ANIMAL BREEDING NOTES

CHAPTER 14

THE MATRIX OF ADDITIVE RELATIONSHIPS AND ITS INVERSE

Assumptions

(a) n loci, n arbitrary,

(b) r_i alleles per locus, r_i arbitrary, and

(c) no linkage.

Breeding Value

Genetic value of an individual based on the mean genotypic value of its progeny. Because parents pass on their genes (**not** their genotypes) to their progeny, the mean genotypic value of their progeny is determined by the average effects of the parent's alleles (Falconer, 1981, pg. 106). Thus, by definition, the breeding value of animal x for a single trait is:

$$u_x = a_s + a_d \qquad\qquad [1]$$

where

u_x = random variable representing the breeding value of individual x for a trait.

a_s = random variable representing the sum of the average effects of all alleles affecting a trait coming from the gamete of the sire of animal x, i.e.,

$a_s = \displaystyle\sum_{k=1}^{2n} \delta_k a_{sk}$, a_{sk} belongs to the sire of animal x, n = number of loci, and δ_k is a Kronecker delta, i.e., $\delta_k = 0$ or 1; **δ_k will be zero (2n/2) times and one (2n/2) times, because a random sample of only ½ of the male alleles is being passed on to individual x**.

a_d = random variable representing the sum of the average effects of all alleles affecting a trait, coming from gamete of the dam of animal x, i.e.,

$$a_d = \sum_{k=1}^{2n} \delta_k \, a_{dk}, \; a_{dk} \text{ belongs to the dam of animal x, n = number of loci.}$$

Because average genetic effects are defined as deviations from the average gene at each locus, i.e.,

from $\mu_j = \sum_{c=1}^{r_c} p_{jc} \, A_{jc}$, the expected value of u_x is:

$$
\begin{aligned}
E[u_x] &= E\left[a_s + a_d\right] \\
&= E\left[a_s\right] + E\left[a_d\right] \\
&= E\left[\sum a_{s_k}\right] + E\left[\sum a_{d_k}\right] \\
&= E\left[\sum E\left[a_{s_k} \mid \text{locus}\right]\right] + E\left[\sum E\left[a_{d_k} \mid \text{locus}\right]\right] \\
&= 0 + 0 \\
&= 0
\end{aligned}
$$

The variance of u_x is:

$$
\begin{aligned}
\text{var}(u_x) &= \text{var}(a_s + a_d) \\
&= \text{var}(a_s) + \text{var}(a_d) + 2\,\text{cov}(a_s, a_d)
\end{aligned}
$$

By **conditioning on the breeding values of the sire (u_s) and the dam (u_d) of animal x**, the var(u_x) becomes:

$$
\begin{aligned}
\text{var}(u_x) &= \text{var}(E[a_s \mid u_s]) + E[\text{var}(a_s \mid u_s)] \\
&\quad + \text{var}(E(a_d \mid u_d)) + E[\text{var}(a_d \mid u_d)] \\
&\quad + 2\,\text{cov}(E[a_s \mid u_s], E[a_d \mid u_d]) + 2\,E[\text{cov}(a_s \mid u_s, a_d \mid u_d)]
\end{aligned}
$$

But **a_s is the average effect of ½ of the alleles affecting the trait in the sire**, i.e., **$a_s = \tfrac{1}{2}u_s$**.

Thus,

$$E[a_s | u_s] \quad = \quad E[\tfrac{1}{2} u_s | u_s]$$

$$= \quad \tfrac{1}{2} u_s \text{ [Breeding Value of the sire]}$$

Applying a similar argument to a_d yields:

$$E[a_d | u_d] \quad = \quad \tfrac{1}{2} u_d \text{ [Breeding Value of the dam]}$$

Thus,

$$\text{var}(E[a_s | u_s]) \quad = \quad \text{var}(\tfrac{1}{2} u_s)$$

$$= \quad \tfrac{1}{4} \text{var}(u_s)$$

$$= \quad \tfrac{1}{4} a_{ss} \sigma_A^2$$

$$= \quad \tfrac{1}{4} (1 + F_s) \sigma_A^2 \text{ [var(Breeding Value of the sire)]}$$

and

$$\text{var}(E[a_d | u_d]) \quad = \quad \tfrac{1}{4} (1 + F_d) \sigma_A^2 \text{ [var(Breeding Value of the dam)]}$$

What is $E[\text{var}(a_s | u_s)]$?

$$E[\text{var}(a_s | u_s)] \quad = \quad \text{var}(a_s) - \text{var}(E[a_s | u_s])$$

But

$$\text{var}(a_s) = \quad \text{var}\left(\sum_{k=1}^{2n} \delta_k \, a_k \right)$$

Also, because, by definition,

$$\text{var}\left(\sum_{k=1}^{2n} a_k \right) = \quad \sigma_A^2$$

then,

$$\text{var}(a_s) = \tfrac{1}{2} \sigma_A^2$$

Thus,

$$E[var(a_s \mid u_s)] \quad = \quad \tfrac{1}{2}\,\sigma_A{}^2 - \tfrac{1}{4}\,(1 + F_s)\,\sigma_A{}^2$$

$$= \quad \tfrac{1}{4}\,\sigma_A{}^2 - \tfrac{1}{4}\,F_s\,\sigma_A{}^2$$

$$= \quad \tfrac{1}{4}\,(1 - F_s)\,\sigma_A{}^2 \text{ [var(Mendelian sampling in the sire)]}$$

Similarly, for the dam of animal x, $E[var(a_d \mid u_d)]$ is:

$$E[var(a_d \mid u_d)] \quad = \quad \tfrac{1}{4}\,\sigma_A{}^2 - \tfrac{1}{4}\,F_d\,\sigma_A{}^2$$

$$= \quad \tfrac{1}{4}\,(1 - F_d)\,\sigma_A{}^2 \text{ [var(Mendelian sampling in the dam)]}$$

The **covariance terms of var(u$_x$)** are:

$$2\,cov(E[a_s \mid u_s], E[a_d \mid u_d]) \quad = \quad 2\,cov(\tfrac{1}{2}\,u_s, \tfrac{1}{2}\,u_d)$$

$$= \quad \tfrac{1}{2}\,cov(u_s, u_d)$$

$$= \quad \tfrac{1}{2}\,a_{sd}\,\sigma_A{}^2 \text{ [2*cov(BV sire, BV dam)]}$$

$$= \quad F_x\,\sigma_A{}^2$$

The value of **$2\,E[cov(a_s \mid u_s, a_d \mid u_d)] = 0$** because the sire and the dam random samples of ½ of their respective set of alleles are taken **independently** of each other, i.e., **there is no connection between the formation of sire gametes and dam gametes (biological fact)**. This biological rationale can be shown as follows. On one hand, adding the components of var(u$_x$) excluding 2 $E[cov(a_s \mid u_s, a_d \mid u_d)]$, yields:

$$var(u_x) \quad = \quad \tfrac{1}{4}\,(1 + F_s)\,\sigma_A{}^2 + \tfrac{1}{4}\,(1 - F_s)\,\sigma_A{}^2$$

$$+ \tfrac{1}{4}\,(1 + F_d)\,\sigma_A{}^2 + \tfrac{1}{4}\,(1 - F_d)\,\sigma_A{}^2$$

$$+ F_x\,\sigma_A{}^2 + 0$$

$$var(u_x) \quad = \quad \tfrac{1}{2}\,\sigma_A{}^2 + \tfrac{1}{2}\,\sigma_A{}^2 + F_x\,\sigma_A{}^2$$

$$\text{var}(u_x) \quad = \quad (1 + F_x)\,\sigma_A{}^2$$

On the other hand, we know that:

$$\text{var}(u_x) \quad = \quad a_{xx}\,\sigma_A{}^2$$

$$= (1 + F_x)\,\sigma_A{}^2$$

$\Rightarrow \ \text{cov}(a_s \mid u_s, a_d \mid u_d)$ must necessarily be equal to zero.

Equivalent model for the breeding value of an animal for a single trait

According to Henderson (1985), models that have the same first and second moments are linearly equivalent, i.e., linearly equivalent models have the same expected values and mean square errors.

Thus, an **equivalent model to the single trait breeding value model**, i.e.,

$$u_x \quad = \quad a_s + a_d$$

$$E[u_x] \quad = \quad 0$$

$$\text{var}(u_x) = \quad (1 + F_x)\,\sigma_A{}^2$$

is:

$$u_x = \quad \tfrac{1}{2}\,u_s + \tfrac{1}{2}\,u_d + \tfrac{1}{2}\,\varepsilon_s + \tfrac{1}{2}\,\varepsilon_d \qquad\qquad [2]$$

where

$u_x \ = \ $ breeding value of animal x (random),

$u_s \ = \ $ breeding value of sire s (random),

$u_d \ = \ $ breeding value of dam d (random),

$\varepsilon_s \ = \ $ Mendelian sampling occurring during gametogenesis in sire s (random), and

$\varepsilon_d \ = \ $ Mendelian sampling occurring during gametogenesis in dam d (random).

The Mendelian sampling terms ε_s and ε_d are independent from each other and independent

from the breeding values. All random variables have expected values equal to zero, i.e.,

$$E[u_x] \;=\; 0$$

and

$$\text{var}(u_x) \;=\; \text{var}(\tfrac{1}{2}\,u_s + \tfrac{1}{2}\,u_d) + \text{var}(\tfrac{1}{2}\,\varepsilon_s) + \text{var}(\tfrac{1}{2}\,\varepsilon_d)$$

where

$$
\begin{aligned}
\text{var}(\tfrac{1}{2}\,u_s + \tfrac{1}{2}\,u_d) \;&=\; \text{var}(\tfrac{1}{2}\,u_s) + \text{var}(\tfrac{1}{2}\,u_d) + 2\,\text{cov}(\tfrac{1}{2}\,u_s,\, \tfrac{1}{2}\,u_d) \\[4pt]
&=\; \tfrac{1}{4}\,(1 + F_s)\,\sigma_A^2 + \tfrac{1}{4}\,(1 + F_d)\,\sigma_A^2 + F_x\,\sigma_A^2 \\[4pt]
&=\; [\tfrac{1}{2} + \tfrac{1}{4}(F_s + F_d) + F_x]\,\sigma_A^2 \\[4pt]
&=\; \tfrac{1}{2}\,\sigma_A^2 + F_x\,\sigma_A^2 + \tfrac{1}{4}\,F_s\,\sigma_A^2 + \tfrac{1}{4}\,F_d\,\sigma_A^2
\end{aligned}
$$

Thus, to obtain $\text{var}(u_x) = (1 + F_x)\,\sigma_A^2$, we need the variance of $\text{var}(\tfrac{1}{2}\,\varepsilon_s) + \text{var}(\tfrac{1}{2}\,\varepsilon_d)$ to be equal to $(\tfrac{1}{2}\,\sigma_A^2 - \tfrac{1}{4}\,F_s\,\sigma_A^2 - \tfrac{1}{4}\,F_d\,\sigma_A^2)$. **But the sampling process during gamete formation (Mendelian sampling) in the male and female gametes is completely independent of one another. Thus, any loss of variation during the process of gamete formation due to (i) the inbreeding of the male occurs only in the male gamete, and (ii) the inbreeding of the female occurs only in the female gamete.** Consequently,

$$
\begin{aligned}
\text{var}(\tfrac{1}{2}\,\varepsilon_s) \;&=\; \tfrac{1}{4}\,\sigma_A^2 - \tfrac{1}{4}\,F_s\,\sigma_A^2 \\[4pt]
&=\; \tfrac{1}{4}\,(1 - F_s)\,\sigma_A^2, \text{ and} \\[6pt]
\text{var}(\tfrac{1}{2}\,\varepsilon_d) \;&=\; \tfrac{1}{4}\,\sigma_A^2 - \tfrac{1}{4}\,F_d\,\sigma_A^2 \\[4pt]
&=\; \tfrac{1}{4}\,(1 - F_d)\,\sigma_A^2
\end{aligned}
$$

and

$$\text{var}(u_x) \;=\; (1 + F_x)\,\sigma_A^2$$

For the analysis of a single population only, a **simpler equivalent model** can be written. Let

$$\varphi \quad = \quad \tfrac{1}{2}\,\varepsilon_s + \tfrac{1}{2}\,\varepsilon_d$$

Then,

$$u_x \quad = \quad \tfrac{1}{2}\,u_s + \tfrac{1}{2}\,u_d + \varphi \qquad\qquad [3]$$

$$E[u_x] \quad = \quad 0$$

$$var(u_x) \quad = \quad var(\tfrac{1}{2}\,u_s + \tfrac{1}{2}\,u_d) + var\,(\varphi)$$

where

$$var(\tfrac{1}{2}\,u_s + \tfrac{1}{2}\,u_d) \quad = \quad [\tfrac{1}{2} + \tfrac{1}{4}(F_s + F_d) + F_x]\,\sigma_A^2$$

$$var(\varphi) \quad = \quad [\tfrac{1}{2} - \tfrac{1}{4}(F_s + F_d)]\,\sigma_A^2$$

Hence,

$$var(u_x) \quad = \quad (1 + F_x)\,\sigma_A^2$$

Remarks: **$var(\varphi) = var(\tfrac{1}{2}\,\varepsilon_s) + var(\tfrac{1}{2}\,\varepsilon_d)$ represents the variability that exists among gametes in the sire and in the dam. Thus, it is affected negatively by the level of inbreeding in the sire (F_s) and dam (F_d) and it is independent of the level of inbreeding of the individual (F_x).**

Derivation of the rules to compute the inverse of the additive relationship matrix directly

Model [3] can be generalized to include not only the case when both parents are identified, but also the cases when only the sire, only the dam or neither parent is known.

The **unidentified parents** are assumed to be **non-inbred and unrelated** among themselves and to all other identified animals in the population, just like base animals.

Base animals are those which all other animals in the population descend from. They are assumed to be unrelated and non-inbred.

The extended version of model [3] with animals ordered such that parents precede progeny (e.g.,

by birth date), in matrix notation, is:

$$u = \tfrac{1}{2} P u + \varphi \tag{4}$$

where

u = vector breeding values of animals where parents precede progeny;

P = lower triangular matrix relating parents to progeny. A row of P contains ones in the columns corresponding to the known parents and zeroes elsewhere. Thus, a row of P contains:

(i) two 1's if both parents are known,

(ii) one 1 if either the sire or the dam of an animal is known,

(iii) zeroes if both parents are unknown;

φ = vector of independent random variables representing:

(i) Mendelian sampling in the sire and in the dam, if both parents of animal i are known, i.e.,

$$\varphi_i = \tfrac{1}{2} \varepsilon_s + \tfrac{1}{2} \varepsilon_d$$

(ii) Mendelian sampling in the sire and the dam plus:

(a) the breeding value of the dam, if only the sire of animal i is known, i.e.,

$$\varphi_i = \tfrac{1}{2} u_d + \tfrac{1}{2} \varepsilon_s + \tfrac{1}{2} \varepsilon_d$$

(b) the breeding value of the sire, if only the dam animal i is known, i.e.,

$$\varphi_i = \tfrac{1}{2} u_s + \tfrac{1}{2} \varepsilon_s + \tfrac{1}{2} \varepsilon_d$$

(iii) the breeding value of animal i if neither its sire nor its dam are known, i.e.,

$$\varphi_i = u_i$$

From [4] we can see that:

$$(I - \tfrac{1}{2} P) u = \varphi$$

$$\Rightarrow \quad \mathbf{u} \;=\; (\mathbf{I} - \tfrac{1}{2}\,\mathbf{P})^{-1}\,\varphi$$

$$\Rightarrow \quad \mathbf{E[u]} \;=\; (\mathbf{I} - \tfrac{1}{2}\,\mathbf{P})^{-1}\,\mathbf{E}[\varphi]$$

$$=\; 0$$

$$\Rightarrow \quad \mathrm{var}(\mathbf{u}) \;=\; (\mathbf{I} - \tfrac{1}{2}\,\mathbf{P})^{-1}\,\mathrm{var}(\varphi)\,(\mathbf{I} - \tfrac{1}{2}\,\mathbf{P}')^{-1}$$

$$\mathbf{var(u)} \;=\; (\mathbf{I} - \tfrac{1}{2}\,\mathbf{P})^{-1}\,\mathbf{D}\,(\mathbf{I} - \tfrac{1}{2}\,\mathbf{P}')^{-1}\,\sigma_A{}^2$$

where

$$\mathbf{D} \;=\; \mathrm{diag}\,\{d_{ii}\}$$

The $\mathbf{var(\varphi_i)} \;=\; \mathbf{d_{ii}\,\sigma_A{}^2}$ **are:**

(i) $\mathrm{var}\left(\dfrac{1}{2}\,\varepsilon_{s_i} + \dfrac{1}{2}\,\varepsilon_{d_i}\right) \;=\; \mathrm{var}\,(u_i) - \mathrm{var}\left(\dfrac{1}{2}\,u_{s_i} + \dfrac{1}{2}\,u_{d_i}\right)$

$$=\; \left[\left(1 + \frac{1}{2}\,a_{s_i\,d_i}\right) - \left(\frac{1}{4}\,a_{s_i\,s_i} + \frac{1}{4}\,a_{d_i\,d_i} + \frac{1}{2}\,a_{s_i\,d_i}\right)\right]\sigma_A^2$$

$$=\; \left[1 - \frac{1}{4}\,a_{s_i\,s_i} - \frac{1}{4}\,a_{d_i\,d_i}\right]\sigma_A^2$$

$$=\; \left[1 - \frac{1}{4}\left(1 + F_{s_i}\right) - \frac{1}{4}\left(1 + F_{d_i}\right)\right]\sigma_A^2$$

$$=\; \left[\frac{1}{2} - \frac{1}{4}\left(F_{s_i} + F_{d_i}\right)\right]\sigma_A^2$$

(ii) $\mathrm{var}\left(\dfrac{1}{2}\,u_{d_i} + \dfrac{1}{2}\,\varepsilon_{s_i} + \dfrac{1}{2}\,\varepsilon_{d_i}\right) \;=\; \mathrm{var}\,(u_i) - \mathrm{var}\left(\dfrac{1}{2}\,u_{s_i}\right)$

$$=\; \left[1 - \frac{1}{4}\,a_{s_i\,s_i}\right]\sigma_A^2$$

$$=\; \left[1 - \frac{1}{4}\left(1 + F_{s_i}\right)\right]\sigma_A^2$$

$$= \left[\frac{3}{4} - \frac{1}{4} F_{s_i} \right] \sigma_A^2$$

if s_i is known only,

(iii) $\text{var} \left(\frac{1}{2} u_{s_i} + \frac{1}{2} \varepsilon_{s_i} + \frac{1}{2} \varepsilon_{d_i} \right) = \text{var} \left(u_i \right) - \text{var} \left(\frac{1}{2} u_{d_i} \right)$

$$= \left[1 - \frac{1}{4} a_{d_i d_i} \right] \sigma_A^2$$

$$= \left[1 - \frac{1}{4} \left(1 + F_{d_i} \right) \right] \sigma_A^2$$

$$= \left[\frac{3}{4} - \frac{1}{4} F_{d_i} \right] \sigma_A^2$$

if d_i is known only,

(iv) $\text{var} \left(\frac{1}{2} u_{s_i} + \frac{1}{2} u_{d_i} + \frac{1}{2} \varepsilon_{s_i} + \frac{1}{2} \varepsilon_{d_i} \right) = \text{var}(u_i)$

$$= \sigma_A{}^2$$

if neither s_i nor d_i are known.

But

$$\text{var}(u) = A \sigma_A{}^2$$

where

A= matrix of additive genetic relationships.

Thus,

$$\text{var}(u) = \left(I - \frac{1}{2} P \right)^{-1} D \left(I - \frac{1}{2} P' \right)^{-1} \sigma_A^2$$

$$= A \sigma_A^2$$

$\Rightarrow \qquad A \quad = \quad \left(I - \dfrac{1}{2}P\right)^{-1} D \left(I - \dfrac{1}{2}P'\right)^{-1}$

$\Rightarrow \qquad A^{-1} \quad = \quad \left(I - \dfrac{1}{2}P'\right) D^{-1} \left(I - \dfrac{1}{2}P\right)$

$\qquad A^{-1} \quad = \quad D^{-1} - \tfrac{1}{2} D^{-1} P - \tfrac{1}{2} P' D^{-1} + \tfrac{1}{4} P' D^{-1} P$

$\downarrow \qquad\qquad \downarrow \qquad\qquad \downarrow \qquad\qquad\qquad \downarrow$

diagonals   parent–progeny   parent–parent

Let $P = \begin{bmatrix} p_1{}' \\ p_2{}' \\ \vdots \\ p_n{}' \end{bmatrix}$, where $p_i{}'$ is a vector with at most two 1's and the rest zeroes.

Thus,

$-\tfrac{1}{2} D^{-1} P \quad = \quad \begin{bmatrix} -\dfrac{1}{2} d_{11}^{-1} p_1' \\ \vdots \\ -\dfrac{1}{2} d_{nn}^{-1} p_n' \end{bmatrix}$

$= \left\{ \begin{matrix} & [\text{sire}_i] & & [\text{dam}_i] & \\ & \vdots & & \vdots & \\ \cdots & -\dfrac{1}{2} d_{ii}^{-1} & \cdots & -\dfrac{1}{2} d_{ii}^{-1} & \cdots & [\text{calf}_i] \\ & \vdots & & \vdots & \end{matrix} \right\}$

$-\tfrac{1}{2} P' D^{-1} \quad = \quad \begin{bmatrix} -\dfrac{1}{2} d_{11}^{-1} p_1 & \cdots & -\dfrac{1}{2} d_{nn}^{-1} p_n \end{bmatrix}$

$$= \left\{ \begin{array}{cccc} & & [\text{calf}_i] & \\ & & \vdots & \\ \cdots & -\dfrac{1}{2}\,d_{ii}^{-1} & \cdots & [\text{sire}_i] \\ & & \vdots & \\ \cdots & -\dfrac{1}{2}\,d_{ii}^{-1} & \cdots & [\text{dam}_i] \\ & & \vdots & \end{array} \right\}$$

$$\tfrac{1}{4}\,P'\,D^{-1}\,P \quad = \quad \sum_{i=1}^{n} d_{ii}^{-1}\,p_i\,p_i{}'$$

$$= \left\{ \begin{array}{ccccccc} & [\text{sire}_i] & & [\text{dam}_i] & & \\ & \vdots & & \vdots & & \\ \cdots & \dfrac{1}{4}\,d_{ii}^{-1} & \cdots & \dfrac{1}{4}\,d_{ii}^{-1} & \cdots & [\text{sire}_i] \\ & \vdots & & \vdots & & \\ \cdots & \dfrac{1}{4}\,d_{ii}^{-1} & \cdots & \dfrac{1}{4}\,d_{ii}^{-1} & \cdots & [\text{dam}_i] \\ & \vdots & & \vdots & & \end{array} \right\}$$

Based on the **pattern of contributions of the four matrices contributing to A^{-1}**, the following

rules to compute A^{-1} directly can be inferred:

(1) if both the sire (s_i) and the dam (d_i) of animal i are identified, add:

$$d_{ii}^{-1} \quad \text{to} \quad i \times i$$

$$-\frac{1}{2}\,d_{ii}^{-1} \quad \text{to} \quad i \times s_i,\ i \times d_i,\ s_i \times i,\ d_i \times i$$

$$\frac{1}{4}\,d_{ii}^{-1} \quad \text{to} \quad s_i \times s_i,\ s_i \times d_i,\ d_i \times s_i,\ d_i \times d_i$$

where

$$d_{ii}^{-1} = \left[1 - \frac{1}{4}\,a_{s_i s_i} - \frac{1}{4}\,a_{d_i d_i} \right]^{-1}$$

(2) if only the sire (s_i) is known, add:

$$d_{ii}^{-1} \quad \text{to} \quad i \times i$$

$$-\frac{1}{2} d_{ii}^{-1} \quad \text{to} \quad i \times s_i, s_i \times i$$

$$\frac{1}{4} d_{ii}^{-1} \quad \text{to} \quad s_i \times s_i$$

where

$$d_{ii}^{-1} = \left[1 - \frac{1}{4} a_{s_i s_i} \right]^{-1}$$

(3) if only the dam (d_i) is known, add:

$$d_{ii}^{-1} \quad \text{to} \quad i \times i$$

$$-\frac{1}{2} d_{ii}^{-1} \quad \text{to} \quad i \times d_i, d_i \times i$$

$$\frac{1}{4} d_{ii}^{-1} \quad \text{to} \quad d_i \times d_i$$

where

$$d_{ii}^{-1} = \left[1 - \frac{1}{4} a_{d_i d_i} \right]^{-1}$$

(4) if neither s_i nor d_i are known, add:

$$d_{ii}^{-1} \quad \text{to} \quad i \times i$$

where

$$d_{ii}^{-1} = 1$$

These are called **Henderson's rules**.

In order to apply these rules we must know the d_{ii}. If there is no inbreeding the d_{ii} can be easily

computed using the above formulae substituting 1's for the relationships of parents with themselves. But, if there is inbreeding, the computation of the d_{ii} requires knowledge of the coefficients of inbreeding of their parents. However, it is easier to compute the d_{ii} directly using a recursive procedure based on computing L, where $LL' = A$. This approach will be used here.

Non-Inbred Population

If all animals in a population are non-inbred then:

d_{ii} = ½ if both s_i and d_i are known,

= ¼ if only s_i or d_i is known,

= 1 if neither s_i nor d_i are known.

and **Henderson's rules** simplify to:

(1) if both s_i and d_i are identified, add:

2   to $i \times i$

-1   to $i \times s_i, i \times d_i, s_i \times i, d_i \times i$

$\dfrac{1}{2}$ to $s_i \times s_i, s_i \times d_i, d_i \times s_i, d_i \times d_i$

(2) if s_i is identified only, add:

$\dfrac{4}{3}$ to $i \times i$

$-\dfrac{2}{3}$ to $i \times s_i, s_i \times i$

$\dfrac{1}{3}$ to $s_i \times s_i$

(3) if d_i is identified only, add:

$\dfrac{4}{3}$ to $i \times i$

$-\dfrac{2}{3}$ to $i \times d_i$, $d_i \times i$

$\dfrac{1}{3}$ to $d_i \times d_i$

(4) if neither s_i nor d_i are known, add:

1   to $i \times i$.

Example of A^{-1} in a non-inbred population

	Animal	Sire	Dam
Parents	1		
	2		
	3		2
Non-parents	4	1	
	5	1	2
	6	1	3

$$P = \begin{bmatrix} 0 & & & | & & & \\ 0 & 0 & & | & & & \\ 0 & 1 & 0 & | & & & \\ - & - & - & | & - & - & - \\ 1 & 0 & 0 & | & 0 & & \\ 1 & 1 & 0 & | & 0 & 0 & \\ 1 & 0 & 1 & | & 0 & 0 & 0 \end{bmatrix}, \quad D^{-1} = \begin{bmatrix} 1 & & & | & & & \\ & 1 & & | & & & \\ & & \frac{4}{3} & | & & & \\ - & - & - & | & - & - & - \\ & & & | & \frac{4}{3} & & \\ & & & | & & 2 & \\ & & & | & & & 2 \end{bmatrix}$$

$$-\tfrac{1}{2}\,D^{-1}P = -\frac{1}{2}\begin{bmatrix} 1 & & & | & & & \\ & 1 & & | & & & \\ & & \frac{4}{3} & | & & & \\ - & - & - & | & - & - & - \\ & & & | & \frac{4}{3} & & \\ & & & | & & 2 & \\ & & & | & & & 2 \end{bmatrix}\begin{bmatrix} 0 & & & | & & & \\ 0 & 0 & & | & & & \\ 0 & 1 & 0 & | & & & \\ - & - & - & | & - & - & - \\ 1 & 0 & 0 & | & 0 & & \\ 1 & 1 & 0 & | & 0 & 0 & \\ 1 & 0 & 1 & | & 0 & 0 & 0 \end{bmatrix}$$

$$= \begin{bmatrix} 0 & & & | & & & \\ 0 & 0 & & | & & & \\ 0 & -\frac{2}{3} & 0 & | & & & \\ - & - & - & | & - & - & - \\ -\frac{2}{3} & 0 & 0 & | & 0 & & \\ -1 & -1 & 0 & | & 0 & 0 & \\ -1 & 0 & -1 & | & 0 & 0 & 0 \end{bmatrix}$$

$$-\tfrac{1}{2}\,P'\,D^{-1} \;=\; \begin{bmatrix} 0 & 0 & 0 & | & -\dfrac{2}{3} & -1 & -1 \\[2mm] & 0 & -\dfrac{2}{3} & | & 0 & -1 & 0 \\[2mm] & & 0 & | & 0 & 0 & -1 \\[2mm] - & - & - & | & - & - & - \\[2mm] & & & | & 0 & 0 & 0 \\[2mm] & & & | & & 0 & 0 \\[2mm] & & & | & & & 0 \end{bmatrix}$$

$$\tfrac{1}{4}\,P'\,D^{-1}\,P \;\;=\;\; (-\tfrac{1}{2}\,P'\,D^{-1})(-\tfrac{1}{2}\,P)$$

$$=\; \begin{bmatrix} 0 & 0 & 0 & | & -\dfrac{2}{3} & -1 & -1 \\[2mm] & 0 & -\dfrac{2}{3} & | & 0 & -1 & 0 \\[2mm] & & 0 & | & 0 & 0 & -1 \\[2mm] - & - & - & | & - & - & - \\[2mm] & & & | & 0 & 0 & 0 \\[2mm] & & & | & & 0 & 0 \\[2mm] & & & | & & & 0 \end{bmatrix} \begin{bmatrix} 0 & & & | \\[2mm] 0 & 0 & & | \\[2mm] 0 & -\dfrac{1}{2} & 0 & | \\[2mm] - & - & - & | & - & - & - \\[2mm] -\dfrac{1}{2} & 0 & 0 & | & 0 \\[2mm] -\dfrac{1}{2} & -\dfrac{1}{2} & 0 & | & 0 & 0 \\[2mm] -\dfrac{1}{2} & 0 & -\dfrac{1}{2} & | & 0 & 0 & 0 \end{bmatrix}$$

$$
=\begin{bmatrix}
\left(\dfrac{1}{3}+\dfrac{1}{2}+\dfrac{1}{2}\right) & \left(\dfrac{1}{2}\right) & \left(\dfrac{1}{2}\right) & | & 0 & 0 & 0 \\[2mm]
 & \left(\dfrac{1}{3}+\dfrac{1}{2}\right) & 0 & | & 0 & 0 & 0 \\[2mm]
 & & \left(\dfrac{1}{2}\right) & | & 0 & 0 & 0 \\[2mm]
\text{-------} & \text{-----} & \text{---} & | & - & - & - \\[1mm]
 & & & | & 0 & 0 & 0 \\
 & & & | & & 0 & 0 \\
 & & & | & & & 0
\end{bmatrix}
$$

$$A^{-1} \;=\; D^{-1} - \tfrac{1}{2}\,D^{-1}\,P - \tfrac{1}{2}\,P'\,D^{-1} + \tfrac{1}{4}\,P'\,D^{-1}\,P$$

$$
A^{-1} \;=\;\begin{bmatrix}
\left(1+\dfrac{1}{3}+\dfrac{1}{2}+\dfrac{1}{2}\right) & \left(\dfrac{1}{2}\right) & \left(\dfrac{1}{2}\right) & | & \left(-\dfrac{2}{3}\right) & (-1) & (-1) \\[3mm]
 & \left(1+\dfrac{1}{3}+\dfrac{1}{2}\right) & \left(-\dfrac{2}{3}\right) & | & 0 & (-1) & 0 \\[3mm]
 & & \left(\dfrac{4}{3}+\dfrac{1}{2}\right) & | & 0 & 0 & (-1) \\[3mm]
\text{---------} & \text{--------} & \text{-----} & | & \text{---} & \text{---} & \text{---} \\[2mm]
 & & & | & \left(\dfrac{4}{3}\right) & 0 & 0 \\[3mm]
 & & & | & & (2) & 0 \\[2mm]
 & & & | & & & (2)
\end{bmatrix}
\begin{array}{l} \\[3mm] \textit{parents} \\[6mm] \ \\[6mm] \\[3mm] \textit{nonparents} \\[6mm] \ \end{array}
$$

$$\downarrow \qquad\qquad\qquad\qquad \downarrow$$

parents   *non-parents*

Inbred Population

The additive relationship of an animal with itself is equal to:

$$a_{ii} = 1 + \frac{1}{2} a_{s_i d_i}$$

or

$$a_{ii} = 1 + F_i$$

where

$a_{s_i d_i}$ =   additive genetic relationship between the sire (s_i) and the dam (d_i) of animal i

F_i =   coefficient of inbreeding of animal i

= $\frac{1}{2} a_{s_i d_i}$

In an inbred population the diagonal elements of the matrix D, i.e., the d_{ii}, will depend on the coefficient of inbreeding of the parents of the animals included in the relationship matrix A. Thus, the d_{ii} cannot be computed based on knowledge of σ_A^2 only, as it was the case in a non-inbred population, but must also know the coefficients of inbreeding of the parents in the population. One possibility would be to obtain these coefficients of inbreeding by computing A first. However, we only need the diagonals of A, because

$$d_{ii} = 1 - \frac{\delta_{s_i}}{4} \left(a_{s_i s_i} \right) - \frac{\delta_{d_i}}{4} \left(a_{d_i d_i} \right)$$

where

$$\delta_{s_i} \left(\delta_{d_i} \right) = \begin{cases} 1 & \text{if } s_i \left(d_i \right) \text{is known} \\ 0 & \text{otherwise} \end{cases}$$

Thus, what is needed is an efficient method to compute the diagonal elements of A, i.e., the a_{ii}. A fast method to compute the a_{ii}, based on some previous work by Henderson (1976), was described by Quaas (1976).

Recursive method to compute the a_{ii}

The relationship matrix A is equal to:

$$A = \left(I - \frac{1}{2}P\right)^{-1} D \left(I - \frac{1}{2}P'\right)^{-1}$$

Claim:

$$\left(I - \frac{1}{2}P\right)^{-1} = I + \frac{1}{2}P + \left(\frac{1}{2}P\right)^2 + \left(\frac{1}{2}P\right)^3 + \ldots + \left(\frac{1}{2}P\right)^m$$

where

  m = maximum number of generations separating two individuals in A.

  $m \leq n$, n   = order of matrix A

         = number of animals in the pedigree

Proof (Quaas, 1986):

P is a lower triangular matrix with zeroes on and above the diagonal. Thus, $P^{m+1} = 0$ for $m \leq n$.

Consider,

$$T = I + \frac{1}{2}P + \left(\frac{1}{2}P\right)^2 + \ldots + \left(\frac{1}{2}P\right)^m$$

and

$$\left(\frac{1}{2}P\right)T = \frac{1}{2}P + \left(\frac{1}{2}P\right)^2 + \left(\frac{1}{2}P\right)^3 + \ldots + \left(\frac{1}{2}P\right)^m + \left(\frac{1}{2}P\right)^{m+1}$$

Subtract the second term from the first term:

$$T - \left(\frac{1}{2}P\right)T = I - \left(\frac{1}{2}P\right)^{m+1}$$

But

$$\left(\frac{1}{2}P\right)^{m+1} = 0$$

Thus,

$$\Rightarrow \quad T\left(I - \frac{1}{2}P\right) = I$$

$$\Rightarrow \quad T = \left(I - \frac{1}{2}P\right)^{-1}$$

$$\Rightarrow \quad \left(I - \frac{1}{2}P\right)^{-1} = I + \frac{1}{2}P + \left(\frac{1}{2}P\right)^{2} + \ldots + \left(\frac{1}{2}P\right)^{m}$$

Remarks:

The rows of the matrices P, P^2, P^3, ..., identify parents, grandparents, great-grandparents, ..., i.e.,

Rows of	identify
P	parents
P^2	grandparents
P^3	great-grandparents
⋮	⋮
P^m	ancestors m generations back from the current generation

Example of A⁻¹ in an inbred population

	Animal	Sire	Dam
Parents	1		
	2	1	
	3	1	2
	4	3	2
Non-parents	5	3	4
	6	3	4

$$
P = \begin{bmatrix}
0 & & & & | & & \\
1 & 0 & & & | & & \\
1 & 1 & 0 & & | & & \\
0 & 1 & 1 & 0 & | & & \\
- & - & - & - & | & - & - \\
0 & 0 & 1 & 1 & | & 0 & \\
0 & 0 & 1 & 1 & | & 0 & 0
\end{bmatrix}
$$

$$
P^2 = PP = \begin{bmatrix}
0 & & & & | & & \\
1 & 0 & & & | & & \\
1 & 1 & 0 & & | & & \\
0 & 1 & 1 & 0 & | & & \\
- & - & - & - & | & - & - \\
0 & 0 & 1 & 1 & | & 0 & \\
0 & 0 & 1 & 1 & | & 0 & 0
\end{bmatrix}
\begin{bmatrix}
0 & & & & | & & \\
1 & 0 & & & | & & \\
1 & 1 & 0 & & | & & \\
0 & 1 & 1 & 0 & | & & \\
- & - & - & - & | & - & - \\
0 & 0 & 1 & 1 & | & 0 & \\
0 & 0 & 1 & 1 & | & 0 & 0
\end{bmatrix}
= \begin{bmatrix}
0 & & & & | & & \\
0 & 0 & & & | & & \\
1 & 0 & 0 & & | & & \\
2 & 1 & 0 & 0 & | & & \\
- & - & - & - & | & - & - \\
1 & 2 & 1 & 0 & | & 0 & \\
1 & 2 & 1 & 0 & | & 0 & 0
\end{bmatrix}
$$

↓ parents   ↓ grandparents

$$
\mathbf{P}^3 = \mathbf{P}^2\,\mathbf{P} =
\begin{bmatrix}
0 & & & & | & & \\
0 & 0 & & & | & & \\
1 & 0 & 0 & & | & & \\
2 & 1 & 0 & 0 & | & & \\
- & - & - & - & | & - & - \\
1 & 2 & 1 & 0 & | & 0 & \\
1 & 2 & 1 & 0 & | & 0 & 0
\end{bmatrix}
\begin{bmatrix}
0 & & & & | & & \\
1 & 0 & & & | & & \\
1 & 1 & 0 & & | & & \\
0 & 1 & 1 & 0 & | & & \\
- & - & - & - & | & - & - \\
0 & 0 & 1 & 1 & | & 0 & \\
0 & 0 & 1 & 1 & | & 0 & 0
\end{bmatrix}
=
\begin{bmatrix}
0 & & & & | & & \\
0 & 0 & & & | & & \\
0 & 0 & 0 & & | & & \\
1 & 0 & 0 & 0 & | & & \\
- & - & - & - & | & - & - \\
3 & 1 & 0 & 0 & | & 0 & \\
3 & 1 & 0 & 0 & | & 0 & 0
\end{bmatrix}
$$

$\downarrow$

great-grandparents

$$
\mathbf{P}_4 = \mathbf{P}^3\,\mathbf{P} =
\begin{bmatrix}
0 & & & & | & & \\
0 & 0 & & & | & & \\
0 & 0 & 0 & & | & & \\
1 & 0 & 0 & 0 & | & & \\
- & - & - & - & | & - & - \\
3 & 1 & 0 & 0 & | & 0 & \\
3 & 1 & 0 & 0 & | & 0 & 0
\end{bmatrix}
\begin{bmatrix}
0 & & & & | & & \\
1 & 0 & & & | & & \\
1 & 1 & 0 & & | & & \\
0 & 1 & 1 & 0 & | & & \\
- & - & - & - & | & - & - \\
0 & 0 & 1 & 1 & | & 0 & \\
0 & 0 & 1 & 1 & | & 0 & 0
\end{bmatrix}
=
\begin{bmatrix}
0 & & & & | & & \\
0 & 0 & & & | & & \\
0 & 0 & 0 & & | & & \\
0 & 0 & 0 & 0 & | & & \\
- & - & - & - & | & - & - \\
1 & 0 & 0 & 0 & | & 0 & \\
1 & 0 & 0 & 0 & | & 0 & 0
\end{bmatrix}
$$

$\downarrow$

great-great-grandparents

$$
\mathbf{P}^5 = \mathbf{P}^4\,\mathbf{P} =
\begin{bmatrix}
0 & & & & | & & \\
0 & 0 & & & | & & \\
0 & 0 & 0 & & | & & \\
0 & 0 & 0 & 0 & | & & \\
- & - & - & - & | & - & - \\
1 & 0 & 0 & 0 & | & 0 & \\
1 & 0 & 0 & 0 & | & 0 & 0
\end{bmatrix}
\begin{bmatrix}
0 & & & & | & & \\
1 & 0 & & & | & & \\
1 & 1 & 0 & & | & & \\
0 & 1 & 1 & 0 & | & & \\
- & - & - & - & | & - & - \\
0 & 0 & 1 & 1 & | & 0 & \\
0 & 0 & 1 & 1 & | & 0 & 0
\end{bmatrix}
= \{0\}
$$

$\Rightarrow$ Animals in the current generation have no known ancestors beyond their 4th ancestral generation.

Also,

$$\left(I-\frac{1}{2}P\right)^{-1} = \begin{bmatrix} 1 & & & & & \\ -\frac{1}{2} & 1 & & & & \\ -\frac{1}{2} & -\frac{1}{2} & 1 & & & \\ 0 & -\frac{1}{2} & -\frac{1}{2} & 1 & & \\ 0 & 0 & -\frac{1}{2} & -\frac{1}{2} & 1 & \\ 0 & 0 & -\frac{1}{2} & -\frac{1}{2} & 0 & 1 \end{bmatrix}^{-1}$$

$$= \begin{bmatrix} 1.0 & & & & & \\ 0.5 & 1.0 & & & & \\ 0.75 & 0.5 & 1.0 & & & \\ 0.625 & 0.75 & 0.5 & 1.0 & & \\ 0.6875 & 0.625 & 0.75 & 0.5 & 1.0 & \\ 0.6875 & 0.625 & 0.75 & 0.5 & 0 & 1.0 \end{bmatrix}$$

Alternatively,

$$\left(I-\frac{1}{2}P\right)^{-1} = I+\frac{1}{2}P+\left(\frac{1}{2}P\right)^{2}+\left(\frac{1}{2}P\right)^{3}+\left(\frac{1}{2}P\right)^{4}$$

$$= \begin{bmatrix} 1 & & & & & \\ & 1 & & & & \\ & & 1 & & & \\ & & & 1 & & \\ & & & & 1 & \\ & & & & & 1 \end{bmatrix} + \begin{bmatrix} 0 & & & & & \\ 0.5 & 0 & & & & \\ 0.5 & 0.5 & 0 & & & \\ 0 & 0.5 & 0.5 & 0 & & \\ 0 & 0 & 0.5 & 0.5 & 0 & \\ 0 & 0 & 0.5 & 0.5 & 0 & 0 \end{bmatrix}$$

$$+ \begin{bmatrix} 0 & & & & & \\ 0 & 0 & & & & \\ 0.25 & 0 & 0 & & & \\ 0.50 & 0.25 & 0 & 0 & & \\ 0.25 & 0.50 & 0.25 & 0 & 1 & \\ 0.25 & 0.50 & 0.25 & 0 & 0 & 1 \end{bmatrix} + \begin{bmatrix} 0 & & & & & \\ 0 & 0 & & & & \\ 0 & 0 & 0 & & & \\ 0.125 & 0 & 0 & 0 & & \\ 0.375 & 0.125 & 0 & 0 & 0 & \\ 0.375 & 0.125 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$+ \begin{bmatrix} 0 & & & & & \\ 0 & 0 & & & & \\ 0 & 0 & 0 & & & \\ 0 & 0 & 0 & 0 & & \\ 0.0625 & 0 & 0 & 0 & 0 & \\ 0.0625 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$= \begin{bmatrix} 1 & & & & & \\ 0.5 & 1 & & & & \\ 0.75 & 0.5 & 1 & & & \\ 0.625 & 0.75 & 0.5 & 1 & & \\ 0.6875 & 0.625 & 0.75 & 0.5 & 1 & \\ 0.6875 & 0.625 & 0.75 & 0.5 & 0 & 1 \end{bmatrix}$$

Let us look at the sums $I + \sum_{c=1}^{j} \left(\frac{1}{2} P \right)^{c}$, $j \le 4$, more closely.

$$I + \frac{1}{2} P \quad = \quad \begin{bmatrix} 1.0 & & & & & \\ 0.5 & 1.0 & & & & \\ - & - & - & - & - & - \\ 0.5 & 0.5 & 1.0 & & & \\ 0 & 0.5 & 0.5 & 1.0 & & \\ 0 & 0 & 0.5 & 0.5 & 1.0 & \\ 0 & 0 & 0.5 & 0.5 & 0 & 1.0 \end{bmatrix} \quad \text{parental rows from generation 1}$$

$$I + \sum_{c=1}^{2}\left(\frac{1}{2}P\right)^c \;=\; \begin{bmatrix} 1.0 & & & & & \\ 0.5 & 1.0 & & & & \\ \text{----} & \text{----} & \text{----} & \text{---} & \text{---} & \text{---} \\ 0.75 & 0.5 & 1.0 & & & \\ \text{----} & \text{----} & \text{----} & \text{---} & \text{---} & \text{---} \\ 0.50 & 0.75 & 0.5 & 1.0 & & \\ 0.25 & 0.50 & 0.75 & 0.5 & 1.0 & \\ 0.25 & 0.50 & 0.75 & 0.5 & 0 & 1.0 \end{bmatrix}$$

parental rows from generation 1

parental row from generation 2

$$I + \sum_{c=1}^{3}\left(\frac{1}{2}P\right)^c \;=\; \begin{bmatrix} 1.0 & & & & & \\ 0.5 & 1.0 & & & & \\ \text{----} & \text{----} & \text{----} & \text{---} & \text{---} & \text{---} \\ 0.75 & 0.5 & 1.0 & & & \\ \text{----} & \text{----} & \text{----} & \text{---} & \text{---} & \text{---} \\ 0.625 & 0.75 & 0.5 & 1.0 & & \\ \text{-----} & \text{-----} & \text{----} & \text{----} & \text{---} & \text{---} \\ 0.625 & 0.625 & 0.75 & 0.5 & 1.0 & \\ 0.625 & 0.625 & 0.75 & 0.5 & 0 & 1.0 \end{bmatrix}$$

parental rows from generation 1

parental row from generation 2

parental row from generation 3

$$I + \sum_{c=1}^{4}\left(\frac{1}{2}P\right)^c \;=\; \begin{bmatrix} 1.0 & & & & & \\ 0.5 & 1.0 & & & & \\ \text{------} & \text{-----} & \text{----} & \text{---} & \text{---} & \text{---} \\ 0.75 & 0.5 & 1.0 & & & \\ \text{------} & \text{-----} & \text{----} & \text{---} & \text{---} & \text{---} \\ 0.625 & 0.75 & 0.5 & 1.0 & & \\ \text{------} & \text{-----} & \text{----} & \text{----} & \text{---} & \text{---} \\ 0.6875 & 0.625 & 0.75 & 0.5 & 1.0 & \\ 0.6875 & 0.625 & 0.75 & 0.5 & 0 & 1.0 \end{bmatrix}$$

parental rows from generation 1

parental row from generation 2

parental row from generation 3

Generalizing:

(1) The ith row of $T = \left(I - \frac{1}{2}P\right)^{-1}$ is equal to the sum of the ith rows of I, $\frac{1}{2}P$, $\left(\frac{1}{2}P\right)^2$, ..., $\left(\frac{1}{2}P\right)^m$,

   i.e., the ith row of T is equal to the sum of the ith rows of I, $\frac{1}{2}P$, $\left(\frac{1}{2}P\right)^2$, ..., $\left(\frac{1}{2}P\right)^m$.

   However, the ith row of T is also equal to the sum of the ith rows of I, $\frac{1}{2}P$, $\left(\frac{1}{2}P\right)^2$, ..., $\left(\frac{1}{2}P\right)^{m_i}$,

   where m_i $(m_i \leq m)$ is the number of generations separating animal i from its oldest known ancestor.

(2)   The parental rows of $I - \frac{1}{2}P$ are the same as the corresponding ones of

$$I + \frac{1}{2}P + \left(\frac{1}{2}P\right)^2 , \quad I + \frac{1}{2}P + \left(\frac{1}{2}P\right)^2 + \left(\frac{1}{2}P\right)^3, \quad ...$$

and

$$I + \frac{1}{2}P + \left(\frac{1}{2}P\right)^2 + \left(\frac{1}{2}P\right)^3 + ... + \left(\frac{1}{2}P\right)^m \equiv T$$

Similarly, the parental rows of $I + \frac{1}{2}P + \left(\frac{1}{2}P\right)^2$ are the same as the corresponding ones of

$$I + \frac{1}{2}P + \left(\frac{1}{2}P\right)^2 + \left(\frac{1}{2}P\right)^3 , \quad ...,$$ and of T; etc. The reason for this is that the differences that exist

between

$$I + \sum_{c=1}^{j-1} \left(\frac{1}{2}P\right)^c \qquad \text{and} \qquad I + \sum_{c=1}^{j} \left(\frac{1}{2}P\right)^c$$

are related to accounting for the passage of alleles from ancestors c generations removed form each

animal, to these same individuals. For instance, if c = 3, the difference between $I + \sum_{c=1}^{2}\left(\frac{1}{2}P\right)^c$ and

$I + \sum_{c=1}^{3}\left(\frac{1}{2}P\right)^c$, are the elements of $\left(\frac{1}{2}P\right)^3$ which reflect the passage of alleles from great-

grandparents to great-grandprogeny. Thus, rows of animals with unknown ancestors from the cth

generation backwards remain unchanged, i.e., **when the passage of alleles from all known**

ancestors of an animal has been explained, its row will not change anymore. These fixed rows

are called **parental rows** if these animals have progeny. In particular, notice that:

$$\left\{ \begin{array}{c} \text{the parental rows of} \\ \\ I + \sum_{c=1}^{m_i-1}\left(\frac{1}{2}P\right)^c \end{array} \right\} = \left\{ \begin{array}{c} \text{the parental rows of} \\ \\ I + \sum_{c=1}^{m_i}\left(\frac{1}{2}P\right)^c \end{array} \right\}$$

because the animals from the last generation have not become parents yet.

(3)   The ith row of T is a linear function of the rows of the parents of animals i, i.e.,

$$i^{th} \text{ row of } \left\{ I + \sum_{c=1}^{m_i}\left(\frac{1}{2}P\right)^c \right\} = i^{th} \text{ row of } \left\{ I + \frac{1}{2}P\left[I - \sum_{c=1}^{m_i-1}\left(\frac{1}{2}P\right)^c \right] \right\}$$

$$= 1 \text{ on diag} + \frac{1}{2}p_i'\left[I + \sum_{c=1}^{m_i-1}\left(\frac{1}{2}P\right)^c \right]$$

where

    $p_i' = $ i^{th} row of P, it has at most two non-zero elements: a 1 on the column corresponding to

the sire of animal i (s_i) and another 1 on the column of the dam of animal i (d_i), i.e.,

$$p_i' = [0 \dots 010 \dots 010 \dots 0]$$

$$\downarrow \qquad \downarrow$$
$$s_i \qquad d_i$$

(4) Because T contains all the parental rows and the row for an animal is a linear function of the rows of its parents, a **recursive procedure to compute T** can be outlined as follows:

(i) Order animals such that parents precede progeny, numbering them from 1 (oldest) to n (youngest).

(ii) Compute the elements of $T = \{t_{ij}\}$, one row or one column at a time, as follows:

(a) $t_{ij} \quad = \quad \dfrac{1}{2} t_{s_i,j} + \dfrac{1}{2} t_{d_i,j}$ for $j<i$ if s_i and d_i are known

$\qquad = \quad \dfrac{1}{2} t_{s_i,j}$ for $j<i$ if s_i is known only

$\qquad = \quad \dfrac{1}{2} t_{d_i,j}$ for $j<i$ if d_i is known only

$\qquad = \quad 0$ for $j<i$ if neither s_i nor d_i is known

$\qquad = \quad 0$ for $j>i$

(b) $t_{ii} \quad = \quad 1$

The matrix A, written in terms of T, is:

$$A \quad = \quad T D T'$$

Because D is diagonal and positive, $D = D^{½} D^{½}$. Thus,

$$A \quad = \quad T D^{½} D^{½} T'$$

$$A \quad = \quad C C'$$

where

$$C \quad = \quad T D^{½}$$

$$C = \text{Cholesky decomposition of A.}$$

The elements of C can be computed recursively, using the procedure to compute T, as follows:

(i) $\quad c_{ij} = t_{ij}\, d_{jj}^{1/2}$

$$= \frac{1}{2}\left(\delta_{s_i}\, t_{s_i,j} + \delta_{d_i}\, t_{d_i,j}\right) d_{jj}^{1/2} \quad \text{for } j < i$$

where

$$\delta_{s_i}\,(\delta_{d_i}) \quad = \quad 1 \quad \text{if } s_i\,(d_i) > 0$$

$$= \quad 0 \quad \text{if } s_i\,(d_i) = 0$$

(ii) $\quad c_{ii} = d_{ii}^{-1}$

$$c_{ii}^2 = d_{ii}$$

$$= 1 - \frac{1}{4}\delta_{s_i}\, a_{s_i s_i} - \frac{1}{4}\delta_{d_i}\, a_{d_i d_i}$$

But

$$A = CC'$$

$$\Rightarrow \quad a_{s_i s_i} = \sum_{k=1}^{s_i} c_{s_i,k}^2$$

$$a_{d_i d_i} = \sum_{k=1}^{d_i} c_{d_i,k}^2$$

$$\Rightarrow \quad c_{ii}^2 = 1 - \frac{1}{4}\delta_{s_i}\sum_{k=1}^{s_i} c_{s_i,k}^2 - \frac{1}{4}\delta_{d_i}\sum_{k=1}^{d_i} c_{d_i,k}^2$$

$\Rightarrow$ to compute the $d_{ii} = c_{ii}^2$ we only need the squares of the diagonal elements of Cholesky matrix C. Also, computations can proceed **one column at a time**. Consequently, the matrix C does **not** need to be stored to compute the a_{ii}.

The **computational procedure to obtain the a_{ii}, proceeding one column at a time (Quaas, 1976)**, is as follows:

[1] Define:

u $\quad=\quad$ vector of sums of squares of the elements of a row of C

v $\quad=\quad$ vector containing the diagonal elements of C and work vector (used to store offdiagonal elements of C temporarily)

[2] Order animals so that parents precede progeny and number them from 1 to n. Set the numbers of unknown parents to zero.

[3] For the ith round (i.e., the ith animal) compute:

(a) $\quad v_i \;=\; c_{ii}$

$$= \; \left[1 - \frac{1}{4}\left(u_{s_i} + u_{d_i}\right)\right]^{\frac{1}{2}} \qquad \text{if } s_i, d_i > 0$$

$$= \; \left[1 - \frac{1}{4} u_{s_i}\right]^{\frac{1}{2}} \qquad \text{if } s_i > 0, d_i = 0$$

$$= \; \left[1 - \frac{1}{4} u_{d_i}\right]^{\frac{1}{2}} \qquad \text{if } s_i = 0, d_i > 0$$

$$= \; 1 \qquad \text{if } s_i = d_i = 0$$

(b) $\quad v_j \;=\; c_{ji} \qquad \text{for } j = i + 1, \ldots, n$

$$= \; \frac{1}{2} v_{s_j} + \frac{1}{2} v_{d_j} \qquad \text{if } i \leq s_j, d_j$$

$$= \; \frac{1}{2} v_{s_j} \qquad \text{if } d_j < i \leq s_j$$

$$= \; \frac{1}{2} v_{d_j} \qquad \text{if } s_j < i \leq d_j$$

$$= \quad 0 \qquad\qquad\qquad \text{if } s_j, d_j < i$$

(c) $\quad u_j \quad = \quad u_j + (v_j)^2 \quad$ for $j = i, \dots, n$

(d) $\quad d_{ii}^{-1} \quad = \quad (v_i)^{-2}$

[4] Compute and sum the contributions of the ith animal to A^{-1} using Henderson's rules. If the matrix is too big to be kept in core, use a linked-list subroutine to sum and store only the non-zero elements of A^{-1}.

[5] Repeat steps [3] and [4] until the last animal is processed, i.e., do steps [3] and [4] for $i = 1, \dots, n$.

[6] If matrix A^{-1} is to be stored on disk or type, copy the non-zero elements accompanied by their row and column numbers.

Computation of the d$_{ii}$ in the example of an inbred population using Quaas' (1976) procedure

(j)	Round (i)					
	1	2	3	4	5	6
u_1	1.0	1.0	1.0	1.0	1.0	1.0
u_2	$(0.5)^2$	$u_{2(1)} + 0.75$	1.0	1.0	1.0	1.0
u_3	$(0.75)^2$	$u_{3(1)} + (v_{3(2)})^2$	$u_{3(2)} + 0.5$	1.25	1.25	1.25
u_4	$(0.625)^2$	$u_{4(1)} + (v_{4(2)})^2$	$u_{4(2)} + (v_{4(3)})^2$	1.375	1.375	1.375
u_5	$(0.6875)^2$	$u_{5(1)} + (v_{5(2)})^2$	$u_{5(2)} + (v_{5(3)})^2$	$u_{5(3)} + (v_{5(4)})^2$	1.5	1.5
u_6	$(0.6875)^2$	$u_{6(1)} + (v_{6(2)})^2$	$u_{6(2)} + (v_{6(3)})^2$	$u_{5(3)} + (v_{5(4)})^2$	$u_{6(4)} + (0.0)^2$	1.5
	1	2	3	4	5	6
v_1	$(1.0)^{1/2}$	1.0	1.0	1.0	1.0	1.0
v_2	0.5	$(0.75)^{1/2}$	$(0.75)^{1/2}$	$(0.75)^{1/2}$	$(0.75)^{1/2}$	$(0.75)^{1/2}$
v_3	0.75	$\frac{1}{2}(0.75)^{1/2}$	$(0.5)^{1/2}$	$(0.5)^{1/2}$	$(0.5)^{1/2}$	$(0.5)^{1/2}$
v_4	0.625	$\frac{3}{4}(0.75)^{1/2}$	$\frac{1}{2}(0.5)^{1/2}$	$(0.4375)^{1/2}$	$(0.4375)^{1/2}$	$(0.4375)^{1/2}$
v_5	0.6875	$\frac{5}{8}(0.75)^{1/2}$	$\frac{3}{4}(0.5)^{1/2}$	$\frac{1}{2}(0.34375)^{1/2}$	$(0.34375)^{1/2}$	$(0.34375)^{1/2}$
v_6	0.6875	$\frac{5}{8}(0.75)^{1/2}$	$\frac{3}{4}(0.75)^{1/2}$	$\frac{1}{2}(0.4375)^{1/2}$	0.0	$(0.34375)^{1/2}$

Thus, the matrix D = diag $\{(v_i)^2\}$, is:

$$D = \begin{bmatrix} 1.0 & & & & & \\ & 0.75 & & & & \\ & & 0.5 & & & \\ & & & 0.4375 & & \\ & & & & 0.34375 & \\ & & & & & 0.34375 \end{bmatrix}$$

The matrix A^{-1}, computed using Henderson's rules, is:

$$A^{-1} = \begin{bmatrix} A^{11} & A^{12} \\ A^{12'} & A^{22} \end{bmatrix}$$

where

$$A^{11} = \begin{bmatrix} 1 + \dfrac{1}{4}\left[\dfrac{1}{0.75} + \dfrac{1}{0.5}\right] & -\dfrac{1}{2}\left[\dfrac{1}{0.75}\right] + \dfrac{1}{4}\left[\dfrac{1}{0.5}\right] & & -\dfrac{1}{2}\left[\dfrac{1}{0.5}\right] & 0 \\[4mm] & \dfrac{1}{0.75} + \dfrac{1}{4}\left[\dfrac{1}{0.5}\right] + \dfrac{1}{0.4375} & -\dfrac{1}{2}\left[\dfrac{1}{0.5}\right] + \dfrac{1}{4}\left[\dfrac{1}{0.4375}\right] & -\dfrac{1}{2}\left[\dfrac{1}{0.34375}\right] \\[4mm] & & \dfrac{1}{0.5} + \dfrac{1}{4}\left[\dfrac{1}{0.4375} + \dfrac{2}{0.34375}\right] & -\dfrac{1}{2}\left[\dfrac{1}{0.4375}\right] + \dfrac{1}{4}\left[\dfrac{2}{0.34375}\right] \\[4mm] & & & \dfrac{1}{0.4375} + \dfrac{1}{4}\left[\dfrac{2}{0.34375}\right] \end{bmatrix}$$

$$A^{12} = \begin{bmatrix} 0 & 0 \\[3mm] 0 & 0 \\[3mm] -\dfrac{1}{2}\left[\dfrac{1}{0.34375}\right] & -\dfrac{1}{2}\left[\dfrac{1}{0.34375}\right] \\[3mm] -\dfrac{1}{2}\left[\dfrac{1}{0.34375}\right] & -\dfrac{1}{2}\left[\dfrac{1}{0.34375}\right] \end{bmatrix}$$

$$A^{22} = \begin{bmatrix} \dfrac{1}{0.34375} & 0 \\[4mm] & \dfrac{1}{0.34375} \end{bmatrix}$$

Thus,

$$A^{-1} = \begin{bmatrix} 1.8333 & -0.1667 & -1.0000 & 0 & | & 0 & 0 \\ & 2.4048 & -0.4286 & -1.1429 & | & 0 & 0 \\ & & 4.0260 & 0.3117 & | & -1.4545 & -1.4545 \\ & & & 3.7403 & | & -1.4545 & -1.4545 \\ - & - & - & - & | & - & - \\ & Symmetric & & & | & 2.9091 & 0 \\ & & & & | & & 2.9091 \end{bmatrix}$$

$$A^{-1} = (I - \tfrac{1}{2}\,P')\,D^{-1}\,(I - \tfrac{1}{2}\,P)$$

For the sake of completeness, the relationship matrix A is:

$$A = (I - \tfrac{1}{2} P)^{-1} D (I - \tfrac{1}{2} P')^{-1}$$

$$
A = \begin{bmatrix}
1.0 & 0.5 & 0.75 & 0.625 & | & 0.6875 & 0.6875 \\
 & 1.0 & 0.75 & 0.875 & | & 0.8125 & 0.8125 \\
 & & 1.25 & 1.0 & | & 1.125 & 1.125 \\
 & & & 1.375 & | & 1.1875 & 1.1875 \\
- & - & - & - & | & - & - \\
 & \textit{Symmetric} & & & | & 1.5 & 1.15625 \\
 & & & & | & & 1.5
\end{bmatrix}
$$

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