

3. Properties of the relationship matrix

3.1 Partitioning of the relationship matrix

The additive relationship matrix, **A**, can be written as the product of a lower triangular matrix, **T**, a diagonal matrix, **D**, and **T'**:

$$\mathbf{A} = \mathbf{T}\mathbf{D}\mathbf{T}'$$

D is a diagonal matrix with a simple structure:

1. If both parents, s and d, of animal i are known, the diagonal element of **D** is

$$d_{ii} = 0.5 - 0.25 (F_s + F_d)$$
2. If one parent is known, say s,

$$d_{ii} = 0.75 - 0.25 F_s$$
3. If no parents are known, which is the case in the base population, then

$$d_{ii} = 1.$$

T is a lower triangular matrix with ones along the diagonal. All elements in the upper triangle are zeros. The lower off-diagonal elements are computed as follows:

1. If both parents, s and d, of animal i are known, then $t_{ij} = 0.5(t_{sj} + t_{dj})$ for $j = 1, 2, \dots, i-1$.
2. If one parent is known, say s, then $t_{ij} = 0.5 t_{sj}$
3. If neither parent is known, then $t_{ij} = 0$.

Example 3.1

The following example is from a publication by Henderson from 1976. Given the following:

Animal	Sire	Dam
3	1	
4	1	2
5	3	4
6	1	4
7	5	6

The **A** matrix is

			1.	1.2	3.4	1.4	5.6
	1	2	3	4	5	6	7
1	1	0	0.5	0.5	0.5	0.75	0.625
2	0	1	0	0.5	0.25	0.25	0.25
3	0.5	0	1	0.25	0.625	0.375	0.5
4	0.5	0.5	0.25	1	0.625	0.75	0.6875

5	0.5	0.25	0.625	0.625	1.125	0.5625	0.84375
6	0.75	0.25	0.375	0.75	0.5625	1.25	0.90625
7	0.625	0.25	0.5	0.6875	0.84375	0.90625	1.28125

The **D** matrix is set up by following the above rules. Animals 1 and 2 have unknown parents, and $d_{11} = d_{22} = 1$.

One of the parents of animal 3 is known. Therefore $d_{33} = 0.75$.

The remaining animals have known parents. Animals 4,5 and 6 have non-inbred parents, and the elements corresponding to these animals are 0.5.

The parents of animal 7 (5 and 6) are inbred ($F_5 = 0.125$ and $F_6 = 0.25$). Therefore,

$$d_{77} = 0.5 - 0.25(0.125 + 0.25) = 0.40625.$$

Hence,

$$D = \text{diag} \{1, 1, 0.75, 0.5, 0.5, 0.5, 0.40625\}$$

T is most easily set up as shown below. To the left of each row, the number of the animal, its sire and dam is shown. In each i-row, enter the average of the s- and d-rows.

s	d	i	1	2	3	4	5	6	7
		1	1	0	0	0	0	0	0
		2	0	1	0	0	0	0	0
1		3	0.5	0	1	0	0	0	0
1	2	4	0.5	0.5	0	1	0	0	0
3	4	5	0.5	0.25	0.5	0.5	1	0	0
1	4	6	0.75	0.25	0	0.5	0	1	0
5	6	7	0.625	0.25	0.25	0.5	0.5	0.5	1

$\mathbf{T}^{-1}$ has a very simple structure. It is a lower triangular matrix with ones along the diagonal and -0.5 for columns corresponding to the parents. The rest of the elements are zero. The $\mathbf{T}^{-1}$ matrix is

s	d	i	1	2	3	4	5	6	7
		1	1	0	0	0	0	0	0
		2	0	1	0	0	0	0	0
1		3	-0.5	0	1	0	0	0	0
1	2	4	-0.5	-0.5	0	1	0	0	0
3	4	5	0	0	-0.5	-0.5	1	0	0
1	4	6	-0.5	0	0	-0.5	0	1	0
5	6	7	0	0	0	0	-0.5	-0.5	1

Let u_i denote the breeding value of animal i . Then $\mathbf{u}$ is a vector of breeding values and the product $\mathbf{T}^{-1} \mathbf{u}$ is

$$\begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ -0.5 & 0 & 1 & 0 & 0 & 0 & 0 \\ -0.5 & -0.5 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & -0.5 & -0.5 & 1 & 0 & 0 \\ -0.5 & 0 & 0 & -0.5 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & -0.5 & -0.5 & 1 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \\ u_6 \\ u_7 \end{bmatrix} = \begin{bmatrix} u_1 \\ u_2 \\ u_3 - \frac{1}{2}u_1 \\ u_4 - \frac{1}{2}u_1 - \frac{1}{2}u_2 \\ u_5 - \frac{1}{2}u_3 - \frac{1}{2}u_4 \\ u_6 - \frac{1}{2}u_1 - \frac{1}{2}u_4 \\ u_7 - \frac{1}{2}u_5 - \frac{1}{2}u_6 \end{bmatrix}$$

Since an animal receives half its genes from its sire and half from its dam, the expected breeding value of the animal is the average of the breeding values of its parents. However each parent contributes a random half of its genes to the progeny and the breeding value of the progeny is therefore

$$u_o = \frac{1}{2} u_s + \frac{1}{2} u_d + m, \quad (31)$$

where m is a deviation from the average of the breeding values of the parents and is called Mendelian sampling. Thus,

$$\mathbf{m} = \mathbf{u}_o - \frac{1}{2} \mathbf{u}_s - \frac{1}{2} \mathbf{u}_d$$

The product $\mathbf{T}^{-1} \mathbf{u}$ is therefore $\mathbf{m}$, the Mendelian sampling vector.

While the variance of $\mathbf{u}_o$ is reduced by directional selection because the variance of $\frac{1}{2} \mathbf{u}_s + \frac{1}{2} \mathbf{u}_d$ is affected by selection of the parents, Bulmer (1971) has shown that if the number of loci affecting a trait is large, $\mathbf{m}$ is unaffected by selection and independent of $\mathbf{u}_s$ and $\mathbf{u}_d$.

As shown above

$$\mathbf{m} = \mathbf{u}_o - \frac{1}{2}(\mathbf{u}_s + \mathbf{u}_d) \quad (32)$$

The variance of $\mathbf{m}$ is therefore

$$\begin{aligned} V(\mathbf{m}) &= V(\mathbf{u}_o) - V(\frac{1}{2}(\mathbf{u}_s + \mathbf{u}_d)) \\ &= V(\mathbf{u}_o) - \frac{1}{4}(V(\mathbf{u}_s) + V(\mathbf{u}_d)) - 2Cov(\mathbf{u}_s \mathbf{u}_d) \\ &= V(\mathbf{u}_o) - \frac{1}{4}V(\mathbf{u}_s) - \frac{1}{4}V(\mathbf{u}_d) - \frac{1}{2}Cov(\mathbf{u}_s \mathbf{u}_d) \\ &= (1 + F)\sigma_A^2 - \frac{1}{4}a_{ss}\sigma_A^2 - \frac{1}{4}a_{dd}\sigma_A^2 - \frac{1}{2}a_{sd}\sigma_A^2 \end{aligned}$$

where a_{ss} , and a_{dd} are diagonal elements of the additive relationship matrix corresponding to sire and dam, and a_{sd} is the additive relationship between sire and dam. Then

$$\frac{V(\mathbf{m})}{\sigma_A^2} = (1 + F) - \frac{1}{4}a_{ss} - \frac{1}{4}a_{dd} - \frac{1}{2}a_{sd}$$

For $F = 0$ this is equal to $\frac{1}{2}$, $\frac{3}{4}$ or 1 if 2, 1 or no parent is known. These are the diagonal element of the $\mathbf{D}$ -matrix. Therefore $V(\mathbf{m}) = \mathbf{D}^{-1} \sigma_A^2$.

This can also be shown by noting that $\mathbf{m} = \mathbf{T}^{-1} \mathbf{u}$. Then $V(\mathbf{m}) = V(\mathbf{T}^{-1} \mathbf{u})$:

$$\begin{aligned}
V(\mathbf{T}^{-1}\mathbf{u}) &= \mathbf{T}^{-1}V(\mathbf{u})\mathbf{T}'^{-1} \\
&= \mathbf{T}^{-1}\mathbf{A}\sigma_A^2\mathbf{T}'^{-1} \\
&= \mathbf{T}^{-1}\mathbf{A}\mathbf{T}'^{-1}\sigma_A^2 \\
&= \mathbf{T}^{-1}\mathbf{T}\mathbf{D}\mathbf{T}'\mathbf{T}'^{-1}\sigma_A^2 \\
&= \mathbf{D}\sigma_A^2
\end{aligned}$$

Unbiased estimates of breeding values under selection is obtained only if $\mathbf{m}$ solely represents Mendelian sampling. This is the case only if both parents are identified and accounted for in $\mathbf{T}$ except for the unrelated base population. If only one or no parents are identified, $\mathbf{m}$ contains a genetic component in addition to Mendelian sampling, the variance of which will be affected by selection. The assumption that the base population is unselected need also not be true.

3.2. Computation of $\mathbf{A}^{-1}$

Since $\mathbf{A} = \mathbf{T}\mathbf{D}\mathbf{T}'$ then $\mathbf{A}^{-1} = (\mathbf{T}^{-1})'\mathbf{D}^{-1}\mathbf{T}^{-1}$. $\mathbf{D}$ is a diagonal matrix. Therefore $\mathbf{D}^{-1}$ is easily obtained. As shown above, also $\mathbf{T}^{-1}$ has a very simple structure that does not require knowledge of $\mathbf{T}$. The inverse of the relationship matrix, $\mathbf{A}^{-1}$, can therefore be computed directly without computing $\mathbf{A}$.

Consider the following pedigree:

Animal	Sire		Dam
1	-		-
2	-		-
3	1		2

Then

$$\mathbf{T}^{-1} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -\frac{1}{2} & -\frac{1}{2} & 1 \end{bmatrix} \quad \mathbf{D}^{-1} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 2 \end{bmatrix}$$

Performing the multiplication $(\mathbf{T}^{-1})'\mathbf{D}^{-1}\mathbf{T}^{-1}$ gives first

$$(\mathbf{T}^{-1})'\mathbf{D}^{-1} = \begin{bmatrix} 1 & 0 & -\frac{1}{2} \\ 0 & 1 & -\frac{1}{2} \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 2 \end{bmatrix} = \begin{bmatrix} 1 & 0 & -1 \\ 0 & 1 & -1 \\ 0 & 0 & 2 \end{bmatrix}$$

and next

$$\mathbf{A}^{-1} = (\mathbf{T}^{-1'} \mathbf{D}^{-1}) \mathbf{T}^{-1} = \begin{bmatrix} 1 & 0 & -1 \\ 0 & 1 & -1 \\ 0 & 0 & 2 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -\frac{1}{2} & -\frac{1}{2} & 1 \end{bmatrix} = \begin{bmatrix} \frac{1}{2} & \frac{1}{2} & -1 \\ \frac{1}{2} & \frac{1}{2} & -1 \\ -1 & -1 & 2 \end{bmatrix}$$

It is seen that the diagonal of $\mathbf{A}^{-1}$ is $\mathbf{D}^{-1}$ with addition of $\frac{1}{2}$ to the elements corresponding to each of the parents. The off-diagonal elements (1,2) and (2,1), corresponding to the intersection of row and column of the parents, is $\frac{1}{2}$ and the elements corresponding to the intersection of rows and columns of parents and offspring are -1. Similar exercises can be made for relationship matrices when one or no parents are known. From this the following general rule for setting up $\mathbf{A}^{-1}$ directly has been developed:

First set $\mathbf{A}^{-1} = 0$. Let $\mathbf{d}$ be a vector of diagonal elements of $\mathbf{D}^{-1}$. Then if both parents of the i^{th} individual, s and d are known, then add

- $\mathbf{d}_i$ to element (i,i),
- $-\mathbf{d}_i/2$ to elements (s,i), (i,s), (d,i) and (i,d) and
- $\mathbf{d}_i/4$ to element (s,s), (d,d), (s,d) and (d,s)

If only one parent, s, is known then add

- $\mathbf{d}_i$ to element (i,i)
- $-\mathbf{d}_i/2$ to elements (s,i) and (i,s) and
- $\mathbf{d}_i/4$ to element (s,s).

If neither parent is known add

- $\mathbf{d}_i$ to element (i,i).

For non-inbred populations, the values of $\mathbf{d}_i$ are 2, 4/3 or 1 if both, one or no parents are known, respectively.

