

Appendix

DERIVATION OF MULTIVARIATE VARIANCE-COMPONENTS MODEL

Here we present a simplified derivation of a multivariate version of Willham's (1963, 1972) variance-components model. The standard version of this model assumes that the vector of phenotypes (\mathbf{z}) can be partitioned into additive genetic (\mathbf{a}) and environmental components (\mathbf{e}), or

$$\mathbf{z} = \mathbf{a}_d + \mathbf{a}'_m + \mathbf{e}_d + \mathbf{e}'_m, \quad (\text{A1})$$

where subscript d denotes the direct effects of an individual's genes or environment, and subscript m denotes genetic and environmental maternal effects. (For simplicity, we ignore dominance and epistasis here.) In equation (A1) and below, primes denote that the value of the maternal components come from a different individual, *i.e.*, the mother. An underlying assumption of equation (A1) is that the phenotype of the grandmother does not affect the offspring's phenotype except via direct transmission of genes. Such an effect may either arise from what is defined in the text from what is defined in the text as a "cascading maternal effect," or less likely, from a direct grandmaternal effect. Willham (1972) considered a more complex model incorporating a cascading maternal effect into a grandmaternal effect term.

The vector of total breeding values, which represent an individual's total heritable contribution to the population mean (Bijma et al. 2007), can be written as

$$\mathbf{A} = \mathbf{a}_d + \mathbf{a}_m. \quad (\text{A2})$$

Note the absence of a prime on the maternal breeding value in equation (A2): the maternal breeding value reflects an individual's expected maternal contribution to its own offspring rather than the phenotypic effect of its own mother (Willham 1963; Bijma 2006). The variance of total breeding values is thus

$$\mathbf{G}_A = \mathbf{G}_{dd} + \mathbf{G}_{dm} + \mathbf{G}_{md} + \mathbf{G}_{mm} \quad (\text{A3})$$

where \mathbf{G}_{ij} is a variance-covariance matrix when $i = j$ and a square matrix of covariances when $i \neq j$.

To derive a predictive expression for the response to selection for maternally affected traits, we assume that relative fitness (w) can be expressed as linear function of phenotypes, with the strength of directional selection on each character z represented by a selection gradient β (Lande and Arnold 1983). Expressed as a vector equation,

$$w = \alpha + \mathbf{z}^T \boldsymbol{\beta} + \varepsilon, \quad (\text{A4})$$

where α and ε are intercept and error terms, respectively, T denotes transposition, and $\boldsymbol{\beta}$ is a vector of selection gradients. We ignore maternal selection (Kirkpatrick and Lande 1989) here; extensions incorporating it are straightforward (Kirkpatrick and Lande 1992; Hadfield 2012). Using Price's (1970) equation, $\Delta\bar{z} = \text{Cov}(\mathbf{A}, w)$, the change in phenotypic means after one generation can be represented as

$$\Delta\bar{z} = \text{Cov}(\mathbf{A}, \mathbf{z}^T)\boldsymbol{\beta}. \quad (\text{A5})$$

Substituting equations (A1) and (A2) into (A5) and taking the covariance leads to equation (1) in the text (cf. McGlothlin et al. 2010).

TRANSLATION BETWEEN VARIANCE-COMPONENTS AND TRAIT-BASED MODELS

In the trait-based model, the vector of phenotypes can be written as

$$\mathbf{z} = \mathbf{a} + \mathbf{e} + \mathbf{M}\mathbf{z}', \quad (\text{A6})$$

where \mathbf{a} is a vector of additive genetic values, \mathbf{e} is a vector of environmental effects, and \mathbf{M} is a square matrix of maternal effects coefficients. Likewise, the total breeding value can be written as

$$\mathbf{A} = \mathbf{a} + \mathbf{M}\mathbf{A} = (\mathbf{I} - \mathbf{M})^{-1}\mathbf{a} = (\mathbf{I} - \mathbf{M}\mathbf{M})^{-1}(\mathbf{a} + \mathbf{M}\mathbf{a}), \quad (\text{A7})$$

where \mathbf{I} is the identity matrix. The variance of breeding values is

$$\mathbf{G}_A = (\mathbf{I} - \mathbf{M})^{-1}\mathbf{G}(\mathbf{I} - \mathbf{M}^T)^{-1} = (\mathbf{I} - \mathbf{M}\mathbf{M})^{-1}(\mathbf{G} + \mathbf{G}\mathbf{M}^T + \mathbf{M}\mathbf{G} + \mathbf{M}\mathbf{G}\mathbf{M}^T)(\mathbf{I} - \mathbf{M}^T\mathbf{M}^T)^{-1}. \quad (\text{A8})$$

To translate between the two frameworks, we begin by setting equal the terms of equation (A3) and (A8) following McGlothlin and Brodie (2009), finding

$$\mathbf{G}_{dd} = (\mathbf{I} - \mathbf{M}\mathbf{M})^{-1}\mathbf{G}(\mathbf{I} - \mathbf{M}^T\mathbf{M}^T)^{-1} \quad (\text{A9a})$$

$$\mathbf{G}_{dm} = (\mathbf{I} - \mathbf{M}\mathbf{M})^{-1}\mathbf{G}\mathbf{M}^T(\mathbf{I} - \mathbf{M}^T\mathbf{M}^T)^{-1} \quad (\text{A9b})$$

$$\mathbf{G}_{md} = (\mathbf{I} - \mathbf{M}\mathbf{M})^{-1}\mathbf{M}\mathbf{G}(\mathbf{I} - \mathbf{M}^T\mathbf{M}^T)^{-1} \quad (\text{A9c})$$

$$\mathbf{G}_{mm} = (\mathbf{I} - \mathbf{M}\mathbf{M})^{-1}\mathbf{M}\mathbf{G}\mathbf{M}^T(\mathbf{I} - \mathbf{M}^T\mathbf{M}^T)^{-1}. \quad (\text{A9d})$$

These equations allow us to calculate the parameters of the trait-based model from the more readily estimable terms of the variance-components model:

$$\mathbf{M} = \mathbf{G}_{md}\mathbf{G}_{dd}^{-1} \quad (\text{A10a})$$

$$\mathbf{G} = (\mathbf{I} - \mathbf{MM})\mathbf{G}_{da}(\mathbf{I} - \mathbf{M}^T\mathbf{M}^T), \quad (\text{A10b})$$

(cf. McGlothlin and Brodie [2009], equation 14). Equations (A9-A10) assume that all traits that mediate maternal effects have been measured.

To translate between equations for response to selection in the two frameworks, we first express Willham's model in the terms of Kirkpatrick and Lande's model by substituting (A9) into (1):

$$\Delta\bar{z} = (\mathbf{I} - \mathbf{MM})^{-1}(\mathbf{G} + \frac{1}{2}\mathbf{GM}^T + \mathbf{MG} + \frac{1}{2}\mathbf{MGM}^T)(\mathbf{I} - \mathbf{M}^T\mathbf{M}^T)^{-1}\boldsymbol{\beta}. \quad (\text{A11})$$

By a simple algebraic manipulation, the asymptotic trait-based model (equation 5) can be rewritten in a similar form. Because any matrix can be multiplied by \mathbf{I} without altering it, and because multiplying any invertible matrix by its inverse yields \mathbf{I} , it is possible to express equation (5) as

$$\Delta\bar{z} = (\mathbf{I} - \mathbf{M})^{-1}[(\mathbf{I} + \mathbf{M})^{-1}(\mathbf{I} + \mathbf{M})]\mathbf{G}[(\mathbf{I} + \frac{1}{2}\mathbf{M}^T)(\mathbf{I} + \frac{1}{2}\mathbf{M}^T)^{-1}](\mathbf{I} - \frac{1}{2}\mathbf{M}^T)^{-1}\boldsymbol{\beta} \quad (\text{A12}),$$

where the quantities inserted into equation (5) are enclosed within brackets. Expansion and rearrangement yields equation (9) in the text.

LITERATURE CITED

- Bijma, P. 2006. Estimating maternal genetic effects in livestock. *J. Anim. Sci.* 84:800-806.
- Bijma, P., W. M. Muir, and J. A. M. Van Arendonk. 2007. Multilevel selection 1: quantitative genetics of inheritance and response to selection. *Genetics* 175:277-288.
- Hadfield, J. D. 2012. The quantitative genetic theory of parental effects. Pp. 267-284 *in* N. J. Royle, P. T. Smiseth, and M. Kölliker, eds. *The evolution of parental care*. Oxford Univ. Press, Oxford.
- Kirkpatrick, M., and R. Lande. 1989. The evolution of maternal characters. *Evolution* 43:485-503.
- . 1992. The evolution of maternal characters: errata. *Evolution* 46:284.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210-1226.
- McGlothlin, J. W., and E. D. Brodie, III. 2009. How to measure indirect genetic effects: the congruence of trait-based and variance-partitioning approaches. *Evolution* 63:1785-1795.
- McGlothlin, J. W., A. J. Moore, J. B. Wolf, and E. D. Brodie, III. 2010. Interacting phenotypes and the evolutionary process. III. Social evolution. *Evolution* 64:2558-2574.
- Price, G. R. 1970. Selection and covariance. *Nature* 227:520-521.
- Willham, R. L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* 19:18-27.
- . 1972. The role of maternal effects in animal breeding. III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35:1288-1293.

Table S1. The maternal effects matrix (M), recalculated as described in the text from Galloway et al. (2009). Elements reveal the effect of specific maternal traits on offspring trait expression. All traits were transformed as described in the text, but were not standardized as in Galloway et al. (2009).

		Maternal			
		Days to germ.	Rosette size	Days to flower	Biomass
Offspring	Days to germ.	0.216	0.054	-0.705	0.268
	Rosette size	-0.747	-0.654	0.610	0.611
	Days to flower	-0.247	0.025	-0.289	0.250
	Biomass	-0.279	0.011	0.073	-0.214

Table S2. Selection gradients (β) for ln days to flower for four selection lines (two early flowering, E1 and E2, and two late flowering, L1 and L2) each selected for three generations.

Generation of selection		Selection line			
		E1	E2	L1	L2
1	-4.83	-2.41	6.56	3.32	
2	-6.94	-7.68	6.15	7.65	
3	-7.97	-14.14	9.32	11.76	

Table S3. Estimate of the additive genetic (co)variance matrix (G) for four traits using an animal model (ASReml 3.0) that ignored maternal effects.

	Days to germ.	Rosette size	Days to flower	Biomass
Days to germ.	0.02307			
Rosette size	-0.14386	1.51804		
Days to flower	0.00617	-0.05802	0.01568	
Biomass	0.00839	-0.08689	0.02070	0.03391

Table S4. Estimate of the additive genetic (co)variance matrix (G) for four traits calculated using equation (A10b) and results from Table S1 and Galloway et al. (2009, Table 3a).

	Days to germ.	Rosette size	Days to flower	Biomass
Days to germ.	0.00460			
Rosette size	-0.02897	0.29551		
Days to flower	0.00174	0.00243	0.00768	
Biomass	0.00159	-0.00150	0.01072	0.02334