

Bivariate VT-SEM

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1 Multivariate path tracing rules:

- Matrices are untransposed when traveling the direction against the arrows, and transposed when direction of the arrows. Stated another way, when tracing, begin with an untransposed matrix, always go through a double-headed arrow at which point matrices thereafter are transposed. Traversing μ resets this rule.
- When creating a new matrix (e.g., Ω), always define the untransposed matrix in a way that it travels *against the direction* of the arrows, at least at the beginning of the tracing (they might change direction later). E.g., Ω should be $cov(Y_p, T_p)$ where we travel Y_p to T_p because this is the direction in which we would not transpose when tracing the first individual component paths (e.g., δ). To do it the other way would invite confusion. Often but not always, this means that the untransposed matrices have component matrices that are also untransposed.
- In drawing out expected 2-by-2 covariance matrices between two different variables, always put the starting variable (the one with arrows pointing to it) on the left (defines rows) and the ending variables (arrows coming from it) on the top (defines columns).
- Great care is needed when putting matrices into the expected total var/covar matrix. Try to have the untransposed matrices above the diagonal and transposed ones below it. To do this, the variables must be placed in the right order (e.g., Y 's come before $[N]T$'s in the case of Ω). However, it

will probably be impossible to order the variables in such a way that the untransposed expectations are *always* above the diagonal.

- Var/covar matrices between the same 2 variables are always symmetric. On the other hand, covariance matrices between 2 different variables, such that the variables on top (defining columns) are different than the 2 variables on the side (defining rows), are typically full, although there are exceptions (e.g., g_c between T_p and NT_p , where there is no biological reason for these to be different since the meiosis differentiating transmitted vs. untransmitted occurs in the focal individuals' [parent's] gametes). The reason these covariance matrices are asymmetric is because these 2-by-2 matrices are actually submatrices (the upper right 2-by-2) of larger 4-by-4 symmetric var/covar matrices. E.g., the complete var/covar matrix between F_1 , F_2 , $[N]T_1$, and $[N]T_2$ is a 4-by-4 matrix and is symmetric. However, we define w to be the upper right 2-by-2 submatrix of this complete var/covar matrix, and thus it is not symmetric (and w' is the lower left 2-by-2 submatrix of this complete var/covar matrix). We use the terminology "covariance matrices" to denote these asymmetric 2-by-2 matrices, and "var/covar matrices" to denote symmetric matrices.
- Because covariance matrices are asymmetric, we need a path tracing rule to denote when they should be transposed and when they should not. When moving in the direction of the variable on the left (defining rows) to variables on the top (defining columns), the covariance matrix is untransposed. When moving in the opposite direction, the covariance matrix is transposed. To clarify these two situations in a path diagram, we place a \triangleright in the middle of the curved covariance line with double-headed arrows. The \triangleright points in the direction for which path coefficients should not be transposed.
- Path tracing across the μ matrix also has a special rule in multivariate settings. It is untransposed when going left to right (Y_m to Y_f), but transposed when going right to left (Y_f to Y_m). Note that μ is full and that the copath from $Y_{11,m}$ (on left) to $Y_{22,f}$ (on right) is μ_{12} and between $Y_{22,m}$ and $Y_{11,f}$ is μ_{21} .
- Note that there are now 2 g matrices: g_t ("g trans," which is asymmetric) and g_c ("g cis," which is symmetric). g_t is the covariance between hap-

lotypic PGS's between spouses – e.g., $cov(T_p, T_m)$. There are 4 of them (g_2, g_3, g_4, g_5 in our old nomenclature). g_t is full because $cov(T_{1,p}, T_{2,m})$ doesn't necessarily equal $cov(T_{2,p}, T_{1,m})$. g_c is symmetric because meiosis has mixed alleles of different parental origins together (or we're using the "transmitted" vs. "untransmitted" with respect to the offspring, which is a random mix of the two parents' set of alleles), and so cannot be differentiated by the sex of the parent from whence they came. There are 6 of them – $g_1, g_6, g_7, g_8, g_9, g_{10}$ in our old nomenclature.

- The i_t matrix is also also special. As with the other trans haplotypic covariances, i_t is transposed when going from M to P , and not transposed when going from P to M . However, $cov(LT_p, T_m) \neq cov(T_p, LT_m)$. Therefore, we need two i_t 's, such that $i_{t1} = cov(LT_p, T_m)$ and $i_{t2} = cov(T_p, LT_m)$, with their respective transposes being the flipped versions of those covariances.

2 Matrices:

2.1 Full Matrices

Note: subscripts p, m, s , and d denote paternal, maternal, son, and daughter, respectively. These are used to incorporate sex and generational effects in our model. For example, w_d represents the genetic nurture effect for females in the offspring generation (i.e., "daughters"), whereas w_m represents that of females in the paternal generation ("mothers").

MCK: all of these have been checked

$$\mu (Y_p \text{ to } Y_m) = \begin{matrix} & Y_{1m} & Y_{2m} \\ \begin{matrix} Y_{1p} \\ Y_{2p} \end{matrix} & \begin{bmatrix} \mu_{11} & \mu_{12} \\ \mu_{21} & \mu_{22} \end{bmatrix} \end{matrix}$$

$$\mu' (Y_m \text{ to } Y_p) = \begin{array}{c} Y_{1p} \quad Y_{2p} \\ Y_{1m} \left[\begin{array}{cc} \mu_{11} & \mu_{21} \\ \mu_{12} & \mu_{22} \end{array} \right] \\ Y_{2m} \end{array}$$

μ should be full in order for the expected covariance matrix between mates, as well as the expected covariance of the g_t matrix, to agree with the observed matrices that correspond to these, which may be asymmetric. It is true that, once genes from male/female ancestors are mixed via meiosis, the within-person (or cis) expectations of the off-diagonal elements of g (g_c) are the same. Nevertheless, this symmetry isn't true of g_t and the expected phenotypic $cov(Y_p, Y_m)$ between mates, and thus μ must be full. Note that the paternal goes on the left (defines rows) and maternal on the top (defines columns) of this matrix, and thus $\mu_{12} = \mu_{1p,2m}$ (i.e., 1 is the paternal Y_1 and 2 is the maternal Y_2), and $\mu_{21} = \mu_{2p,1m}$

$$f (F_o \text{ to } Y_{[p/m]}) = \begin{array}{c} Y_{1[p/m]} \quad Y_{2[p/m]} \\ F_{1o} \left[\begin{array}{cc} f_{11} & f_{12} \\ f_{21} & f_{22} \end{array} \right] \\ F_{2o} \end{array}$$

$$f' (Y_{[p/m]} \text{ to } F_o) = \begin{array}{c} F_{1o} \quad F_{2o} \\ Y_{1[p/m]} \left[\begin{array}{cc} f_{11} & f_{21} \\ f_{12} & f_{22} \end{array} \right] \\ Y_{2[p/m]} \end{array}$$

Note that this is full not because of sex of origin effects, but because the influence of parental trait Y_1 on offspring trait Y_2 (f_{12}) isn't necessarily the same as the influence of parental trait Y_2 on offspring trait Y_1 (f_{21}). However, because we do need to account for parental and offspring sex effects there are four different full f matrices, one for each combination of parent/ offspring sex. For example:

$$f_{sm} (F_s \text{ to } Y_m) = \begin{array}{c} Y_{1m} \quad Y_{2m} \\ F_{1s} \left[\begin{array}{cc} f_{1m1s} & f_{1m2s} \\ f_{2m1s} & f_{2m2s} \end{array} \right] \\ F_{2s} \end{array}$$

models the effect of a mother's phenotype on a son's familial environment.

$$w (2(F \text{ to } [N]T)) = \begin{matrix} & [N]T_1 & [N]T_2 \\ F_1 & \begin{bmatrix} w_{11} & w_{12} \end{bmatrix} \\ F_2 & \begin{bmatrix} w_{21} & w_{22} \end{bmatrix} \end{matrix}$$

$$w' (2([N]T \text{ to } F)) = \begin{matrix} & F_1 & F_2 \\ [N]T_1 & \begin{bmatrix} w_{11} & w_{21} \end{bmatrix} \\ [N]T_2 & \begin{bmatrix} w_{12} & w_{22} \end{bmatrix} \end{matrix}$$

Note that w is also a full matrix. When the path is traversed from F to $[N]T$, the coefficient is $\frac{1}{2}w$, and when the path is traversed from $[N]T$ to F , the coefficient is $\frac{1}{2}w'$. For more on w , see notes under its derivation below.

$$q (2(F \text{ to } L[N]T)) = \begin{matrix} & L[N]T_1 & L[N]T_2 \\ F_1 & \begin{bmatrix} q_{11} & q_{12} \end{bmatrix} \\ F_2 & \begin{bmatrix} q_{21} & q_{22} \end{bmatrix} \end{matrix}$$

$$q' (2(L[N]T \text{ to } F)) = \begin{matrix} & F_1 & F_2 \\ L[N]T_1 & \begin{bmatrix} q_{11} & q_{21} \end{bmatrix} \\ L[N]T_2 & \begin{bmatrix} q_{12} & q_{22} \end{bmatrix} \end{matrix}$$

Note that q is also a full matrix. When the path is traversed from F to $L[N]T$, the coefficient is $\frac{1}{2}q$, and when the path is traversed from $L[N]T$ to F , the coefficient is $\frac{1}{2}q'$. For more on q , see notes under its derivation below.

$$g_t ([N]T_p \text{ to } [N]T_m) = \begin{matrix} & [N]T_{1m} & [N]T_{2m} \\ [N]T_{1p} & \begin{bmatrix} g_{t11} & g_{t12} \end{bmatrix} \\ [N]T_{2p} & \begin{bmatrix} g_{t21} & g_{t22} \end{bmatrix} \end{matrix}$$

$$g'_t ([N]T_m \text{ to } [N]T_p) = \begin{matrix} & [N]T_{1p} & [N]T_{2p} \\ [N]T_{1m} & \begin{bmatrix} g_{t11} & g_{t21} \end{bmatrix} \\ [N]T_{2m} & \begin{bmatrix} g_{t12} & g_{t22} \end{bmatrix} \end{matrix}$$

Note that in this matrix, the variable defining rows (e.g., T_{1p} and T_{2p}) is different than the variable defining columns (e.g., T_{1m} and T_{2m}), and thus this matrix is asymmetric: $g_{t,12} \neq g_{t,21}$; e.g., $cov(T_{1p}, T_{2m}) \neq cov(T_{2p}, T_{1m})$.

$$h_t (L[N]T_p \text{ to } L[N]T_m) = \begin{matrix} & L[N]T_{1m} & L[N]T_{2m} \\ L[N]T_{1p} & \begin{bmatrix} h_{t11} & h_{t12} \end{bmatrix} \\ L[N]T_{2p} & \begin{bmatrix} h_{t21} & h_{t22} \end{bmatrix} \end{matrix}$$

$$h'_t (L[N]T_m \text{ to } L[N]T_p) = \begin{matrix} & L[N]T_{1p} & L[N]T_{2p} \\ L[N]T_{1m} & \begin{bmatrix} h_{t11} & h_{t21} \end{bmatrix} \\ L[N]T_{2m} & \begin{bmatrix} h_{t12} & h_{t22} \end{bmatrix} \end{matrix}$$

As with g_t , the variable defining rows (e.g., LT_{1p} and LT_{2p}) is different than the variable defining columns (e.g., LT_{1m} and LT_{2m}), and thus this matrix is asymmetric: $h_{t,12} \neq h_{t,21}$; e.g., $cov(LT_{1p}, LT_{2m}) \neq cov(LT_{2p}, LT_{1m})$.

$$i_{t_{LO}} (L[N]T_p \text{ to } [N]T_m) = \begin{matrix} & [N]T_{1m} & [N]T_{2m} \\ L[N]T_{1p} & \begin{bmatrix} i_{t_{LO}11} & i_{t_{LO}12} \end{bmatrix} \\ L[N]T_{2p} & \begin{bmatrix} i_{t_{LO}21} & i_{t_{LO}22} \end{bmatrix} \end{matrix}$$

$$i'_{t_{LO}} ([N]T_m \text{ to } L[N]T_p) = \begin{matrix} & L[N]T_{1p} & L[N]T_{2p} \\ [N]T_{1m} & \begin{bmatrix} i_{t_{LO}11} & i_{t_{LO}21} \end{bmatrix} \\ [N]T_{2m} & \begin{bmatrix} i_{t_{LO}12} & i_{t_{LO}22} \end{bmatrix} \end{matrix}$$

$$i_{t_{OL}} ([N]T_p \text{ to } L[N]T_m) = \begin{matrix} & L[N]T_{1m} & L[N]T_{2m} \\ \begin{matrix} [N]T_{1p} \\ [N]T_{2p} \end{matrix} & \begin{bmatrix} i_{t_{OL}11} & i_{t_{OL}12} \\ i_{t_{OL}21} & i_{t_{OL}22} \end{bmatrix} \end{matrix}$$

$$i'_{t_{OL}} (L[N]T_m \text{ to } [N]T_p) = \begin{matrix} & [N]T_{1p} & [N]T_{2p} \\ \begin{matrix} L[N]T_{1m} \\ L[N]T_{2m} \end{matrix} & \begin{bmatrix} i_{t_{OL}11} & i_{t_{OL}21} \\ i_{t_{OL}12} & i_{t_{OL}22} \end{bmatrix} \end{matrix}$$

$$i_c (L[N]T_m \text{ to } [N]T_m) = \begin{matrix} & [N]T_{1m} & [N]T_{2m} \\ \begin{matrix} L[N]T_{1m} \\ L[N]T_{2m} \end{matrix} & \begin{bmatrix} i_{c11} & i_{c21} \\ i_{c12} & i_{c22} \end{bmatrix} \end{matrix}$$

$$i'_c ([N]T_m \text{ to } L[N]T_m) = \begin{matrix} & L[N]T_{1m} & L[N]T_{2m} \\ \begin{matrix} [N]T_{1m} \\ [N]T_{2m} \end{matrix} & \begin{bmatrix} i_{c11} & i_{c12} \\ i_{c21} & i_{c22} \end{bmatrix} \end{matrix}$$

Two important things to note: First, while m subscripts are used above, the same matrix applies for the paternal PGS's and i_c is equal across parents. Secondly, despite being within-person, the terms on the matrix y-axis are different from those on the x-axis. Thus, i_c is a full matrix. In other words, $\text{cov}(LT_{1p}, T_{2p}) \neq \text{cov}(T_{1p}, LT_{2p})$ necessarily.

2.2 Symmetric Matrices

MCK: all of these have been checked

$$g_c (T_p \text{ to } NT_p \text{ or } T_m \text{ to } NT_m) = \begin{matrix} & NT_{1p} & NT_{2m} \\ \begin{matrix} T_{1p} \\ T_{2p} \end{matrix} & \begin{bmatrix} g_{c11} & g_{c12} \\ g_{c12} & g_{c22} \end{bmatrix} \end{matrix}$$

Note that this matrix is symmetric - i.e., $g_{c,12}$ in element (1,2) = $g_{c,21}$ = $g_{c,12}$ in element (2,1). This is because, within-person, there is no distinction between the parental origins of alleles in NT and T .

$$h_c (LT_p \text{ to } LNT_p \text{ or } LT_m \text{ to } LNT_m) = \begin{matrix} & LNT_{1m} & LNT_{2m} \\ LT_{1p} & \begin{bmatrix} h_{c11} & h_{c12} \\ h_{c12} & h_{c22} \end{bmatrix} \\ LT_{2p} & \end{matrix}$$

Like g_c , this matrix is symmetric - i.e., $g_{c,12}$ in element (1,2) = $g_{c,21}$ = $g_{c,12}$ in element (2,1). This is because, within-person, there is no distinction between the parental origins of alleles in NT and T .

$$k = \begin{matrix} & T_{1m} & T_{2m} \\ T_{1m} & \begin{bmatrix} k_{11} & k_{12} \\ k_{12} & k_{22} \end{bmatrix} \\ T_{2m} & \end{matrix}$$

k is entirely within-PGS and applies for both T and NT . k_{12} is the covariance between the observed haplotypes at time 0 (i.e., the covariance due to pleiotropy).

$$j = \begin{matrix} & LT_{1m} & LT_{2m} \\ LT_{1m} & \begin{bmatrix} j_{11} & j_{12} \\ j_{12} & j_{22} \end{bmatrix} \\ LT_{2m} & \end{matrix}$$

j is entirely within-PGS and applies for both LT and LNT . j_{12} is the covariance between the latent haplotypes at time 0 (i.e., the covariance due to pleiotropy).

$$V_{Fp} = \begin{matrix} & F_{1p} & F_{2p} \\ F_{1p} & \begin{bmatrix} V_{Fp,11} & V_{Fp,12} \\ V_{Fp,12} & V_{Fp,22} \end{bmatrix} \\ F_{2p} & \end{matrix}$$

This particular example shows the V_F matrix for a father, but it's important to note that there are also separate V_F matrices for mothers, sons, and daughters.

These will all be identical the one above, but with m , s , and d subscripts in place of the p subscripts above.

$$V_{\epsilon p} = \begin{matrix} & \epsilon_{1p} & \epsilon_{2p} \\ \epsilon_{1p} & \left[\begin{array}{cc} V_{\epsilon p,11} & V_{\epsilon p,12} \\ V_{\epsilon p,12} & V_{\epsilon p,22} \end{array} \right] \\ \epsilon_{2p} & \end{matrix}$$

As with V_F , this particular example shows the V_ϵ matrix for a father, but it's important to note that there are also separate V_ϵ matrices for mothers, sons, and daughters. These will all be identical the one above, but with m , s , and d subscripts in place of the p subscripts above.

2.3 Diagonal Matrices

MCK: all of these have been checked

$$\delta_p (Y_p \text{ to } [N]T_p) = \begin{matrix} & [N]T_{1p} & [N]T_{2p} \\ Y_{1p} & \left[\begin{array}{cc} \delta_{11p} & 0 \\ 0 & \delta_{22p} \end{array} \right] \\ Y_{2p} & \end{matrix}$$

$$\delta_m (Y_m \text{ to } [N]T_m) = \begin{matrix} & [N]T_{1m} & [N]T_{2m} \\ Y_{1m} & \left[\begin{array}{cc} \delta_{11m} & 0 \\ 0 & \delta_{22m} \end{array} \right] \\ Y_{2m} & \end{matrix}$$

$$a_p = (Y_p \text{ to } L[N]T_p) = \begin{matrix} & L[N]T_{1p} & L[N]T_{2p} \\ Y_{1p} & \left[\begin{array}{cc} a_{11p} & 0 \\ 0 & a_{22p} \end{array} \right] \\ Y_{2p} & \end{matrix}$$

$$a_m = (Y_m \text{ to } [N]T_m) = \begin{matrix} Y_{1m} \\ Y_{2m} \end{matrix} \begin{bmatrix} L[N]T_{1m} & L[N]T_{2m} \\ a_{11m} & 0 \\ 0 & a_{22m} \end{bmatrix}$$

3 Expectations

3.1 Model 2 with Parental Effects

3.1.1 ≥ 2 generations of AM

$$\begin{aligned} \Omega_p &= Y_p \text{ to } [N]T_p \\ &= 2a_p i_c + 2\delta_p g_c + \delta_p k + \frac{1}{2}w_p \end{aligned}$$

$$\begin{aligned} \Omega'_p &= [N]T_p \text{ to } Y_p \\ &= 2i'_c a'_p + 2g_c \delta'_p + k\delta'_p + \frac{1}{2}w'_p \end{aligned}$$

$$\begin{aligned} \Omega_m &= Y_m \text{ to } [N]T_m \\ &= 2a_m i_c + 2\delta_m g_c + \delta_m k + \frac{1}{2}w_m \end{aligned}$$

$$\begin{aligned} \Omega'_m &= [N]T_m \text{ to } Y_m \\ &= 2i'_c a'_m + 2g_c \delta'_m + k\delta'_m + \frac{1}{2}w'_m \end{aligned}$$

$$\begin{aligned} \Gamma_p &= Y_p \text{ to } L[N]T_p \\ &= 2\delta_p i'_c + 2a_p h_c + a_p j + \frac{1}{2}q_p \end{aligned}$$

$$\begin{aligned} \Gamma'_p &= L[N]T_p \text{ to } Y_p \\ &= 2i_c \delta'_p + 2h_c a'_p + j a'_p + \frac{1}{2}q'_p \end{aligned}$$

$$\begin{aligned} \Gamma_m &= Y_m \text{ to } L[N]T_m \\ &= 2a_m h_c + 2\delta_m i'_c + a_m j + \frac{1}{2}q_m \end{aligned}$$

$$\Gamma'_m = L[N]T_m \text{ to } Y_m$$

$$= 2i_c \delta_m + 2h_c a'_m + j a'_m + \frac{1}{2} q'_m$$

$$g_t = [N]T_p \text{ to } [N]T_m$$

$$= \Omega'_p \mu \Omega_m$$

$$g_c = g_{cis} (NT_p \text{ to } T_p \text{ and } T_p \text{ to } NT_p) \text{ or } (NT_m \text{ to } T_m \text{ and } T_m \text{ to } NT_m)$$

$$g_c = g'_c = \frac{1}{2}(g_t + g'_t)$$

$$h_t = L[N]T_p \text{ to } L[N]T_m$$

$$= \Gamma'_p \mu \Gamma_m$$

$$h_c = h_{cis} (LNT_p \text{ to } LT_p \text{ and } LT_p \text{ to } LNT_p) \text{ or } (LNT_m \text{ to } LT_m \text{ and } LT_m \text{ to } LNT_m)$$

$$h_c = h'_c = \frac{1}{2}(h_t + h'_t)$$

$$i_{t_{LO}} (L[N]T_p \text{ to } [N]T_m)$$

$$i_{t_{LO}} = \Gamma'_p \mu \Omega_m$$

$$i'_{t_{LO}} ([N]T_m \text{ to } L[N]T_p)$$

$$i'_{t_{LO}} = \Omega'_m \mu' \Gamma_p$$

$$i_{t_{OL}} ([N]T_p \text{ to } L[N]T_m)$$

$$i_{t_{OL}} = \Omega'_p \mu \Gamma_m$$

$$i'_{t_{OL}} (L[N]T_m \text{ to } [N]T_p)$$

$$i'_{t_{OL}} = \Gamma'_m \mu' \Omega_p$$

$$i_c = i_{cis} (L[N]T_p \text{ to } [N]T_p) \text{ or } (L[N]T_m \text{ to } [N]T_m)$$

$$i_c = \frac{1}{2}(i_{t_{LO}} + i'_{t_{OL}})$$

$$i'_c = i'_{cis} ([N]T_p \text{ to } L[N]T_p) \text{ or } ([N]T_m \text{ to } L[N]T_m)$$

$$i'_c = \frac{1}{2}(i_{t_{OL}} + i'_{t_{LO}})$$

MCK: I updated all the i 's above to make it more explicit exactly what each one is. Thankfully, we won't have to have the $i_{t_{LO}}$ (etc.) terms in the actual path diagram because they're implied. Only the i_c ones will be in there.

$$\begin{aligned}
V_{Fp} &= f_{sp}V_{Yp}f'_{sp} + f_{sm}V_{Ym}f'_{sm} + f_{sp}V_{Yp}\mu V_{Ym}f'_{sm} + f_{sm}V_{Ym}\mu' V_{Yp}f'_{sp} \\
&= V_{Fs}
\end{aligned}$$

$$\begin{aligned}
V_{Fm} &= f_{dp}V_{Yp}f'_{dp} + f_{dm}V_{Ym}f'_{dm} + f_{dp}V_{Yp}\mu V_{Ym}f'_{dm} + f_{dm}V_{Ym}\mu' V_{Yp}f'_{dp} \\
&= V_{Fd}
\end{aligned}$$

MCK: updated the above two formulas to include the correct transposition of f matrices (the 2nd one wasn't transposed before), given that they are full. I've done the same for V_F formulas below.

$$\begin{aligned}
w_p &= F_p \text{ to } [N]T_p \\
&= f_{sp}\Omega_p + f_{sm}\Omega_m + f_{sp}V_{Yp}\mu\Omega_m + f_{sm}V_{Ym}\mu'\Omega_p \\
&= w_s
\end{aligned}$$

$$\begin{aligned}
w_m &= F_m \text{ to } [N]T_m \\
&= f_{dp}\Omega_p + f_{dm}\Omega_m + f_{dp}V_{Yp}\mu\Omega_m + f_{dm}V_{Ym}\mu'\Omega_p \\
&= w_d
\end{aligned}$$

$$\begin{aligned}
q_p &= F_p \text{ to } L[N]T_p \\
&= f_{sp}\Gamma_p + f_{sm}\Gamma_m + f_{sp}V_{Yp}\mu\Gamma_m + f_{sm}V_{Ym}\mu'\Gamma_p \\
&= q_s
\end{aligned}$$

$$\begin{aligned}
q_m &= F_m \text{ to } L[N]T_m \\
&= f_{dp}\Gamma_p + f_{dm}\Gamma_m + f_{dp}V_{Yp}\mu\Gamma_m + f_{dm}V_{Ym}\mu'\Gamma_p \\
&= q_d
\end{aligned}$$

$$\begin{aligned}
\theta_{NTs} &= Y_s \text{ to } NT_* \\
&= 2\delta_s g_c + 2a_s i_c + a_s i_{t_{LO}} + a_s i'_{t_{OL}} + \delta_s g_t + \delta_s g'_t + w_s \\
&= 4\delta_s g_c + 4a_s i_c + w_s
\end{aligned}$$

MCK: this reduces to the final line bc $g_t + g'_t = 2g_c$ and similarly for i . Similar reductions can be done throughout but it's nice to show both steps for clarity. Also, we need to note that θ is not symmetric

$$\begin{aligned}
\theta_{NTd} &= Y_d \text{ to } NT_* \\
&= 2\delta_d g_c + 2a_d i_c + a_d i_{t_{LO}} + a_d i'_{t_{OL}} + \delta_d g_t + \delta_d g'_t + w_d \\
&= 4\delta_d g_c + 4a_d i_c + w_d
\end{aligned}$$

$$\begin{aligned}\theta_{Ts} &= Y_s \text{ to } T_* \\ &= 2\delta_s k + \theta_{NTs}\end{aligned}$$

$$\begin{aligned}\theta_{Td} &= Y_d \text{ to } T_* \\ &= 2\delta_d k + \theta_{NTd}\end{aligned}$$

$$\begin{aligned}\theta_{LNTs} &= Y_s \text{ to } LNT_* \\ &= 2\delta_s i'_c + 2a_s h_c + a_s h_t + a_s h'_t + \delta_s i_{tOL} + \delta_s i'_{tLO} + q_s\end{aligned}$$

$$\begin{aligned}\theta_{LNTd} &= Y_d \text{ to } LNT_* \\ &= 2\delta_d i'_c + 2a_d h_c + a_d h_t + a_d h'_t + \delta_d i_{tOL} + \delta_d i'_{tLO} + q_d\end{aligned}$$

$$\begin{aligned}\theta_{LTs} &= Y_s \text{ to } LT_* \\ &= 2a_s j + \theta_{LNTs}\end{aligned}$$

$$\begin{aligned}\theta_{LTd} &= Y_d \text{ to } LT_* \\ &= 2a_d j + \theta_{LNTd}\end{aligned}$$

$$V_{Yp} = 2\Omega_p \delta_p + 2\Gamma_p a_p + \delta_p w'_p + a_p q'_p + V_{Fp} + V_{\epsilon p}$$

$$\begin{aligned}V_{Ym} &= 2\Omega_m \delta'_m + 2\Gamma_m a'_m + \delta_m w'_m + a_m q'_m + V_{Fm} + V_{\epsilon m} \\ &= V_{Yd}\end{aligned}$$

JVB: I added $\delta_p w'_p + a_p q'_p$ (and the maternal equivalent to these two expectations) paths to the VY expectations above. We were missing these four paths (those that go through w' and q') in the previous math. I've made the change throughout.

MCK: Jared, I think this is a place where not making the δ and a inverses explicit created confusion. Even though $\delta = \delta'$, it's very helpful to include the proper transpositions because it helps you and others see exactly which paths are being traced. Adding the paths you have makes it correct but it's still not that illuminating how the paths are being traced (I don't think). Below, I provide an alternative that to me makes it clearer, starting at Yp and tracing up each individual path, first to $[N]T_p$, then to $L[N]T_p$, then to F_p , then to ϵ_p . But in general, I'd go through each equation and (a) make the first line be the most

verbose (don't simplify yet), and then collapse terms/simplify after that; and
(b) make sure all transpositions are included and are correct.

$$\begin{aligned} V_{Y_p} &= V_{Y_s} = \delta_p \Omega'_p + \delta_p \Omega'_p + a_p \Gamma'_p + a_p \Gamma'_p + V_{F_p} + \frac{w}{2} \delta'_p + \frac{w}{2} \delta'_p + \frac{q}{2} a'_p + \frac{q}{2} a'_p + V_{\epsilon_p} \\ &= 2\delta_p \Omega'_p + 2a_p \Gamma'_p + V_{F_p} + w\delta'_p + qa'_p + V_{\epsilon_p} \end{aligned}$$

$$\begin{aligned} \text{https://www.overleaf.com/project/5ff8ea9e98e578a48c817d14 } V_{Y_s} &= 2\delta_s k \delta'_s + \\ &2\delta_s g_c \delta'_s + 2a_s j a'_s + 2a_s h_c a'_s + 2a_s i_c \delta'_s + 2\delta_s i'_c a'_s + \delta_s w'_s + w_s \delta'_s + a_s q'_s + q_s a'_s + \delta_s g_t \delta'_s + \\ &\delta_s g'_t \delta'_s + \delta_s i_{t_{OL}} a'_s + a_s i'_{t_{OL}} \delta'_s + a_s h_t a'_s + a_s h'_t a'_s + a_s i_{t_{LO}} \delta'_s + \delta_s i'_{t_{LO}} a'_s + V_{F_s} + V_{\epsilon_s} \end{aligned}$$

$$\begin{aligned} V_{Y_d} &= 2\delta_d k \delta'_d + 2\delta_d g_c \delta'_d + 2a_d j a'_d + 2a_d h_c a'_d + 2a_d i_c \delta'_d + 2\delta_d i'_c a'_d + \delta_d w'_d + w_d \delta'_d + \\ &a_d q'_d + q_d a'_d + \delta_d g_t \delta'_d + \delta_d g'_t \delta'_d + \delta_d i_{t_{OL}} a'_d + a_d i'_{t_{OL}} \delta'_d + a_d h_t a'_d + a_d h'_t a'_d + a_d i_{t_{LO}} \delta'_d + \\ &\delta_d i'_{t_{LO}} a'_d + V_{F_d} + V_{\epsilon_d} \end{aligned}$$

MCK: I added transposes to δ and a terms above for consistency with multivariate path tracing rules (even though this doesn't change the expectations bc they're diagonal).

$$V_{G_{Obs,p}} = 2\delta_p k \delta'_p + 4\delta_p g_c \delta'_p$$

$$V_{G_{Obs,m}} = 2\delta_m k \delta'_m + 4\delta_m g_c \delta'_m$$

$$V_{G_{Lat,p}} = 2a_p j a'_p + 4a_p h_c a'_p$$

$$V_{G_{Lat,m}} = 2a_m j a'_m + 4a_m h_c a'_m$$

$$COV_{G_{Obs,Lat,p}} = 4\delta_p i'_c a'_p + 4a_p i_c \delta'_p$$

$$COV_{G_{Obs,Lat,m}} = 4\delta_m i'_c a'_m + 4a_m i_c \delta'_m$$

$$V_{G_{tot,p}} = 2\delta_p k \delta'_p + 4\delta_p g_c \delta'_p + 4\delta_p i'_c a'_p + 2a_p j a'_p + 4a_p h_c a'_p + 4a_p i_c \delta'_p$$

$$V_{G_{tot,m}} = 2\delta_m k \delta'_m + 4\delta_m g_c \delta'_m + 4\delta_m i'_c a'_m + 2a_m j a'_m + 4a_m h_c a'_m + 4a_m i_c \delta'_m$$

$$COV_{GE_p} = \delta_p w'_p + w_p \delta'_p + a_p q'_p + q_p a'_p$$

$$COV_{GE_m} = \delta_m w'_m + w_m \delta'_m + a_m q'_m + q_m a'_m$$

MCK: The above equations are just repackaging of what comes above, but I think it's helpful to recast the above in chunks that are readily interpretable. It also helps with checking the observed simulated data vs. the algebra.

3.1.2 After 1 Generation of AM

$$\begin{aligned} \Omega_p &= Y_p \text{ to } [N]T_p \\ &= \delta_p k + \frac{1}{2} w_p \end{aligned}$$

$$\begin{aligned} \Omega_m &= Y_m \text{ to } [N]T_m \\ &= \delta_m k + \frac{1}{2} w_m \end{aligned}$$

$$\begin{aligned} \Gamma_p &= Y_p \text{ to } L[N]T_p \\ &= a_p j + \frac{1}{2} q_p \end{aligned}$$

$$\begin{aligned} \Gamma_m &= Y_m \text{ to } L[N]T_m \\ &= a_m j + \frac{1}{2} q_m \end{aligned}$$

$$\begin{aligned} g_t &= [N]T_p \text{ to } [N]T_m \\ &= \Omega'_p \mu \Omega_m \end{aligned}$$

$$\begin{aligned} h_t &= L[N]T_p \text{ to } L[N]T_m \\ &= \Gamma'_p \mu \Gamma_m \end{aligned}$$

$$\begin{aligned} i_{t_{LO}} &= L[N]T_p \text{ to } [N]T_m \\ &= \Gamma'_p \mu \Omega_m \end{aligned}$$

$$i_{t_{OL}} = [N]T_p \text{ to } L[N]T_m$$

$$= \Omega'_p \mu \Gamma_m$$

$$g_c = h_c = i_c = 0$$

$$V_{Fp} = f_{sp} V_{Yp} f'_{sp} + f_{sm} V_{Ym} f'_{sm}$$

$$V_{Fm} = f_{dp} V_{Yp} f'_{dp} + f_{dm} V_{Ym} f'_{dm}$$

$$V_{Fs} = f_{sp} V_{Yp} f'_{sp} + f_{sm} V_{Ym} f'_{sm} + f_{sp} V_{Yp} \mu V_{Ym} f'_{sm} + f_{sm} V_{Ym} \mu' V_{Yp} f'_{sp}$$

$$V_{Fd} = f_{dp} V_{Yp} f'_{dp} + f_{dm} V_{Ym} f'_{dm} + f_{dp} V_{Yp} \mu V_{Ym} f'_{dm} + f_{dm} V_{Ym} \mu' V_{Yp} f'_{dp}$$

$$\begin{aligned} w_p &= F_p \text{ to } [N]T_p \\ &= f_{sp} \Omega_p + f_{sm} \Omega_m \end{aligned}$$

$$\begin{aligned} w_m &= F_m \text{ to } [N]T_m \\ &= f_{dp} \Omega_p + f_{dm} \Omega_m \end{aligned}$$

$$\begin{aligned} w_s &= F_s \text{ to } [N]T_* \\ &= f_{sp} \Omega_p + f_{sm} \Omega_m + f_{sp} V_{Yp} \mu \Omega_m + f_{sm} V_{Ym} \mu' \Omega_p \end{aligned}$$

$$\begin{aligned} w_d &= F_d \text{ to } [N]T_* \\ &= f_{dp} \Omega_p + f_{dm} \Omega_m + f_{dp} V_{Yp} \mu \Omega_m + f_{dm} V_{Ym} \mu' \Omega_p \end{aligned}$$

$$\begin{aligned} q_p &= F_p \text{ to } L[N]T_p \\ &= f_{sp} \Gamma_p + f_{sm} \Gamma_m \end{aligned}$$

$$\begin{aligned} q_m &= F_m \text{ to } L[N]T_m \\ &= f_{dp} \Gamma_p + f_{dm} \Gamma_m \end{aligned}$$

$$\begin{aligned} q_s &= F_s \text{ to } L[N]T_* \\ &= f_{sp} \Gamma_p + f_{sm} \Gamma_m + f_{sp} V_{Yp} \mu \Gamma_m + f_{sm} V_{Ym} \mu' \Gamma_p \end{aligned}$$

$$\begin{aligned} q_d &= F_d \text{ to } L[N]T_* \\ &= f_{dp} \Gamma_p + f_{dm} \Gamma_m + f_{dp} V_{Yp} \mu \Gamma_m + f_{dm} V_{Ym} \mu' \Gamma_p \end{aligned}$$

$$\begin{aligned}\theta_{NT_s} &= Y_s \text{ to } NT_* \\ &= a_s i_{t_{LO}} + a_s i'_{t_{OL}} + \delta_s g_t + \delta_s g'_t + w_s\end{aligned}$$

$$\begin{aligned}\theta_{NT_d} &= Y_d \text{ to } NT_* \\ &= a_d i_{t_{LO}} + a_d i'_{t_{OL}} + \delta_d g_t + \delta_d g'_t + w_d\end{aligned}$$

$$\begin{aligned}\theta_{T_s} &= Y_s \text{ to } T_* \\ &= 2\delta_s k + \theta_{NT_s}\end{aligned}$$

$$\begin{aligned}\theta_{T_d} &= Y_d \text{ to } T_* \\ &= 2\delta_d k + \theta_{NT_d}\end{aligned}$$

$$\begin{aligned}\theta_{LNT_s} &= Y_s \text{ to } LNT_* \\ &= a_s h_t + a_s h'_t + \delta_s i_{t_{OL}} + \delta_s i'_{t_{LO}} + q_s\end{aligned}$$

$$\begin{aligned}\theta_{LNT_d} &= Y_d \text{ to } LNT_* \\ &= a_d h_t + a_d h'_t + \delta_d i_{t_{OL}} + \delta_d i'_{t_{LO}} + q_d\end{aligned}$$

$$\begin{aligned}\theta_{LT_s} &= Y_s \text{ to } LT_* \\ &= 2a_s j + \theta_{LNT_s}\end{aligned}$$

$$\begin{aligned}\theta_{LT_d} &= Y_d \text{ to } LT_* \\ &= 2a_d j + \theta_{LNT_d}\end{aligned}$$

$$V_{Y_p} = 2\Omega_p \delta_p + 2\Gamma_p a_p + \delta_p w'_p + a_p q'_p + V_{Fp} + V_{\epsilon p}$$

$$V_{Y_m} = 2\Omega_m \delta_m + 2\Gamma_m a_m + \delta_m w'_m + a_m q'_m + V_{Fm} + V_{\epsilon m}$$

$$\begin{aligned}V_{Y_s} &= 2\delta_s k \delta'_s + 2a_s j a'_s + \delta_s w'_s + w_s \delta'_s + a_s q'_s + q_s a'_s + \delta_s g_t \delta'_s + \delta_s g'_t \delta'_s + \delta_s i_{t_{OL}} a'_s + \\ &+ a_s i'_{t_{OL}} \delta'_s + a_s h_t a'_s + a_s h'_t a'_s + a_s i_{t_{LO}} \delta'_s + \delta_s i'_{t_{LO}} a'_s + V_{Fs} + V_{\epsilon s}\end{aligned}$$

$$\begin{aligned}V_{Y_d} &= 2\delta_d k \delta'_d + 2a_d j a'_d + \delta_d w'_d + w_d \delta'_d + a_d q'_d + q_d a'_d + \delta_d g_t \delta'_d + \delta_d g'_t \delta'_d + \delta_d i_{t_{OL}} a'_d + \\ &+ a_d i'_{t_{OL}} \delta'_d + a_d h_t a'_d + a_d h'_t a'_d + a_d i_{t_{LO}} \delta'_d + \delta_d i'_{t_{LO}} a'_d + V_{Fd} + V_{\epsilon d}\end{aligned}$$

3.1.3 No AM

$$\begin{aligned}\Omega_p &= Y_p \text{ to } [N]T_p \\ &= \delta_p k + \frac{1}{2}w_p\end{aligned}$$

$$\begin{aligned}\Omega_m &= Y_m \text{ to } [N]T_m \\ &= \delta_m k + \frac{1}{2}w_m\end{aligned}$$

$$\begin{aligned}\Gamma_p &= Y_p \text{ to } L[N]T_p \\ &= a_p j + \frac{1}{2}q_p\end{aligned}$$

$$\begin{aligned}\Gamma_m &= Y_m \text{ to } L[N]T_m \\ &= a_m j + \frac{1}{2}q_m\end{aligned}$$

$$g_t = h_t = i_{t_{LO}} = i_{t_{OL}} = 0$$

$$g_c = h_c = i_c = 0$$

$$\begin{aligned}V_{Fp} &= f_{sp}V_{Yp}f'_{sp} + f_{sm}V_{Ym}f'_{sm} \\ &= V_{Fs}\end{aligned}$$

$$\begin{aligned}V_{Fm} &= f_{dp}V_{Yp}f'_{dp} + f_{dm}V_{Ym}f'_{dm} \\ &= V_{Fd}\end{aligned}$$

$$w_s = w_p = (F_s \text{ to } [N]T_p + F_s \text{ to } [N]T_m) = f_{sp}\Omega_p + f_{sm}\Omega_m$$

$$w_d = w_m = (F_d \text{ to } [N]T_p + F_d \text{ to } [N]T_m) = f_{dp}\Omega_p + f_{dm}\Omega_m$$

$$\begin{aligned}q_p &= F_p \text{ to } L[N]T_p \\ &= f_{sp}\Gamma_p + f_{sm}\Gamma_m \\ &= q_s\end{aligned}$$

$$q_m = F_m \text{ to } L[N]T_m$$

$$\begin{aligned}
&= f_{dp}\Gamma_p + f_{dm}\Gamma_m \\
&= q_d
\end{aligned}$$

$$\begin{aligned}
\theta_{NT_s} &= Y_s \text{ to } NT_* \\
&= w_s
\end{aligned}$$

$$\begin{aligned}
\theta_{NT_d} &= Y_d \text{ to } NT_* \\
&= w_d
\end{aligned}$$

$$\begin{aligned}
\theta_{T_s} &= Y_s \text{ to } T_* \\
&= 2\delta_s k + \theta_{NT_s}
\end{aligned}$$

$$\begin{aligned}
\theta_{T_d} &= Y_s/d \text{ to } T_* \\
&= 2\delta_d k + \theta_{NT_d}
\end{aligned}$$

$$\begin{aligned}
\theta_{LNT_s} &= Y_s/d \text{ to } LNT_* \\
&= q_s
\end{aligned}$$

$$\begin{aligned}
\theta_{LNT_d} &= Y_s/d \text{ to } LNT_* \\
&= q_d
\end{aligned}$$

$$\begin{aligned}
\theta_{LT_s} &= Y_s/d \text{ to } LT_* \\
&= 2a_s j + \theta_{LNT_s}
\end{aligned}$$

$$\begin{aligned}
\theta_{LT_d} &= Y_s/d \text{ to } LT_* \\
&= 2a_d j + \theta_{LNT_d}
\end{aligned}$$

$$V_{Y_p} = 2\Omega_p \delta_p + 2\Gamma_p a_p + \delta_p w'_p + a_p q'_p + V_{Fp} + V_{\epsilon p}$$

$$V_{Y_m} = 2\Omega_m \delta_m + 2\Gamma_m a_m + \delta_m w'_m + a_m q'_m + V_{Fm} + V_{\epsilon m}$$

$$V_{Y_s} = \delta_s w'_s + w_s \delta_s + a_s q'_s + q_s a_s + V_{Fs} + V_{\epsilon s}$$

$$V_{Y_d} = \delta_d w'_d + w_d \delta_d + a_d q'_d + q_d a_d + V_{Fd} + V_{\epsilon d}$$

3.2 Model 1 with Parental Effects

3.2.1 ≥ 2 generations of AM

$$\begin{aligned}\Omega_p &= Y_p \text{ to } [N]T_p \\ &= 2\delta_p g_c + \delta_p k + \frac{1}{2}w_p\end{aligned}$$

$$\begin{aligned}\Omega_m &= Y_m \text{ to } [N]T_m \\ &= 2\delta_m g_c + \delta_m k + \frac{1}{2}w_m\end{aligned}$$

$$\begin{aligned}g_t &= [N]T_p \text{ to } [N]T_m \\ &= \Omega'_p \mu \Omega_m\end{aligned}$$

$$\begin{aligned}V_{Fp} &= f_{sp}V_{Yp}f'_{sp} + f_{sm}V_{Ym}f'_{sm} + f_{sp}V_{Yp}\mu V_{Ym}f'_{sm} + f_{sm}V_{Ym}\mu' V_{Yp}f'_{sp} \\ &= V_{Fs}\end{aligned}$$

$$\begin{aligned}V_{Fm} &= f_{dp}V_{Yp}f'_{dp} + f_{dm}V_{Ym}f'_{dm} + f_{dp}V_{Yp}\mu V_{Ym}f'_{dm} + f_{dm}V_{Ym}\mu' V_{Yp}f'_{dp} \\ &= V_{Fd}\end{aligned}$$

$$\begin{aligned}w_p &= F_p \text{ to } [N]T_p \\ &= f_{sp}\Omega_p + f_{sm}\Omega_m + f_{sp}V_{Yp}\mu\Omega_m + f_{sm}V_{Ym}\mu'\Omega_p \\ &= w_s\end{aligned}$$

$$\begin{aligned}w_m &= F_m \text{ to } [N]T_m \\ &= f_{dp}\Omega_p + f_{dm}\Omega_m + f_{dp}V_{Yp}\mu\Omega_m + f_{dm}V_{Ym}\mu'\Omega_p \\ &= w_d\end{aligned}$$

$$\begin{aligned}\theta_{NTs} &= Y_s \text{ to } NT_* \\ &= 2\delta_s g_c + \delta_s g_t + \delta_s g'_t + w_s \\ \theta_{NTd} &= Y_d \text{ to } NT_* \\ &= 2\delta_d g_c + \delta_d g_t + \delta_d g'_t + w_d\end{aligned}$$

$$\begin{aligned}\theta_{Ts} &= Y_s \text{ to } T_* \\ &= 2\delta_s k + \theta_{NTs}\end{aligned}$$

$$\begin{aligned}\theta_{Td} &= Y_d \text{ to } T_* \\ &= 2\delta_d k + \theta_{NTd}\end{aligned}$$

$$\begin{aligned}V_{Yp} &= 2\Omega_p \delta_p + \delta_p w'_p + V_{Fp} + V_{\epsilon p} \\ &= V_{Ys}\end{aligned}$$

$$\begin{aligned}V_{Ym} &= 2\Omega_m \delta_m + \delta_p w'_p + V_{Fm} + V_{\epsilon m} \\ &= V_{Yd}\end{aligned}$$

$$V_{Ys} = \delta_s w'_s + w_s \delta'_s + \delta_s g_t \delta'_s + \delta_s g'_t \delta'_s + V_{Fs} + V_{\epsilon s}$$

$$V_{Yd} = \delta_d w'_d + w_d \delta'_d + \delta_d g_t \delta'_d + \delta_d g'_t \delta'_d + V_{Fd} + V_{\epsilon d}$$

3.2.2 After 1 Generation of AM

$$\begin{aligned}\Omega_p &= Y_p \text{ to } [N]T_p \\ &= \delta_p k + \frac{1}{2}w_p\end{aligned}$$

$$\begin{aligned}\Omega_m &= Y_m \text{ to } [N]T_m \\ &= \delta_m k + \frac{1}{2}w_m\end{aligned}$$

$$\begin{aligned}g_t &= [N]T_p \text{ to } [N]T_m \\ &= \Omega'_p \mu \Omega_m\end{aligned}$$

$$g_c = 0$$

$$V_{Fp} = f_{sp} V_{Yp} f'_{sp} + f_{sm} V_{Ym} f'_{sm}$$

$$V_{Fm} = f_{dp} V_{Yp} f'_{dp} + f_{dm} V_{Ym} f'_{dm}$$

$$V_{Fs} = f_{sp}V_{Yp}f'_{sp} + f_{sm}V_{Ym}f'_{sm} + f_{sp}V_{Yp}\mu V_{Ym}f'_{sm} + f_{sm}V_{Ym}\mu' V_{Yp}f'_{sp}$$

$$V_{Fd} = f_{dp}V_{Yp}f'_{dp} + f_{dm}V_{Ym}f'_{dm} + f_{dp}V_{Yp}\mu V_{Ym}f'_{dm} + f_{dm}V_{Ym}\mu' V_{Yp}f'_{dp}$$

$$\begin{aligned} w_p &= F_p \text{ to } [N]T_p \\ &= f_{sp}\Omega_p + f_{sm}\Omega_m \end{aligned}$$

$$\begin{aligned} w_m &= F_m \text{ to } [N]T_m \\ &= f_{dp}\Omega_p + f_{dm}\Omega_m \end{aligned}$$

$$\begin{aligned} w_s &= F_s \text{ to } [N]T_* \\ &= f_{sp}\Omega_p + f_{sm}\Omega_m + f_{sp}V_{Yp}\mu\Omega_m + f_{sm}V_{Ym}\mu'\Omega_p \end{aligned}$$

$$\begin{aligned} w_d &= F_d \text{ to } [N]T_* \\ &= f_{dp}\Omega_p + f_{dm}\Omega_m + f_{dp}V_{Yp}\mu\Omega_m + f_{dm}V_{Ym}\mu'\Omega_p \end{aligned}$$

$$\begin{aligned} \theta_{NTs} &= Y_s \text{ to } NT_* \\ &= \delta_s g_t + \delta_s g'_t + w_s \end{aligned}$$

$$\begin{aligned} \theta_{NTd} &= Y_d \text{ to } NT_* \\ &= \delta_d g_t + \delta_d g'_t + w_d \end{aligned}$$

$$\begin{aligned} \theta_{Ts} &= Y_s \text{ to } T_* \\ &= 2\delta_s k + \theta_{NTs} \end{aligned}$$

$$\begin{aligned} \theta_{Td} &= Y_d \text{ to } T_* \\ &= 2\delta_d k + \theta_{NTd} \end{aligned}$$

$$V_{Yp} = 2\Omega_p\delta_p + \delta_p w'_p + V_{Fp} + V_{\epsilon p}$$

$$V_{Ym} = 2\Omega_m\delta_m + \delta_m w'_m + V_{Fm} + V_{\epsilon m}$$

$$V_{Ys} = \delta_s w'_s + w_s \delta'_s + \delta_s g_t \delta'_s + \delta_s g'_t \delta'_s + V_{Fs} + V_{\epsilon s}$$

$$V_{Yd} = \delta_d w'_d + w_d \delta'_d + \delta_d g_t \delta'_d + \delta_d g'_t \delta'_d + V_{Fd} + V_{\epsilon d}$$

3.2.3 No AM

$$\begin{aligned}\Omega_p &= Y_p \text{ to } [N]T_p \\ &= \delta_p k + \frac{1}{2}w_p\end{aligned}$$

$$\begin{aligned}\Omega_m &= Y_m \text{ to } [N]T_m \\ &= \delta_m k + \frac{1}{2}w_m\end{aligned}$$

$$g_t = 0$$

$$g_c = 0$$

$$\begin{aligned}V_{Fp} &= f_{sp}V_{Yp}f'_{sp} + f_{sm}V_{Ym}f'_{sm} \\ &= V_{Fs}\end{aligned}$$

$$\begin{aligned}V_{Fm} &= f_{dp}V_{Yp}f'_{dp} + f_{dm}V_{Ym}f'_{dm} \\ &= V_{Fd}\end{aligned}$$

$$\begin{aligned}w_s &= w_p = F_s \text{ to } [N]T_p + F_s \text{ to } [N]T_m \\ &= f_{sp}\Omega_p + f_{sm}\Omega_m\end{aligned}$$

$$\begin{aligned}w_d &= w_m = F_d \text{ to } [N]T_p + F_d \text{ to } [N]T_m \\ &= f_{dp}\Omega_p + f_{dm}\Omega_m\end{aligned}$$

MCK: All good above

$$\begin{aligned}\theta_{NTs} &= Y_s \text{ to } NT_* \\ &= w_s\end{aligned}$$

$$\begin{aligned}\theta_{NTd} &= Y_d \text{ to } NT_* \\ &= w_d\end{aligned}$$

$$\theta_{Ts} = Y_s \text{ to } T_*$$

$$= 2\delta_s k + \theta_{NTs}$$

$$\theta_{Td} = Y_s/d \text{ to } T_*$$

$$= 2\delta_d k + \theta_{NTd}$$

$$V_{Yp} = 2\Omega_p \delta_p + \delta_p w'_p + V_{Fp} + V_{\epsilon p}$$

$$V_{Ym} = 2\Omega_m \delta_m + \delta_m w'_m + V_{Fm} + V_{\epsilon m}$$

$$V_{Ys} = \delta_s w'_s + w_s \delta'_s + V_{Fs} + V_{\epsilon s}$$

$$V_{Yd} = \delta_d w'_d + w_d \delta'_d + V_{Fd} + V_{\epsilon d}$$

3.3 Models 0 and 1 [OUTDATED MATH, DO NOT USE]

$$f_{dp} * \Gamma_p + f_{dm} * V_{Ym} * \mu' * \Gamma_p$$

$$f_{dp} \Gamma_p + f_{dm} V_{Ym} \mu' \Gamma_p$$

Note: The text "to" in the below shows the directionality of the untransposed covariances– for asymmetric covariance matrices, they show which 2 variables should be on the left (defining rows) "to" which 2 variables should be on the top (defining columns). Unfortunately, the use of a directional arrows in this document would have caused confusion because it's the opposite of a path diagram arrow directionality.

$$\Omega (Y \text{ to } [N]T) = \begin{matrix} & [N]T_1 & [N]T_2 \\ Y_1 & \Omega_{11} & \Omega_{12} \\ Y_2 & \Omega_{21} & \Omega_{22} \end{matrix}$$

$$\Omega = \delta(k + g_c) + \frac{1}{2}w + \delta g_c$$

$$\Omega = \delta k + 2\delta g_c + \frac{1}{2}w$$

MCK: checked

$$\Omega' ([N]T \text{ to } Y) = \begin{matrix} & Y_1 & Y_2 \\ [N]T_1 & \Omega_{11} & \Omega_{21} \\ [N]T_2 & \Omega_{12} & \Omega_{22} \end{matrix}$$

$$\Omega' = (k + g_c)\delta' + \frac{1}{2}w' + g_c\delta'$$

$$\Omega' = k\delta' + 2g_c\delta' + \frac{1}{2}w'$$

MCK: checked

$$g_t = g_{trans} (T_p \text{ to } T_m) = \begin{matrix} & [N]T_{1m} & [N]T_{2m} \\ [N]T_{1p} & g_{t,pp} & g_{t,pm} \\ [N]T_{2p} & g_{t,mp} & g_{t,mm} \end{matrix}$$

$$g_t = \Omega'_p \mu \Omega_m$$

$$g'_t = g'_{trans} (T_m \text{ to } T_p) = \begin{matrix} & [N]T_{1p} & [N]T_{2p} \\ [N]T_{1m} & \begin{bmatrix} g_{t,pp} & g_{t,mp} \end{bmatrix} \\ [N]T_{2m} & \begin{bmatrix} g_{t,pm} & g_{t,mm} \end{bmatrix} \end{matrix}$$

$$g'_t = \Omega'_m \mu' \Omega_p$$

MCK: checked

Note: it is crucial to use g_t when traversing T_p to T_m and to use g'_t when traversing T_m to T_p . This should only matter for finding covariances between mates as most other g 's used in expectations are g_c .

$$g_c = g_{cis} = \frac{1}{2}(g_t + g'_t)$$

MCK: I have checked (via simulation) that it's actually the arithmetic mean we need here and not the geometric mean (see comments in main.tex). This makes g_c off-diagonal elements be the same, and equal to the arithmetic mean of the off-diagonal elements of g_t .

$$\begin{aligned} V_Y &= \delta(k + g_c)\delta' + \delta\frac{1}{2}w' + \delta g_c\delta' + \frac{1}{2}w\delta' + V_F + \frac{1}{2}w\delta' + \delta(k + g_c)\delta' + \delta\frac{1}{2}w' + \delta g_c\delta' + V_\epsilon \\ &= 2\Omega\delta' + w\delta' + V_F + V_\epsilon \end{aligned}$$

$$\begin{aligned} V_F &= 2fV_Y f' + 2fV_Y \mu V_Y f' \\ &= 2fV_Y (f' + \mu V_Y f') \end{aligned}$$

MCK: still needs to be checked

$$w_{sp} (F_s \text{ to } [N]T_p) = \begin{matrix} & [N]T_{1p} & [N]T_{2p} \\ F_{1s} & \begin{bmatrix} w_{s11} & w_{12} \end{bmatrix} \\ F_{2s} & \begin{bmatrix} w_{21} & w_{22} \end{bmatrix} \end{matrix}$$

$$w = 2f\Omega + 2fV_Y \mu' \Omega$$

$$w = 2f(\Omega + V_Y \mu' \Omega)$$

$$w' ([N]T \text{ to } F) = \begin{matrix} F_1 & F_2 \\ [N]T_1 & \begin{bmatrix} w_{11} & w_{21} \end{bmatrix} \\ [N]T_2 & \begin{bmatrix} w_{12} & w_{22} \end{bmatrix} \end{matrix}$$

$$w' = 2\Omega' f' + 2\Omega' \mu V_Y f'$$

$$w' = 2\Omega'(f' + \mu V_Y f')$$

MCK: Both w and w' have been checked in mathematica and are correct, including the μ' in the w equality. Therefore, when the path is traversed from F to $[N]T$, the coefficient is $\frac{1}{2}w$, and when the path is traversed from $[N]T$ to F , the coefficient is $\frac{1}{2}w'$. The asymmetry of w has nothing to do with parental origin effects (f_p vs. f_f). Rather, it is intrinsic to w : $cov(F_1, [N]T_2) \neq cov(F_2, [N]T_1)$, which is a consequence of f and μ being full.

However, if we do have sex-specific parental f , one could trace F_o to $[N]T_p$, or F_o to $[N]T_m$, and these will be different. This would lead to two different w 's: w_p (to the father) and w_m (to the mother). Which w should be used within-person? In this case, the paternally and maternally derived alleles are again mixed (ala g_c), and thus $w = \frac{1}{2}(w_p + w_m)$. Note that unlike g_c , however, this equality should not be $w = \frac{1}{2}(w_p + w'_m)$ - that would lead to a symmetric matrix w which cannot be correct. Instead, we want the two off-diagonals of w to be the geometric means of the two off-diagonals w_p and w_m respectively.

MCK: Both w and w' need to be re-checked. I checked that the above (and it worked) when tracing from F_o to $[N]T_p$ but not F_o to $[N]T_m$. From looking at it, these should differ according to our rules for μ - it should be the same as above but with μ transposed when untransposed above, and vice-versa. I think therefore that we actually have to separate w_p from w_m , even when there are no sex-specific effects of f , and if so, we'd need to find w (within-person g-e covariance) as the geometric mean, as discussed above.

MCK: OK, both F_o to $[N]T_p$ and F_o to $[N]T_m$ have been checked and they are not the same things. Take the extreme example where male traits aren't heritable but female ones are, then F_o to $[N]T_p$ will be 0 but F_o to $[N]T_m$ will be > 0 . So we need to have separate coefficients (we'll call them w_p and w_m respectively) for each. And for the same reasons that g_c is the arithmetic mean of g_t and g'_t , w (within-person, regardless of their sex) should be the arithmetic mean of w_p and w_m (not w'_m).

$$\begin{aligned} \theta_{NT} &= Y_o \text{ to } NT \\ &= 2[f\Omega + fV_Y\mu\Omega + \delta g' + \delta\Omega'\mu\Omega] \\ &= 4\delta g + w \end{aligned}$$

(In our paper's supplement, $\theta_{NT} = 4\delta g + 2w$, but I think this might be a mistake?)

MCK: This is checked is correct. The paper supp is wrong

$$\begin{aligned}
\theta_T &= Y \text{ to } T \\
&= 2[\delta(k+g) + f\Omega + \delta\Omega'\mu\Omega + fV_Y\mu\Omega] \\
&= 2\delta k + 4\delta g + w \\
&= 2\delta k + \theta_{NT}
\end{aligned}$$

MCK: this is checked

$$\begin{aligned}
\theta_T - \theta_{NT} &= 2\delta k \\
&= 2 \begin{bmatrix} \delta_{11}k_{11} & \delta_{11}k_{12} \\ \delta_{22}k_{12} & \delta_{22}k_{22} \end{bmatrix}
\end{aligned}$$

MCK: Note that I removed the r_o that was originally in the off-diagonals of this matrix - it's undefined. I believe the above is the correct way. Unf I forgot to save the old way you had it

3.4 Model 2

JVB: The changes I'm making below are largely for the purpose of incorporating/ differentiating trans and cis covariances, and the asymmetric mu matrix

$$\begin{aligned}
\Omega &= Y \text{ to } [N]T \\
&= ai + \delta(k+g) + \frac{1}{2}w + \delta g^* + ai \\
&= \delta k + 2ai + 2\delta g + \frac{1}{2}w
\end{aligned}$$

JVB:

$$\begin{aligned}
\Omega &= ai_c + \delta(k+g_c) + \frac{1}{2}w + \delta g_c + ai_c \\
&= \delta k + 2\delta g_c + 2ai_c + \frac{1}{2}w
\end{aligned}$$

$$\begin{aligned}
\Omega' &= [N]T \text{ to } Y \\
&= i'a' + (k+g)\delta' + \frac{1}{2}w'g^*\delta' + i'a' \\
&= k\delta' + 2i'a' + 2g\delta' + \frac{1}{2}w'
\end{aligned}$$

JVB:

$$\Omega' = (k+g_c)\delta + \frac{1}{2}w' + g_c\delta + i'_c a + i'_c a$$

$$k\delta + 2g_c\delta + 2i'_c a + \frac{1}{2}w'$$

$$\begin{aligned}\Gamma &= Y \text{ to } L[N]T \\ &= a(j+h) + \delta i' + \frac{1}{2}v + \delta i' + ah^* \\ &= aj + 2ah + 2\delta i' + \frac{1}{2}v\end{aligned}$$

JVB:

$$\begin{aligned}\Gamma &= a(j+h_c) + \delta i'_c + \frac{1}{2}v + \delta i'_c + ah_c \\ &= aj + 2ah_c + 2\delta i'_c + \frac{1}{2}v\end{aligned}$$

$$\begin{aligned}\Gamma' &= L[N]T \text{ to } Y \\ &= (j+h)a' + i\delta' + \frac{1}{2}v' + i\delta' + h^*a \\ &= ja' + 2ha' + 2i\delta' + \frac{1}{2}v'\end{aligned}$$

$$\begin{aligned}h &= LNT \text{ to } LT \\ h &= \Gamma'\mu\Gamma\end{aligned}$$

$$\begin{aligned}i &= L[N]T \text{ to } [N]T \\ &= \Gamma'\mu\Omega\end{aligned}$$

$$\begin{aligned}g &= NT \text{ to } T \\ &= \Omega'\mu\Omega\end{aligned}$$

$$V_Y = 2\Gamma a' + 2\Omega\delta' + \delta w' + av' + V_F + V_\epsilon$$

$$\begin{aligned}w &= F \text{ to } [N]T \\ &= 2(f\Omega + fV_Y\mu\Omega)\end{aligned}$$

$$\begin{aligned}w' &= [N]T \text{ to } F \\ &= 2(\Omega'f' + \Omega'\mu V_Y f')\end{aligned}$$

$$\begin{aligned}
v &= F \text{ to } L[N]T \\
&= 2(f\Gamma + fV_Y\mu\Gamma)
\end{aligned}$$

$$\begin{aligned}
v' &= L[N]T \text{ to } F \\
&= 2(\Gamma'f' + \Gamma'\mu V_Y f')
\end{aligned}$$

$$\begin{aligned}
\theta_{NT} &= Y \text{ to } NT \\
&= 2(\tfrac{1}{2}w + \delta g' + ai + \delta g' + ai) \\
&= 4\delta g' + 4ai + w
\end{aligned}$$

$$\begin{aligned}
\theta_T &= Y \text{ to } T \\
&= 2(\tfrac{1}{2}w + \delta(k + g) + ai + \delta g + ai) \\
&= 2\delta k + 4\delta g + 4ai + w \\
&= 2\delta k + \theta_{NT}
\end{aligned}$$

$$\begin{aligned}
\theta_{LNT} &= Y \text{ to } LNT \\
&= 2(\tfrac{1}{2}v + \delta i' + ah' + \delta i' + ah') \\
&= 4\delta i' + 4ah' + v
\end{aligned}$$

$$\begin{aligned}
\theta_{LT} &= Y \text{ to } LT \\
&= 2(\tfrac{1}{2}v + \delta i' + a(j + h) + \delta i' + ah) \\
&= 2aj + 4\delta i' + 4ah + v \\
&= 2aj + \theta_{LNT}
\end{aligned}$$

4 Expanded Matrices

4.1 Models 0 and 1

$$\begin{aligned}
\Omega &= \begin{bmatrix} 2\delta_1 g_1 + \delta_1 k_1 + 0.5w_1 & 2\delta_1 g_{12} + \delta_1 k_{12} + 0.5w_{12} \\ 2\delta_2 g_{12} + \delta_2 k_{12} + 0.5w_{21} & 2\delta_2 g_2 + \delta_2 k_2 + 0.5w_2 \end{bmatrix} \\
g &= \begin{bmatrix} \Omega_1(\mu_1\Omega_1 + \mu_{12}\Omega_{21}) + \Omega_{21}(\mu_{12}\Omega_1 + \mu_2\Omega_{21}) & \Omega_{12}(\mu_1\Omega_1 + \mu_{12}\Omega_{21}) + \Omega_2(\mu_{12}\Omega_1 + \mu_2\Omega_{21}) \\ \Omega_1(\mu_1\Omega_{12} + \mu_{12}\Omega_2) + (\mu_{12}\Omega_{12} + \mu_2\Omega_2)\Omega_{21} & \Omega_{12}(\mu_1\Omega_{12} + \mu_{12}\Omega_2) + \Omega_2(\mu_{12}\Omega_{12} + \mu_2\Omega_2) \end{bmatrix}
\end{aligned}$$

$$\begin{aligned}
V_Y &= \begin{bmatrix} VE_1 + VF_1 + 2\delta_1(2\delta_1g_1 + \delta_1k_1 + 0.5w_1) + \delta_1w_1 & VE_{12} + VF_{12} + 2\delta_2(2\delta_1g_{12} + \delta_1k_{12} + 0.5w_{12}) + \delta_1w_{12} \\ VE_{12} + VF_{12} + 2\delta_1(2\delta_2g_{12} + \delta_2k_{12} + 0.5w_{21}) + \delta_1w_{21} & VE_2 + VF_2 + 2\delta_2(2\delta_2g_2 + \delta_2k_2 + 0.5w_2) + \delta_2w_2 \end{bmatrix} \\
\theta_{NT} &= \begin{bmatrix} 4\delta_1g_1 + w_1 & 4\delta_1g_{12} + w_{12} \\ 4\delta_2g_{12} + w_{21} & 4\delta_2g_2 + w_2 \end{bmatrix} \\
\theta_T &= \begin{bmatrix} 4\delta_1g_1 + 2\delta_1k_1 + w_1 & 4\delta_1g_{12} + 2\delta_1k_{12} + w_{12} \\ 4\delta_2g_{12} + 2\delta_2k_{12} + w_{21} & 4\delta_2g_2 + 2\delta_2k_2 + w_2 \end{bmatrix}
\end{aligned}$$

4.2 Model 2

$$\begin{aligned}
\Omega &= \begin{bmatrix} 2\delta_1g_1 + 2a_1i_1 + \delta_1k_1 + 0.5w_1 & 2\delta_1g_{12} + 2a_1i_{12} + \delta_1k_{12} + 0.5w_{12} \\ 2\delta_2g_{12} + 2a_2i_{12} + \delta_2k_{12} + 0.5w_{21} & 2\delta_2g_2 + 2a_2i_2 + \delta_2k_2 + 0.5w_2 \end{bmatrix} \\
\Gamma &= \begin{bmatrix} 2a_1h_1 + 2\delta_1i_1 + a_1j_1 + 0.5v_1 & 2a_1h_{12} + 2\delta_1i_{12} + a_1j_{12} + 0.5v_{12} \\ 2a_2h_{12} + 2\delta_2i_{12} + a_2j_{12} + 0.5v_{21} & 2a_2h_2 + 2\delta_2i_2 + a_2j_2 + 0.5v_2 \end{bmatrix} \\
\theta_{NT} &= \begin{bmatrix} 4\delta_1g_1 + 4a_1i_1 + w_1 & 4\delta_1g_{12} + 4a_1i_{12} + w_{12} \\ 4\delta_2g_{12} + 4a_2i_{12} + w_{21} & 4\delta_2g_2 + 4a_2i_2 + w_2 \end{bmatrix} \\
\theta_T &= \begin{bmatrix} 4\delta_1g_1 + 4a_1i_1 + 2\delta_1k_1 + w_1 & 4\delta_1g_{12} + 4a_1i_{12} + 2\delta_1k_{12} + w_{12} \\ 4\delta_2g_{12} + 4a_2i_{12} + 2\delta_2k_{12} + w_{21} & 4\delta_2g_2 + 4a_2i_2 + 2\delta_2k_2 + w_2 \end{bmatrix} \\
\theta_{LNT} &= \begin{bmatrix} 4a_1h_1 + 4\delta_1i_1 + v_1 & 4a_1h_{12} + 4\delta_1i_{12} + v_{12} \\ 4a_2h_{12} + 4\delta_2i_{12} + v_{21} & 4a_2h_2 + 4\delta_2i_2 + v_2 \end{bmatrix} \\
\theta_{LT} &= \begin{bmatrix} 4a_1h_1 + 4\delta_1i_1 + 2a_1j_1 + v_1 & 4a_1h_{12} + 4\delta_1i_{12} + 2a_1j_{12} + v_{12} \\ 4a_2h_{12} + 4\delta_2i_{12} + 2a_2j_{12} + v_{21} & 4a_2h_2 + 4\delta_2i_2 + 2a_2j_2 + v_2 \end{bmatrix}
\end{aligned}$$