



Dominance effects in domestic populations

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ABSTRACT

The objective of this study was to provide an extensive discussion about background of the dominance effects connected to animal improvement. Because estimation of dominance effects requires large magnitude of full sibs they are mostly relevant in multipara species (pig, poultry and fish). Genetic evaluations taking into account dominance effects make more precise breeding value estimation possible. Besides, utilization of dominance effects is useful in developing mating schemes. The concept of dominance and its definition as an estimable parameter was introduced several decades ago. Yet because its application is complicated, until recently dominance was not in the central interest of animal breeders contrary to its important role in the genetic evaluation. However, since the software (SAS, PEST, VCE) used for genetic evaluation are extended with new procedures capable estimating this genetic component recent studies showed substantial dominance components for numerous traits justifying the relevance of dominance effects in animal breeding.

(Keywords: dominance, farm animals)

INTRODUCTION

Dominance variance is one of the main features whose properties determine genetic variance. Genetic evaluation in commercial programs nowadays is widely based on BLUP, ensuring unbiased estimates if the full relationship matrix and all data used in selection are included in the evaluation (*Blasco and Toro, 2014*). Selection efficiency also depends on the magnitude of the non-additive variances. An intensive research is now being developed in this area. However, including non-additive effects like dominance effect in the applied models produces further complications. Thus, understanding the basis of dominance effect plays a vital role in the genetic improvement of farm animals. In this article, the conception and research background of the dominance effects were summarized the strategies and methods were reviewed. The challenges and possible developments in future researches were also discussed.

A brief history

The concept of dominance, originally formulated by Gregor Mendel (*Bennett, 1965*) is fundamental to genetics. Though Mendel, "The Father of Genetics", first used the term in the 1860s, it was not widely known until the early twentieth century. The evolution of dominance was proposed initially by *Fisher* (1928) to explain the observed partial or complete dominance of wild-type alleles to the overwhelming majority of deleterious mutations. Nevertheless, *Wright* (1929, 1934) believed that the main explanation for dominance should be based on physiological factors, and selection for modifiers was not a primary force. The theoretical models and empirical experiments suggest that

substantial selection for dominance modifiers exists during the spread of adaptive alleles (Bourguet, 1999). According to Schlager (1974) genetic analysis yielded significant additive and dominance components in the inheritance of systolic blood pressure in mice. The estimates of non-additive components were highly variable but generally small compared to the additive genetic estimates in chicken populations (Silva *et al.*, 1976). Genetic variance estimated from twin data into additive and dominance variances was presented using Falconer's variance component model, which seems to be the least affected by fluctuations in the magnitudes of dominance and environmental variances (Kang *et al.*, 1977). Dominance components were two to four times the magnitude of additive components for dairy characters (Thomas *et al.*, 1985). Mixed models including additive and non-additive genetic effects have been developed (Henderson, 1988; Meyer, 1989; Hoeschele and VanRaden, 1991). Egg production is also influenced by dominance (Fairfull and Gowe, 1990). Dominance influences all genetic parameters related to cross-breeding (Wei *et al.*, 1991a, b). VanRaden (1989), Hoeschele (1991), and Tempelman and Burnside (1991) have reported such estimation of dominance variance for dairy cattle traits. The results on dominance were in good agreement with heterosis and inbreeding depression for these egg production traits and it was described by Ming *et al.* (1993). Varona *et al.* (1999) found that the largest changes after adding the dominance effect to the model were for animals with no own records and having many progenies by a single mate, e.g. dams of a single embryo-transfer batch in cattle. Non-additive genetic effects appear to be of sizeable magnitude for fertility traits and should be included in models intended for estimating additive genetic merit (Palucci *et al.*, 2007). The use of the complete dominance relationship matrix may improve the estimation of additive genetic variances and breeding values in pigs (Dufrasne *et al.*, 2014). Ignoring the dominance resulted in a slight overestimation of permanent environmental effects and these two effects showed partial confounding (Nagy *et al.*, 2014).

Definition

Non-additive genetic variation results from interactions between genes and the most important non-additive genetic effects are those of dominance (Gengler *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). The prediction of additive and dominance genetic effects concurrently should allow for a more precise prediction of total genetic merit and breeding value and 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). However, large populations are required to obtain acceptable accuracies for breeding values (Goddard and Hayes, 2009).

Genetic parameters

Cattle

The estimates of dominance effect and heritability for productive traits of cattle were generally different in magnitude and ranged from very low to moderate (Table 1).

Table 1. Additive and dominance components of reproductive traits in cattle

No.	References	Breed	Data size	Productive traits	Dominance effect	Heritability	
1	<i>Allaire et al., 1965</i>	Holsteins	12,631	Milk yield	0.16	0.24	
				Fat yield	0.24	0.23	
2	<i>Tempelman et al., 1990</i>	Holsteins	60,892	Milk yield	0.06	0.4	
				Fat yield	0.24	0.32	
3	<i>Tempelman et al., 1991</i>	Holsteins	24,695	Milk yield	0.19	0.39	
				Fat yield	0.34	0.43	
4	<i>Lawlor et al., 1992</i>	Holsteins	55,641	Milk yield	0.12	0.32	
5	<i>Fuerst et al., 1994</i>	SIM_PB_CB	375,093	MY1	0.08	0.18	
		SIM_PB	322,166		0.09	0.20	
		BVx BS	170,465		0.06	0.15	
		SIM_PB_CB	254,441	MY2	0.07	0.15	
		SIM_PB	217,310		0.07	0.16	
		BVx BS	120,754		0.11	0.13	
		SIM_PB_CB	168,744	MY3	0.05	0.17	
		SIM_PB	143,865		0.04	0.18	
		BVx BS	80,825		0.03	0.18	
		SIM_PB_CB	208,857	LPL	0.21	0.13	
		SIM_PB	198,483		0.19	0.13	
		BVx BS	116,432		0.35	0.13	
6	<i>Miglior et al., 1995</i>	Holsteins	176916	LSCS	0.013	0.165	

(5) SIM_PB_CB = Simmental including crossbreds, SIM_PB = pure bred Simmental, and BV x BS = population of Braunvieh and crossbreds of Braunvieh with Brown Swiss; MY1 = milk yield of lactation 1, MY2 = milk yield of lactation 2, MY3 = milk yield of lactation 3; LPL= length of productive life, and LFCM = lifetime production of fat corrected milk; (6) LSCS = lactation mean of somatic cell score for first lactation.

Allaire and Henderson (1965) presented the computed estimates of the dominance effects and heritabilities for first lactation records of milk and fat yields. With advances in the development of effective algorithms for large data sets, Tempelman and Burnside (1990, 1991) and Lawlor (1992) reported considerable dominance effects for the same traits in Holstein Friesian population. The lowest dominance and highest heritability values were found in the study which was based on the biggest dataset (Tempelman and Burnside, 1990). Thus, these significant differences can mainly be due to variances of the data size and an increasing frequency of families with non-additive relationships (three-quarter sibs, full sibs, and clones) and substantial improvement in the available hardware and software allowing the estimation of non-additive genetic variances from large files of field data (Fuerst and Sölkner, 1994).

For lactation traits, levels of dominance were quite constant through the tested breeds, except for the BV x BS data for second lactation, in which dominance was very high. Dominance and heritability estimates were highest (Table 1) in the first lactation among three lactations; estimating the second lactation were equal to or lower than that for third lactation and heritability decreased from first to third lactations (Strandberg, 1991).

Fuerst and Sölkner (1994) reported that dominance variance was important for most lifetime performance traits dominance was definitely higher than additive variance. Particularly, dominance variance was high for both traits and for all breeds especially for the population of Braunvieh and crossbreds of Braunvieh with Brown Swiss (BV x BS) data. Heritability estimates for LPL was unchanged over all breeds (Table 1). Estimates for LFCM for BV x BS were outside of parameter limits because of high standard errors (0.06-0.1) and possible correlations between the genetic variances (VanRaden *et al.*, 1992). McAllister *et al.*, 1990 found significant heterosis for most lifetime performance traits in a crossbred population of Holsteins. Heritability estimated by Miglior *et al.*, (1995) for lactational measures of somatic cell score for first lactation was almost twice as large as the dominance component, but, overall, non-additive genetic variance was low. Accurate estimation of dominance variances is difficult because proportions of variance shared by relatives maybe small and confounded with other genetic or environmental effects (Fuerst and Sölkner, 1994). Inclusion of dominance effects in genetic evaluation models can improve estimation of additive effects and should be considered in breeding programs.

The results of several studies examining fertility traits are presented in Table 2. Dominance variance was equal or larger than heritability for artificial insemination, days open (DO), service period (days between first and last insemination-SP) and service period with an upper bound of 91 days traits (SP91), excepting days open with an upper bound of 150 days trait (DO150) but dominance variance relied clearly on upper bounds. Dominance effect was negligible for DO and DO150, SP and SP91 although its value increased to double with upper bound days (Table 2). Heritability was equal levels for days open, service period and artificial insemination traits (Table 2). Alteration in female reproduction is owing to variations among cow in ability to conceive and that of the embryo to survive. Genetic variation in ability to conceive and in embryonic survival may have been reduced because all cows were fertile as heifers and were successful conceptions themselves (Hoeschele, 1991).

Table 2. Numerous estimates of dominance variance and heritability for reproductive trait of cattle

No.	References	Breed	Data size	Reproductive trait	Dominance effect	Heritability
1	<i>Hoeschele et al.</i> , 1990	Holsteins	379,009	DO	0.023	0.02
				DO150	0.005	0.021
				SP	0.014	0.008
				SP91	0.028	0.008
2	<i>Hoeschele</i> , 1991	Holsteins	379,009	DO	0.02	0.02
				AI period	0.01	0.01
3	<i>DeStefano et al.</i> , 1992	Cows	400	Mating strategy 1	0.05	0.05
				Mating strategy 2	0.1	0.15
				Mating strategy 3	0.15	0.25
4	<i>Fuerst et al.</i> , 1992	Simmental	304,493	CI 1	0.04	0.02
			191,772	CI 2	0.02	0.02
			126,969	CI 3	0.00	0.03
5	<i>Fuerst et al.</i> , 1994	SI(all)	354,247	CI1	0.04	0.02
		SI (pure)	304,493		0.04	0.02
		BVx BS	148,105		0.01	0.01
		SI(all)	224,130	CI2	0.02	0.01
		SI (pure)	191,772		0.02	0.02
		BVx BS	99,973		0	0.02
		SI(all)	149,017	CI3	0	0.03
		SI (pure)	126,969		0	0.03
		BVx BS	66,740		0	0.01
6	<i>VanRaden et al.</i> , 2006	Cows	1,739,055	Embryo loss	0.028	0.01
7	<i>Palucci et al.</i> , 2007	Cattle	486,012(heifers)	AFS	0.14-0.18	0.1-0.21
			507,315(cows)	NRR (heifers)	0.007- 0.019	0.005
				CTFS	0.062-0.073	0.1-0.11
				NRR (cows)	0.006-0.012	0.067-0.14

DO = Days open, DO150 = days open with an upper bound of 150 d, SP = service period (days between first and last insemination), SP91 = service period with an upper bound of 91day, AI = artificial insemination, CI 1 = Calving interval for lactations 1, CI 2= Calving interval for lactations 2, CI 3 = Calving interval for lactations 3; SI (all) =Simmental including crossbreds, SI (pure) =pure bred Simmental, and BV x BS = population of Braunvieh and crossbreds of Braunvieh with Brown Swiss; AFS = age at first service; NRR = non-return-rate; CTFS = interval from calving to first service

Turning to examine three mating strategies were shown by *DeStefano et al.*, (1992) such as mating strategy 1 allocated sires to cows based on predicted specific combining ability (PSCA) among service sires and sires of the cows such that average PSCA was maximized by linear programming, mating strategy 2 were ranked by sire x maternal grandsires (MGS) combination effect and chosen sequentially sequential allocation by specific combining ability (SEQ) and mating strategy 3 were the average PSCA calculated for each MGS over all 10 service sires, to simulate the increase in progeny performance, heritability and the ratio of dominance to phenotypic variance, both showed increasing trend from the first mating strategy to the third one relied on predicted specific combining abilities among sires and maternal grandsires through random mating to avoid inbreeding that do not use specific combining ability.

Fuerst and *Sölkner* (1994) reported about six inbred lines of Holsteins and their reciprocal crosses, the results for calving interval about estimates of heritability computed in the present studies were in agreement with others at three lactation periods. Except for the population of Braunvieh and crossbreds of Braunvieh with Brown Swiss (BV x BS), dominance effect was equal or larger than do heritability and interestingly, equals to zero in term of calving interval 3. Comparison of the three period of lactation, heritability estimates did not decrease except for BV x BS in the third period. However, it has to be noted that, the magnitude of heritability and dominance estimates were all close to zero.

Beckett et al., (1979) concluded that specific gene combinations and the way in which they were assembled can have an important influence on reproductive performance. Non-return rate (NR) at day 70 after first insemination was evaluated as a trait of the embryo loss, which is caused by lethal recessive genes. Heritability estimates for this trait is substantially smaller compared to dominance variance. Dominance genetic variances were greater than heritability for age to first service, heifer non return rate, and interval from calving to first service and found the agreement with the findings of *Miglior et al.*, (1995). *Table 2* showed the results of several models estimating several non-additive genetic variances including dominance (D), additive-by dominance (AD) and dominance-by-dominance (DD), together with the additive genetic variance (A) and the model including only additive genetic effect. Comparing genetic variance estimates between heifer and cow in non-return rate, non-additive genetic variance estimates were similar in value. On the contrary the additive component was much greater for cows than for heifers. The possible reason may be that non-return rate in cows is influenced by other factors that regulate ovarian activity and may have a heritability value greater than that of non-return rate (*Palucci et al.*, 2007). Heritability in the narrow sense (i.e. additive genetic variance to phenotypic variance) was lower when accounting for dominance genetic variances than using an additive animal model. This phenomenon was reported by *Palucci* (2007) in *Table 2*. Whenever gene interactions are omitted from the model their variance gets split between the additive and the residual effect therefore determining the additive effect to be overestimated. The consequences of this study on genetic evaluations for fertility traits, and maybe other traits, are that the ratio of the variance explained by non-additive genetic effects to phenotypic variance appears larger than heritability in the narrow sense for age at first service, heifer non-return rate and calving to first service (*Palucci et al.*, 2007). Ignoring dominance genetic variances may result in additive genetic effects to be overestimated and possibly biased, as seen by comparison of the results in *Table 2* with numerous studies on this issue.

Table 3. Numerous estimates of dominance variance and heritability for confirmative traits of cattle

No.	References	Breed	Data size	confirmative traits	Dominance effect	Heritability	Note
1	<i>Rodríguez et al., 1995</i>	Rhodes	3,992	Birth weight	0.00-0.39	0.31-0.6	
				Birth hip height	0.14-0.53	0.39-0.52	
				205-day weight	0.00-0.56	0.14-0.44	
		McNay	2,877	Birth weight	0.00-0.3	0.39-0.63	
				Birth hip height	0.00-0.33	0.1-0.51	
				205-day weight	0.16-0.27	0.19-0.37	
2	<i>Misztal et al., 1997</i>	Holsteins	600,678	Stature	0.069±0.012	0.453±0.003	
				Strength	0.08±0.007	0.278±0.005	
				Body depth	0.098±0.007	0.345±0.003	
				Dairy form	0.053±0.001	0.234±0.004	
				Rump angle	0.027±0.007	0.345±0.006	
				Thurl width	0.025±0.008	0.254±0.002	
				Rear led set	0.036±0.012	0.187±0.002	
				Foot angle	0.022±0.013	0.122±0.006	
				Fore udder att	0.047±0.007	0.243±0.005	
				Udder height	0.035±0.007	0.228±0.004	
				Udder width	0.034±0.006	0.19±0.003	
				Udder cleft	0.031±0.008	0.179±0.003	
				Udder depth	0.036±0.007	0.301±0.003	
Front teat	0.029±0.009	0.252±0.003					
3	<i>Gengler et al., 1998</i>	Limousin cattle	215,326	Postweaning gain	0.103±0.014	0.206±0.011	Original contemporary model
					0.184±0.018	0.0195±0.006	Alternative contemporary model

Estimates of dominance variance and heritability together with their standard errors of the eighteen confirmative traits are given in *Table 3*. These results suggest that significant differences existed in the estimates of dominance genetic variance and heritability between Rhodes and McNay lines (*Table 3*). The range of estimates was from low to moderately high. Particularly, the highest estimates of dominance variance were for WW; therefore, this trait is expected to present the largest degree of heterosis (*Willham, 1970*). The lowest estimates of dominance variance were observed for BWT, BH, and WH for both lines. Estimates of dominance variance and heritability were generally higher at the Rhodes herd than at the McNay herd for BWT, BH, and WW (*Tables 3*). These differences could be due to sampling variance only; more records were available at Rhodes and the inverses of the dominance relationship matrices were more dense for the data subsets from this herd, which could have resulted in better estimates of the parameter (*Rodríguez et al., 1995*).

Estimates of dominance and additive variances were obtained for next 14 linear confirmative traits in Holsteins. These traits are scored on a unified scale of one to 50, and have a similar phenotypic standard deviation of about 6.0, thus simplifying comparisons among them (*Thompson et al., 1983*). No clear relationship was found between the estimates of dominance and heritability and, particularly, larger estimates of dominance variances were generally associated with higher additive variances, but that association was weak. (*Misztal et al., 1997*); *Table 3* presents estimates of dominance and heritability variances for the 14 traits are expressed as ratio of the phenotypic variance with the standard deviations. All traits with larger estimates of dominance were strength, body depth, dairy form traits. estimate of dominance variance was highest level for body depth and lowest for foot angle (*Table 3*). For all traits, the dominance variance was, on average, 10 times lower than the heritability. The estimates of the dominance variance are low for some traits but there is a substantial variability for their magnitude.

Another study based on Limousin cattle, estimates of dominance variances were higher than heritability expressed as percentage of the phenotypic variance (*Table 3*) based on alternative contemporary model. The high values may indicate that dominance effect is important for post-weaning gain trait. Results showed the advantage of an individual dominance approach based on sire-dam combinations; therefore, expected gains through the use of specific combination ability as a part of the mating selection criteria for growth might be high (*Gengler et al., 1998*). A potential candidate for such variation in PWG could be the performance differences between males and females. Some changes may happen in estimated breeding values obtained with or without dominance genetic effects in the models. This approach should be superior to using expected heterosis on a breed level in commercial selection because allele interaction is directly modelled on a sire-dam base independently from breed origin (*Gengler et al., 1998*). Use of specific combining ability as described by *Henderson (1989)* might permit the exploitation of the observed dominance variance in commercial situations, upgrading, or purebred populations.

Pigs and rabbits

Dominance and heritability measurements for reproductive traits of pig and rabbit are presented in *Table 4*.

Table 4. Numerous estimates of dominance variance and heritability for reproductive traits of pig and rabbit

No.	References	Animal	Data size	Traits	Dominance effect	Heritability	Model		
1	<i>Culbertson et al., 1998</i>	Yorkshire pig	179,485	NBA	0.022 ± 0.007	0.088±0.0005			
				LWT	0.063 ± 0.009	0.081±0.0011			
2	<i>Ishida et al., 2001</i>	Pig	285	NP	0.2	0.11±0.14			
				NW	0.00	0.05±0.1			
3	<i>Norris et al., 2006</i>	Landrace pigs	26,223	NBA	0.068 ± 0.011	0.103 ± 0.011			
			21,335	LWT	0.019 ± 0.015	0.067 ± 0.009			
			16,370	FI	0.025 ± 0.02	0.020 ± 0.009			
4	<i>Norris et al., 2010</i>	Duroc Pig	10,703	NBA	0.037±0.022	0.084±0.016			
			6,883	LWT	0.015±0.011	0.103±0.017			
			6,881	FI	0.01±0.009	0.018±0.011			
5	<i>Angkuraseranee, 2010</i>	Duroc Pig	1,481	NBA	0.1024	0.1716			
			1,477	BW	0.1625	0.1737			
			1,422	NW	0.0470	0.3720			
			1,421	WW	0.1536	0.1516			
6	<i>Nagy et al., 2013</i>	Rabbit	3,883	NBA	0.118±0.024	0.089±0.01	AD		
					0.117 ±0.024	0.089±0.01	ADF		
					0.05±0.024	0.055±0.01	ADPe		
					0.048 ±0.024	0.055±0.011	ADPeF		
					NBD	0.058 ±0.02	0.02±0.006	AD	
						0.059±0.02	0.02±0.006	ADF	
						0.052±0.024	0.019 ±0.007	ADPe	
						0.053±0.024	0.019 ±0.006	ADPeF	
						TNB	0.152 ±0.028	0.098 ±0.01	AD
							0.152 ±0.028	0.098 ±0.01	ADF
							0.08 ±0.032	0.062 ±0.01	ADPe
			0.081 ±0.032	0.062 ±0.01	ADPeF				
7	<i>Nagy et al., 2014</i>	Rabbit	11,582	NBA	0.048±0.008	0.094±0.018	single-trait		
					NBD	0.037±0.01	0.068±0.006		
					TNB	0.117±0.018	0.005±0.007		
					NBA	0.046 ±0.007	0.085 ±0.015	two-trait	
			NBD	0.065 ±0.006	0.029 ±0.011				

NBA = number born alive, LWT = 21-d litter weight, NP= the number of piglet born in total, NW = number weaned, FI = interval between parities, BW = birth weight; WW = weaning weight, NBD = number of kits born dead; TNB = total number of kits born, AD = model with additive and dominance effects; ADPe = model with permanent environmental, additive, and dominance effects; ADF= model with additive, dominance, and inbreeding (doe and litter) effects; ADPeF = model with permanent environmental, additive, dominance, and inbreeding (doe and litter)

All variances are expressed as a ratio of the phenotypic variance. Estimates of dominance variance were moderate and lower than additive variance for NBA and LWT on pig. According to *Norris et al.* (2006), the proportion of phenotypic variance accounted for by dominance effects for farrowing interval was larger than the heritability of additive effects for this trait, indicating the importance of dominance effects on this trait, although according to the study of *Norris et al.* (2010), dominance variance were lower than additive variance. This could be due to the small data size and the standard errors were large for the observed estimates especially the dominance. However, a simulation study by *Norris et al.* (2002) revealed that even when the data set is small, as long as the magnitude of the dominance genetic variance is large, dominance genetic variances can be estimated with relatively good accuracies. Estimating the additive and dominance genetic variances for birth weight (BW), number weaned (NW), and weaning weight (WW) substantial magnitudes were found. For the number of piglet born in total trait, the narrow-sense heritability was smaller than dominance in the minor level. These ratios of the variance because of dominance effects were also not statistically significant largely due to the large standard errors. The results suggest that dominance genetic effects affect expression of the traits studied. Several authors (*Hoeschele*, 1991; *Fuerst and Sölkner*, 1994) indicated that non-additive genetic variance could be relatively important in fertility traits since these traits show low additive genetic variance.

The estimated variance components based on rabbit data is presented in *Table 4*. Additive, dominance, and permanent environmental variance components were estimated for the number of kits born alive, number of kits born dead, and total number of kits born of a synthetic rabbit line (called Pannon Ka). Using the models without and with dominance components such as AD, model with additive and dominance effects; ADPe, model with permanent environmental, additive, and dominance effects; ADF, model with additive, dominance, and inbreeding (doe and litter) effects; ADPeF, model with permanent environmental, additive, dominance, and inbreeding (doe and litter) effects it was found that heritability estimates were low for all traits (NBA, NBD, and TNB). The examined traits were evaluated using single-trait and two-trait (number of kits born alive-dead) animal models containing all or part of the following effects: additive genetic effects, permanent environmental effects, dominance effects (*Nagy et al.*, 2014). Results showed that the dominance components for number born alive (NBA), number of kits born dead (NBD) and total number of kits born (TNB) were smaller or larger than heritability and various levels among the different models with the dominance effects (*Table 4*). Ignoring the dominance resulted in a slight overestimation of permanent environmental effects and these two effects showed partial confounding (*Nagy et al.*, 2013). Accuracy of genetic evaluations could be increased when dominance genetic effects are considered in the model of evaluation (*deBoer and Van Arendonk*, 1992; *Misztal*, 1997; *VanRaden et al.*, 1992; *Johansson et al.*, 1993). These findings justify including dominance effects in models of litter size traits in populations that reveal significant dominance relationships.

Table 5. Numerous estimates of dominance variance and heritability for growth traits of pig

No.	References	Breed	Data size	Traits	Dominance effect	Heritability	Note	
1	Lutaaya et al., 2001	Landrace	6,022	LDG	0.39	0.51	line A	
			24,170		0.16	0.38	line B	
			6,135		0.29	0.29	line C	
2	Culbertson et al., 1998	Yorkshire	239,354	DAYS	0.103 ±0.015	0.332±0.04		
				BF	0.048±0.007	0.436±0.09		
3	Ishida et al., 2001	Landrace	1,528	BL	0.19	0.38±0.07		
				HG	0.16	0.16±0.06		
				CC	0.26	0.28±0.07		
				WH	0.28	0.32±0.08		
				CD	0.1	0.04±0.03		
				SW	0.03	0.21±0.05		
				CW	0.18	0.07±0.04		
				HW	0.39	0.18±0.08		
				HH	0.19	0.42±0.07		
				DG	0.9	0.09±0.41		
				567	BWS	0.00	0.05±0.07	
					CWT	0.00	0.12±0.08	
					CL	0.00	0.5±0.11	
					CWD	0.01	0.26±0.1	
					BLI	0.24	0.32±0.14	
					BLII	0.09	0.31±0.11	
					PS	0.13	0.09±0.09	
	PH	0.47	0.07±0.15					
	MLA	0.49	0.32±0.2					
	MLL	0.00	0.21±0.09					
	MLW	0.00	0.2±0.09					
	ABF	0.28	0.33±0.15					
	AGF	0.53	0.47±0.21					
	KFW	0.29	0.44±0.16					
	NVT	0.14	0.19±0.1					
4	DufRASne et al., 2014	Piétrain × Landrace	22,197	Body weight	0.22 - 0.4	0.19 - 0.42	Model 2	
					0.05 - 0.11	0.31 - 0.53	Mode 3	

LDG = lifetime daily gain; Days = days to 104.5 kg; BF = back fat at 104.5 kg; BL = body length; HG = Heart girth; CC = cannon circumference; WH = withers height; CD = chest depth; SW = shoulder width; CW = chest width; HW = hip width; HH = hip height; DG = average daily gain; BWS = body weight before slaughter; CWT = cold carcass weight; CL = carcass length; CWD = carcass width; BLI = black loin I; BLII = back loin II; PS = percentage of shoulder weight; PH = percentage of ham weight; MLA = M. longissimusthoracis area; MLL = M. longissimusthoracis length; MLW = M. longissimusthoracis weight; ABF = average back fat thickness; AGF = average M. gluteus medius back fat thickness; KFW = kidney fat weight; NVT = the number of Vertebrae thoracicae.

Studies analyzing growth traits of pig presented in *Table 5*. Data on lifetime daily gain from two purebred lines A, B, and their reciprocal crosses C were used to estimate dominance variance and heritability. The ratio of parental dominance to phenotypic variance was moderate for lines A, B, and C. These ratios are very large, suggesting that the parental dominance variance may be inflated and may also contain other variances, including full-sib environmental variances and non-additive variances other than dominance (*Lutaaya et al.*, 2001). However, the dominance variation should be accounted for lifetime daily gain. Heritability estimates for purebred lines were different to those for the crossbred line. Estimates of heritability for purebred lines obtained were generally higher than dominance effect, whereas both genetic parameters have the same ratio in the crossbred line. Animals ranked best as purebred are not necessarily breeding the best crossbreds (*Lutaaya et al.*, 2001). Estimates dominance variance and heritability were obtained for days to 104.5 kg (DAYS), and back fat at 104.5 kg (BF). All variances are expressed as a ratio of the phenotypic variance. Estimates of dominance variance were small magnitude for DAYS and BF. Dominance variance for DAYS and BF were estimated to be less than the additive variance in the narrow sense. Although the dominance variance for DAYS would seem large, similar results were found for growth traits in beef cattle (*Gengler et al.*, 1997). The results indicate that dominance effects may be important for reproductive and growth traits in swine. The amount of dominance variance varied among traits. It is not surprising because the variance depends largely on gene frequencies at loci concerned and changes during selection (*Ishida et al.*, 2001). However, the degree of dominance variances for chest depth (CD), chest width (CW), hip width (HW), average daily gain (DG), percentage of shoulder weight (PS), percentage of ham weight (PH); M. longissimus thoracis area (MLA); average M. gluteus medius back fat thickness (AGF) are greatly higher than that of heritability. Dominance effects could not be detected body weight before slaughter (BWS), cold carcass weight (CWT), carcass length (CL), M. longissimusthoracis length (MLL), M. longissimusthoracis weight (MLW), although the number of the piglet born in total (NP) and body length (BL) were affected. It appears necessary to consider the dominance effects in genetic evaluation of the selected lines. *Dufrasne et al.*, (2014), estimated the dominance variance for repeated live BW records in a crossbred population of pigs from 50 to 210 d of age. 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. Dominance variance was computed as 4 times the estimated parental subclass variance. Results presented that dominance effects exist for growth traits are reasonably smaller than heritability. Therefore, genetic variability in the studied population remains quite large and could explain the large heritability estimates for this population (*Dufrasne et al.*, 2014). Estimated heritability and dominance effect in model 2 appeared to be lower compared with Model 3. 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.

Poultry and fish

Table 6.

Numerous estimates of dominance variance and heritability for growth traits of poultry and fish

No.	References	Animal	Data size	Traits	Dominance effect, %	Heritability	Note
1	<i>Rye et al., 1998</i>	Salmon	58,920	Body weight	0.087	0.074	
			62,161		0.054	0.063	
			55,251		0.016	0.129	
			51,969		0.027	0.047	
2	<i>Mielenz et al., 2006</i>	Quails	7,934	BW42f	0.46±0.05	0.33±0.03	Line 1
				BW200f	0.09±0.04	0.38±0.03	
				BW42m	0.44±0.05	0.50±0.03	
				BW200m	0.21±0.08	0.49±0.04	
			7,214	BW42f	0.35±0.05	0.38±0.03	Line 2
				BW200f	0.001±0.02	0.38±0.04	
				BW42m	0.28±0.04	0.55±0.03	
				BW200m	0.23±0.08	0.52±0.04	
3	<i>Gallardo et al., 2010</i>	Salmon	11,833	Harvest weight	0.19	0.21	Even population
			10,327		0.06	0.37	Odd population

BW42f = the body weight of 42-day-old females; BW200f = body weight at an age of 200 days females; BW42m = the body weight of 42-day-old males; BW200m = body weight at an age of 200 days males

Dominance genetic variance and heritability estimates for growth traits of poultry and fish are summarized in *Table 6*. These traits were examined in numerous studies. Dominance genetic variance was smaller than additive genetic variance, except one population of 58,920 records where dominance variance was larger than additive genetic variance. The magnitude of dominance genetic variance and their effected the estimates of heritability found in this study encouraged significantly that dominance genetic variance should be considered in genetic evaluations for growth traits in salmon. Furthermore, estimates of heritability from models ignoring non-additive genetic effects were strongly biased upwards, illustrating a significant confounding between additive and non-additive genetic effects (*Rye et al., 1998*). Substantial reduction in the heritability estimates by including dominance effects in the model was previously reported for egg production traits in poultry (*Wei and van der Werf, 1993*). Ignoring non-additive genetic effects will likely have greater undesirable consequences in salmon than in cattle, as salmon populations have a higher level of average non-additive genetic relationships (*Rye et al., 1998*).

The estimated heritability and dominance genetic variance values of the body weight of 42-day-old females (BW42f), body weight at an age of 200 days females (BW200f), the body weight of 42-day-old males (BW42m), body weight at an age of 200 days males (BW200m), a total of 7,934 records for line 1 and 7,214 records for line 2 from 21 generations are shown in *Table 6*. The estimates are similar in both lines. The calculated values are high BW42m and BW200m, medium for BW42f and slight for BW200f. The magnitude of heritability was higher than for a larger parental dominance variance (*Table 6*). Surprisingly, high estimates of dominance values were reported for the body weight at an age of 42 days for both lines. This may be because of the fact that unknown environmental effects influenced on the early growth rate of the quails; a second explanation for the overestimation mentioned above may be the fact that the parental dominance variance includes maternal, common environmental and epistatic variances; and last but not least, a third reason might be the insufficient amount of data (*Mielenz et al., 2006*). Any estimation of the dominance variance requires much larger data sets than an estimation of the additive variance (*Misztal et al., 1997*). Additionally, the high dominance variance estimates for BW may be due to the change of the allele frequencies caused by the selection of the egg weight over more than 20 generations (*Mielenz et al., 2006*). Using the dominance model to get a more precise estimation of heritability in a narrow sense should be applied.

Heritability and dominance genetic variance on harvest weight in two populations of *Oncorhynchus kisutch*, forming two classes such as odd and even-year spawners were also estimated. A high heritability for harvest weight was estimated in both populations but heritabilities decreased to even and odd populations moderately. Interestingly, the magnitude of the dominance variance was significantly decreased in both populations. In fact, the magnitude of these effects may be very different in different populations. However, ranking of the 30 best males and the 100 best females per generation changed when a high dominance variance was estimated, as was the case in one of the two populations (even) and dominance and common environmental variance may be important components of variance in harvest weight in *O. kisutch*, thus not including them may produce an overestimation of the predicted response; moreover, genetic evaluation was seen to be partially affected, since the ranking of selected animals changed with the inclusion of non-additive effects in the animal model (*Gallardo et al., 2010*).

The estimates of dominance variance and heritability for egg production traits are presented in *Table 7*. These traits were examined egg number (EN) produced at 18 to 25 (EN1), 26 to 65 (EN2), and 18 to 65 week of age (EN3); egg weight (EW) measured at 30 to 35 (EW1) and 40 to 45 week (EW2); and egg specific gravity (ESG) measured at 30 to 35 (ESG1) and 40 to 45 week (ESG2); egg production at an age of 42 to 200 days (EN200); average egg weight for the first 11 weeks of their laying season (EW1); the average egg weight from weeks 12 to 23 (EW2). Within three White Leghorn lines, estimates for dominance variance and heritability were similar. The heritability estimates were moderately high and mostly higher than the proportion of dominance variance compared to the total phenotypic variance. However, the proportion of dominance variance was larger than the heritability for EN3 (line 3) and the dominance estimates were also obtained in low level for all traits. The approximate standard errors for genetic estimates were small laying hens because in poultry the proportion of full sibs is high enough to detect dominance relationships precisely. Significant dominance variation was found for all egg production traits, especially egg number (*Wei et al., 1993*).

Table 7.

Numerous estimates of dominance variance and heritability for reproductive traits of poultry

No.	References	Animal	Data size	Traits	Dominance effect, %	Heritability
1	<i>Wei et al., 1993</i>	Poultry	6001 (line1)	EN1	0.11±0.046	0.52±0.057
				EN2	0.15±0.055	0.35±0.051
				EN3	0.15±0.051	0.36±0.058
				EW1	0.01±0.045	0.55±0.056
				EW2	0.06±0.038	0.63±0.048
				ESG1	0.08±0.046	0.31±0.043
				ESG2	0.01±0.042	0.39±0.048
			12610 (line2)	EN1	0.1±0.054	0.48±0.043
				EN2	0.2±0.06	0.28±0.039
				EN3	0.18±0.057	0.35±0.04
				EW1	0.07±0.04	0.41±0.047
				EW2	0.02±0.046	0.52±0.039
				ESG1	0.11±0.054	0.34±0.04
				ESG2	0.05±0.053	0.4±0.039
10038 (line3)	EN1	0.19±0.055	0.33±0.048			
	EN2	0.11±0.46	0.15±0.031			
	EN3	0.16±0.05	0.12±0.031			
	EW1	0.13±0.053	0.38±0.048			
	EW2	0.04±0.046	0.48±0.049			
	ESG1	0.13±0.049	0.33±0.043			
	ESG2	0.05±0.044	0.32±0.037			
2	<i>Misztal et al., 2000</i>	Laying hen	26265	EN1	0.00-0.13	0.32
				EN2	0.10-0.14	0.19
				EN3	0.01-0.08	0.14-0.18
				EW	0.08	0.64-0.65
				SS	0.13-0.14	0.23-0.24
3	<i>Mielenz et al., 2006</i>	Quails	7934 (line 1)	EN200	0.07±0.08	0.32±0.05
				EW1	0.22±0.08	0.56±0.02
				EW2	0.17±0.07	0.44±0.03
		7214 (line 2)	EN200	0.12±0.11	0.16±0.05	
			EW1	0.06±0.06	0.54±0.05	
			EW2	0.45±0.12	0.24±0.06	

EN1, EN2, and EN3 = transformed egg numbers produced between 18 and 25, 26 and 65, and 18 and 65 week of age; EW1 and EW2 = egg weights measured at 30 to 35 and 40 to 45 week; ESG1 and ESG2 = egg specific gravities measured at 30 to 35 and 40 to 45 week; (2)EN1 = eggs laid between 19 and 25 weeks; EN2 = 26 and 38 weeks; EN3 = 26 and 54 weeks; EW = egg weigh; SS = shell strength; (3) EN200 = egg production at an age of 42 to 200 days; EW1 = average egg weight for the first 11 weeks of their laying season; EW2 = the average egg weight from weeks 12 to 23;

Estimates of dominance variance and heritability for five egg traits on 26265 laying hens were shown in *Table 7*. A model for estimation of dominance variance should also include the full-sib or a similar effect, provided the data set is large (*Misztal et al., 2000*). The estimates of the dominance variances heritability were changed slightly for the models on the group includes the number of eggs laid between 19 and 25 weeks (EN1), 26 and 38 weeks (EN2), and 26 and 54 weeks (EN3), the egg characteristic traits were average egg weight (EW) and shell strength (SS), both measured between 38 and 54 weeks of age. Three reasons may explain such a confounding. The first one is the low variability of EN2. This trait corresponds to the egg production during the peak period, when the lay intensity, above 90%, is approaching the biological limit of one egg per day per hen; the second reason is related to the mating structure, which is mainly hierarchical, and the last one, but not the least, is an insufficient amount of data (*Misztal et al., 2000*).

This study estimates the dominance variance and heritability for egg production traits of two lines of quails from a long-term selection. For 1,717 records (line 1) and 1,671 records (line 2) at the age of 42 to 200 days (EN200), on the average egg weight for the first 11 weeks of their laying season (EW1), on the average egg weight from weeks 12 to 23 (EW2), and on their body weight at an age of 200 days (BW200f). For on the average egg weight for the first 11 weeks of their laying season, the heritability values were similar but the dominance variances were different. For the first line, the respective ratio of the dominance variance to the phenotypic variance for EN200, EW1, EW1 were larger than those of the values for the second line. The estimated h^2 values for lines 1 and 2 from dominance models were smaller than those from the additive model. The differences between the heritability estimates were higher than dominance variance. The results were in accordance with reports for the egg production trait for chickens (*Wei and Van der Werf, 1993; Mielenz et al., 2003*). According to *Wei and Van der Werf (1993)*, any resemblance between relatives is partly due to dominance effects. Since the highest standard error was calculated for this estimated value (*Table 7*), the small sample size might be one explanation for the partial overestimation of dominance ratios of the egg weight trait (*Mielenz et al., 2006*). Therefore, it is reasonable to expect the existence of dominance variance for the egg weight as well.

CONCLUSION

Based on the numerous studies it can be concluded that dominance effects are important and should be included in animal models in the course of breeding value estimation. Neglecting dominance effects results in confounding that is the dominance effects will appear in other random effects such as additive genetic effects or permanent environmental effects thus breeding value estimation becomes less precise. However it has to be kept in mind that precise estimation of dominance effect requires large datasets and large number of full sibs.

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