in commercial environments.

Third, either the definition or the measurement of the trait may differ between purebred and crossbred animals, causing the r_{pc} to be smaller than 1. An example of a trait for which different measurement methods are used is backfat thickness, which can either be measured using ultrasound on live animals, or directly from the carcass after slaughtering the animals (Standal, 1977; Zumbach et al., 2007). Because purebred animals are measured to support selection decisions for the breeding program, backfat is generally measured using ultrasound on live animals, in contrast to crossbred animals, which are generally measured after slaughtering (Zumbach et al., 2007). The correlations between ultrasound and carcass measurements of the same animals are reported to be around 0.85 (Giles et al., 1981; Lo et al., 1992). This indicates that even though the correlation between both measurements is high, the r_{pc} for backfat is affected by measuring purebreds and crossbreds in different ways.

The Importance of r_{pc}

Here, we will give a brief review of quantitative genetics theory relevant to explain the importance of the r_{pc}. Naturally, this will provide a list of parameters that are important when measuring and interpreting the r_{pc}.

The response to selection per unit of time is computed using the breeder's equation: $R = \frac{i \times \rho \times \sigma_a}{L}$, where i is the intensity of selection, ρ is the accuracy of selection, σ_a is the genetic standard deviation of the trait under selection, and L is the generation interval. In many breeding programs where the breeding goal is to improve CB performance on commercial farms, actual selection takes place based on PB performance in nucleus herds. In this case, indirect selection is applied based on a correlated response (Falconer and Mackay, 1996). Alternatively, the purebreds can be directly selected for CB performance, based on the performance records of their crossbred relatives. A combination of both selection methods is possible as well, but for simplicity, here we either consider the response to direct selection or indirect selection.

When purebreds are selected based on PB performance, the direct response to selection (*R(PB)*) in purebreds is for PB performance:

$$R(PB)_{PB} = \frac{i \times \rho_{PB,PB} \times \sigma_{a_{PB,PB}}}{L},$$

where $\sigma_{a_{PB,PB}}$ represents the genetic standard deviation in purebreds for PB performance, and $\rho_{PB,PB}$ is the accuracy of selecting purebreds for PB performance. This selection method results in a correlated response to selection in the purebreds for CB performance, which is equal to

$$R(PB)_{CB} = r_{PC} \frac{i \times \rho_{PB,PB} \times \sigma_{a_{PB,CB}}}{L} = r_{PC} \frac{\sigma_{a_{PB,CB}}}{\sigma_{a_{PB,PB}}} R(PB)_{PB},$$

where $\sigma_{a_{PB,CB}}$ is the genetic standard deviation in purebreds for CB performance.

When purebreds are selected based only on CB performance, the direct response to selection (*R(CB)*) in purebreds for CB performance is

$$R(CB)_{CB} = \frac{i \times \rho_{PB,CB} \times \sigma_{a_{PB,CB}}}{L},$$

where $\rho_{PB,CB}$ is the accuracy of selecting purebreds for CB performance. The correlated response to this selection in the purebreds for PB performance is

$$R(CB)_{PB} = r_{PC} \frac{i \times \rho_{PB,CB} \times \sigma_{a_{PB,PB}}}{L} = r_{PC} \frac{\sigma_{a_{PB,PB}}}{\sigma_{a_{PB,CB}}} R(CB)_{CB}.$$

The purebred animals only contribute half of their genes to the crossbred offspring. Therefore, the response to selection in CB performance of the crossbreds due to genetic progress for CB performance in one specific purebred parent line is only half the response in the purebreds, assuming that the genetic standard deviations for CB performance are the same in purebreds and crossbreds.

The previous equations indicate that to obtain the same response to selection in crossbreds for CB performance using both selection strategies, the ratio in response to selection for PB performance is

$$R(PB)_{CB} = R(CB)_{CB}$$

$$r_{PC} \frac{\sigma_{a_{PB,CB}}}{\sigma_{a_{PB,PB}}} R(PB)_{PB} = \frac{1}{r_{PC}} \frac{\sigma_{a_{PB,CB}}}{\sigma_{a_{PB,PB}}} R(CB)_{PB}$$

$$R(PB)_{PB} = \frac{1}{r_{pc}^2} R(CB)_{PB}.$$

So, to obtain the same response in CB performance, the response to selection in purebreds for PB performance should be $\frac{1}{r_{pc}^2}$ as large when selection is based on PB performance compared to selection based on CB performance. Conversely, direct selection for CB performance reduces the response to selection in purebreds for PB performance by a factor $\frac{1}{r_{pc}^2}$, when achieving the same CB response as obtained with indirect selection based on PB performance. This implies that direct selection for CB performance leads to less extreme PB performances and thus potentially easier management in the nucleus, especially for traits with low r_{pc}.

Regardless whether PB or CB performance is used as information source, the parameter i still reflects the intensity of selection of purebred animals, and $\sigma_{a_{PB,PB}}$ and $\sigma_{a_{PB,CB}}$ still reflect the genetic standard deviation for either PB or CB performance in purebred animals. The generation interval, L, can be slightly longer when selecting purebreds for crossbred performance because it might take more time to estimate accurate breeding values. However, for simplicity, we will assume that this difference is reflected in the accuracy of breeding values and that the generation interval is the same. Therefore, when comparing different breeding programs using either PB or CB performance as information source, we assume that i, $\sigma_{a_{PB,PB}}$, $\sigma_{a_{PB,CB}}$, and L are constant.

So, the only parameter that likely differs when selecting animals based on PB or CB performance is the accuracy of selection. In practical breeding programs, the accuracy of selecting purebred animals for CB performance is expected to be lower than the accuracy of selecting for PB performance. This is mainly a result of the level of relationships between the selection candidates and the animals with performance records. Breeding values for PB performance may be based on performance records of the PB selection candidate itself, its parents, full- and half-sibs, and progeny. Breeding values for CB performance may be based on performance records of half-sibs, progeny, or even more distant descendants of the PB selection candidate, but no own performance, parent, or full-sib information can be used. This substantially reduces the relationships between the animals with performance records and the selection candidates, which reduces the accuracy for both traditional (Mrode and Thompson, 2005) and genomic selection (Habier et al., 2007a). Moreover, the accuracy of selection for PB and CB performance depends on the heritability, which can be different for PB (h_{PB}^2) and CB (h_{CB}^2) performance. When the heritability for CB performance is lower than for PB performance, this can further reduce the accuracy of selecting for CB performance for both traditional (Mrode and Thompson, 2005) and genomic selection (Meuwissen et al., 2001; Daetwyler et al., 2008). The above formulas, however, show that selecting based on CB performance is already beneficial when the accuracy of selecting for CB performance in purebred animals ($\rho_{PB,CB}$) is at least $r_{pc} \times \rho_{PB,PB}$. So, when r_{pc} is 0.5, selection based on CB performance is already beneficial when its accuracy is at least half the accuracy of selection for PB performance.

Before, it was shown that a difference in accuracy of selection is the only reason why response to selection for CB performance can be different when selecting purebred animals based on either PB performance or CB performance. The accuracy of selection is both depending on the level of relationships between selection candidates and animals with performance records as well as on the heritability. Therefore, next to the r_{pc}, the values of h_{PB}^2 and h_{CB}^2 are also important when comparing the expected benefits of selection based on PB versus CB performance. In addition, $\sigma_{a_{PB,PB}}$ and $\sigma_{a_{PB,CB}}$ can be used to estimate the response to selection in crossbreds when knowing the response to selection in purebreds, and should be reported as well.

Review of Existing Literature

In this review, 201 estimates of r_{pc} in pigs from 27 studies were considered. The studies were published between 1964 and 2017 (Fig. 1), and an extensive overview of the reviewed papers is given in Table S1. In this section, we will start by giving an overview of the different methods and models to compute r_{pc}, followed by the empirical values for different trait categories and the relation of r_{pc} to the heritability. Thereafter, we discuss the contributions of each of the 3 components to the r_{pc}.

Methods and Models to Compute r_{pc}

In the majority of the studies, the experimental setup involves a limited number of sires with both PB and CB offspring, whose performance is measured. Over time, methods used to compute the r_{pc} have changed. The earliest studies typically computed the correlation between the average PB and CB offspring performance. From the late 1990s onward, all studies used animal models. The use of animal models to estimate r_{pc} has been boosted by the development of restricted maximum likelihood (**REML**; Patterson and Thompson, 1971) and Gibbs sampling (Wang et al., 1993), and the implementation thereof in software packages (Misztal, 1994). In addition, computers became increasingly more powerful, which made solving of the computationally more complex animal models possible.

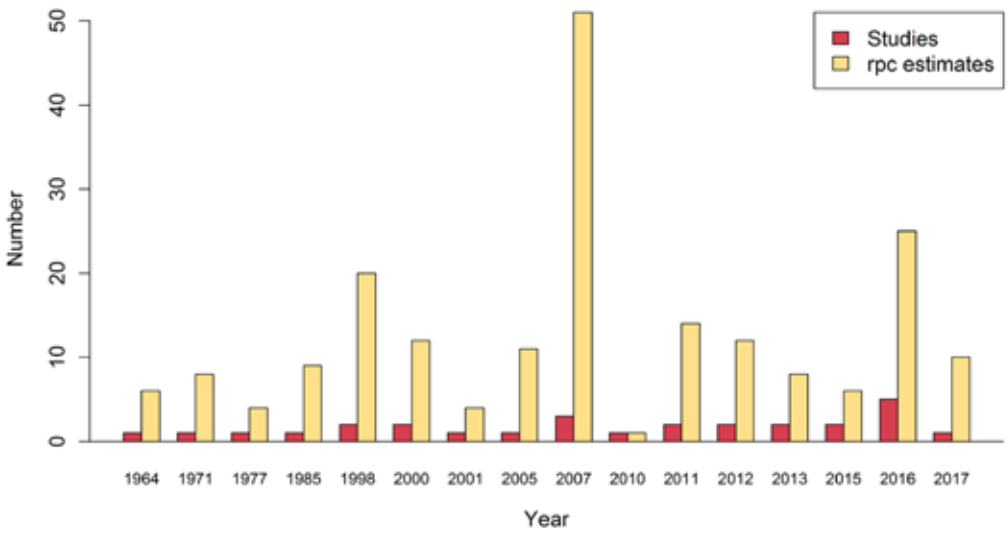

Figure 1. Distribution of the number of studies and r_{pc} estimates over the years used in the review. In this review, the following studies were included: Robinson et al. (1964), Wong et al. (1971), Standal (1977), McLaren et al. (1985), Brandt and Täubert (1998), Merks and Hanenberg (1998), Bösch et al. (2000), Täubert and Brandt (2000), Lutaaya et al. (2001), Nakavisut et al. (2005), Habier et al. (2007b), Stamer et al. (2007), Zumbach et al. (2007), Cecchinato et al. (2010), Ibáñez-Escriche et al. (2011), Nagyné Kiszlinger et al. (2011), Bloemhof et al. (2012), Nagyné Kiszlinger et al. (2012), Nagyné Kiszlinger et al. (2013), Hidalgo et al. (2015a), Hidalgo et al. (2015b), Abell et al. (2016), Nielsen et al. (2016), Tusell et al. (2016), Xiang et al. (2016a), Xiang et al. (2016b), and R. M. Godinho, Animal Breeding and Genomics, Wageningen University and Research, Wageningen, personal communication.

Animal models traditionally rely on the use of pedigree relationships. In those models, it is essential to have close family relationships between the purebred and crossbred animals of which performance records are available. It has been shown that in those models the standard error of the estimated r_{pc} depends on the number of common sires between the purebred and crossbred animals, the value of the r_{pc}, and the reliabilities of sire estimated breeding values reflecting the number of offspring with performance records (Bijma and Bastiaansen, 2014). In total, 11 studies reported the number of common sires between purebred and crossbred animals as well as the standard error of the r_{pc} estimate. Across those studies, it was indeed shown that a higher number of common sires resulted in lower standard errors (Fig. 2).

Recently, estimation of both breeding values and variance component is increasingly more often based on genomic instead of pedigree relationships. An important benefit of the use of genomic relationships, in the context of estimation of the r_{pc}, is that information of crossbred animals without pedigree information can be used. In addition, because genomic relationships are more precise than pedigree relationships,

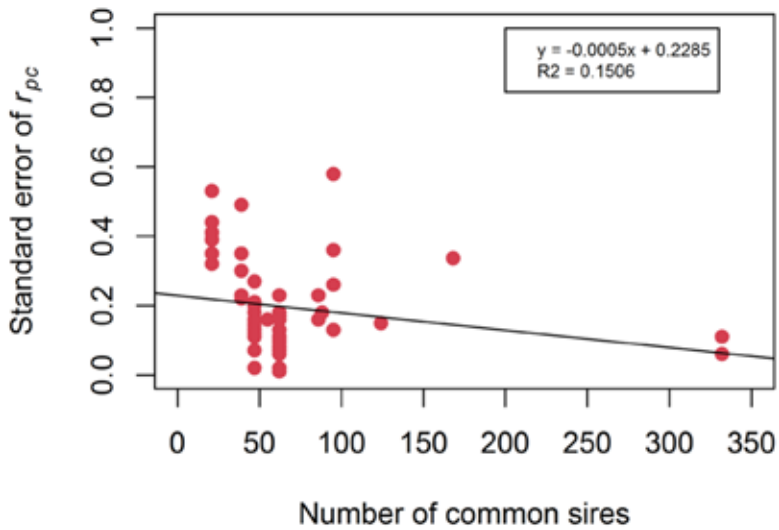

Figure 2. Number of common sires between purebred and crossbred animals versus the standard error of the r_{pc}.

Table 1. Overview of the 6 different trait categories

Trait category	Traits (Number of r_{pc} estimates per trait)	Total number of r_{pc} estimates	Avg. h^2 PB	Avg. h^2 CB	Avg. r_{pc}
Growth	Average daily gain (28), Body weight (13), Age at test weight (2)	43	0.32	0.31	0.66
Meat amount	Backfat (30), Lean meat content (16), Muscle depth (3), Carcass length (2), Meat content (2), Muscle area (2), Meat:Fat content (2), Ham content (2), Body length (1), Belly meat content (1), Lipid deposition (1), Protein deposition (1)	63	0.41	0.42	0.69
Meat quality	pH meat (11), Conductivity (5), Meat clarity (2), Meat quality score (1), Drip loss (1), Intramuscular fat (1)	21	0.34	0.28	0.67
Fertility	Total number born (21), Total number born alive (16), Number of piglets raised (4), Gestation length (4), Farrowing rate (4), Age at first insemination (3), Birth weight (2), Heat tolerance (2), Farrowing interval (2), Litter birth weight (2), Litter variation (1), Longevity (1)	62	0.15	0.18	0.54
Feed	Feed conversion ratio (4), Feed efficiency (2), Feed intake (1), Residual energy intake (1) Residual feed intake (1)	9	0.20	0.27	0.67
Index	Index (3)	3	0.40	0.43	0.50

their use is expected to lead to a smaller standard error of the r_{pc} (Xiang et al., 2016a; Xiang et al., 2016b).

Empirical Values

Estimated r_{pc} values were reported for 39 different traits, covering a wide range of traits measured in pig production. We divided the traits into 6 trait categories, namely: Growth, Meat amount, Meat quality, Fertility, Feed, and Index (Table 1). For 4 out of the 6 trait categories (Growth, Meat amount, Meat quality, and Fertility), a considerable number (> 20) of r_{pc} estimates were obtained. For the other 2 trait categories, Feed and Index, only 9 and 3 r_{pc} estimates were obtained. Over all traits, estimates of r_{pc} covered the whole range of possible correlation estimates (−1 to 1), with even some estimates outside this range. The average r_{pc} estimate was 0.63, with 50% of the estimates between 0.45 and 0.87. Standard errors of the estimates were reasonably high, ranging from 0.002 to 0.58 with an average standard error of 0.16, with 50% of the estimated standard errors between 0.06 and 0.19.

Traits

The estimates of the r_{pc} for the different trait categories are highly variable (Fig. 3). This indicates that either the r_{pc} estimates are highly variable across traits in 1 trait category and/or across different purebred-crossbred combinations or that accurately estimating the r_{pc} is difficult. This figure, however, clearly shows that for all 6 trait categories the true r_{pc} is likely different from 1. Average r_{pc} estimates are slightly above 0.6 for Growth, Meat amount, Meat quality, and Feed, and slightly below 0.6 for Fertility and Index (Table 1). For all traits, the average r_{pc} was below 0.8, suggesting that it is important to use a combined crossbred and purebred selection scheme (**CCPS**) for all traits (Wei and Van der Werf, 1994).

The range of estimates is smaller for Feed and Index traits, which is probably due to the low number of estimates. The 4 trait categories with a considerable amount of information show more or less the same range in r_{pc} estimates, although the average r_{pc} is slightly lower for Fertility than for the production traits (Growth, Meat Amount, and Meat Quality). Three out of the 4 studies estimating r_{pc} for fertility traits and production traits in the same animals also showed lower r_{pc} estimates for fertility traits (Robinson et al., 1964; Wong et al., 1971; McLaren et al., 1985; Nakavisut et al., 2005). It has been suggested that nonadditive effects, like epistasis and dominance, are more important for traits with a low heritability, like fertility, than for traits with a high heritability, like production traits (Sellier, 1976; Nakavisut et al., 2005). This is in agreement with the larger dominance variance relative to the additive variance for fertility traits compared to production traits reported in purebred Yorkshire pigs (Culbertson et al., 1998). As explained before, nonadditive effects in combination with differences in allele frequency between the parental populations can result in an r_{pc} below 1. From the small and nonsignificant differences between the trait categories in our review study, however, no final conclusion can be drawn about the difference in r_{pc} across traits.

Heritability Estimates

Besides r_{pc} estimates, most studies also reported h^2 estimates for PB and CB performance. Generally, traits with a higher h^2 for PB performance also had a higher h^2 for CB performance (Fig. 4). The average h^2 for PB and CB performance was similar. Wei et al. (1991a) theoretically showed that for traits with dominant gene

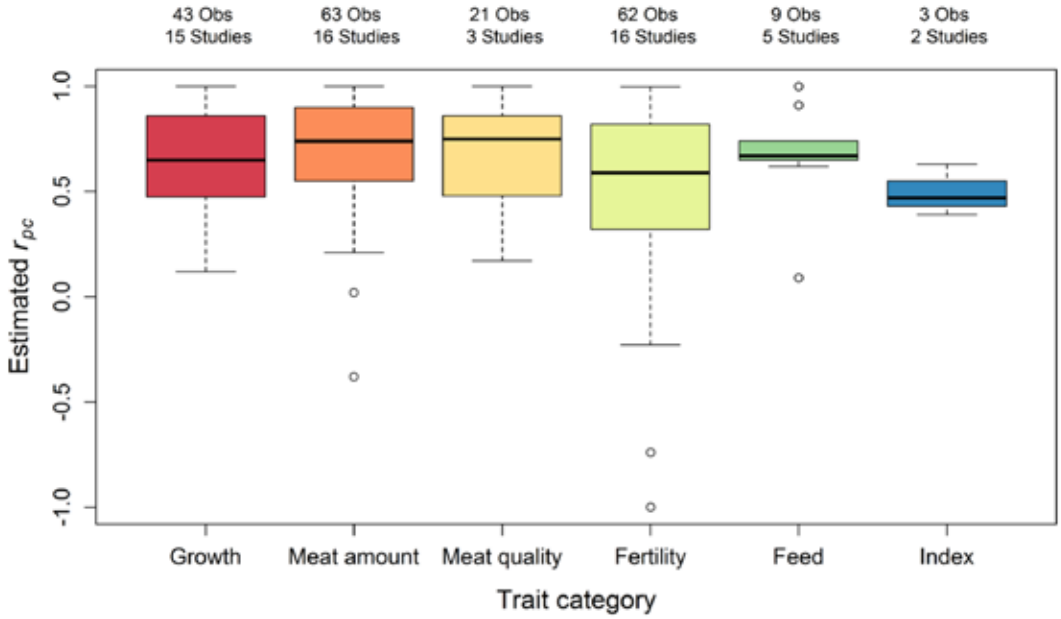

Figure 3. Estimated r_{pc} values for the 6 different trait categories.

action, the additive genetic variance is expected to be higher in crossbreds compared to purebreds. The expected difference in additive genetic variance depends on the difference in allele frequency between both parent populations and the level of dominance for the trait. For instance, when the dominance effect is half the additive effect, the additive genetic variance in crossbreds can be up to 50% larger than the average additive genetic variances in both purebred parent populations. Although in a number of studies additive genetic variances were indeed greater for crossbreds compared to purebreds (e.g., Brandt and Täubert, 1998; Cecchinato et al., 2010; Bloemhof et al., 2012; Tusell et al., 2016), there was no general trend across the studies that confirmed this expectation. So, the similar average h^2 estimates for PB and CB performance indicate that either the studied traits are not largely affected by dominance, or that environmental variance is greater in crossbreds as well. Because r_{pc} estimates are different from 1, it is likely that dominance effects are present. Therefore, it is more likely that the environmental variance is greater in crossbreds, which is indeed confirmed by several studies (Täubert and Brandt, 2000; Habier et al., 2007b; Zumbach et al., 2007; Bloemhof et al., 2012), although no general trend is observed across all studies. This larger environmental variance for crossbreds might be a result of a scale effect (Habier et al., 2007b), because crossbreds tend to outperform their purebred parents, or might

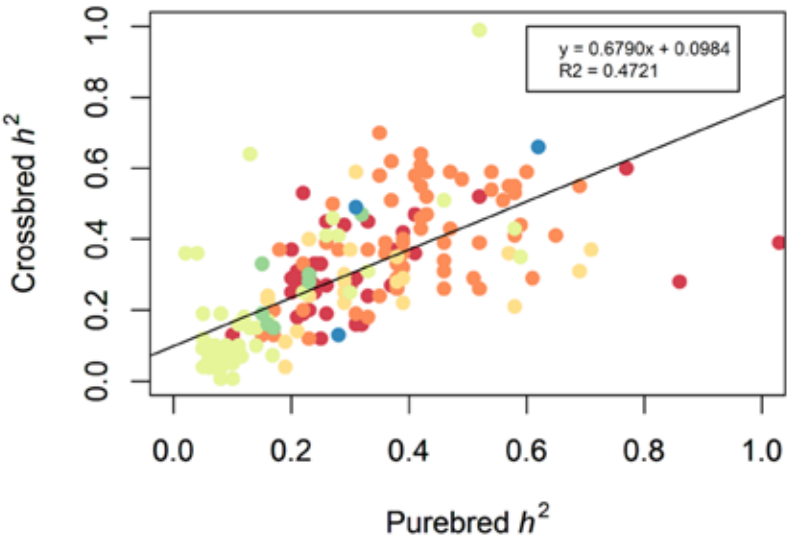

Figure 4. Heritability in crossbreds versus heritability in purebreds. Different colors represent the different trait categories (red = Growth; orange = Meat amount; yellow = Meat quality; light green = Fertility; green = Feed; blue = Index).

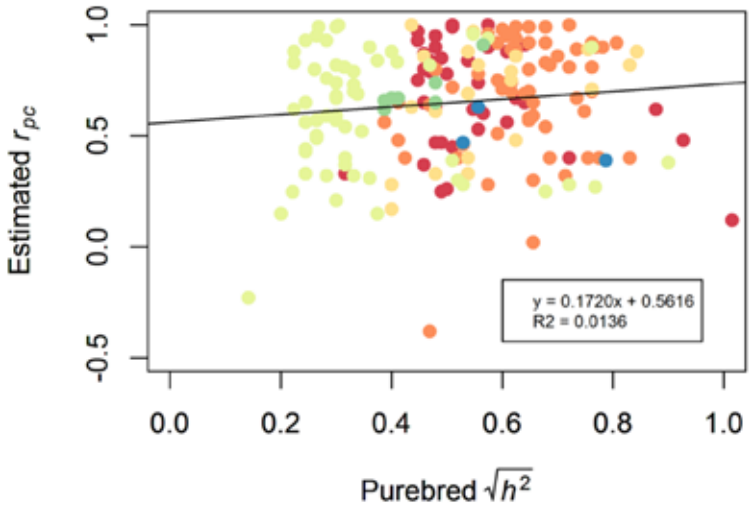

Figure 5. Estimated r_{pc} versus the square root of the heritability in purebreds. Different colors represent the different trait categories (red = Growth; orange = Meat amount; yellow = Meat quality; light green = Fertility; green = Feed; blue = Index).

be a result of the less controlled and therefore more variable commercial conditions under which crossbreds are generally kept (Wei and van der Werf, 1995).

Brandt and Täubert (1998) suggested a relation between r_{pc} and h^2 of a trait, with higher r_{pc} values for traits with a higher h^2. This is in agreement with the suggestion that nonadditive effects, which reduce r_{pc}, may be more important for traits with a low heritability (Sellier, 1976; Nakavisut et al., 2005). We investigated this suggested relationship across all 26 reviewed studies that reported both r_{pc} and h^2 estimates. As indicated before, the r_{pc} is the square root of the proportion of genetic variance in one trait that could be explained by the genetic variance in the other trait. The h^2 of a trait is the proportion of the total variation that could be explained by genetics. To get r_{pc} and h^2 on comparable scales, r_{pc} estimates were related to the square root of the h^2 values. Both the square root of the h^2 for PB performance (Fig. 5) as well as the h^2 for CB performance (Fig. 6) seem to be unrelated to the r_{pc} value (R^2 = 0.0136 and R^2 = 0.0023, respectively). So, across all studies, there is no evidence for the suggested relationship between r_{pc} and h^2.

Estimates of r_{pc} and the 3 Components of r_{pc}

As indicated before, the r_{pc} consists of 3 main components: 1) genotype by genotype interactions, 2) genotype by environment interactions, and 3) differences in methods to measure the traits. Here, we will try to disentangle the 3 components. In total, 92 r_{pc} estimates from 11 studies are between purebreds and crossbreds in the same environment and using the same method to measure the trait. Those estimates reflect the r_{pc} due

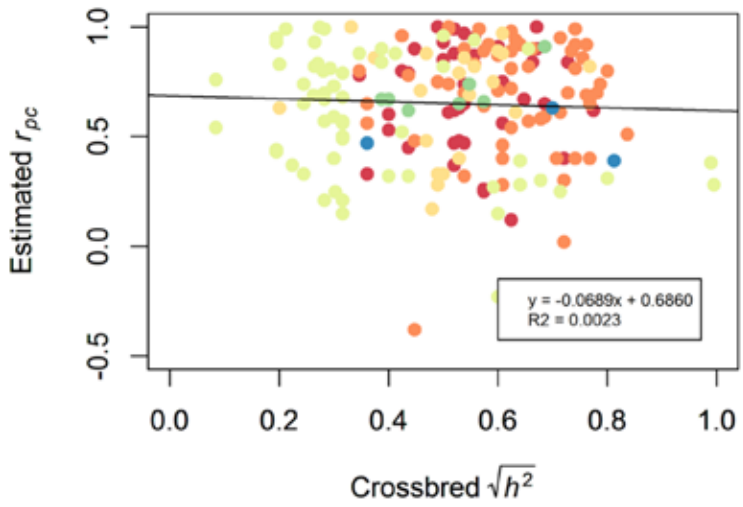

Figure 6. Estimated r_{pc} versus the square root of the heritability in crossbreds. Different colors represent the different trait categories (red = Growth; orange = Meat amount; yellow = Meat quality; light green = Fertility; green = Feed; blue = Index).

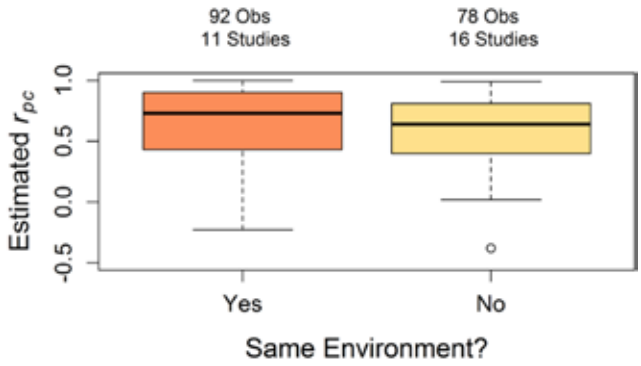

Figure 7. Estimated r_{pc} values for studies housing purebreds and crossbreds in the same or different environments.

to genotype by genotype interactions. Moreover, 78 r_{pc} estimates from 16 studies are between purebreds and crossbreds in different environments and using the same methods to measure the trait. Those estimates reflect the r_{pc} due to both genotype by genotype interactions and genotype by environment interactions. Finally, 19 r_{pc} estimates from 3 studies are between purebreds and crossbreds in different environments and using different methods of measuring the trait. Those r_{pc} estimates reflect the r_{pc} due to all 3 components.

In Fig. 7, the r_{pc} estimates for the first 2 classes, either including or excluding differences in environments, are shown. Unfortunately, the number of studies and observations using different methods to measure the trait is too low to investigate the effect of this component; therefore, this class is not included. Figure 7 shows that the range of estimates is wide for both classes. The average r_{pc} estimate of 0.66 between purebreds and crossbreds in the same environment indicates that genotype by genotype interactions have a large effect on the r_{pc}. Including genotype by environment interactions resulted in a slightly lower average r_{pc} of 0.61, which shows that there is a small effect of genotype by environment interactions. This minor decrease in r_{pc} suggests that the effect of genotype by environment interactions is smaller than the effect of genotype by genotype interactions.

Recommendations and Guidelines

As explained in the theory section, the value for r_{pc} as well as the heritabilities for PB and CB performance are required for the optimization of breeding programs for CB performance. An accurate estimation of r_{pc} is difficult and requires a substantial amount of data (Robertson, 1959; Bijma and Bastiaansen, 2014). Therefore, we recommend studies investigating r_{pc} to report both h^2 values and r_{pc} estimates with standard errors or confidence intervals. The additive genetic variances for both PB and CB performance, together with the r_{pc}, can be used to estimate the response to selection in crossbreds when knowing the response to selection in purebreds. Therefore, we recommend to report additive genetic variances for PB and CB performance as well.

For comparing r_{pc} estimates of different studies, it is important to clearly describe the environments in which purebred and crossbred animals were kept, even when both groups were kept in the same environment. It is for example relevant to know whether the same biosecurity level and feeding regimes were applied, or whether group size was the same. For instance, feeding animals ad libitum or not might affect the results, yet only 2 studies included in this review reported that information (Zumbach et al., 2007; R. M. Godinho, Animal Breeding and Genomics, Wageningen University and Research, Wageningen, personal communication).

The r_{pc} may have different values for each combination of purebred parental line and crossbred. In a number of studies, however, 1 r_{pc} was estimated between 2 or more parental purebred lines and 1 or more types of crossbreds. In traditional pedigree BLUP models, relationships between the parental lines are all zero; therefore, the value of the genetic correlation between the lines is not relevant. In contrast, in GBLUP models, relationships between the lines vary around 0. Therefore, modeling performance of different parental lines as the same trait in GBLUP assumes a genetic correlation of 1 between both purebred parental lines. This assumption is very unrealistic given the differences in genetic background between lines in combination with nonadditive effects (Fisher, 1918; Falconer and Mackay, 1996), as has been shown by estimated genetic correlations between different cattle breeds ranging from −0.01 to 0.79 (e.g., Karoui et al., 2012; Zhou et al., 2014). Furthermore, the 10 studies that estimated r_{pc} separately for each purebred-crossbred combination showed absolute differences in r_{pc} between the purebred lines ranging from 0.01 to 0.86, with an average of 0.23. This confirms our expectation that r_{pc} values are likely to differ across combinations of purebred lines and crossbreds. Moreover, we expect the r_{pc} to be lower between a purebred dam line and its 3-way cross offspring compared to its 2-way cross offspring, because the genetic background is more different. Unfortunately, the data were too limited to investigate this expectation in the reviewed studies. Altogether, we strongly recommend estimating and presenting separate r_{pc} values for each unique purebred-crossbred combination.

Genomic relationships instead of pedigree relationships are increasingly more often used in estimation of both breeding values and variance components. Generally, genomic relationships are more precise than

pedigree relationships, because they capture variation between relatives due to Mendelian sampling and take relationships between founder individuals in the pedigree into account (Nejati-Javaremi et al., 1997; Hill and Weir, 2011). Particularly for distant relationships, genomic relationships are more precise (Hill and Weir, 2011), due to the build-up of Mendelian sampling over generations. The commercial crossbred animals are generally distantly related to the purebred selection candidates, stressing the benefit of using genomic information for purebred and crossbred analyses. Moreover, by using genomic information, crossbred animals without pedigree information can be included, which increases the amount of information that can be used. It is indeed shown that genomic information reduces the standard error of estimating r_{pc} (Xiang et al., 2016a,b). Therefore, we strongly recommend that future studies estimating r_{pc} use genomic information.

The r_{pc} can be different from 1 due to 3 different components. To predict the genetic progress in crossbreds due to selection in purebred animals, the value of r_{pc} is important, regardless of the impact of each of the 3 different components on this r_{pc} value. For optimizing breeding programs, however, it is useful to know whether the r_{pc} is different from unity due to differences in genetic backgrounds, environments, or trait measurements. When the r_{pc} is mainly influenced by differences in genetic background, measuring crossbred animals, either in commercial or nucleus environments, is essential. However, when the r_{pc} is mainly influenced by differences in the environment of purebred versus crossbred animals, genetic progress could be increased by measuring purebred animals in commercial environments. For example, full-sibs of the selection candidates could be measured in a commercial environment, which increases the relationships between selection candidates and performance records and can increase the response to selection.

Based on the reviewed studies, it appears that the effect of differences in genetic background on r_{pc} is larger than of differences in environment. Unfortunately, it was not possible to investigate the effect of differences in trait measurements due to the low amount of data. The high correlations (~0.85) between ultrasound and carcass measurements on the same animals (Giles et al., 1981; Lo et al., 1992), however, suggest that differences in trait measurements have a relatively small contribution to r_{pc}. For a more conclusive dissection of the components of the r_{pc}, more research is needed. The ideal experiment involves a design where purebreds and crossbreds are kept under both nucleus and commercial conditions and data are collected on all animals using the method generally used in purebreds and the method generally used in crossbreds (Fig. 8). In Fig. 8, the gray boxes represent the data that are generally collected (purebreds in nucleus environment and crossbreds in commercial environment). Collecting data in all 4 boxes using the 2 methods of data collection enables the estimation of genotype by genotype interactions ($r_{G\times G}$), genotype by environment interactions ($r_{G\times E}$), correlation due to trait measurement (r_T), and the purebred-crossbred correlation (r_{pc}). We recommend at least measuring animals in 1 of the boxes using the 2 different methods to investigate r_T. When it is only possible to collect data from 3 different boxes, we recommend collecting data from purebreds in commercial environments (white box) as well as purebreds in nucleus and crossbreds in commercial environments (gray boxes), which still enables us to disentangle the different components from the r_{pc}. This is because collecting data of purebreds under commercial conditions can be beneficial for the breeding program when the r_{pc} is mainly a result of genotype by environment interactions, as explained before.

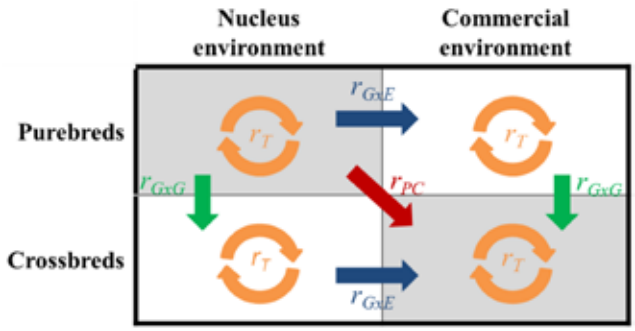

Figure 8. Experimental design to disentangle the effect of the different components on r_{pc}. Currently, data are collected only in the gray boxes using 1 method to measure the trait. The arrows within the boxes indicate the correlation due to trait measurements (r_T) when measurements are done using 2 different methods. The different arrows between the boxes indicate genotype by genotype interactions ($r_{G\times G}$), genotype by environment interactions ($r_{G\times E}$), and the total purebred-crossbred correlation (r_{pc}).

Genotype by environment interactions might not only play a role between nucleus and commercial farms, but also among purebred farms and among crossbred farms. Due to differences in management and housing conditions, the nucleus environment is not exactly the same for all purebred animals and the commercial environment is not exactly the same for all crossbred animals. The extent of genotype by environment interaction among nucleus or commercial herds is, however, not known. This can complicate the estimation of r_{pc} when information from multiple purebred and crossbred farms are combined. Investigating the underlying nature of the r_{pc} is probably easiest by focusing on 1 purebred and 1 crossbred farm. For estimating the r_{pc} relevant for a breeding program, however, we recom-

mend combining information from a group of purebred farms and a group of crossbred farms.

Conclusion

The genetic correlation between purebreds and crossbreds, r_{pc}, is an important component in pig and poultry breeding. This r_{pc} can be different from 1 due to 3 components: 1) genotype by genotype interactions, 2) genotype by environment interactions, and 3) differences in trait measurements. In this paper, we theoretically showed that direct selection for CB performance reduces the response to selection in purebreds for PB performance by a factor $\frac{1}{r_{PC}^2}$, when achieving the same crossbred response as obtained with indirect selection based on PB performance. This implies that direct selection for CB performance leads to less extreme PB performances and thus potentially easier management in the nucleus, especially for traits with low r_{pc}. The review of r_{pc} in pigs showed that r_{pc} is around 0.6 for all trait categories, e.g., Growth, Meat amount, Meat quality, Feed, and Fertility. Genotype by environment interactions appeared to have a smaller contribution to r_{pc} than genotype by genotype interactions. More research regarding the impact of the different components on the r_{pc} can help to improve breeding programs. Future studies are advised to report characteristics of the herd environments in detail, to report estimated h^2 and additive genetic variances for purebreds and crossbreds and estimated r_{pc} with standard errors or confidence intervals, to estimate separate r_{pc} for different pure lines, and to genotype the animals under study.

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