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ESTIMATES OF GENETIC PARAMETERS FOR DIRECT AND MATERNAL EFFECTS ON EMBRYONIC SURVIVAL IN SWINE[1,2,3]

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ABSTRACT

Survival of 16,838 potential embryos was determined by counting corpora lutea and fetuses at 50 d of gestation for 1,081 litters by 225 sires. These data, coded as 1 or 0 depending on whether an ovulation was represented by a fetus, were used to estimate direct and maternal additive genetic variances and their covariance for embryonic survival. Data were from first-parity gilts of a Large White-Landrace composite population subdivided into two lines, one selected for an index of ovulation rate and embryonic survival for seven generations and a contemporary control line. Variance components were obtained by ANOVA and expectations of covariances among relatives and by derivative-free restricted maximum likelihood (DFREML) in an animal model. As a trait of the embryo, heritability of direct effects obtained with ANOVA was 3.8%, heritability of maternal effects was 1.5%, and the genetic correlation between them was –.51. After adjustment of embryonic survival for ovulation rate, lower estimates of each parameter were obtained with ANOVA. Heritability of embryonic survival as a trait of the dam was 9 to 10%. Estimates of heritability of both direct and maternal effects obtained with DFREML were < 1% and the genetic correlation between them was –.64. When survival of embryos from only those dams with 15 or more ovulations was analyzed, heritability of maternal effects was 4.4%. Estimates of common environmental effects on embryonic survival ranged from 5 to 7%.
Key Words: Pigs, Embryos, Survival, Heritability, Maternal Effects, Genetic Parameters

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Introduction

Sir John Hammond (1914, 1921) first discussed the importance of embryonic and fetal survival in swine, estimating that 25 to 50% of the potential pig population is lost between ovulation and birth. Pope and First (1985) indicated that average embryo mortality is 40 to 50%, with most embryos lost in the first 40 d of gestation. Average survival to term of potential embryos is therefore an important component of litter size and accounts for more of the variation in this trait than ovulation rate does (Johnson et al., 1984).

Variation in survival of embryos results from variation in uterine environment provided by the dam and in the ability of the embryo to survive, which depends in part on its own genes. An interaction also may exist between the genotype of the embryo and of the dam, as shown in mice by Moler et al. (1980). These factors and competition among embryos for uterine space (Dziuk, 1985) or for some critical substances (Bazer et al., 1969; Ulberg and Rampacek, 1974) make embryonic survival a complicated trait.

Heritability estimates for mean survival of embryos analyzed as a trait of the dam range from .15 to .18 in pigs (Johnson et al., 1984;

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Otmesguine, 1984 [cited by Bidanel, 1989]; Neal et al., 1989), and direct selection for mean survival of a litter was successfully practiced in mice (Bradford, 1969). Crossbred pig litters have higher embryonic survival than purebred litters (Johnson and Omtvedt, 1973); thus, individual genetic variation for embryonic survival does exist.

In this work, embryonic survival is regarded as a trait of the potential embryo, with a maternal influence. Therefore, the objective was to obtain estimates of direct and maternal additive genetic variances and their covariance for embryonic survival to 50 d of gestation in pigs.

Materials and Methods

Data. This study was conducted at the University of Nebraska-Lincoln, Field Laboratory, with first-parity gilts of a Large White-Landrace composite population subdivided into two lines, one selected for an index combining ovulation rate and survival of the litter to 50 d of gestation (I) and a contemporary control line (C). Johnson et al. (1984) presented the theory underlying this approach to improve litter size, and Neal et al. (1989) reported on the management, selection procedures, and response to the first five generations of this selection.

In brief, selection was initiated in 1981 by assigning gilts of the F_3 generation of the Large White-Landrace composite to either the I or the C line. In each generation of selection, an average of 147 and 55 gilts were selected in the I and C lines, respectively, and mated to 15 boars of the same line. Laparotomy was performed at 50 d of gestation on all females of the I line to determine ovulation rate and number of fetuses; approximately 40 to 45 gilts per generation were selected to farrow in this line based on the index 10.6 × ovulation rate + 72.6 × survival of the litter. Because the means of these two traits changed due to the first five generations of selection and the optimum coefficients in the index depend on these means, coefficients were changed to 9.9 and 148.9 after Generation 5. Laparotomy was not done on any females in the C line in Generation 0 and it was done on one-half of them in Generations 1 through 4 and 6 through 7 and on all of them in Generation 5. All pregnant females in the C line were farrowed. Selection of replacements in the I line was based on the dam's index, whereas in the C line random selection was practiced. This study includes data from the first seven generations of the experiment.

Analysis. Fertilization occurs for nearly all ova in swine (Wrathall, 1971; Archibong et al., 1987); thus, for the purposes of this analysis, each corpus luteum was considered as a potential embryo and coded as 1 or 0 depending on whether it was represented as a fetus at 50 d of gestation. These coded survival values were then used in the analyses.

In the first procedure, variance components were estimated by ANOVA and genetic components were estimated by equating these variance components to expectations of covariances among relatives, as discussed by Willham (1972). Heritability of embryonic survival was estimated and then the estimate was converted to a normal scale using the procedure described by Dempster and Lerner (1950). This method requires the assumption that there is an underlying normal distribution of genetic and environmental causes, and its robustness has been well demonstrated (Van Vleck, 1972; Olausson and Ronningen, 1975). Three models were used, all including the fixed effects of line and year and, in a second analysis, the linear and quadratic effects of ovulation rate. First the coded survival values (0, 1) were analyzed with a model including the random effects of sire of the litter; expected covariance among paternal half-sibs represented 1/4 of the variance of additive direct effects (σ^2_A). Survival of the litter (number of fetuses at 50 d/number of corpora lutea) was the response variable in the second model, which included the random effects of sire of the gilt. In this case, the expected covariance among the mean survival of litters of paternal half-sib gilts (PHSG) is as follows:

$$E\,[\text{Cov (PHSG)}] = 1/16\ \sigma^2_A + 1/4\ \sigma^2_M + 1/4\ \sigma_{AM}$$

where σ^2_M is the variance of additive maternal effects and σ_{AM} is the covariance between additive direct and maternal effects.

The third model included the regression of the mean survival of the grandprogeny of a maternal grandsire on the mean survival of its

progeny ($b_{\bar{O}'.\bar{O}}$). The diagram in Figure 1 illustrates this case. The expectation of $b_{\bar{O}'.\bar{O}}$ includes σ^2_A, σ^2_M, σ_{AM}, the phenotypic variance (σ^2_p), the intraclass correlation among full-sibs (t_{FS}) and half-sibs (t_{HS}), and is a function of the average number of potential embryos per gilt (n) and the number of gilts mated per sire (d). This expectation (Appendix) is as follows:

$$E[b_{\bar{O}'.\bar{O}}] = \frac{[2 + n\ (d + 1)]\ \sigma^2_A/8 + n\ \sigma^2_M/2 + [2 + n\ (d + 2)]\ \sigma_{AM}/4}{[1 + (n - 1)\ t_{FS} + n\ (d - 1)\ t_{HS}]\ \sigma^2_p}.$$

Given the complexity of these expectations, SE of genetic-parameter estimates could not readily be calculated.

In the second procedure, variance components were estimated by derivative-free restricted maximum likelihood (DFREML; Meyer, 1988) in an individual animal model. Under certain conditions estimation of (co)variance components by maximum-likelihood procedures is free of selection bias (Rothschild et al., 1979; Sorensen and Kennedy, 1984), and use of an animal model allows simultaneous estimation of the (co)variance components of interest. The following mixed model describing the record for each embryo was used:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1u_1} + \mathbf{Z_2u_a} + \mathbf{Z_3u_m} + \mathbf{e}$$

where y is a vector of coded values (0 or 1) for survival of the individual embryo, b is a vector of fixed effects (year, line, and linear and quadratic effects of ovulation rate), $\mathbf{u_1}$ is a vector of random litter effects, $\mathbf{u_a}$ is a vector of additive direct genetic effects, $\mathbf{u_m}$ is a vector of additive maternal genetic effects, e is a vector of residual effects, and X, Z_1, Z_2, and Z_3 are design matrices relating records to the appropriate fixed or random effects. It was assumed that E(y) = Xb and the variance-covariance matrix of the random effects was as follows:

$$V\begin{bmatrix} \mathbf{u_1} \\ \mathbf{u_a} \\ \mathbf{u_m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} I\sigma^2_1 & 0 & 0 & 0 \\ 0 & A\sigma^2_A & A\sigma_{AM} & 0 \\ 0 & A\sigma_{AM} & A\sigma^2_M & 0 \\ 0 & 0 & 0 & I\sigma^2 \end{bmatrix}$$

hence, $V(y) = Z_1Z_1'\sigma^2_1 + Z_2AZ_2'\sigma^2_A + Z_3AZ_3'\sigma^2_M$

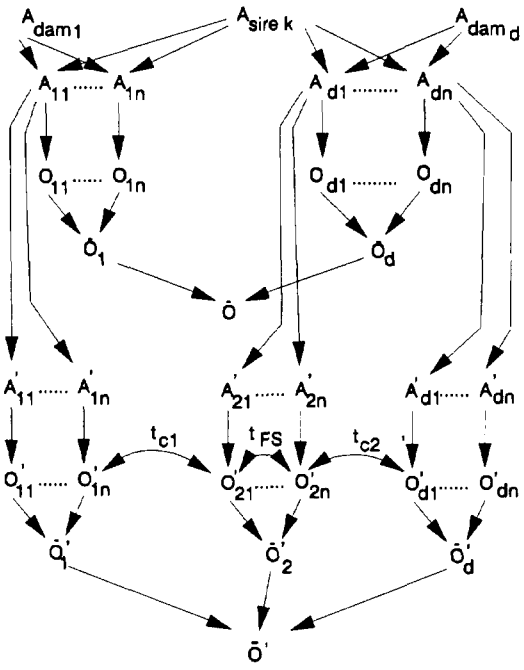

Figure 1. Diagram showing the relationship between the mean survival of the grandprogeny of a sire and the mean survival of its progeny. $A_{sire\ k}$ = breeding value of the sire of progeny O_{ij} and maternal grandsire of grandprogeny O'_{ij}; $A_{dam\ i}$ = breeding value of the i^{th} gilt mated to sire k: A_{ij} and O_{ij} = breeding and phenotypic values, respectively, of embryo j in litter i, progeny of sire k and dam i; A'_{ij} and O'_{ij} = breeding and phenotypic values, respectively, of pig j in litter i, progeny of the i^{th} daughter of sire k; $\bar{O}_i$ and $\bar{O}'_i$ = mean embryonic survival of the i^{th} litter, respectively, of progeny and grandprogeny of sire k; $\bar{O}$ and $\bar{O}'$ = mean survival of the progeny and grandprogeny of sire k, respectively; t_{c1} = intraclass correlation between progeny of paternal half-sib gilts, daughters of sire k; t_{c2} = intraclass correlation between progeny of full-sib gilts, daughters of sire k; t_{FS} = intraclass correlation between full-sib embryos.

TABLE 1. NUMBER OF RECORDS IN ANALYSIS OF VARIANCE AND IN DERIVATIVE-FREE RESTRICTED MAXIMUM-LIKELIHOOD ANALYSIS (DFREML)[a]

Item	ANOVA	DFREML
No. of potential embryos	16,838	14,933
No. of fetuses present	12,265	10,871
No. of litters	1,081	943
No. of sires of litters	225	115

[a]DFREML analyses include only select-line gilts, whereas ANOVA data also include control-line gilts.

$+ (Z_3AZ_2' + Z_2AZ_3')\sigma_{AM} + I\sigma^2$, where I is the identity matrix, σ_l^2 is the variance of litter effects, σ^2 is the residual variance, and A is the numerator relationship matrix among potential embryos. Because not all gilts were measured in the C line, only I-line gilts were included in this analysis.

A second mixed-model analysis was conducted with the same model on data including embryos from only those gilts with ≥ 15 potential embryos. The rationale for this analysis was that genetic variation in uterine capacity, a component of maternal effects for embryonic survival, might be expressed only in gilts challenged by a large number of potential embryos (Bennett and Leymaster, 1989).

In DFREML, the natural log of the likelihood function (L) of the data independent of fixed effects is evaluated explicitly, and the values of the parameters that maximize L are located by a direct search, without the use of derivatives (Meyer, 1989). The procedure was started with priors estimated from the ANOVA and the convergence criterion was $Var[-2 Log(L)] < 1 \times 10^{-6}$. After initial convergence was obtained, the procedure was restarted, to avoid the possibility of convergence to a local maximum (Boldman and Van Vleck, 1990). The values reported are those obtained at the second convergence and are assumed to represent the global maxima.

Smith and Graser (1986) used DFREML with a quadratic term in the parameters of log L to obtain approximate SE for the estimated variances. Meyer (1989), however, showed that this method is not applicable to a model including correlated maternal effects; therefore, approximate SE were not calculated for estimates obtained with DFREML.

To make the estimates of variance due to common litter environmental effects comparable in the two analyses, the expected contribution of additive genetic components of variance ($1/2\ \sigma_A^2 + \sigma_M^2 + \sigma_{AM}$) was subtracted from the covariance among full-sib embryos estimated in ANOVA.

Results

Average embryonic survival to 50 d of gestation was 73%. The number of records, litters, and sires used in the ANOVA and DFREML procedures are presented in Table 1. Data for both the I and C lines were used with the ANOVA procedure, whereas only data for the I line were used in the DFREML procedure. The average number of potential embryos per litter and number of mates per sire were, respectively, 15.63 and 4.86; both were obtained from coefficients of variance components in expected mean squares from the nested ANOVA. The coefficients from the regression of mean survival of the grand-

TABLE 2. ESTIMATES OF VARIANCE COMPONENTS VIA ANALYSIS OF VARIANCE FOR ANALYSES OF EMBRYONIC SURVIVAL AS A TRAIT OF THE EMBRYO (TE) AND SURVIVAL OF THE LITTER AS A TRAIT OF THE DAM (TD)

	Unadjusted for ovulation rate		Adjusted for ovulation rate	
Component[a]	TE	TD	TE	TD
S	.001863	.000623	.001170	.000658
D	.016353	.001781	.012748	.001798
W	.179505	.026413	.179505	.023417

[a]S, D, and W are estimates of sire, dam, and progeny variance components, respectively.

TABLE 3. GENETIC PARAMETER ESTIMATES FOR EMBRYONIC SURVIVAL FROM ANALYSIS OF VARIANCE[a]

Item	Unadjusted for ovulation rate	Adjusted for ovulation rate
h_a^2	.038	.024
h_m^2	.015	.011
r_{am}	−.507	−.206
c^2	.070	.052
h_{dam}^2	.087	.102

[a] h_a^2, h_m^2, r_{am}, and c^2 are, respectively, estimates of heritability of direct effects, heritability of maternal effects, correlation between direct and maternal effects, and ratio of variance of common environmental effects to total variance for embryo survival as a trait of the embryo; h_{dam}^2 is estimated heritability of survival of the litter as a trait of the dam.

progeny of a maternal grandsire on the mean survival of its progeny before and after adjustment for ovulation rate were, respectively, .0781 and .1146, obtained from 265 pairs.

Estimates of the sire, dam, and progeny variance components obtained with the ANOVA method are presented in Table 2. Estimates of the heritability of additive direct and maternal genetic effects, the correlation between the two, common environmental effects, and heritability of survival of the litter regarded as a trait of the dam are presented in Table 3. Differences between estimates obtained before and after adjustment for ovulation rate were minor. The estimates of heritability for direct effects were approximately 2 and 4%, and those for maternal effects were approximately 1 and 2%, but a negative correlation existed between the two. As a trait of the dam, estimated heritability of survival of the litter was approximately 9 to 10%.

The estimates of heritabilities obtained with DFREML (Table 4) were < 1% for both additive direct and maternal effects, and a negative correlation between the two was obtained. In all analyses, the estimated ratio of the variance of litter environmental effects (excluding any additive effects) to phenotypic variance was between 5 and 7%.

There were 10,428 potential embryos from 593 litters with at least 15 potential embryos (Table 4). Analysis of these data with DFREML again resulted in an estimate of the heritability of direct effects of < 1%, but the estimated heritability of maternal effects increased to approximately 4%.

Estimated heritability of mean survival of a litter regarded as a trait of the dam, calculated from the estimated (co)variance components obtained by DFREML, was only 3% when all data on the select line were used but 24% in the truncated data set.

Discussion

No estimates of heritability of additive direct or maternal effects for embryonic survival in polytocous species were found in

TABLE 4. GENETIC PARAMETER ESTIMATES FOR EMBRYONIC SURVIVAL WITH DERIVATIVE-FREE RESTRICTED MAXIMUM LIKELIHOOD ANALYSIS, FOR THE FULL DATA SET AND FOR A DATA SET INCLUDING ONLY LITTERS WITH AT LEAST 15 POTENTIAL EMBRYOS[a]

Item	Full data set	Truncated data set
h_a^2	.006	.001
h_m^2	.006	.044
r_{am}	−.639	−.721
c^2	.060	.061

[a] h_a^2, h_m^2, r_{am}, and c^2 are, respectively, estimates of heritability of direct effects, heritability of maternal effects, correlation between direct and maternal effects, and ratio of variance of common environmental effects to total variance for embryo survival as a trait of the embryo.

the literature. Our results indicate that, even though it is very small, additive genetic variation may exist for the ability of an embryo to survive. When converted to a normal scale using the procedure described by Dempster and Lerner (1950), the ANOVA estimates of heritability of direct effects were approximately 4 to 7%. Genes affecting embryonic growth rate could contribute to individual effects on embryonic survival, as shown in mice by the presence of a major gene affecting preimplantation embryonic development (Warner, 1986).

The heritability of maternal effects was lower than anticipated, even though embryonic survival is often regarded as a trait of the dam. One possible reason for this low estimate is that uterine capacity, a major component of maternal ability for embryonic survival, does not play a major role until approximately 30 or 40 d of gestation (Webel and Dziuk, 1974; Knight et al., 1977) and in this analysis embryonic survival was estimated at 50 d of gestation. At the same time, maternal genetic variation in uterine capacity likely is expressed only if the uterus is challenged by a sufficiently large number of potential embryos (Bennett and Leymaster, 1989). Therefore, including data from gilts with ovulation rates lower than uterine capacity would tend to reduce the heritability of maternal effects. After truncation of the data to include only gilts with $\geq$ 15 potential embryos, presumably close to the mean uterine capacity of this line (Johnson and Neal, 1988), the heritability of maternal effects did increase to approximately 4%.

Factors involved in genetic differences in maternal effects could include uterine space (Dziuk, 1985) or characteristics of the uterine environment (Ulberg and Rampacek, 1974). Wilmut et al. (1986) emphasized the importance of a nearly perfect synchrony between developmental stages of the embryo and uterus. Heterogeneity of embryonic development within a litter frequently has been observed, and the probability of survival of smaller embryos is reduced in these circumstances (Bazer et al., 1990). Ovulation takes approximately 6 h in pigs and, as duration of ovulation increases, embryonic heterogeneity and mortality also increase (Pope and First, 1985). If embryonic heterogeneity contributes to differences in embryonic survival, genetic variation in duration of ovulation would be present in the heritability of maternal effects.

A large negative correlation between additive direct and maternal effects indicates that selection for only one of these traits will result in reduction in the other, strongly suggesting the use of index selection procedures combining the breeding values for both direct and maternal effects as the best approach to genetically improve embryonic survival in swine.

The relatively large component of variance for common environmental effects, after exclusion of additive genetic effects, indicates that nonadditive individual genetic effects and maternal environmental effects play an important role in embryonic survival.

Higher estimates of heritability obtained with ANOVA than with DFREML were unexpected, because ANOVA estimates are biased downward when selection occurs, whereas REML estimates are affected less (Sorensen and Kennedy, 1984). One possible explanation is that data were not exactly the same for both analyses because only data for the I line were used in the DFREML analysis, whereas data for both the I and C lines were used in the ANOVA estimates. Estimates did not differ greatly and discrepancies may be due to sampling.

Implications

Selection among dams based on the mean embryonic survival of their litter should be an effective way to improve embryonic survival in swine. Most of the response is expected to be due to improved maternal genetic effects and not to direct genetic effects of the embryo. Selection for embryonic survival is expected to be most effective in lines with high ovulation rates. Procedures to standardize the number of potential embryos at numbers that provide an adequate challenge to the uterus of each female also should enhance response to selection. Practical procedures to select for embryonic survival in industry herds need to be developed.

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Appendix

Let:

$V(X)$ = variance of X
$Cov(X.Y)$ = covariance between X and Y
σ^2_A = additive direct genetic variance
σ^2_M = additive maternal genetic variance
σ_{AM} = covariance between additive direct and maternal effects
t_{FS} = intraclass correlation between full-sibs
t_{HS} = intraclass correlation between paternal half-sibs

$\bar{O}'$ and $\bar{O}$ are, respectively, the mean survival rates of the grandprogeny and progeny of a sire, and assume d litters/sire, n pigs/litter, and s daughters selected/sire.

$$b_{\bar{O}'.\bar{O}} = \frac{\text{Cov}\,(\bar{O}'.\bar{O})}{V\,(\bar{O})}$$

Expectations

1. $\text{Cov}\,(\bar{O}'.\bar{O})$

$$= \text{Cov}\,\{[\,1/s(\bar{O}'_1 + \bar{O}'_2 + \ldots + \bar{O}'_s)]\cdot[\,1/d\,(\bar{O}_1 + \bar{O}_2 + \ldots + \bar{O}_d)]\}$$

$$= \text{Cov}\,\{[1/s\,(1/n\,(O'_{11} + \ldots + O'_{1n}) + \ldots + 1/n\,(O'_{s1} + \ldots + O'_{sn}))]$$
$$[1/d\,(1/n\,(O_{11} + \ldots + O_{1n}) + \ldots + 1/n\,(O_{d1} + \ldots + O_{dn}))]\}$$

$$= \text{Cov}\left[\left(1/sn \sum_{i=1}^{s}\sum_{j=1}^{n} O'_{ij}\right)\left(1/dn \sum_{i=1}^{d}\sum_{j=1}^{n} O_{ij}\right)\right].$$

Ignoring genetic covariances between individuals with relationships smaller than .25 and assuming that environmental covariances between individuals other than full-sibs are zero, three types of covariances may exist between O'_{ij} and O_{ij}, as follows:

Covariance between progeny of dam d and:	Expectation	No. of covariances
Dam d	$1/2\,\sigma^2_A + 1/2\,\sigma^2_M + 5/4\,\sigma_{AM}$	sn
Full-sibs of dam d	$1/4\,\sigma^2_A + 1/2\,\sigma^2_M + 3/4\,\sigma_{AM}$	$sn\,(n-1)$
Paternal half-sibs of dam d	$1/8\,\sigma^2_A + 1/4\,\sigma_{AM}$	$sn^2\,(d-1)$

Therefore:

$E\,[\,\text{Cov}\,(\bar{O}'.\bar{O})\,]$

$$= 1/dsn^2\,[sn\,(1/2\,\sigma^2_A + 1/2\,\sigma^2_M + 5/4\,\sigma_{AM}) + sn\,(n-1)\,(1/4\,\sigma^2_A + 1/2\,\sigma^2_M + 3/4\,\sigma_{AM}) + sn^2\,(d-1)\,(1/8\,\sigma^2_A + 1/4\,\sigma_{AM})]$$

$$= 1/dn\,[1/2\,\sigma^2_A + 1/2\,\sigma^2_M + 5/4\,\sigma_{AM} + (n-1)/4\,\sigma^2_A + (n-1)/2\,\sigma^2_M + 3\,(n-1)/4\,\sigma_{AM} + n(d-1)/8\,\sigma^2_A + n(d-1)/4\,\sigma_{AM}]$$

$$= 1/dn\,\{\,[1/2 + (n-1)/4 + n(d-1)/8]\,\sigma^2_A + [1/2 + (n-1)/2]\,\sigma^2_M + [5/4 + 3(n-1)/4 + n(d-1)/4]\,\sigma_{AM}\}$$

$$= 1/dn\left\{[2 + n(d+1)]/8\,\sigma^2_A + n/2\,\sigma^2_M + [2 + n(d+2)]/4\,\sigma_{AM}\right\}$$

2. $V(\bar{O})$

$$= V\,[\,1/d\,(\,\bar{O}_1 + \bar{O}_2 + \ldots + \bar{O}_d\,)]$$

$$= 1/d^2\left[\sum_{i=1}^{d} V(\bar{O}_i) + \text{Cov}\,(\bar{O}_1.\bar{O}_2) + \ldots + \text{Cov}\,(\bar{O}_i.\bar{O}_{i'}) + \ldots + \text{Cov}\,(\bar{O}_d.\bar{O}_{d-1})\right]$$

And, with the same assumptions as for $\text{Cov}\,(\bar{O}'.\bar{O})$:

Type of variance or covariance	Expectation	No. of (co)variances
$V(\bar{O}_i)$	$[1 + (n-1)\, t_{FS}]/n\, \sigma_p^2$	d
Cov $(\bar{O}_i \cdot \bar{O}_{i'})$	$t_{HS}\sigma_p^2$	d (d – 1)

Therefore:

$$\begin{aligned} E[\,V(\bar{O})\,] &= 1/d^2 \left\{ d[1 + (n-1)\, t_{FS}]/n\, \sigma_p^2 + d(d-1)\, t_{HS}\, \sigma_p^2 \right\} \\ &= 1/d \left\{ [1 + (n-1)\, t_{FS}]/n\, \sigma_p^2 + [n(d-1)\, t_{HS}]/n\, \sigma_p^2 \right\} \\ &= 1/dn\, [1 + (n-1)\, t_{FS} + n(d-1)\, t_{HS}]\, \sigma_p^2 \end{aligned}$$

Hence:

$$E\left[\, b_{\bar{O}' \cdot \bar{O}} \,\right] = \frac{\left[\, 2 + n(d+1) \,\right]/8\, \sigma_A^2 + n/2\, \sigma_M^2 + [\, 2 + n(d+2)\,]/4\, \sigma_{AM}}{\left[1 + (n-1)\, t_{FS} + n(d-1)\, t_{HS} \right] \sigma_p^2}.$$