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The exact moments of estimators of the heritability coefficients for the twofold balanced nested model*

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SUMMARY

Heritability coefficients defined as the ratios of genotypic variance to total phenotypic variance are estimated by the ANOVA technique. The resulting estimators take the form of the ratio of two quadratic forms of the vector of observations. We derive the exact formulas for moments of these estimators in the case of a twofold nested random model assuming normality. These formulas express the moments as definite integrals of rational and irrational functions. Tables of expected values, standard deviations and relative biases of the estimators are supplied.

KEY WORDS: estimators of heritability coefficients, exact moments, standard deviations, relative bias.

1. Introduction

The heritability coefficient is a measure of degree of genetic determination of a quantitative character of animals and plants. In a broad sense, it is the ratio of genotypic variance to the total phenotypic variance. The phenotypic variance can be divided into paternal, maternal and environmental components. Each of these components can be separately estimated by the technique of the analysis of variance. This method leads to unbiased estimators, which are substituted in formulas for the coefficients of heritability (CH). The resulting estimators of CH are biased, because the expectation of the ratio is not equal to the ratio of expectations. This estimator takes a form of the ratio of two dependent quadratic forms of a random vector. Approximate formulas for the variance of the estimator of CH that ignore this dependency are in common use. Magnus (1986) has derived the exact formula for the moments of the

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ratio of two stochastically dependent quadratic forms of a normal random vector. We use this result to derive moments of the estimator of CH. Similar problem for intraclass correlation has been solved in Niedokos (1997). The resulting formula expresses the moment as a definite integral of rational and irrational functions with coefficients being functions of variance components.

2. The balanced twofold nested model

Let us consider an experimental design in which each of s sires or paternal plants is mated with d dams or maternal plants, and each mating produces r progeny. Then the observation of the quantitative character on the k-th offspring of the ij-th sire-dam mating can be represented as

$$y_{ijk} = \mu + s_i + d_{ij} + e_{ijk}, \qquad (i = 1, ..., s;\ j = 1, ..., d;\ k = 1, ..., r) \tag{1}$$

where μ is a common mean, s_i is the effect of the i-th sire, d_{ij} is the effect of the j-th dam mated to the i-th sire and e_{ijk} are uncontrolled environmental and genetic deviations attributed to the individuals. The effects are assumed to be normally distributed, completely independent random variables with zero means and variances σ_s^2, σ_d^2 and σ_e^2, i.e.

$$s_i \sim NID(0, \sigma_s^2), \quad d_{ij} \sim NID(0, \sigma_d^2), \quad e_{ijk} \sim NID(0, \sigma_e^2).$$

The variances are referred to as variance components. Then the phenotypic variance is

$$\sigma_y^2 = \sigma_s^2 + \sigma_d^2 + \sigma_e^2,$$

and the paternal and maternal heritability coefficients are defined as

$$h_s^2 = SCH = \frac{4\sigma_s^2}{\sigma_y^2}, \quad h_d^2 = DCH = \frac{4\sigma_d^2}{\sigma_y^2}.$$

3. Notation

We will use the following notation:

$\mathbf{Y}$ – denotes the vector of $n = sdr$ observations y_{ijk} ordered lexicographically,
$\mathbf{I}_s$ – is the identity matrix of order $s \times s$,
$\mathbf{J}_s$ – is the $s \times s$ matrix of ones,
$\mathbf{1}_s$ – is the $s \times 1$ column vector of ones,
$\mathbf{1}_s^1$ – is the $s \times 1$ vector with the only nonzero element equal to one on the first position,
$\mathbf{E}_s^{11} = \mathbf{1}_s^1 \mathbf{1}_s^1$

$\mathcal{E}$ – is the expectation operator,
E – stands for "estimator of".
We will use the following projection operators

$$\mathbf{P}_s = \left(\mathbf{I}_s - \frac{1}{s}\mathbf{J}_s\right) \otimes \frac{1}{d}\mathbf{J}_d \otimes \frac{1}{r}\mathbf{J}_r, \quad \mathbf{P}_d = \mathbf{I}_s \otimes \left(\mathbf{I}_d - \frac{1}{d}\mathbf{J}_d\right) \otimes \frac{1}{r}\mathbf{J}_r,$$

$$\mathbf{P}_e = \mathbf{I}_s \otimes \mathbf{I}_d \otimes \left(\mathbf{I}_r - \frac{1}{r}\mathbf{J}_r\right), \quad \mathbf{P}_0 = \mathbf{I}_s \otimes \frac{1}{d}\mathbf{J}_d \otimes \frac{1}{r}\mathbf{J}_r,$$

where $\otimes$ denotes the Kronecker multiplication. The following identities will be useful

$$\begin{aligned} &\mathbf{P}_s\mathbf{P}_d = \mathbf{P}_s\mathbf{P}_e = \mathbf{P}_d\mathbf{P}_0 = \mathbf{P}_e\mathbf{P}_0 = \mathbf{0} \\ &\mathbf{P}_s\mathbf{P}_0 = \mathbf{P}_s, \qquad \mathbf{P}_0 + \mathbf{P}_d + \mathbf{P}_e = \mathbf{I}_n \end{aligned} \tag{2}$$

The Helmert matrix $\mathbf{H}_f$ of order $f \times f$ has elements

$$h_{i1} = 1/\sqrt{f}, \quad i = 1, ..., f,$$

$$h_{ii} = -(i-1)/\sqrt{i(i-1)}, \quad i = 2, ..., f,$$

$$h_{ij} = 0, \quad i = 3, ..., f; \quad j < i.$$

It is easy to show that

$$\mathbf{H}_f'\mathbf{H}_f = \mathbf{I}_f, \quad \mathbf{H}_f'\frac{1}{f}\mathbf{J}_f\mathbf{H}_f = \mathbf{E}_f^{11}, \quad \mathbf{H}_f'\mathbf{1}_f = \sqrt{f}\mathbf{1}_f^1, \quad \mathbf{H}_f'\frac{1}{f}\mathbf{J}_f\mathbf{1}_f = \sqrt{f}\mathbf{1}_f^1. \tag{3}$$

4. Estimation of variance components and coefficients of heritability

The analysis of variance of the model (1) takes the form of Table 1.

Equating the mean squares to their expectations and solving the resulting equations, gives estimators of variance components. We obtain the following estimators

Table 1. The analysis of variance for model (1)

Source of variation	Degrees of freedom	Sum of squares	Mean square	Expectation of mean square
Sires	$v_s = s-1$	$SS_s = \mathbf{Y}'\mathbf{P}_s\mathbf{Y}$	$MS_s = \frac{SS_s}{v_s}$	$\lambda_s = \sigma_e^2 + r\sigma_d^2 + rd\sigma_s^2$
Dams	$v_d = s(d-1)$	$SS_d = \mathbf{Y}'\mathbf{P}_d\mathbf{Y}$	$MS_d = \frac{SS_d}{v_d}$	$\lambda_d = \sigma_e^2 + r\sigma_d^2$
Progeny	$v_e = sd(r-1)$	$SS_e = \mathbf{Y}'\mathbf{P}_e\mathbf{Y}$	$MS_e = \frac{SS_e}{v_e}$	$\lambda_e = \sigma_e^2$

in terms of mean squares

$$\hat{\sigma}_e^2 = MS_e, \qquad \hat{\sigma}_d^2 = \frac{1}{r}(MS_d - MS_e), \qquad \hat{\sigma}_s^2 = \frac{1}{dr}(MS_s - MS_d),$$

hence

$$\begin{aligned} sdr\hat{\sigma}_s^2 &= \mathbf{Y}'(\frac{s}{s-1}\mathbf{P}_s - \frac{1}{d-1}\mathbf{P}_d)\mathbf{Y}, \\ sdr\hat{\sigma}_d^2 &= \mathbf{Y}'(\frac{d}{d-1}\mathbf{P}_d - \frac{1}{r-1}\mathbf{P}_e)\mathbf{Y}, \\ sdr\hat{\sigma}_y^2 &= \mathbf{Y}'(\frac{s}{s-1}\mathbf{P}_s + \mathbf{P}_d + \mathbf{P}_e)\mathbf{Y}. \end{aligned}$$

The CH are estimated as follows

$$\begin{aligned} \hat{h}_s^2 = ESCH = 4\frac{\mathbf{Y}'(\frac{s}{s-1}\mathbf{P}_s - \frac{1}{d-1}\mathbf{P}_d)\mathbf{Y}}{\mathbf{Y}'(\frac{s}{s-1}\mathbf{P}_s + \mathbf{P}_d + \mathbf{P}_e)\mathbf{Y}} = 4\frac{\mathbf{Y}'\mathbf{S}\mathbf{Y}}{\mathbf{Y}'\mathbf{K}\mathbf{Y}}, \\ \hat{h}_d^2 = EDCH = 4\frac{\mathbf{Y}'(\frac{d}{d-1}\mathbf{P}_d - \frac{1}{r-1}\mathbf{P}_e)\mathbf{Y}}{\mathbf{Y}'(\frac{s}{s-1}\mathbf{P}_s + \mathbf{P}_d + \mathbf{P}_e)\mathbf{Y}} = 4\frac{\mathbf{Y}'\mathbf{D}\mathbf{Y}}{\mathbf{Y}'\mathbf{K}\mathbf{Y}}. \end{aligned} \tag{4}$$

Magnus (1986) has developed a formula for moments of the ratio of two dependent quadratic forms of a normal vector. Under our assumptions the observation vector $\mathbf{Y}$ is multivariate normal $N(\boldsymbol{\mu}, \mathbf{V})$, where

$$\begin{aligned} \boldsymbol{\mu} &= (\mathbf{1}_s \otimes \mathbf{1}_d \otimes \mathbf{1}_r)\mu, \\ \mathbf{V} &= \sigma_s^2(\mathbf{I}_s \otimes \mathbf{J}_d \otimes \mathbf{J}_r) + \sigma_d^2(\mathbf{I}_s \otimes \mathbf{I}_d \otimes \mathbf{J}_r) + \sigma_e^2(\mathbf{I}_s \otimes \mathbf{I}_d \otimes \mathbf{I}_r). \end{aligned}$$

The covariance matrix has the spectral decomposition

$$\mathbf{V} = \lambda_s\mathbf{P}_0 + \lambda_d\mathbf{P}_d + \lambda_e\mathbf{P}_e, \tag{5}$$

because it follows from (2) that $\mathbf{P}_o$, $\mathbf{P}_d$ and $\mathbf{P}_e$ are idempotent, mutually orthogonal matrices whose sum is the identity matrix. The λ_s, λ_d and λ_e are characteristic roots of $\mathbf{P}_o$, $\mathbf{P}_d$ and $\mathbf{P}_e$ with the multiplicities $v_s + 1$, v_e and v_e, respectively. We are interested in derivation of a formula for the expectation of the form

$$\mathcal{E}(\mathbf{Y}'\mathbf{G}\mathbf{Y}/\mathbf{Y}'\mathbf{K}\mathbf{Y})^s, \qquad s = 1, 2, 3.$$

It will enable us to investigate an expectation, bias, variance, standard deviation, the coefficient of variation and the asymmetry of the estimators of CH.

In our case the mean vector is proportional to the vector $\mathbf{1}_n$. This fact allows to simplify the formula of Magnus. In order to calculate the moments according to this formula, we have worked out the following algorithm:

Input data: $\mathbf{V}, \mathbf{G}, \mathbf{K}$, where $\mathbf{G}$ stands for $\mathbf{S}$ or $\mathbf{D}$. These matrices are defined in (4).
A1. Calculate $\mathbf{L}$ such that $\mathbf{L}'\mathbf{L} = \mathbf{V}$.
A2. Calculate $\mathbf{L}'\mathbf{K}\mathbf{L}$.
A3. Calculate $\mathbf{Q}$ such that $\mathbf{Q}'\mathbf{L}'\mathbf{K}\mathbf{L}\mathbf{Q} = \mathbf{\Lambda}$ (a diagonal matrix).
A4. Calculate $\mathbf{\Delta} = (\mathbf{I}_n + 2t\mathbf{\Lambda})^{-\frac{1}{2}}$.
A5. Calculate determinant $|\mathbf{\Delta}|$.
A6. Calculate $\mathbf{G}^* = \mathbf{Q}'\mathbf{L}'\mathbf{G}\mathbf{L}\mathbf{Q}$.
A7. Calculate $\mathbf{R} = \mathbf{\Delta}\mathbf{G}^*\mathbf{\Delta}$, $\mathbf{R}^2$ and $\mathbf{R}^3$.
A8. Find nonnegative integer solutions $w = (n_1, n_2, ..., n_m)$ for $m = 1, 2, 3$ of the equation

$$n_1 + 2n_2 + 3n_3 + \cdots + mn_m = m$$

A9. Calculate

$$\gamma_m(w) = m!\, 2^m \prod_{j=1}^{m} (n_j!(2j)^{n_j})^{-1}.$$

Then the formula of Magnus becomes

$$\mathcal{E}\left[(\hat{h}^2)^m\right] = \frac{4^m}{(m-1)!}\left\{\sum_w \gamma_m(w) \int_0^\infty |\Delta| \prod_{i=1}^{m} \left[tr\mathbf{R}^j\right]^{n_j} dt\right\}, \tag{6}$$

where summing up is over all vectors $\mathbf{v} = (n_1, ..., n_m)$ calculated according to A8. Our interest is limited to

$$m = 1, \quad w = (n_1) = (1), \quad \gamma_1(1) = 1,$$

$$m = 2, \quad w = (n_1, n_2) = (2,0), (0,1), \quad \gamma_2(2,0) = 1, \quad \gamma_2(0,1) = 2,$$

$$m = 3, \quad w = (n_1, n_2, n_3) = (3,0,0), (1,1,0,), (0,0,1),$$

$$\gamma_3(3,0,0) = 1, \quad \gamma_3(1,1,0) = 6, \quad \gamma_3(0,0,1) = 8$$

Let us implement the algorithm for $\mathbf{V}$, $\mathbf{G}$ and $\mathbf{K}$ given by (4) and (5).
A1. Using the spectral decomposition (5) we obtain

$$\mathbf{L} = \sqrt{\lambda_s}\mathbf{P}_0 + \sqrt{\lambda_d}\mathbf{P}_d + \sqrt{\lambda_e}\mathbf{P}_e = \mathbf{L}'.$$

A2. Next we calculate

$$\mathbf{LKL} = \frac{s\lambda_s}{s-1}\mathbf{P}_s + \lambda_d\mathbf{P}_d + \lambda_e\mathbf{P}_e.$$

A3. In order to diagonalize $\mathbf{LKL}$ we define

$$\mathbf{Q} = \mathbf{H}_s \otimes \mathbf{H}_d \otimes \mathbf{H}_r,$$

with $\mathbf{H}_f$ defined in Section 3. We have

$$\begin{aligned}
\mathbf{Q}'\mathbf{P}_s\mathbf{Q} &= (\mathbf{H}'_s \otimes \mathbf{H}'_d \otimes \mathbf{H}_r)\left[\left(\mathbf{I}_s - \frac{1}{s}\mathbf{I}_s\right) \otimes \frac{1}{d}\mathbf{J}_d \otimes \frac{1}{r}\mathbf{J}_r\right](\mathbf{H}_s \otimes \mathbf{H}_d \otimes \mathbf{H}_r) \\
&= \left(\mathbf{H}'_s\mathbf{H}_s - \mathbf{H}'_s\frac{1}{s}\mathbf{J}_s\mathbf{H}_s\right) \otimes \mathbf{H}'_d\frac{1}{d}\mathbf{J}_d\mathbf{H}_d \otimes \mathbf{H}'_r\frac{1}{r}\mathbf{J}_r\mathbf{H}_r \\
&= (\mathbf{I}_s - \mathbf{E}_s^{11}) \otimes \mathbf{E}_d^{11} \otimes \mathbf{E}_r^{11}
\end{aligned}$$

and similarly

$$\begin{aligned}
\mathbf{Q}'\mathbf{P}_d\mathbf{Q} &= \mathbf{I}_s \otimes (\mathbf{I}_d - \mathbf{E}_d^{11}) \otimes \mathbf{E}_r^{11} \\
\mathbf{Q}'\mathbf{P}_e\mathbf{Q} &= \mathbf{I}_s \otimes \mathbf{I}_d \otimes (\mathbf{I}_r - \mathbf{E}_r^{11}).
\end{aligned}$$

Next, we obtain

$$\begin{aligned}
\Lambda &= \mathbf{Q}'\mathbf{LKLQ} \\
&= \frac{s\lambda_s}{s-1}(\mathbf{I}_s - \mathbf{E}_s^{11}) \otimes \mathbf{E}_d^{11} \otimes \mathbf{E}_r^{11} \\
&\quad + \lambda_d\mathbf{I}_s \otimes (\mathbf{I}_d - \mathbf{E}_d^{11}) \otimes \mathbf{E}_r^{11} + \lambda_e\mathbf{I}_s \otimes \mathbf{I}_d \otimes (\mathbf{I}_r - \mathbf{E}_r^{11}).
\end{aligned}$$

A4. We define a diagonal matrix by the formula

$$\mathbf{\Delta}^{-2} = \mathbf{I}_n + 2t\mathbf{\Lambda}.$$

The pivotal element of $\mathbf{\Delta}$ is equal to one, other diagonal elements are:

$$\begin{aligned}
&1 + 2t\tfrac{s\lambda_s}{s-1} && - \quad \text{occurs } v_s \text{ times,} \\
&1 + 2t\lambda_d && - \quad \text{occurs } v_d \text{ times,} \\
&1 + 2t\lambda_e && - \quad \text{occurs } v_e \text{ times.}
\end{aligned}$$

Therefore,

$$\begin{aligned}
\mathbf{\Delta} &= \mathbf{E}_s^{11} \otimes \mathbf{E}_d^{11} \otimes \mathbf{E}_r^{11} + \left(1 + 2t\frac{s\lambda_s}{s-1}\right)^{-\frac{1}{2}}(\mathbf{I}_s - \mathbf{E}_s^{11}) \otimes \mathbf{E}_d^{11} \otimes \mathbf{E}_r^{11} \\
&\quad + (1 + 2\lambda_d t)^{-\frac{1}{2}}\mathbf{I}_s \otimes (\mathbf{I}_d - \mathbf{E}_d^{11}) \otimes \mathbf{E}_r^{11} \\
&\quad + (1 + 2\lambda_e t)^{-\frac{1}{2}}\mathbf{I}_s \otimes \mathbf{I}_d \otimes (\mathbf{I}_r - \mathbf{E}_r^{11}).
\end{aligned}$$

A5. Now, we calculate the determinant

$$|\Delta| = \left(1 + \frac{2s\lambda_s}{s-1}t\right)^{-0.5v_s}(1 + 2\lambda_d t)^{-0.5v_d}(1 + 2\lambda_e t)^{-0.5v_e}.$$

The steps from A1 to A5 are common for both the coefficients SCH and DCH. Starting from step A6 calculation for the SCH and DCH are done separately. We will present the derivation for the SCH.

AS6. Using methods similar to those in A3, we obtain

$$\mathbf{S}^* = \mathbf{Q}'\mathbf{LSLQ} = \frac{s\lambda_s}{s-1}\left(\mathbf{I}_s - \mathbf{E}_s^{11}\right) \otimes \mathbf{E}_d^{11} \otimes \mathbf{E}_r^{11} - \frac{\lambda_d}{d-1}\mathbf{I}_s \otimes \left(\mathbf{I}_d - \mathbf{E}_d^{11}\right) \otimes \mathbf{E}_r^{11}.$$

AS7. Next, we calculate

$$\begin{aligned}
\mathbf{R}_s &= \mathbf{\Delta S}^*\mathbf{\Delta} = \\
&= \frac{s\lambda_s}{s-1}\left(1+\frac{2s\lambda_s}{s-1}t\right)^{-1}\left(\mathbf{I}_s - \mathbf{E}_s^{11}\right) \otimes \mathbf{E}_d^{11} \otimes \mathbf{E}_r^{11} \\
&\quad -\frac{\lambda_d}{d-1}(1+2\lambda_d t)^{-1}\mathbf{I}_s \otimes \left(\mathbf{I}_d - \mathbf{E}_d^{11}\right) \otimes \mathbf{E}_r^{11}
\end{aligned}$$

and

$$\begin{aligned}
\mathbf{R}_s^m &= \left(\frac{s\lambda_s}{s-1}\right)^m \left(1+\frac{2s\lambda_s}{s-1}t\right)^{-m}\left(\mathbf{I}_s - \mathbf{E}_s^{11}\right) \otimes \mathbf{E}_d^{11} \otimes \mathbf{E}_r^{11} \\
&\quad + \left(\frac{-\lambda_d}{d-1}\right)^m (1+2\lambda_d t)^{-m}\mathbf{I}_s \otimes \left(\mathbf{I}_d - \mathbf{E}_d^{11}\right) \otimes \mathbf{E}_r^{11}.
\end{aligned}$$

AS8. The trace which occurs in (6) can be expressed as

$$tr\mathbf{R}_s^m = v_s\left(\frac{s\lambda_s}{s-1}\right)^m\left(1+\frac{2s\lambda_s}{s-1}t\right)^{-m} + v_d\left(\frac{-\lambda_d}{d-1}\right)^m(1+2\lambda_d t)^{-m}.$$

5. Main results

Substituting the results of A5 and AS8 into (6) we obtain formulas for the following three moments

$$\begin{aligned}
m_{s1} &= \mathcal{E}(\hat{h}_s^2) = 4\int_0^\infty f(t)g_s(t)dt, \\
m_{s2} &= \mathcal{E}\left[(\hat{h}_s^2)^2\right] = 16\int_0^\infty tf(t)\left[g_s(t)\right]^2 dt + 32\int_0^\infty tf(t)h_s(t)dt, \\
m_{s3} &= \mathcal{E}\left[(\hat{h}_s^2)^3\right] = 32\int_0^\infty t^2 f(t)\left[g_s(t)\right]^3 dt + 196\int_0^\infty t^2 f(t)g_s(t)h_s(t)dt \\
&\quad +256\int_0^\infty t^2 f(t)k_s(t)dt,
\end{aligned} \tag{7}$$

where

$$
\begin{aligned}
&f(t) = |\mathbf{\Delta}|, \\
&g_s(t) = \frac{v_s s\lambda_s}{s-1}\left(1+\frac{2s\lambda_s}{s-1}t\right)^{-1} - \frac{v_d\lambda_d}{d-1}(1+2\lambda_d t)^{-1}, \\
&h_s(t) = v_s\left(\frac{s\lambda_s}{s-1}\right)^2\left(1+\frac{2s\lambda_s}{s-1}t\right)^{-2} + v_d\left(\frac{\lambda_d}{d-1}\right)^2(1+2\lambda_d t)^{-2}, \\
&k_s(t) = v_s\left(\frac{s\lambda_s}{s-1}\right)^3\left(1+\frac{2s\lambda_s}{s-1}t\right)^{-3} - v_d\left(\frac{\lambda_d}{d-1}\right)^3(1+2\lambda_d t)^{-3}.
\end{aligned}
\tag{8}
$$

Similar derivation leads to formulas for the moments of EDCH:

$$
\begin{aligned}
m_{d1} &= \mathcal{E}(\hat{h}_d^2) = 4\int_0^\infty f(t)g_d(t)dt, \\
m_{d2} &= \mathcal{E}\left[(\hat{h}_d^2)^2\right] = 16\int_0^\infty tf(t)\left[g_d(t)\right]^2 dt + 32\int_0^\infty tf(t)h_d(t)dt, \\
m_{d3} &= \mathcal{E}\left[(\hat{h}_d^2)^3\right] = 32\int_0^\infty t^2 f(t)\left[g_d(t)\right]^3 dt + 196\int_0^\infty t^2 f(t)g_d(t)h_d(t)dt \\
&\quad +256\int_0^\infty t^2 f(t)k_d(t)dt,
\end{aligned}
$$

where

$$
\begin{aligned}
g_d(t) &= v_d\frac{d\lambda_d}{d-1}\left(1+\frac{2d\lambda_d}{d-1}t\right)^{-1} - v_e\frac{\lambda_e}{r-1}(1+2\lambda_e t)^{-1}, \\
h_d(t) &= v_d\left(\frac{d\lambda_d}{d-1}\right)^2\left(1+\frac{2d\lambda_d}{d-1}t\right)^{-2} + v_e\left(\frac{\lambda_e}{r-1}\right)^2(1+2\lambda_e t)^{-2}, \\
k_d(t) &= v_d\left(\frac{d\lambda_d}{d-1}\right)^3\left(1+\frac{2d\lambda_d}{d-1}t\right)^{-3} - v_e\left(\frac{\lambda_e}{r-1}\right)^3(1+2\lambda_e t)^{-3}.
\end{aligned}
$$

6. Numerical results

To illustrate the theory described in the previous section, we will work out an example of the model (1) with $(\sigma_s^2, \sigma_d^2, \sigma_e^2) = (0.2, 0.1333, 1)$ and $(s, d, r) = (20, 6, 3)$. It yields $\lambda_s = 25.6$, $\lambda_d = 1.6$, $\lambda_e = 1$ and $v_s = 19$, $v_d = 100$, $v_e = 240$. The true values of *CH* are $h_s^2 = 0.6$ and $h_d^2 = 0.4$. Now, we find from A5 and (6) that

$$
|\mathbf{\Delta}| \;=\; f(t) = (1+\frac{824}{19}t)^{-9.5}(1+3.2t)^{-50}(1+2t)^{-120},
$$

$$trR_s = 512(1+\frac{824}{19}t)^{-1} - 80(1+3.2t)^{-1},$$
$$trR_s^2 = \frac{512^2}{19}(1+\frac{824}{19}t)^{-2} + 64(1+3.2t)^{-2}.$$

Substituting these expressions into (7) we obtain

$m_{s1} = E(\hat{h}_s^2) = 0.58843,$ $\quad bias(\hat{h}_s^2) = -0.01157,$

$E[(\hat{h}_s^2)^2] = 0.40068,$ $\quad SD(\hat{h}_s^2) = 0.23330$ (standard deviation).

Let us define the relative bias as follows

$$relbias((\hat{h}_s^2) = \frac{E(\hat{h}_s^2) - h_s^2}{h_s^2}.$$

Table 2. Expected values of estimators of the coefficients of heritability ($\mathcal{E}$ESCH for sires, $\mathcal{E}$EDCH for dams), their standard deviations (SDS and SDD) and relative biases (RBS and RBD). $s = 20$ (sires), $d = 6$ (dams), $r = 3$ (progeny), $n = sdr = 360$ (total number of progeny).

h_s^2	h_d^2	$\mathcal{E}$ESCH ± SDS	RBS (%)	$\mathcal{E}$EDCH ± SDD	RBD (%)
0.2	0.2	0.1976 ± 0.1386	–1.2	0.1974 ± 0.2226	–1.30
0.2	0.4	0.1974 ± 0.1460	–1.3	0.3960 ± 0.2306	–0.99
0.2	0.6	0.1972 ± 0.1535	–1.4	0.5946 ± 0.2364	–0.89
0.2	0.8	0.1970 ± 0.1609	–1.5	0.7932 ± 0.2401	–0.84
0.4	0.2	0.3939 ± 0.1855	–1.5	0.1978 ± 0.2120	–1.10
0.4	0.4	0.3935 ± 0.1926	–1.6	0.3968 ± 0.2204	–0.81
0.4	0.6	0.3931 ± 0.1997	–1.7	0.5957 ± 0.2270	–0.72
0.4	0.8	0.3928 ± 0.2069	–1.8	0.7941 ± 0.2316	–0.67
0.6	0.2	0.5890 ± 0.2266	–1.8	0.1983 ± 0.2015	–0.85
0.6	0.4	0.5884 ± 0.2333	–1.9	0.3977 ± 0.2106	–0.58
0.6	0.6	0.5879 ± 0.2401	–2.0	0.5970 ± 0.2181	–0.50
0.6	0.8	0.5875 ± 0.2471	–2.1	0.7964 ± 0.2240	–0.45
0.8	0.2	0.7831 ± 0.2618	–2.1	0.1989 ± 0.1912	–0.55
0.8	0.4	0.7825 ± 0.2682	–2.2	0.3987 ± 0.2010	–0.31
0.8	0.6	0.7819 ± 0.2748	–2.3	0.5986 ± 0.2098	–0.23
0.8	0.8	0.7813 ± 0.2815	–2.3	0.7985 ± 0.2174	–0.19

Then, for our data, we obtain

$$relbias((\hat{h}_s^2) = (0.58843 - 0.6)/0.6 = -0.01928 \approx -1.9\%.$$

The results of such calculations for selected values of SCH and DCH for the design $(s, d, r) = (20, 6, 3)$ and $n = 360$ are given in Table 2.

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Dokładne momenty estymatorów współczynników odziedziczalności dla dwustopniowego zrównoważonego modelu hierarchicznego

Streszczenie

Współczynniki odziedziczalności określane są jako stosunki wariancji genotypowej do wariancji fenotypowej. Ich estymatory otrzymuje się metodą analizy wariancji, mają one postać ilorazów dwóch form kwadratowych wektora obserwacji. Wyprowadzono dokładne wzory na momenty tych estymatorów dla modelu dwustopniowej klasyfikacji hierarchicznej przy założeniu normalności. Wzory te przedstawiają momenty estymatorów jako całki oznaczone pewnych funkcji wymiernych i niewymiernych. Dołączono tablicę wartości oczekiwanych, odchyleń standardowych i obciążeń względnych estymatorów dla wybranych wartości parametrów.

Słowa kluczowe: estymatory współczynników odziedziczalności, dokładne momenty, odchylenie standardowe, obciążenia względne.