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# Genetic evaluation with autosomal and X-chromosomal inheritance *

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**Summary.** At present, genetic evaluation in livestock using best linear unbiased prediction (BLUP) assumes autosomal inheritance. There is evidence, however, of X-chromosomal inheritance for some traits of economic importance. BLUP can accommodate models that include X-chromosomal in addition to autosomal inheritance. To obtain BLUP with autosomal and X-chromosomal additive inheritance for a population in which allelic frequency is equal in the sexes, and that is in gametic equilibrium, we write $y_i = \boldsymbol{x}_i' \boldsymbol{\beta} + a_i + s_i + e_i$, where $y_i$ is the phenotypic value for individual $i$, $\boldsymbol{x}_i'$, is a vector of constants relating $y_i$ to fixed effects, $\boldsymbol{\beta}$ is a vector of fixed effects, $a_i$ is the additive genetic effect for autosomal loci, $s_i$ is the additive genetic effect for X-chromosomal loci, and $e_i$ is random error. The covariance matrix of $a_i$'s is $\boldsymbol{A}\sigma_A^2$, where $\boldsymbol{A}$ is the matrix of twice the co-ancestries between relatives for autosomal loci, and $\sigma_A^2$ is the variance of additive genetic effects for autosomal loci. The covariance matrix of $s_i$'s is $\boldsymbol{S}\sigma_F^2$, where $\boldsymbol{S}$ is a matrix of functions of co-ancestries between relatives for X-chromosomal loci and $\sigma_F^2$ is the variance of additive genetic effects for X-chromosomal loci for noninbred females. Given the covariance matrices of random effects $a_i$, $s_i$, and $e_i$, BLUPs of autosomal and of X-chromosomal additive effects can be obtained using mixed model equations. Recursive rules to construct $\boldsymbol{S}$ and an efficient algorithm to compute its inverse are given.

**Key words:** X-linkage – Covariance – Genetic evaluation – BLUP

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## Introduction

Methods for genetic evaluation in livestock usually assume only autosomal inheritance. There is evidence, however, that X-linked (X-chromosomal) inheritance may make a contribution that should not be ignored in evaluating individuals genetically for economically important quantitative traits (e.g., Jerome et al. 1956; Thomas et al. 1958; VanRaden 1987).

Best linear unbiased prediction (BLUP) (Henderson 1973) is widely used for genetic evaluation in livestock for traits with autosomal inheritance (e.g., Benyshek et al. 1988; Wiggans et al. 1988; Robinson and Chesnais 1988). BLUP can accommodate models that include X-chromosomal in addition to autosomal inheritance. At present, however, models used for genetic evaluation do not account for X-chromosomal inheritance.

The objective of this paper is to show how BLUP can be used for genetic evaluation in the presence of autosomal and X-chromosomal additive inheritance.

## Theory

*Genetic model*

We assume that the male is heterogametic (XY) and the female is homogametic (XX). The Y chromosome is considered to contain inert loci and is ignored. Further, we assume a population in which allelic frequency is equal in the sexes and that is in gametic equilibrium. Results developed here also are applicable to species in which the male is homogametic (ZZ) and the female is heterogametic (ZW), such as poultry.

Consider a single X-chromosomal locus. We define the additive genotypic value for a trait in male $M$ to be $g_M$ and for the same trait in female $F$ to be $g_F$. Male $M$ receives its allele $x$ from its maternal parent and female $F$ receives alleles $x_m$ from its maternal parent $m$, and $x_p$ from its paternal parent $p$. Then, for male $M$,

$$g_M = \alpha$$

and, for female $F$,

$$g_F = \alpha_m + \alpha_p ,$$

where $\alpha$ is the additive genetic effect for the maternal allele ($x$) in male $M$, and where $\alpha_m$ and $\alpha_p$ are additive genetic effects for the maternal ($x_m$) and paternal ($x_p$) allele in female $F$. We assume that additive effects for the same allele in males and females are equal. Therefore, because allelic frequency is equal in the sexes,

$$V(\alpha) = V(\alpha_m) = V(\alpha_p). \quad (1)$$

Thus, additive genotypic variance for males, $V(g_M)$, and for non-inbred females, $V(g_F)$, are

$$V(g_M) = V(\alpha)$$

and

$$\begin{aligned} V(g_F) &= V(\alpha_m + \alpha_p) \\ &= V(\alpha_m) + V(\alpha_p) \\ &= 2V(\alpha) \\ &= 2V(g_M), \end{aligned}$$

from Eq. (1).

For a trait determined by many such loci, therefore, additive genetic variance for noninbred females ($\sigma_F^2$) is twice additive genetic variance for males ($\sigma_M^2$). Variance for inbred females is $\sigma_F^2(1+f)$, where $f$ is the coefficient of inbreeding for X-chromosomal loci (Wright 1933).

Consider again a single X-chromosomal locus. Additive genotypic covariance between two males $M$ and $M'$ is

$$\begin{aligned} C(g_M, g_{M'}) &= C(\alpha, \alpha') = V(\alpha)\, P(x \equiv x') \\ &= V(\alpha)\, r_{MM'} \\ &= \tfrac{1}{2} V(g_F)\, r_{MM'}, \end{aligned}$$

where $P(x \equiv x')$ denotes the probability that allele $x$ is identical by descent to allele $x'$, and where the co-ancestry between males ($r_{MM'}$) is the probability that allele $x$ in $M$ is identical by descent to the allele $x'$ in $M'$ (Grossman and Eisen 1989).

Additive genotypic covariance between two females $F$ and $F'$ is

$$\begin{aligned} C(g_F, g_{F'}) &= C(\alpha_m, \alpha_{m'}) + C(\alpha_m, \alpha_{p'}) + C(\alpha_p, \alpha_{m'}) + C(\alpha_p, \alpha_{p'}) \\ &= V(\alpha_m)\,[P(x_m \equiv x_{m'}) + P(x_m \equiv x_{p'}) + P(x_p \equiv x_{m'}) + P(x_p \equiv x_{p'})] \\ &= V(\alpha_m)\,(4 r_{FF'}) \\ &= \tfrac{1}{2} V(g_F)\,(4 r_{FF'}) \\ &= 2 V(g_F)\, r_{FF'}, \end{aligned}$$

where the co-ancestry between females ($r_{FF'}$) is the probability that an allele drawn at random from $F$ is identical by descent to an allele drawn at random from $F'$ (Grossman and Eisen 1989).

Additive genotypic covariance between male $M$ and female $F$ is

$$C(g_M, g_F) = C(\alpha, \alpha_m) + C(\alpha, \alpha_p).$$

Because additive effects for the same allele in the sexes are equal,

$$\begin{aligned} C(g_M, g_F) &= V(\alpha)\,[P(x \equiv x_m) + P(x \equiv x_p)] \\ &= V(\alpha)\,(2 r_{MF}) \\ &= \tfrac{1}{2} V(g_F)\,(2 r_{MF}) \\ &= V(g_F)\, r_{MF}, \end{aligned}$$

where the co-ancestry between male and female ($r_{MF}$) is the probability that the allele $x$ in $M$ is identical by descent to an allele drawn at random from $F$ (Grossman and Eisen 1989).

For a trait determined by many such loci, therefore, additive genetic covariance between males is $\frac{1}{2}(\sigma_F^2)\, r_{MM'}$, between females it is $2(\sigma_F^2)\, r_{FF'}$, and between male and female, $(\sigma_F^2)\, r_{MF}$.

*Best linear unbiased prediction*

Total additive genetic effect for animal $i$ can be written as the sum of its additive genetic effect for autosomal loci ($a_i$) and its additive genetic effect for X-chromosomal loci ($s_i$). To obtain BLUP of $a_i$ and $s_i$, we write

$$y_i = \boldsymbol{x}_i' \boldsymbol{\beta} + a_i + s_i + e_i , \quad (2)$$

where $y_i$ is the phenotypic value for individual $i$, $\boldsymbol{x}_i'$ is a row vector of constants relating $y_i$ to fixed effects, $\boldsymbol{\beta}$ is a column vector of fixed effects, and $e_i$ is random error.

The covariance matrix of $a_i$'s is $\boldsymbol{A}\sigma_A^2$, where $\boldsymbol{A}$ is the matrix of twice the co-ancestries between relatives for autosomal loci (Henderson 1976) and $\sigma_A^2$ is the variance of additive genetic values for autosomal loci. The covariance matrix of $s_i$'s is $\boldsymbol{S}\sigma_F^2$, where $\boldsymbol{S}$ is a matrix whose elements are functions of co-ancestries between relatives for X-chromosomal loci. The covariance matrix of $e_i$'s is assumed to be $\boldsymbol{I}\sigma^2$.

Given the covariance matrices of effects $a_i$, $s_i$, and $e_i$ and one record for each individual, BLUPs of autosomal effects ($\hat{\boldsymbol{a}}$) and of X-chromosomal effects ($\hat{\boldsymbol{s}}$) are obtained using mixed model equations (MMEs) (Henderson 1973):

$$\begin{bmatrix} \boldsymbol{X}'\boldsymbol{X} & \boldsymbol{X}' & \boldsymbol{X}' \\ \boldsymbol{X} & \boldsymbol{I} + \boldsymbol{A}^{-1}\sigma^2/\sigma_A^2 & \boldsymbol{I} \\ \boldsymbol{X} & \boldsymbol{I} & \boldsymbol{I} + \boldsymbol{S}^{-1}\sigma^2/\sigma_F^2 \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}^\circ \\ \hat{\boldsymbol{a}} \\ \hat{\boldsymbol{s}} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}'\boldsymbol{y} \\ \boldsymbol{y} \\ \boldsymbol{y} \end{bmatrix}$$

The inverse of $\boldsymbol{A}$ can be obtained simply by an algorithm described by Henderson (1976). The construction of $\boldsymbol{S}$ and the simple, efficient computation of its inverse follow.

## Construction of $S$ via the tabular method

The tabular method to construct $\boldsymbol{S}$ is based on the following linear models for additive genotypic values for X-chromosomal loci in male $M$ with a maternal parent $m$ and in female $F$ with a maternal parent $m$ and a paternal parent $p$.

$$\text{Male:} \quad s_M = \tfrac{1}{2} s_m + \varepsilon_M \quad (3)$$

$$\text{Female:} \quad s_F = \tfrac{1}{2} s_m + s_p + \varepsilon_F \quad (4)$$

*Theorem*

For individuals $i$ and $j$, where $i$ is not a direct descendent of $j$, the covariance between $s_i$ and $\varepsilon_j$ is null.

*Proof*

See 'Appendix'.

Now, covariance between an individual $i$ and male $M$, where $i$ is not a direct descendent of $M$, can be written as

$$\begin{aligned} C(s_i, s_M) &= C(s_i, \tfrac{1}{2} s_m + \varepsilon_M) \\ &= \tfrac{1}{2} C(s_i, s_m) + C(s_i, \varepsilon_M) \\ &= \tfrac{1}{2} C(s_i, s_m), \end{aligned} \quad (5)$$

because $C(s_i, \varepsilon_m)$ is zero from 'Theorem'.

Covariance between individual $i$ and female $F$, where $i$ is not a direct descendent of $F$, can be written as

$$\begin{aligned} C(s_i, s_F) &= C(s_i, \tfrac{1}{2}s_m + s_p + \varepsilon_F) \\ &= \tfrac{1}{2}C(s_i, s_m) + C(s_i, s_p) + C(s_i, \varepsilon_F) \\ &= \tfrac{1}{2}C(s_i, s_m) + C(s_i, s_p), \end{aligned} \quad (6)$$

because $C(s_i, \varepsilon_F)$ is zero from 'Theorem'.

From Eqs. (5) and (6), recursive rules to construct the $\boldsymbol{S}$ matrix, similar to those of Henderson (1976), are given below.

(1) Number individuals such that progeny follow parents.
(2) For females, set diagonal elements to 1.
(3) For males, set diagonal elements to $\frac{1}{2}$.
(4) For female $i$ with mother $m$ and father $p$, element $j$ of row $i$ ($s_{ij}$) in $\boldsymbol{S}$ is computed as

$$s_{ij} = \tfrac{1}{2}s_{mj} + s_{pj}, \quad \text{for} \quad j = 1, \ldots, i-1.$$

(4.1) Elements in column $i$ are obtained by symmetry.
(4.2) Add $s_{mp}$ to $s_{ii}$.
(5) For male $i$ with mother $m$, element $s_{ij}$ is computed as

$$s_{ij} = \tfrac{1}{2}s_{mj}, \quad \text{for} \quad j = 1, \ldots, i-1.$$

(5.1) Elements in column $i$ are obtained by symmetry.

*Numerical example for constructing* $\boldsymbol{S}$

Consider the pedigree in Fig. 1. Following Henderson (1976), we can tabulate this information as in Table 1. To construct $\boldsymbol{S}$ (Table 2), set diagonal elements to $\frac{1}{2}$ for males 1, 3, 5, and 7. Set diagonal elements to 1 for females 2, 4, 6, and 8. Off-diagonal elements for the upper left $2 \times 2$ submatrix are zero because base-population individuals 1 and 2 are assumed to be unrelated.

Row elements below the diagonal are obtained by rules 4 and 5. Column elements above the diagonal are obtained by symmetry. Row elements for male 3 are zero because its mother is unknown. Each row element for female 4 is obtained by taking one-half the corresponding element in row 2 plus the corresponding element in row 1. Each row element for male 5 is obtained by taking one-half the corresponding element in row 4. Each row element for female 6 is obtained in a manner similar to row 4, except that rows 4 and 1 are used. Note that parents of female 6 are related, so that element $s_{41} = \frac{1}{2}$ is added to the diagonal element for female 6. Elements in rows and columns 7 and 8 are obtained in a similar manner.

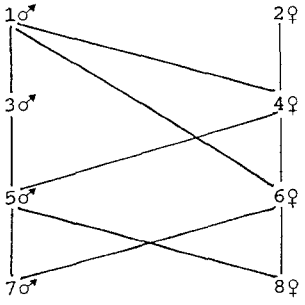


**Fig. 1.** Pedigree involving inbreeding, with individuals distinguished by sex (adapted from Henderson 1976)

**Table 1.** Individuals and their parents from Fig. 1

| Individual | Parents |
|---|---|
| 1♂ | unknown |
| 2♀ | unknown |
| 3♂ | 1 and unknown |
| 4♀ | 1 and 2 |
| 5♂ | 3 and 4 |
| 6♀ | 1 and 4 |
| 7♂ | 5 and 6 |
| 8♀ | 5 and 6 |

**Table 2.** $\boldsymbol{S}$ matrix

| | 1♂ | 2♀ | 3♂ | 4♀ | 5♂ | 6♀ | 7♂ | 8♀ |
|---|---|---|---|---|---|---|---|---|
| 1♂ | 1/2 | 0 | 0 | 1/2 | 1/4 | 3/4 | 3/8 | 5/8 |
| 2♀ | 0 | 1 | 0 | 1/2 | 1/4 | 1/4 | 1/8 | 3/8 |
| 3♂ | 0 | 0 | 1/2 | 0 | 0 | 0 | 0 | 0 |
| 4♀ | 1/2 | 1/2 | 0 | 1 | 1/2 | 1 | 1/2 | 1 |
| 5♂ | 1/4 | 1/4 | 0 | 1/2 | 1/2 | 1/2 | 1/4 | 3/4 |
| 6♀ | 3/4 | 1/4 | 0 | 1 | 1/2 | 1+1/2 | 3/4 | 5/4 |
| 7♂ | 3/8 | 1/8 | 0 | 1/2 | 1/4 | 3/4 | 1/2 | 5/8 |
| 8♀ | 5/8 | 3/8 | 0 | 1 | 3/4 | 5/4 | 5/8 | 1+1/2 |

**Computation of $\boldsymbol{S}$ inverse**

Following Quaas et al. (1984), Eqs. (3) and (4) are used to write the vector ($s$) of additive genetic effects for X-chromosomal loci:

$$s = Ps + \varepsilon,$$

where $\boldsymbol{P}$ is a matrix in which each row contains one or two nonzero elements, if parents are known, or all zeros, if parents are unknown. From Eq. (3), the row for a male contains an element $\frac{1}{2}$ in the column corresponding to its maternal parent. From Eq. (4), the row for a female contains an element $\frac{1}{2}$ in the column corresponding to its maternal parent and an element 1 in the column corresponding to its paternal parent.

It is shown below that the covariance matrix of $\varepsilon$ is $V\sigma_F^2$, where $V$ is a diagonal matrix of order $n$, the number of individuals in the pedigree. For any two individuals, one will not be a direct descendent of the other. Thus, without loss of generality, let $i$ be an individual that is not a direct descendent of $j$, which has maternal and paternal parents $m$ and $p$. Covariances of $s_i$, $s_m$, and $s_p$ with $\varepsilon_j$ are

null, from 'Theorem', because parents $m$ and $p$ are not and cannot be direct descendents of individual $j$. Hence, from Eqs. (3) and (4), the covariance between $\varepsilon_i$ and $\varepsilon_j$ is also null and $V$ is diagonal.

To proceed, we need the diagonal elements of $V$ for males and for females when parents are known and unknown. If parents $m$ and $p$ are known, the diagonal element for a male [from Eq. (3)] or for a female [from Eq. (4)] is $\frac{1}{4}(1-f)$, where $f$ is the coefficient of inbreeding for the maternal parent $m$. If maternal parent $m$ is unknown, the diagonal element for a male or for a female is $\frac{1}{2}$. If paternal parent $p$ is unknown, the diagonal element for a male is $\frac{1}{4}(1-f)$ and the diagonal element for a female is $\frac{1}{4}(3-f)$. If both parents are unknown, the diagonal element for a male is $\frac{1}{2}$ and for a female is 1.

Again, following Quaas et al. (1984), $s$ can be written as

$$s=(I-P)^{-1}\,\varepsilon$$

and the covariance matrix of $s$ as

$$V(s)=S\,\sigma_F^2=(I-P)^{-1}\,V(I-P')^{-1}\,\sigma_F^2.$$

The inverse of $S$ now can be written as

$$S^{-1}=(I-P')\,V^{-1}(I-P)=Q\,V^{-1}\,Q', \qquad (7)$$

where $Q=(I-P')$. Because $V^{-1}$ is diagonal, Eq. (7) can be written as

$$S^{-1}=\Sigma_i\, q_i\, q_i'\, d_i, \quad \text{for} \quad i=1,\ldots,n,$$

where $q_i$ is column $i$ of $Q$ and $d_i$ is diagonal element $i$ of $V^{-1}$.

Thus, to construct the inverse of $S$ directly,

(1) set $S^{-1}$ to $\mathbf{0}$.
(2) For each individual $i$, with maternal and paternal parents $m$ and $p$, add $d_i$ times the following to the indicated elements of $S^{-1}$:

for males, if $m$ is known, $\frac{1}{4}$ to element $(m, m)$, 1 to element $(i, i)$, and $-\frac{1}{2}$ to elements $(m, i)$ and $(i, m)$. If $m$ is unknown, omit elements involving $m$;

or

for females, if $m$ and $p$ are known, $\frac{1}{4}$ to element $(m, m)$, 1 to elements $(p, p)$ and $(i, i)$, $\frac{1}{2}$ to elements $(m, p)$ and $(p, m)$, $-\frac{1}{2}$ to elements $(m, i)$ and $(i, m)$, and $-1$ to elements $(p, i)$ and $(i, p)$. If $m$ is unknown, omit elements involving $m$. If $p$ is unknown, omit elements involving $p$.

*Numerical example for constructing S inverse*

Consider the pedigree in Fig. 1 and Table 1. We need first to construct the diagonal elements of $V$. Because parents of individuals 1 and 2 are unknown, the diagonal element for male 1 is $\frac{1}{2}$ and the diagonal element for female 2 is 1. The maternal parent of male 3 is unknown so the diagonal element is $\frac{1}{2}$. Parents of individuals 4, 5, and 6 are known, and individuals 2 and 4 (their maternal parents) are noninbred, so the diagonal elements are $\frac{1}{4}$. Parents of individuals 7 and 8 are known, and individual 6 (their maternal parent) is inbred ($f=\frac{1}{2}$), so the diagonal elements are 1/8.

The matrix $P$ for this pedigree is in Table 3. The first three rows are null because maternal parents are unknown for males 1 and 3 and both parents are unknown for female 2. For female 4, with parents 1 and 2, column 1 corresponding to its paternal parent contains 1 and column 2 corresponding to its maternal parent contains $\frac{1}{2}$. For male 5, with parents 3 and 4, column 4 corresponding to its maternal parent contains $\frac{1}{2}$. For remaining individuals, rows are obtained in a similar manner.

The matrix $Q=(I-P')$ is in Table 4. It can be verified that $Q\,V^{-1}\,Q'$ is the inverse of $S$, which is in Table 5.

**Table 3.** $P$ matrix

| | 1♂ | 2♀ | 3♂ | 4♀ | 5♂ | 6♀ | 7♂ | 8♀ |
|---|---|---|---|---|---|---|---|---|
| 1♂ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2♀ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3♂ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4♀ | 1 | 1/2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5♂ | 0 | 0 | 0 | 1/2 | 0 | 0 | 0 | 0 |
| 6♀ | 1 | 0 | 0 | 1/2 | 0 | 0 | 0 | 0 |
| 7♂ | 0 | 0 | 0 | 0 | 0 | 1/2 | 0 | 0 |
| 8♀ | 0 | 0 | 0 | 0 | 1 | 1/2 | 0 | 0 |

**Table 4.** $Q=(I-P')$ matrix

| | 1♂ | 2♀ | 3♂ | 4♀ | 5♂ | 6♀ | 7♂ | 8♀ |
|---|---|---|---|---|---|---|---|---|
| 1♂ | 1 | 0 | 0 | −1 | 0 | −1 | 0 | 0 |
| 2♀ | 0 | 1 | 0 | −1/2 | 0 | 0 | 0 | 0 |
| 3♂ | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 4♀ | 0 | 0 | 0 | 1 | −1/2 | −1/2 | 0 | 0 |
| 5♂ | 0 | 0 | 0 | 0 | 1 | 0 | 0 | −1 |
| 6♀ | 0 | 0 | 0 | 0 | 0 | 1 | −1/2 | −1/2 |
| 7♂ | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 8♀ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

**Table 5.** $S^{-1}=QV^{-1}\,Q'$

| | 1♂ | 2♀ | 3♂ | 4♀ | 5♂ | 6♀ | 7♂ | 8♀ |
|---|---|---|---|---|---|---|---|---|
| 1♂ | 10 | 2 | 0 | −2 | 0 | −4 | 0 | 0 |
| 2♀ | 2 | 2 | 0 | −2 | 0 | 0 | 0 | 0 |
| 3♂ | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| 4♀ | −2 | −2 | 0 | 6 | −2 | −2 | 0 | 0 |
| 5♂ | 0 | 0 | 0 | −2 | 12 | 4 | 0 | −8 |
| 6♀ | −4 | 0 | 0 | −2 | 4 | 8 | −4 | −4 |
| 7♂ | 0 | 0 | 0 | 0 | 0 | −4 | 8 | 0 |
| 8♀ | 0 | 0 | 0 | 0 | −8 | −4 | 0 | 8 |

## Discussion

We have described a tabular method to construct the $\boldsymbol{S}$ matrix for X-chromosomal loci. We also developed a simple and efficient algorithm to compute the inverse of $\boldsymbol{S}$. This development allows for X-chromosomal inheritance to be accounted for in genetic evaluation by including X-chromosomal additive effects, in addition to autosomal additive effects, in a mixed model. This results in an increase in the number of mixed model equations equal to the number of individuals in the pedigree. Equivalent models, such as the reduced animal model, may be used to reduce the number of equations.

Our procedure requires knowledge of variances of autosomal and X-chromosomal additive effects. Based on chromosome numbers for farm animals, Lush (1945) suggested that X-chromosomal inheritance accounts for about 5% of total genetic variance. In species with few chromosomes, such as *D. melanogaster*, variance due to X-chromosomal inheritance can account for a large proportion of total genetic variance for some traits (Cowley et al. 1986).

Differences in heritabilities from the sire component and from the dam component, obtained by estimating sire and dam variance components using Method I (Henderson 1953), suggested that X-chromosomal effects could affect body weight or weight gain in female chickens (Jerome et al. 1956; Thomas et al. 1958). VanRaden (1987) compared variance components for sire and maternal grandsire, and suggested that about 5% of genetic variation for milk and for fat production in Holstein cattle is located on the X-chromosome.

The mixed model presented here can be used to estimate directly variance components for autosomal and X-chromosomal additive effects by restricted maximum likelihood (REML). With this approach, all data and all known relationships are used to estimate the variance components. If data used for selection decisions are included in the analysis, then REML can be computed, ignoring selection (Fernando and Gianola 1990; Im et al. 1989).

We have assumed that allelic frequency in the population is equal in the sexes. This is not a valid assumption for a cross between populations with different allelic frequencies, for example. For a single autosomal locus, a crossbred population will achieve genotypic equilibrium in one or two generations of random mating, whereas for a single X-chromosomal locus the population will achieve equilibrium only in the limit. When the population is in disequilibrium, covariances between relatives can be obtained, but not easily (Grossman and Fernando 1989), and computing genetic evaluations is not straightforward.

Our approach to the analysis of X-chromosomal inheritance could be extended to accommodate other modes of inheritance, such as dosage compensation or X-chromosomal inactivation (Levitan 1988), by constructing the appropriate covariance matrix of $s_i$'s. Alternative modes of inheritance could be tested by comparing likelihoods under the alternative models.

Recent research by Schaeffer et al. (1989) outlines the genetic analysis of autosomally inherited effects when either the paternal or maternal gamete is expressed. Our analysis of X-chromosomally inherited effects is based on the maternal gamete being expressed in the male and in the female, but on the paternal gamete being expressed only in the female.

## Appendix

*Proof of theorem*

Let $s_M$ be the additive genotypic value for X-chromosomal loci in male $M$ with a maternal parent $m$ and let $s_F$ be the additive genotypic value for X-chromosomal loci in female $F$ with maternal and paternal parents $m$ and $p$. Then we can represent these genotypic values in a linear model as a function of additive genetic effects for the maternal ($s_m$) and paternal ($s_p$) parents:

$$s_M = \tfrac{1}{2}s_m + \varepsilon_M$$

and

$$s_F = \tfrac{1}{2}s_m + s_p + \varepsilon_F.$$

From the text, it has been shown that additive genotypic covariance between males $M$ and $M'$ is $\frac{1}{2}(\sigma_F^2)\, r_{MM}$, between females $F$ and $F'$ it is $2(\sigma_F^2)\, r_{FF}$, and between male $M$ and female $F$, $(\sigma_F^2)\, r_{MF}$.

*Female–female.* Covariance between additive genotypic values for females $F$ and $F'$, where $F$ is not a direct descendent of $F'$, is

$$\begin{aligned}\mathrm{C}(s_F, s_{F'}) &= \mathrm{C}(s_F, \tfrac{1}{2}s_{m'} + s_{p'} + \varepsilon_{F'}) \\ &= \tfrac{1}{2}\mathrm{C}(s_F, s_{m'}) + \mathrm{C}(s_F, s_{p'}) + \mathrm{C}(s_F, \varepsilon_{F'}).\end{aligned}$$

From the above, $\mathrm{C}(s_F, s_{F'}) = 2\sigma_F^2 r_{FF'}$, $\mathrm{C}(s_F, s_{m'}) = 2\sigma_F^2 r_{Fm'}$, and $\mathrm{C}(s_F, s_{p'}) = \sigma_F^2 r_{Fp'}$, so that

$$\begin{aligned}2\sigma_F^2 r_{FF'} &= \tfrac{1}{2}\mathrm{C}(s_F, s_{m'}) + \mathrm{C}(s_F, s_{p'}) + \mathrm{C}(s_F, \varepsilon_{F'}) \\ &= \tfrac{1}{2}2\sigma_F^2 r_{Fm'} + \sigma_F^2 r_{Fp'} + \mathrm{C}(s_F, \varepsilon_{F'}) \\ &= \sigma_F^2[r_{Fm'} + r_{Fp'}] + \mathrm{C}(s_F, \varepsilon_{F'}).\end{aligned}$$

From Grossman and Eisen (1989), $[r_{Fm'} + r_{Fp'}] = 2r_{FF'}$. Thus

$$2\sigma_F^2 r_{FF'} = \sigma_F^2\, 2r_{FF'} + \mathrm{C}(s_F, \varepsilon_{F'});$$

hence, $\mathrm{C}(s_F, \varepsilon_{F'}) = 0$.

*Male–female.* Covariance between additive genotypic values for male $M$ and female $F'$, where $M$ is not a direct descendent of $F'$, is

$$\begin{aligned}\mathrm{C}(s_M, s_{F'}) &= \mathrm{C}(s_M, \tfrac{1}{2}s_{m'} + s_{p'} + \varepsilon_{F'}) \\ &= \tfrac{1}{2}\mathrm{C}(s_M, s_{m'}) + \mathrm{C}(s_M, s_{p'}) + \mathrm{C}(s_M, \varepsilon_{F'}).\end{aligned}$$

From the above, $\mathrm{C}(s_M, s_{F'}) = \sigma_F^2 r_{MF'}$, $\mathrm{C}(s_M, s_{m'}) = \sigma_F^2 r_{Mm'}$, and $\mathrm{C}(s_M, s_{p'}) = \frac{1}{2}\sigma_F^2 r_{Mp'}$, so that

$$\begin{aligned}\sigma_F^2 r_{MF'} &= \tfrac{1}{2}\mathrm{C}(s_M, s_{m'}) + \mathrm{C}(s_M, s_{p'}) + \mathrm{C}(s_M, \varepsilon_{F'}) \\ &= \tfrac{1}{2}\sigma_F^2 r_{Mm'} + \tfrac{1}{2}\sigma_F^2 r_{Mp'} + \mathrm{C}(s_M, \varepsilon_{F'}) \\ &= \sigma_F^2 \tfrac{1}{2}[r_{Mm'} + r_{Mp'}] + \mathrm{C}(s_M, \varepsilon_{F'}).\end{aligned}$$

From Grossman and Eisen (1989), $\frac{1}{2}[r_{Mm'} + r_{Mp'}] = r_{MF'}$. Thus

$$\sigma_F^2 r_{MF'} = \sigma_F^2 r_{MF'} + \mathrm{C}(s_M, \varepsilon_{F'});$$

hence, $\mathrm{C}(s_M, \varepsilon_{F'}) = 0$.

*Female–male.* Covariance between additive genotypic values for a female $F$ and male $M'$, where $F$ is not a direct descendent of $M'$, is

$$C(s_F, s_{M'}) = C(s_F, \tfrac{1}{2}s_{m'} + \varepsilon_{M'}) = \tfrac{1}{2}C(s_F, s_{m'}) + C(s_F, \varepsilon_{M'}).$$

From the above, $C(s_F, s_{M'}) = \sigma_F^2 r_{FM'}$, $C(s_F, s_{m'}) = 2\sigma_F^2 r_{Fm'}$, so that

$$\sigma_F^2 r_{FM'} = \tfrac{1}{2}C(s_F, s_{m'}) + C(s_F, \varepsilon_{M'}) = \sigma_F^2 r_{Fm'} + C(s_F, \varepsilon_{M'}).$$

From Grossman and Eisen (1989), $r_{Fm'} = r_{FM'}$. Thus

$$\sigma_F^2 r_{FM'} = \sigma_F^2 r_{FM'} + C(s_F, \varepsilon_{M'});$$

hence, $C(s_F, \varepsilon_{M'}) = 0$.

*Male–male.* Covariance between additive genotypic values for males $M$ and $M'$, where $M$ is not a direct descendent of $M'$, is

$$C(s_M, s_{M'}) = C(s_M, \tfrac{1}{2}s_{m'} + \varepsilon_{M'}) = \tfrac{1}{2}C(s_M, s_{m'}) + C(s_M, \varepsilon_{M'}).$$

From the above, $C(s_M, s_{M'}) = \tfrac{1}{2}\sigma_F^2 r_{MM'}$, $C(s_M, s_{m'}) = \sigma_F^2 r_{Mm'}$, so that

$$\tfrac{1}{2}\sigma_F^2 r_{MM'} = \tfrac{1}{2}C(s_M, s_{m'}) + C(s_M, \varepsilon_{M'}) = \tfrac{1}{2}\sigma_F^2 r_{Mm'} + C(s_M, \varepsilon_{M'}).$$

From Grossman and Eisen (1989), $r_{Mm'} = r_{MM'}$. Thus,

$$\tfrac{1}{2}\sigma_F^2 r_{MM'} = \tfrac{1}{2}\sigma_F^2 r_{MM'} + C(s_M, \varepsilon_{M'});$$

hence, $C(s_M, \varepsilon_{M'}) = 0$.

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