

Animal board invited review: The purebred-crossbred genetic correlation in poultry

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ABSTRACT

The purebred-crossbred genetic correlation (r_{pc}) is a key parameter to determine whether the optimal selection of purebred animals to improve crossbred performance should rely on crossbred phenotypes, purebred phenotypes, or both. We reviewed published estimates of the r_{pc} in poultry. In total, 19 studies were included, of which four were on broilers and 15 on laying hens, with 150 r_{pc} estimates for nine different trait categories. Average reported r_{pc} estimates were highest for egg weight, egg quality and egg colour (0.74–0.82), intermediate for BW, maturity and mortality (0.61–0.70) and egg number (0.58), and low for resilience (0.40) and body conformation (0.14). Most studies were based on measuring purebred and crossbred phenotypes in the same environment and thus did not capture the contribution of genotype by environment interactions to the r_{pc} , suggesting that the presented average estimates may be higher than values that apply in practice. Nearly all studies were based on two-way crossbred animals. We hypothesised that r_{pc} values for a two-way cross are good proxies for r_{pc} of a four-way cross. Only eight out of 19 studies were published in the last 25 years, and only two of those used genomic data. We expect that more studies using genomic data may be published in the coming years, as the required data may be generated when implementing genomic selection for crossbred performance, which will lead to more accurate r_{pc} estimates. Future studies that aim to estimate r_{pc} are encouraged to capture the genotype by environment interaction component by housing purebred and crossbred animals differently as is done in practice. Moreover, there is a need for further studies that enable to explicitly estimate the magnitude of genotype by environment versus genotype by genotype interactions for multiple trait categories. Further, studies are advised to report: the specific housing conditions of the animals, any differences between measurements of purebred versus crossbred performance, and the heritabilities of purebred and crossbred performance.

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Implications

Poultry breeding relies on selection in purebred lines, while commercial animals are crossbreds. The so-called purebred-crossbred genetic correlation determines the genetic similarity between purebred performance recorded in the nucleus and crossbred performance in commercial flocks. Based on a literature search, we found that for the majority of traits, this correlation lies between 0.6 and 0.8. These results imply that for most traits in poultry, it is beneficial to perform selection based on data from both purebred and crossbred performance.

Introduction

In poultry production, the broilers and layers at commercial farms are crossbred (CB) animals arising from crossing purebred

(PB) breeding lines. This routine crossbreeding has been adopted since the 1940s and 1950s (Muir and Aggrey, 2003; Tixier-Boichard et al., 2012). The main reasons to use CB instead of PB animals for commercial production are: (1) making use of the specific strengths of different PB lines that can be selected for in somewhat other directions (Smith, 1964), (2) making use of heterosis (Dickerson, 1973), the phenomenon that CB animals outperform the average of their PB parents, and (3) avoiding the need to distribute PB animals outside the breeding programme, such that competitors do not get access to the PB genetics of a breeding company. In the pyramidal breeding structure used in poultry breeding, selection takes place in PB lines, with the aim to improve the performance of their CB descendants in commercial flocks. Often, PB and CB performance are not the same trait. Both traits have their own genetic SD and heritability, while the genetic correlation between them, known as the purebred-crossbred genetic correlation (r_{pc}) (e.g. Wei and Van der Werf, 1995), tends to be lower than one. The r_{pc} comprises three main components (for more details, see: Wientjes and Calus, 2017): (1) genotype by genotype interac-

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tions (**GxG**), including dominance and epistasis, which can result in different gene effects between PB and CB animals when allele frequencies are different in the parental lines or breeds, (2) genotype by environment interactions (**GxE**), because CB production animals are typically kept in a commercial environment that deviates from the high biosecurity environment in which PB breeding animals are kept, and (3) differences in the method of measuring the same trait in PB and CB animals.

Since poultry breeding programmes ultimately aim to improve CB performance, breeding methods that use records of both PB and CB performance have been developed. One of such methods is reciprocal recurrent selection (**RRS**), in which animals from PB lines are evaluated based on the performance of reciprocal crosses between them (Bell et al., 1950; Wei and van der Steen, 1991). Another method is combined CB and PB selection (**CCPS**), in which selection is based on the performance of both PB and CB offspring (Wei and van der Werf, 1994). It has been recognised for a long time that the optimal use of crossbred information for selection in a pyramidal breeding programme to achieve the maximum response to selection depends heavily on the value of the r_{pc} , with the expected benefit of measuring CB performance being limited for high values of r_{pc} (Hill, 1971; Bell, 1982; Wei and van der Steen, 1991; Bijma and van Arendonk, 1998).

In a genomic breeding programme that aims to improve CB performance, optimal selection decisions may be based only on measured performance in PB animals if the r_{pc} is relatively close to one (i.e. greater than ~ 0.7) (van Grevenhof and van der Werf, 2015; Chu et al., 2018; Wientjes et al., 2020), only on measured performance in CB animals if the r_{pc} is close to 0, or a combination of PB and CB performance for intermediate values of the r_{pc} . It is, therefore, important to have an accurate estimate of the r_{pc} for any trait subject to selection. Accurately estimating the r_{pc} has a number of challenges. Traditionally, when estimating the r_{pc} using pedigree and phenotype data, the most powerful design was to have sires with both PB and CB offspring (Bijma and Bastiaansen, 2014). Such a design may arise in a breeding programme as a by-product of RRS or CCPS, where both PB and CB offspring of the same parents are generated. Alternatively, a dedicated experiment can be set up to generate the required animals. Before any data on CB animals has been recorded, r_{pc} values reported in the literature can be used as a starting point.

The aim of this paper was to review published estimates of the r_{pc} in poultry, including both laying hens and broilers. We start with describing our literature search, followed by a description and more detailed analysis of the published r_{pc} values.

Material and methods

Literature search

As a starting point, we used the 11 references listed in Table 2 of Wei and van der Steen (1991). Subsequently, we performed a literature search in June 2023, in Web of Science (Clarivate Analytics, 2023). The search terms used were ("layer" OR "laying" OR "broiler") AND (("cross*" AND "pure*" AND "genetic") OR "purebred-crossbred") in all fields, including title and abstract. This yielded 84 publications, of which seven reported estimated r_{pc} values. Of those seven studies, one was among the 11 references listed in Table 2 of Wei and van der Steen (1991). Five out of the remaining six citations were published in later years. For all selected publications and the publication of Wei and van der Steen (1991), the reference lists and citations to those papers were screened, yielding another six studies reporting estimated r_{pc} values. Finally, we screened the proceedings of all World Conferences of Genetics Applied to Livestock Production (1st–12th edition), which yielded

another two studies reporting estimated r_{pc} values. This resulted in a total of 25 identified studies that reported at least one estimated r_{pc} value for layers or broilers. From those 25 studies, we removed three that did not report SE of estimated r_{pc} values or numbers of individuals used in the analysis (Comstock and Robinson, 1957; Pirschner and Mergl, 1977; Kumar et al., 2013), and another three that were not written in English (Mergl, 1977; Mielenz and Mueller, 1989; Wang and Pirschner, 1992). For the remaining 19 studies, we gathered information as outlined in Supplementary Table S1. The main aspects were: whether the study investigated broilers or layers, the type of cross and the lines or breeds involved, the traits that were investigated, the numbers of PB and CB animals used, estimated genetic parameters including genetic SDs and heritabilities for PB and CB performance, and the estimated r_{pc} .

Computation of average purebred-crossbred genetic correlations

One of our aims was to provide average estimates of r_{pc} values for traits and trait categories across studies. Duenk et al (2019) estimated r_{pc} using different models, and pedigree or genomic information. For their study, only the estimates based on an animal model using genomic data were included, as these were reported to be more accurate. Two other studies computed r_{pc} values based on common sires as well as common dams of the PB and CB offspring with phenotypes recorded (Pirschner and VonKrosigk, 1973; Besbes and Gibson, 1999). In those cases, we only used the estimates computed based on common sires, because those were expected to be more accurate.

SEs of estimated purebred-crossbred genetic correlations

In total, four of the retained studies did not report the SE of the presented r_{pc} values, of which three did report the numbers of individuals used in the analysis (Hale and Clayton, 1965; Besbes and Gibson, 1999; Cavero et al., 2010), while for the fourth study (Picard Druet et al., 2019) estimated SE were provided to us by P. Le Roy (INRAE, Rennes, France, personal communication). Bijma and Bastiaansen (2014) presented an equation that allows to approximate the SE of the r_{pc} from the number of common sires between PB and CB, and the reliabilities of the sire estimated breeding values for PB and CB performance. To compute the reliabilities of the sire estimated breeding values, we used the formula $\frac{\frac{1}{4}nh^2}{1+\frac{1}{4}(n-1)h^2}$ (Cameron, 1997), where h^2 is the heritability for PB or CB performance, and n is the number of PB or CB offspring, which was approximated by dividing the total number of included PB or CB animals by the number of common sires. For 10 studies with the required input for the Bijma and Bastiaansen equation available, including estimated heritabilities for PB and CB performance, we computed approximate SE values of the reported r_{pc} values. For the seven out of those 10 studies that did report SE values, we compared those against the approximated SE values. For the remaining three studies that did not report SE values, we used the approximated SE values in further comparisons.

Results and discussion

In total, 19 studies with 125 estimated r_{pc} values were retained. Nine of the studies were published until 1983, and the other 10 were between 1990 and 2022 (Fig. 1). An overview of the information that was collected from each study is presented in Supplementary Table S1, while the values for each of those characteristics are presented in Supplementary Table S2. Ten studies made use of data generated from ongoing RRS schemes, while the other nine studies

were based on data from dedicated experiments. All 10 studies published until 1990 and one study published in 2006 computed the r_{pc} based on estimated covariances between progeny means, while the other eight more recent studies all used a sire or animal model implemented using REML. Genomic information was only used in two studies (Duenk et al., 2019; Picard Druet et al., 2019), while all other studies relied on pedigree information only. Only four of the studies included broiler data (Aggarwal and Sinha, 1979; Singh et al., 1983; Duenk et al., 2019; Duijvesteijn et al., 2022), while the other 15 studies included layer data. Thus, we will mainly focus on evaluating the layer estimates.

In total, seven studies reported SE and provided all parameters required to compute approximate SE. We compared the approximated against the reported SE for those seven studies and confirmed that the equation by Bijma and Bastiaansen (2014) provides approximations that are in most cases relatively close to the reported SE (Supplementary Fig. S1).

Estimated purebred-crossbred genetic correlations across different traits and trait categories

The average reported r_{pc} value, across all studies and traits, was 0.63, which was similar to the average reported value in pigs (Wientjes and Calus, 2017). The observed variation in r_{pc} estimates, both within and across trait categories, is greater in poultry (Fig. 2) than in pigs, where a narrower range of estimates was observed (Wientjes and Calus, 2017).

In the layer studies, eight different trait categories were identified, including in total 54 different traits (Fig. 2; Table 1). The broiler studies only included BW and body conformation traits. In total, nine r_{pc} estimates were greater than 1.0; those estimates were set to 1.0 before being included in Fig. 1 and Table 1, while the original estimates were retained in Supplementary Table S2. Most r_{pc} estimates were for the egg-related trait categories. Based on 37 estimates, the average r_{pc} for egg number was 0.58, with 11 estimates being below 0.4. The other three egg-related trait categories (egg weight, egg quality and egg colour) had average r_{pc} values in the range of 0.74 to 0.82, with less variation between estimates than egg number. Maturity of laying hens had an average r_{pc} of 0.64. Mortality and resilience both had six estimates, which in both cases originated from only one study, with average r_{pc} values of 0.70 and 0.40, respectively. The trait category BW was the

only one with estimates from both broilers and layers, with an average value of 0.61 and eight out of 20 estimates being below 0.6. The average across the 13 layer estimates (0.65) was somewhat higher than the average across the seven broiler estimates (0.52). Finally, the lowest average r_{pc} value of 0.14 was observed for body conformation in broilers. While this was based on only five values obtained from two studies, these estimates were all consistently low, ranging between 0.10 and 0.17.

Across all included studies, the reported r_{pc} estimates had a strong relationship with their SE, with lower r_{pc} estimates being associated with on average larger SE (Supplementary Fig. S2). This follows the expectation, given that the SE of a genetic correlation (r_g) is approximately proportional to $(1 - r_g^2)$ (Robertson, 1959). This relationship likely explains the observation that all r_{pc} estimates with a SE below 0.04 had a value of 0.73 or higher. In other words, when the true r_{pc} value is low (e.g. <0.70), a (very) large dataset is required to obtain a small SE (i.e. <0.04).

In all studies, reciprocal crosses resulted in different r_{pc} estimates, while the magnitude of the differences varied across studies (Fig. 3). These differences could not be explained by variation in the evaluated traits across studies, as considerable differences were observed for reciprocal r_{pc} estimates for all trait categories (Supplementary Fig. S3). While some of these differences may be due to inaccuracy of the estimates, comparing the absolute differences of reciprocal r_{pc} estimates against their mean SE did not show a clear pattern (Supplementary Fig. S4), suggesting that other factors play a role here as well. Thus, it seems likely that these differences at least partly reflect real differences in the r_{pc} between the reciprocal crosses.

Estimated r_{pc} values tended to be slightly higher for traits with higher heritability for the PB and CB animals (Supplementary Figs. S5 and S6). Note that estimated r_{pc} values were plotted against the square root of the estimated heritability to put both parameters on the same scale (for an explanation, see: Wientjes and Calus, 2017). Perhaps with higher heritability the impact of GxE is relatively smaller, and non-additive genetic effects play a relatively less important role, which could explain the higher r_{pc} values. In most cases, PB and CB heritabilities were similar, while in a few cases, the PB heritability was considerably higher than the CB heritability (Supplementary Fig. S7). Similar relationships between estimated r_{pc} values and heritabilities were observed in pigs (Wientjes and Calus, 2017).

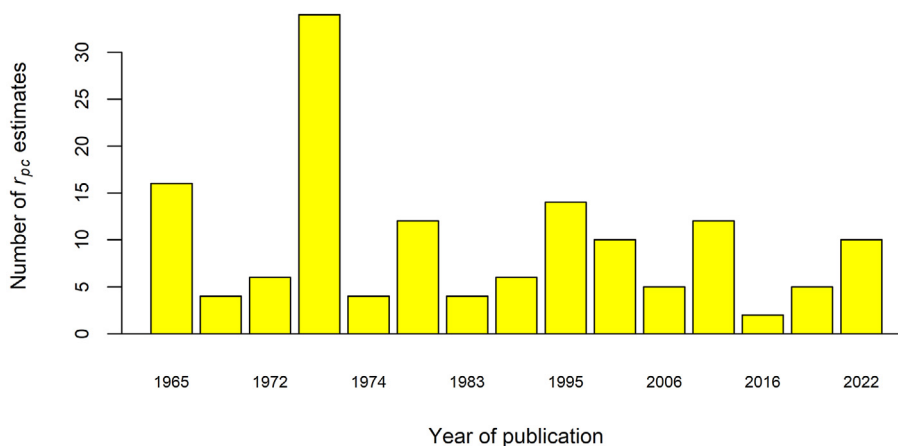


Fig. 1. Overview of all reviewed purebred-crossbred genetic correlation estimates in poultry by year (in 1965, 1979, 2019 and 2022 two studies were published; in all other years only one study). This includes the following 19 studies: (Hale and Clayton, 1965; Krause et al., 1965; Biswas and Craig, 1969; Taran et al., 1972; Pirchner and VonKrosigk, 1973; Singh and Dev, 1974; Aggarwal and Sinha, 1979; Rabsztyn, 1979; Singh et al., 1983; Rabsztyn, 1990; Wei and Van der Werf, 1995; Besbes and Gibson, 1999; Singh and Singh, 2006; Caverio et al., 2010; Mulder et al., 2016; Duenk et al., 2019; Picard Druet et al., 2019; Bedere et al., 2022; Duijvesteijn et al., 2022). Abbreviations: r_{pc} = purebred-crossbred genetic correlation.

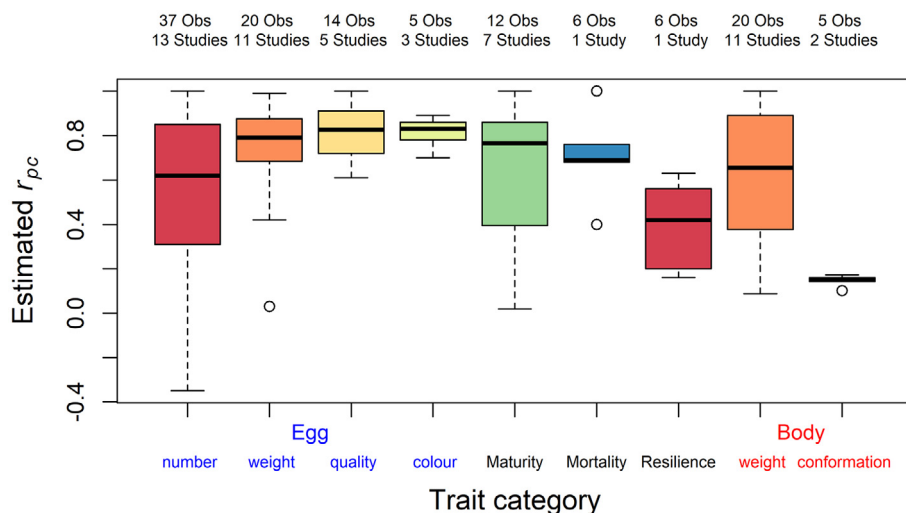


Fig. 2. Overview of all reviewed purebred-crossbred genetic correlation estimates in poultry by trait category. Abbreviations: Obs = Observed number of purebred-crossbred correlation estimates; r_{pc} = estimates of the purebred-crossbred genetic correlation.

Study design

Nearly all studies estimated the r_{pc} between PB lines and two-way CB animals that were derived from crossing the PB lines or breeds. Only one study estimated the r_{pc} between a three-way cross and its PB paternal line A (Duenk et al., 2019). In all 18 other studies, the CB animals were F1's, while in seven of those studies, r_{pc} estimates were reported for both reciprocal crosses. In those seven studies, the r_{pc} was estimated between the sire line and their CB offspring, i.e. between line A and the AB CB animals and between line B and the BA CB animals, where e.g. AB denotes that the sire originates from line A and the dam originates from line B. In one of the other studies, one cross was used to compute the r_{pc} with both PB parental lines, relying on common sires for their line 1 and common dams for their line 2 (Besbes and Gibson, 1999).

In most cases, the (majority of the) information to estimate the r_{pc} came from having common sires between the PB and CB phenotyped animals. One study estimated the r_{pc} between a particular PB line with their two-way offspring both based on common sires and common dams (Pirchner and VonKrosigk, 1973). For instance, the estimates between line C and their crossbred offspring were obtained both using common sires from line C and CD crossbreds, as well as using common dams from line C and DC crossbreds. The comparison of sire versus dam-based estimates in this study may suggest that the dam-based estimates tend to be lower than the sire-based estimates (Supplementary Fig. S8). Considering that common sires generally provide more power due to having larger offspring groups, and thus more accurate estimates than common dams, this difference may, however, also simply be due to common dam-based estimates being less accurate.

Genotype by environment interaction

In seven studies, the PB and CB animals were housed in at least partly different environments (Krause et al., 1965; Pirchner and VonKrosigk, 1973; Wei and Van der Werf, 1995; Cavero et al., 2010; Mulder et al., 2016; Bedere et al., 2022; Duijvesteijn et al., 2022). In five studies, the PB and CB animals were housed in the same environment (Hale and Clayton, 1965; Singh and Dev, 1974; Besbes and Gibson, 1999; Singh and Singh, 2006; Duenk et al., 2019). In the remaining seven studies, the housing conditions were not detailed in the paper. In the seven studies with different environments, the main observed difference is that PB animals

were kept in individual cages, and CB animals in group cages (Krause et al., 1965; Wei and Van der Werf, 1995; Cavero et al., 2010; Mulder et al., 2016; Bedere et al., 2022). This reflects situations in practice where individual housing of the PB animals is needed to enable the recording of individual rather than group phenotypes. This particular difference in housing has two different aspects that affect the observed r_{pc} . The first aspect is that the PB and CB animals are housed in a different environment, with interactions between animals being present in one environment but not in the other, potentially resulting in GxE interactions. The second aspect is that the measurements per se are different, taken from individuals for PB and from groups of individuals for CB animals. This reflects a difference in the trait definition, which may also lower the genetic correlation between the observed PB and CB performance. As an example, Mulder et al (2016) reported a genetic correlation for the trait environmental variance in eggshell colour between individually housed PB and group-housed CB of 0.70. Using the derived genetic correlation between PB hens either individually or group-housed, which was only slightly higher than the estimated r_{pc} , it was predicted that if the trait for both PB and CB would be based on individual phenotypes, the genetic correlation between PB and CB would be ~ 0.95 . This large difference may be specific for traits reflecting environmental variance measured on individuals versus groups and does not necessarily provide an expectation for what this difference could be in other traits. Nevertheless, this example does show that differences in trait definition as applied to PB versus CB animals should be considered, and ideally, its contribution to the r_{pc} should be quantified. Moreover, it shows that when reporting r_{pc} estimates, it is important to also report the housing conditions of the animals.

Given that only seven out of 19 studies had different environments for CB and PB animals, which were a reflection of differences in environments observed in practice, the majority of the studies ignored GxE interactions. The largest numbers of r_{pc} estimates with GxE present or not were observed for the trait categories egg number and egg weight (Supplementary Fig. S9). Across 19 estimates from eight studies that measured egg number in the same environment, the average r_{pc} was 0.69, while across 18 estimates from five studies that measured egg number in different environments, the average was only 0.47. For egg weight, the average r_{pc} was actually higher (0.88) when measured in different, compared to when measured in the same environment (0.66), but the average with different environments was based only on eight estimates from three

Table 1

Overview of the nine trait categories, traits, numbers of estimates and average estimates of reviewed purebred-crossbred genetic correlations in poultry.

Trait category	Number of traits	Number of estimates	h^2 (PB)	h^2 (CB)	r_{pc}	Traits (number of estimates)
Egg number	19	37	0.32	0.27	0.58	18–26 weeks (4) 18–36 weeks (2) 18–64 weeks (2) 19–25 weeks (1) 20–27 weeks (2) 25–83 weeks (2) 26–38 weeks (1) 26–54 weeks (1) 26–65 weeks (2) 28–47 weeks (2) 36–64 weeks (2) 48–68 weeks (2) 3.5-month period in 2nd year (2) First egg to 37 weeks (2) Period undefined (2) Until 40 weeks (1) Until 42 weeks (1) Until 43 weeks (2) Until 64 weeks (4)
Egg weight	9	20	0.56	0.51	0.74	Autumn weight of eggs (4) Av. egg weight at 29, 34 & 45 weeks (2) Av. egg weight at 30–35 and 40–45 weeks (2) Av. egg weight 38–54 weeks (1) Av. egg weight 39–40 weeks (1) Mature egg weight (2) Egg weight (4) Egg weight at 35 weeks (2) Egg weight at 30–35 weeks (2)
Egg quality	8	14	0.41	0.27	0.82	Albumen height at 35 weeks (2) Av. eggshell strength 38–54 weeks (1) Av. eggshell strength at 40, 43 and 46 weeks (2) Blood spots at 35 weeks (2) Eggshell strength (1) Egg specific gravity at 35 weeks (2) Egg specific gravity at 30–35 weeks (2) Egg specific gravity at 40–45 weeks (2)
Egg colour	3	5	0.38	0.40	0.81	Eggshell colour (2) Eggshell colour at 30 weeks (2) Environmental variance of eggshell colour (1)
Maturity	3	12	0.46	0.48	0.64	Age at first egg (6) Age at sexual maturity (4) Maturity (2)
Mortality	4	6	0.05	0.14	0.70	Mortality due to Marek's disease (2) Mortality during adulthood (1) Mortality during growth (2) Mortality of Leukosis (1)
Resilience	3	6	0.07	0.06	0.40	AUTO-R (2) LNVAR (2) SKEW (2)
BW	10	20	0.38	0.47	0.61	BW at day 7 (1) BW at day 35 (1) BW at 8 weeks (1) BW at 10 weeks (2) BW at 18 weeks (4) BW at 20 weeks (6) BW at 40 weeks (1) BW at first egg (2) BW of slow-growing broilers (2)
Body conformation	3	5	NA ¹	NA ¹	0.14	Breast angle (2) Keel length (1) Shank length (2)

Abbreviations: h^2 (PB) = Average heritability for purebreds; h^2 (CB) = Average heritability for crossbreds; r_{pc} = Average estimate of the purebred-crossbred genetic correlation; AUTO-R = the lag-one autocorrelation of the deviations of individual weekly egg production records from the batch average (Bedere et al., 2022); LNVAR = natural logarithm of the variance of an individual's or group's deviations; SKEW = the skewness of the distribution of the deviations.

¹ In both studies that investigated body conformation, no heritabilities were reported.

studies. These results suggest that GxE for egg number may be considerable, and possibly of similar magnitude as GxG.

For all other traits, given that most estimates were based on measuring CB and PB animals in the same environment, deviations from one for most of the reported r_{pc} estimates were solely due to GxG interactions. Thus, the reported average r_{pc} values here should be considered as upper limits, for what would be encountered in

practice. A number of other studies have investigated the extent of GxE interactions by estimating the genetic correlation between performance of PB animals kept in a breeding nucleus or commercial environment. Using PB animals of broiler lines used in commercial breeding programmes, the average values of this correlation within study were reported to be 0.56 (Kapell et al., 2012), 0.51 (Chu et al., 2019), and 0.59 (de Hollander et al., 2023)

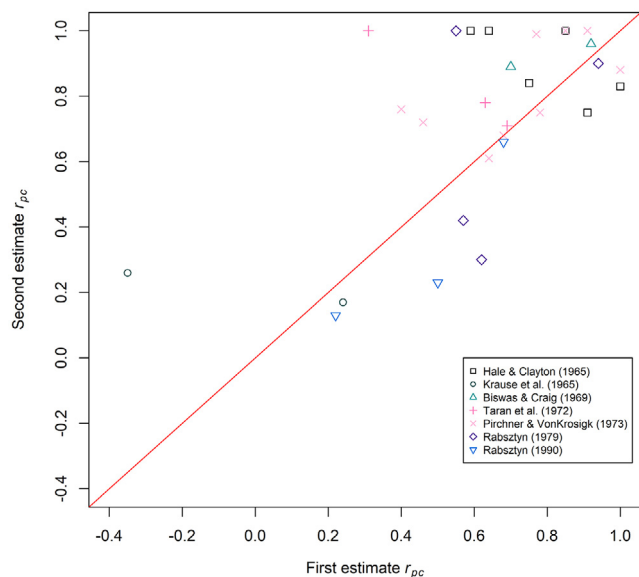


Fig. 3. Estimates of purebred-crossbred genetic correlation estimates in poultry obtained from reciprocal crosses from seven studies. Abbreviations: r_{pc} = purebred-crossbred genetic correlation.

for BW at 35–42 days of age. Using comparable commercial broiler strains and a similar trait, Duenk et al (2019) reported a genetic correlation between PB and CB of 0.9 or greater when housed in the same commercial environment. This suggests that for BW in poultry, the extent of GxE interactions may be considerably higher than the extent of GxG interactions. In contrast, a review of r_{pc} estimates in pigs suggested that in pigs, the extent of GxG may be larger than the extent of GxE (Wientjes and Calus, 2017). In both cases, however, these observations are based on comparing r_{pc} estimates between different studies that either measured PB and CB performance in the same, or in different environments. These apparently conflicting results, both obtained by making comparisons across studies, illustrate the necessity for studies that estimate the impact of GxE and GxG on (partially) the same data. This would require not only measuring phenotypes of PB animals in a nucleus environment and CB animals in a commercial environment but also additionally measuring PB performance in a commercial environment and/or measuring CB performance in a nucleus environment (Wientjes and Calus, 2017). Given limitations to enter animals in a nucleus environment due to stringent biosecurity measures, measuring PB performance in a commercial environment may be the most practical.

Implications and outlook

In both broilers and layers, commercial animals are typically four-way CB animals, while 18 out of the 19 studies included in our overview were based on two-way F1 CB animals. Thus, the reported r_{pc} estimates are applicable to F1 parent stock, which are typically kept in more commercial-like environments. Their performance may be part of the breeding goal, especially for fertility-related traits. However, the main goal of layer and broiler breeding is to improve the performance of four-way CB animals. Therefore, the question arises whether the reported r_{pc} estimates between PB and two-way animals can directly be translated to r_{pc} values between PB and four-way CB animals. In other words, is the true value of r_{pc} expected to be the same for two-way as for four-way crosses? For the GxE component, in the case that both two-way and four-way CB are housed in similar environments,

there are no obvious reasons why GxE is structurally more or less important for four-way CB compared to two-way CB animals. For the GxG component, in the case that we have four lines A, B, C and D, alleles from line A are complemented with alleles from one line in a two-way cross (e.g. from line C in AC crossbreds and from line D in AD crossbreds), and complemented with alleles from two lines in a four-way cross (from both lines C and D in ABxCD crossbreds, which have CD dams). When assuming that GxG is only a result of dominance, we have previously shown that the difference in allele substitution effects between PB performance and CB performance in line A depends on the difference between the allele frequencies in line A and the allele frequencies in the other lines involved in the cross (Duenk et al. 2021). Larger differences in allele substitution effects, in turn, will result in lower r_{pc} values. Assuming uniform allele frequencies for all lines with no correlation between allele frequencies of the different lines, the expected absolute difference in allele frequencies between two lines (e.g. A and C) is ~ 0.33 , while the expected absolute difference between one line (A) and the average of two other lines (C and D) is expected to be ~ 0.29 , and thereby $\sim 12.5\%$ lower. Assuming U-shaped distributed allele frequencies, these are expected to be $\sim 11\%$ lower (see Supplementary Material S1). These results show that the expected difference in allele frequencies only slightly decreases when more lines are involved in the cross. We therefore hypothesise that the r_{pc} for a four-way cross is close to the average r_{pc} of the three two-way crosses that involve the line of interest, and probably somewhat higher.

In this review, we focussed on the reported r_{pc} in poultry, as this is the key parameter to determine the added value of using CB phenotypes in the poultry breeding programme. In traditional pedigree-based selection, the added value of using CB phenotypes not only depends on the r_{pc} but also on the relationships between the PB selection candidates and the CB animals on which the phenotypes are measured. Classical CCPS systems, therefore, typically rely on half-sib information and/or progeny testing (Muir and Aggrey, 2003; Tixier-Boichard et al., 2012). This has a few disadvantages: (1) it requires that the pedigree of the CB animals is recorded, which may not be straightforward in commercial poultry breeding, (2) progeny testing leads to long generation intervals, and (3) the emphasis on half-sib information in pedigree-based selection may result in between family selection, in turn leading to increased rates of inbreeding (Bijma et al., 2001). These limitations can be overcome by genotyping the recorded CB animals, and using their information together with PB genotypes and phenotypes to inform selection decisions (Dekkers, 2007). This has inspired several studies to investigate the benefit of using genomic selection based on CB genotypes and phenotypes to select PB animals when the aim of a breeding programme is to improve CB performance. Studies that evaluated the impact of model parameterisation on the accuracy of genomic prediction relying (partly) on CB data have been reviewed by Stock et al. (2020), while studies that compared strategies to estimate genomic breeding values for CB performance of PB selection candidates have been reviewed by Duenk et al. (2021).

With the implementation of crossbred genotypes and phenotypes in genomic selection, datasets will be created that enable estimation of r_{pc} . With genotypes being available, the need to have strong pedigree links between purebred and crossbred animals can be relaxed, because the genotypes provide information about many small relationships. Nevertheless, stronger pedigree links will still result in more accurate estimates, even when genomic relationships are used. Among the studies included in this review, only two studies made use of genomic data (Duenk et al., 2019; Picard Druet et al., 2019). Of those two studies, only Duenk et al. (2019) estimated r_{pc} based on pedigree and genomic data. This

was done for the traits BW of broilers at 7 days and at 35 days. As expected, SE of the r_{pc} were lower when estimated using genomic relationships, because this provides more accurate information. Using an animal model, the r_{pc} estimates based on genomic relationships were 0.11 and 0.05 higher for BW at 7 days and at 35 days, respectively. While the larger difference at 7 days of age maybe due to the relatively large proportion of phenotypic variance explained by the environmental maternal effect at young age (Chu et al., 2020), which likely can be better disentangled from the direct additive genetic effect if that is modelled using genomic information, this is unlikely the case at 35 days of age where the maternal effect is quite small. Xiang et al. (2016) estimated the r_{pc} in pigs for total number of piglets born using genomic or pedigree data. For a Landrace population, the genomic based r_{pc} of 0.95 (SE 0.06) was much higher than the pedigree-based r_{pc} of 0.75 (SE 0.20), while for a Yorkshire population, the genomic based r_{pc} of 0.44 (0.20) was a bit lower than the pedigree-based r_{pc} of 0.54 (SE 0.30). Although based on a few estimates from two studies, these results may suggest that using pedigree data could lead to somewhat underestimated r_{pc} estimates, but more studies are needed to confirm this finding.

Conclusion

For the majority of trait categories included in this review, the average reported r_{pc} estimates were 0.7 or higher. Lower estimates were found for BW (0.61), egg number (0.58), resilience (0.40) and body conformation (0.14). Given that most studies did not capture the GxE component of the r_{pc} , the reported average values may overestimate the actual r_{pc} encountered in practice. Nearly all studies were based on two-way F1 CB animals. We hypothesise that r_{pc} for a two-way cross are good proxies for r_{pc} of a four-way cross.

Future studies that aim to estimate r_{pc} are encouraged to include a GxE component by housing PB and CB animals as is done in practice. Moreover, they are advised to report: the specific housing conditions of the animals, any differences between measurements of PB versus CB performance, and the heritabilities of PB and CB performance. In particular, there is a need for further studies that enable to explicitly estimate the magnitude of the contribution of GxE and GxG to the r_{pc} .

Supplementary material

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Ethics approval

Not applicable.

Data and model availability statement

Data were not deposited in an official repository. No new datasets were created. The data that are subtracted from the papers included in our review are available in [Supplementary File S2](#).

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence-assisted technologies in the writing process.

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Declaration of interest

None.

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