Selection response in traits with maternal inheritance

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Summary

Maternal inheritance is the non-Mendelian transmission of traits from mothers to their offspring. Despite its presence in virtually all organisms, acting through a variety of mechanisms, the evolutionary consequences of maternal inheritance are not well understood. Here we review and extend a model of the inheritance and evolution of multiple quantitative characters with complex pathways of maternal effects. Extensions of the earlier model include common family environmental effects not associated with maternal phenotype, sexual dimorphism, and paternal effects (non-Mendelian influence of the father on offspring traits). We find that, in contrast to simple Mendelian inheritance, maternal inheritance produces qualitatively different evolutionary dynamics for two reasons: (1) the response to selection on a set of characters depends not only on their additive genetic variances and covariances, but also on maternal characters that influence them, and (2) time lags in the response to selection create a form of evolutionary momentum. These results have important implications for evolution in natural populations and practical applications in the economic improvement of domesticated species. We derive selection indices that maximize either the economic improvement in a single generation of artificial selection or the asymptotic rate of improvement in long-term selection programmes, based on individual merit or a combination of individual and family merit. Numerical examples show that accounting for maternal inheritance can lead to considerable increases in the efficiency of artificial selection.

1. Introduction

Maternal inheritance is the non-Mendelian transmission of phenotypic traits from mothers to their offspring. This can occur through a variety of mechanisms: cytoplasmic heredity (e.g. mitochondrial and chloroplast DNA and maternal RNA transcripts packaged in eggs) or physiology and development (e.g. body size of the mother or egg or seed size affecting the body size of the offspring). Maternal effects are usually strongest early in life and are diluted during development as an individual's own genes are expressed (Rutledge *et al.* 1972; Cheverud *et al.* 1983; Schaal, 1984). However, some maternal effects can persist into adulthood, as for litter size in mice and pigs (Falconer, 1965; Van der Steen, 1985) and age at maturity in springtails (Janssen *et al.* 1988).

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Despite the widespread influence of maternal effects in microorganisms (Grun, 1976), plants (Roach & Wulff, 1987) and animals (Boycott *et al.* 1930; Cundiff, 1972; Bondari *et al.* 1978; Resnick, 1981; Price & Grant, 1985), their evolutionary consequences are poorly understood.

In this paper we review and extend a model (Kirkpatrick & Lande, 1989) of the inheritance and evolution of multiple characters with complex pathways of maternal inheritance. The extensions include common family environmental effects not associated with maternal phenotype, sexual dimorphism or sex-limitation of some characters, and paternal effects (non-Mendelian influence of the father on offspring traits). We also derive selection indices that maximize the rate of economic improvement after a single generation of artificial selection, or in long-term selection programmes, based on individual merit or using information from relatives.

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2. Models of maternal inheritance and selection response

(i) *Basic models*

Dickerson (1947) and Willham (1963) described a model of maternal inheritance in which a single maternal trait, inherited in a purely Mendelian fashion, produces a non-Mendelian effect on a separate trait in the offspring. This model has been used in the animal breeding literature to describe generalized maternal influences on offspring characters such as juvenile growth rate (Cundiff, 1972). Falconer (1965) described a model in which a single character with a partly Mendelian basis exerts a maternal effect on itself in the next generation, and used this to analyze results of breeding and selection experiments on litter size in mice. His model has also been applied to litter size in pigs (Van der Steen, 1985). Riska *et al.* (1985) described a model in which a single maternal trait has a non-Mendelian influence on both itself (in the next generation) and on a separate offspring trait. Although the form of response to a constant intensity of selection is known for the model of Dickerson and Willham (Dickerson, 1947; Hanrahan, 1976; Van Vleck *et al.* 1977) and for Falconer's model (Van der Steen, 1985), a theory of selection response in multiple characters with complex maternal inheritance has only recently been derived by Kirkpatrick & Lande (1989).

We generalized previous models to describe the joint Mendelian and maternal inheritance of a set of k quantitative traits. The phenotypic value of the ith trait in a newborn individual in generation $t+1$ is

$$z_i(t+1) = a_i(t+1) + e_i(t+1) + c_i(t+1) + \sum_{j=1}^{k} M_{ij} z_j^*(t),$$

$$(1)$$

where a_i is the additive genetic component of the trait, e_i is the component attributable to individual environment effects and genetic dominance, and c_i is the effect of common family environment not including maternal influences. Following standard quantitative genetic theory (Falconer, 1981; Bulmer, 1985), we assume that the column vectors $\mathbf{a}$, $\mathbf{e}$ and $\mathbf{c}$ are statistically independent of each other and are multivariate-normally distributed with covariance matrices $\mathbf{G}$, $\mathbf{E}$ and $\mathbf{E_c}$ respectively; the mean values of the environmental components are zero, $\mathbf{e} = \mathbf{0}$ and $\mathbf{c} = \mathbf{0}$; the population mates at random and epistasis is absent. We also assume for simplicity in this section that the population is sexually monomorphic and that selection acts in the same way on males and females. Important modifications of the equations to describe sexually dimorphic or sex-limited traits, such as many maternal characters, are described in the next section.

The summation in (1) represents the component of the trait attributable to maternal inheritance: M_{ij} is the maternal effect coefficient of trait j in the mother on trait i in her offspring, and $z_j^*(t)$ is the phenotype for trait j of the mother (that is, a female who reproduced in generation t). M_{ij} is defined as the regression of the phenotypic value of trait i in offspring on the phenotypic value of trait j in their mothers, holding the genetic component of trait i and the phenotypic values of all other traits constant. This coefficient measures the strength and sign (since M_{ij} can be negative) of effects that mothers have on their offspring through cytoplasmic, physiological, developmental, or other pathways of maternal inheritance. Any network of such pathways between the traits can be described using appropriate values for the M_{ij}s.

The model in equation (1) differs from that in Kirkpatrick & Lande (1989) and Lande & Price (1989) only by the addition of the term $c_i(t+1)$ accounting for common family environmental effects apart from maternal influences. All of their results can be applied to the present model if $\mathbf{E_c}$ is added to $\mathbf{E}$ in various expressions for the phenotypic covariance matrix $\mathbf{P}$ in the former paper. Aside from this change, all of their formulae, including offspring-parent phenotypic covariances and regressions, remain unchanged. (Of course the common family environmental effect $c_i(t+1)$ contributes to the resemblance between full siblings.)

By taking expectations, we can deduce from equation (1) that the evolutionary change caused by selection in the vector of trait means between generations t and $t+1$ is

$$\Delta \bar{z}(t) = [\mathbf{C_{az}} + \mathbf{MP}] \beta(t) + \mathbf{M}\Delta \bar{z}(t-1) - \mathbf{MP}\beta(t-1). \quad (2)$$

where $\mathbf{C_{az}} = \text{Cov}[\mathbf{a}(t), \mathbf{z}(t)^T] \approx \mathbf{G}(\mathbf{I} - \frac{1}{2}\mathbf{M}^T)^{-1}$, and the superscript T denotes matrix transposition (Kirkpatrick & Lande, 1989). $\mathbf{P}$ is the phenotypic covariance matrix, $\mathbf{M}$ is the matrix of maternal effect coefficients, and $\mathbf{I}$ is the identity matrix; these are square matrices of dimension k. The selection gradient vector $\beta(t) = \mathbf{P}^{-1}\mathbf{s}(t)$ is defined in terms of the vector of selection differentials in generation t, $\mathbf{s}(t)$, the difference in mean phenotype between selected and unselected individuals. The elements of the selection gradient indicate the strength and direction of selection acting directly on each trait, and are equivalent to partial regression coefficients of relative fitness on the phenotypic value of each trait (Lande & Arnold, 1983). In the special case that all the M_{ij}s are zero, $\mathbf{C_{az}} = \mathbf{G}$ and (2) becomes the standard equation for the evolution of quantitative traits under pure Mendelian inheritance, $\Delta \bar{z}(t) = \mathbf{G}\beta(t)$ (Lande, 1979).

The three terms on the right side of equation (2) have the following interpretation. The first term is the response to current selection pressures, based on parent-offspring resemblance, since $\mathbf{C_{az}} + \mathbf{MP}$ is the covariance between midparents and offspring (Kirkpatrick & Lande, 1989). The second term represents the delayed effect of evolution in maternal traits on the change they produce in offspring traits; that is, an evolutionary response in maternal traits produces a response in offspring traits in the next generation,
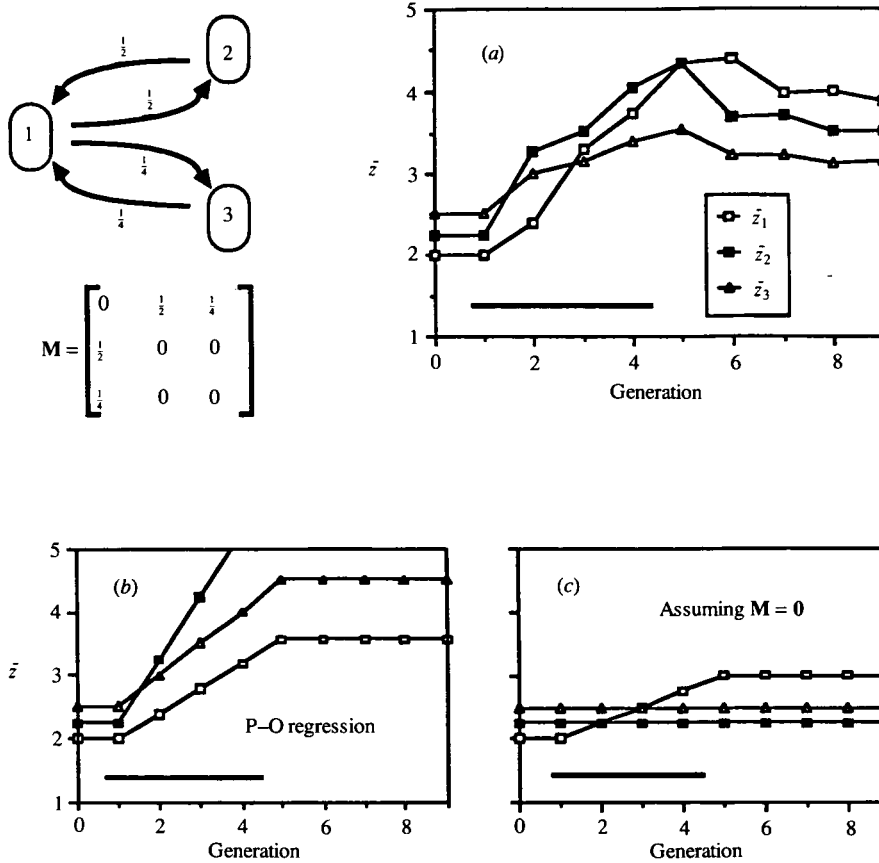
Fig. 1. Numerical example of the evolution of three maternally inherited traits. Top left: schematic of pathways of maternal inheritance, with its corresponding maternal effects matrix. Selection acts only on trait 1 for generations 1–4 (heavy horizontal bars). (*a*) Correct evolutionary trajectories of phenotypic means from equation (2). (*b*) Incorrect trajectories predicted using offspring-midparent regression to estimate the selection response in the first generation and assuming later generations will have the same selection response. (*c*) Incorrect trajectories predicted using the correct genetic covariance matrix but ignoring maternal effects. Models (*b*) and (*c*) incorrectly predict the rank order of the characters by generation 9 as well as the per-generation rates of change. Parameters for all cases: $G = \frac{1}{4} I$, $E = I$, $\beta = (1, 0, 0)^T$. Other parameters in equation (2) calculated as in Kirkpatrick & Lande (1989).

even in the absence of selection on maternal or offspring traits in either generation. The last term in (2) represents the delayed effect of selection on maternal characters on the response of the offspring characters in the next generation.

Two important conclusions follow from equation (2). The first is that the evolution of a set of genetically correlated traits depends not only on additive genetic variances and covariances of those traits, but also involves the inheritance and maternal effect coefficients of all traits exerting maternal effects on the traits of interest. This contrasts with the case of purely Mendelian inheritance, for which hereditary information and selective forces on the characters of interest are sufficient to predict the response to selection (see Fig. 1).

The second conclusion from equation (2) is that the evolution of the trait means depends not only on the current force of selection, $\beta(t)$, but also on the force of selection in the previous generation, $\beta(t-1)$, and the evolutionary change in the previous generation, $\Delta\bar{z}(t-1)$. This also contrasts with purely Mendelian

inheritance, where the evolutionary response to selection depends only on $\beta(t)$. Maternal inheritance therefore generates time lags in the response to selection, producing a form of evolutionary momentum (Kirkpatrick & Lande, 1989).

In an artificial selection programme where generation t is the last generation of selection, so that $\beta(t+\tau) = 0$ *for* $\tau \geq 1$, the evolutionary response in the next generation will be

$$\Delta\bar{z}(t+1) = M\{\Delta\bar{z}(t) - P\beta(t)\},$$

and thereafter the response will be

$$\Delta\bar{z}(t+\tau) = M^{\tau-1}\Delta\bar{z}(t+1).$$

Thus even after selection has ceased evolution will continue for as many generations as there are steps in unclosed pathways of maternal effects, or indefinitely if there are closed pathways or cycles of maternal effects. For example, in Dickerson's (1947) and Willham's (1963) model of a maternal trait affecting a distinct offspring trait, there is a single unclosed pathway of maternal effect of length one; after

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selection has ceased, evolution of the offspring trait will occur in the next generation and there will be no further evolution. (The complete dynamics of response to selection in Willham's model given in equation (10) of Kirkpatrick & Lande (1989) are incorrect, although their more general formula A26 is valid.) If the pathways of maternal effects form cycles, so that **M** has some non-zero eigenvalues, then evolution will continue indefinitely after selection has ceased, although the magnitude of the response will be damped out in proportion to λ^τ where λ is the leading eigenvalue (with the largest modulus) of **M**, which must have modulus less than one, $|\lambda| < 1$ (Kirkpatrick & Lande, 1989). The simplest example of a cycle of maternal effects is Falconer's model of a single character that maternally affects itself, forming a cycle of length one. An interesting consequence of the time lags is that it should be possible to observe a transient response to selection within an inbred line, based on maternally inherited environmental variation.

Figure 1 shows the evolution of three traits connected through a hypothetical network of maternal effects that might correspond to body size (trait 1) and two aspects of maternal performance such as lactation and gestation (traits 2 and 3). Selection acts only on trait 1, and the characters are genetically uncorrelated. We assume for simplicity that the population parameters (**M**, $\mathbf{C_{az}}$ and **P**) and the force of directional selection (β) remain constant, although changes in these parameters can be accommodated by the model. Two consequences of the time lags are evident. First, the rate of evolution of the traits is different in the second and subsequent generations of selection than it is in the first. Second, after selection ceases the traits continue evolving. It can also be seen that the evolution of a trait under selection depends not only on the strength of selection and genetic parameters of that trait, but also on the pathways of maternal inheritance connecting that trait to maternal characters not under selection. These features distinguish maternal inheritance from Mendelian inheritance.

The time lags can cause the initial and final rates of evolution of traits to be substantially different even under a constant intensity and direction of selection, β. The response after a single generation of selection on a population initially at equilibrium at generation 0 is, from equation (2),

$$\Delta \bar{z}(0) = (\mathbf{C_{az}} + \mathbf{MP}) \beta. \tag{3}$$

This can be compared with the population's final rate of evolution, again assuming the parameters remain constant. We find from (2) that the vector of phenotypic means will approach the asymptotic rate of evolution

$$\Delta \bar{z}(\infty) = (\mathbf{I} - \mathbf{M})^{-1} \mathbf{C_{az}} \beta. \tag{4}$$

If there are no cycles of maternal effects in the matrix **M** then under a constant intensity and direction of

selection the asymptotic rate of evolution will be achieved after a number of generations equal to one plus the length of the longest pathway of maternal effects. If there are cycles of maternal effects, then the asymptotic rate of evolution will be approached in proportion to λ^t where λ is the leading eigenvalue of **M**. From data on the magnitude of maternal effect coefficients in papers cited in the introduction, we expect that the asymptotic rate of evolution usually will be approached rapidly, within a few generations in most cases.

(ii) *Sexual dimorphism and sex-limited traits*

Because many maternal traits are sexually dimorphic or sex-limited, it is important to specify how the models can be altered to describe such traits. Hanrahan & Eisen (1973) have experimentally studied the influence of maternal effects on a sexually dimorphic trait, body weight in mice. For a single character with maternal inheritance expressed only in females, such as litter size in mice, $\mathbf{C_{az}}$ should be multiplied by $\frac{1}{2}$ in equations (2) through (4) and the selection gradients, β, then refer to selection on females. This is readily apparent from the fact that the covariance between mothers and daughters is $\frac{1}{2}\mathbf{C_{az}} + \mathbf{MP}$ (Kirkpatrick & Lande, 1989). To describe multiple characters with sexual dimorphism or sex-limited expression, the character vector and the selection gradient vector can be enlarged by treating each trait in each sex as a separate character, such as body size in males and females. The matrices in the above equations can also be enlarged accordingly, allowing for paternal effects (the non-Mendelian influence of father's characters on offspring traits) as well as maternal effects. Details are given in Appendix 1.

3. Artificial selection

The major goal of breeding programs is to economically improve domesticated species by selecting individuals on the basis of a set of correlated characters. The classical approach is to find the combination of characters on which selection will maximize the rate of economic improvement. Equations (3) and (4) suggest two possible strategies: to maximize the immediate improvement following only a single generation of selection, or to maximize the long-term rate of improvement. We consider in turn the cases of selection on unrelated (or distantly related) individuals, and the use of information from relatives.

(i) *Individual selection*

The selection criteria are determined by finding the index weight vector **b** such that artificial selection on the linear combination of characters $\mathbf{b^T z}$ maximizes the rate of economic improvement. The classical

solution, under the assumption of purely Mendelian inheritance, is

$$b = P^{-1}Gd, \tag{5}$$

where d is a vector of relative economic values of the phenotypic traits (Falconer, 1981; Bulmer, 1985). From equation (4), however, we find in Appendix 2 that with maternal effects the ultimate rate of economic improvement is maximized using

$$b = P^{-1}C_{az}^T(I - M^T)^{-1}d. \tag{6}$$

Another alternative is to use the matrix of actual phenotypic regression coefficients of offspring on midparents, $C_{az}P^{-1} + M$, in place of that in the classical selection index, GP^{-1}, so that

$$b = (P^{-1}C_{az}^T + M^T)d. \tag{7}$$

It can be shown from equation (3) that this index maximizes the improvement in the first generation, but in later generations it does not do as well as that based on equation (6).

To compare the rates of economic improvement using these three selection indices on a population with maternal inheritance, consider the example from Fig. 1 and assume trait 1 is the only character of economic value. With equal intensities of selection, using equation (6) yields a 28% increase in the final rate of economic improvement over that using parent-offspring regression and a 27% increase over the classical solution ignoring the maternal effects, as shown in Fig. 2. In this example, using offspring-midparent regression is initially better but ultimately worse than is completely ignoring the maternal effects. Since these are per-generation differences that accumulate across generations, the benefits of accounting for maternal inheritance can be substantial even when the per-generation advantage is modest. The amount of improvement depends on the parameters of genetic and maternal inheritance; other values can produce differences larger or smaller than those seen here.

(ii) *Information from relatives*

The result in equation (6) can also be applied to construct a selection index that maximizes the long-term rate of economic improvement using information from relatives. Thus, in a population consisting of full sib or paternal half sib families, we can derive an optimal index for selection on a combination of individual and family merit. By defining the family mean and the individual deviation from the family mean as separate traits all of the above equations continue to apply, but with vectors and matrices having dimensions twice as large as in the case of individual selection. The special structure of the vectors and matrices are given in Appendix 3. Consider for example the case of a single character, litter size. Falconer (1965) estimated the heritability of litter size
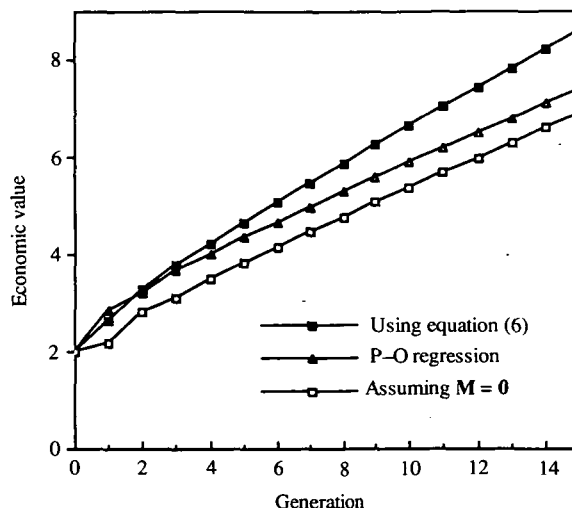

Fig. 2. Comparison of economic improvement under equal intensities of selection obtained by three different methods for calculating the index weight vector, b: (i) maximum long-term rate, from equation (6); (ii) maximum first-generation rate, from equation (7); and (iii) the classical solution in equation (5), which ignores the maternal effects entirely. The selection gradient vector is calculated using $\beta = ib/(b^TPb)^{\frac{1}{2}}$, where i is the standardized selection differential on the index b^Tz. Other parameters are as in Fig. 1, with $i = 1$ and economic weights $d = (1, 0, 0)^T$.

in mice to be $h^2 = 0.22$, the maternal effect coefficient to be $m = -0.13$, and the proportion of phenotypic variance due to common family environment not including maternal effects to be about $c^2 = 0.01$. The
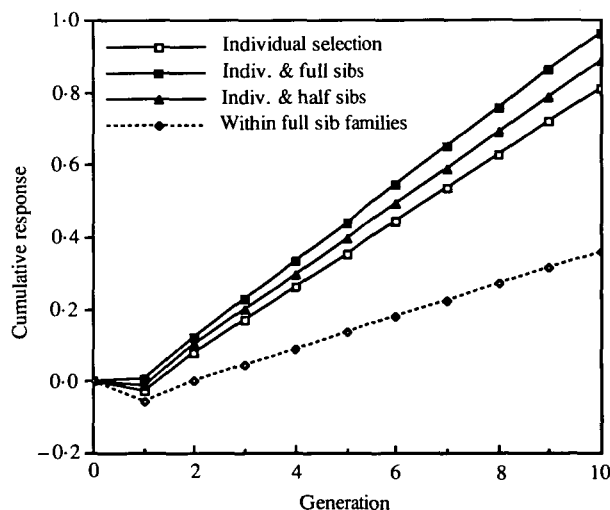

Fig. 3. Cumulative response to selection in units of $i\sigma_z$ for a single character, z, expressed only in females. i is the standardized selection differential on the selection index, and σ_z is the phenotypic standard deviation of the character. Parameters are those estimated by Falconer (1965) for litter size in mice (see text). The response to individual selection is given by equation (2) with C_{az} multiplied by $\frac{1}{2}$ to account for sex-limitation of the character, and responses using an optimal selection index combining individual and family merit (with data on $n = 4$ individuals per family) are described in Appendix 3. The dashed line gives the response to selection only within full sib families, as in Falconer's experiments; note the reversed response to selection in the first generation.

parameters for litter size in pigs are similar (Van der Steen, 1985). Because of the substantial negative maternal effect and the low heritability, the regression of daughter's litter size on that of their mothers, $h^2/(2-m)+m$, is negative. Falconer applied selection within full sib families and observed a marked reversed response to selection in the first generation in both the upward and downward selection lines. Figure 3 compares the dynamics of response to artificial selection on this trait under various schemes of selection.

4. Discussion

Most applications of maternal inheritance theory in animal breeding have been based on the models of Willham (1963, 1972), in which maternal performance is assumed to be unobserved. Without direct observation of the maternal traits it is difficult to estimate the parameters of maternal inheritance, which requires information on many types of relatives (Eisen, 1967). Neither Willham's models nor Van Vleck's (1970, 1976) generalizations can account for closed pathways or cycles of maternal effects, as in Falconer's (1965) model of a single character with a maternal effect on itself in the next generation. The limitations of previous models make it difficult or impossible to incorporate a realistic network of maternal effects. Basic developmental and physiological considerations suggest there are multiple maternal characters that can exert complex pathways of non-Mendelian influence on offspring traits.

Our results indicate that it will be important for evolutionary biologists and breeders to identify networks of maternal effects influencing traits of interest and to measure the relevant parameters, instead of the common practice of lumping all non-Mendelian inheritance into a single maternal effect. Equation (2) demonstrates that to predict the response to selection on a set of characters it is necessary to know not only the phenotypic and additive genetic variances and covariances of the characters, but also the inheritance and maternal effect coefficients of all traits that have maternal effects on the characters of interest. Measurement of maternal characters along with other traits of interest permits both the maternal effect coefficients and the additive genetic variances and covariances of all the characters to be estimated simply from offspring-parent regressions; in some cases this can be accomplished using only daughter-mother regression if it can be assumed that most of the characters do not exert maternal effects (Lande & Price, 1989).

Hayes & Hill (1981) analysed the statistical properties of the classical selection index for multiple characters [equation (5)], and recommended 'bending' the additive genetic variance-covariance matrix, G, to reduce the loss of efficiency in artificial selection caused by sampling errors in the index coefficients

(Harris, 1963). Bending consists of finding the eigenvalues of G and contracting their range (on the real line) around their mean value until there are no negative eigenvalues left, since these correspond to negative additive genetic variance for some combination of characters caused by sampling variance in the estimation of G (Hill & Thompson, 1978). A 'bent' G matrix for use in a selection index is then constructed from the contracted eigenvalues and the original eigenvectors. A similar procedure applied to the matrix of maternal effect coefficients, M, may improve the efficiency of selection indices in equations (6) and (7) based on estimates of G and M. By analogy, this would consist of finding the eigenvalues of M and contracting their range (in the complex plane) around their mean value until there are no eigenvalues with modulus greater than one, since these should not occur except for sampling errors (Kirkpatrick & Lande, 1989). A bent M matrix can then be constructed from the contracted eigenvalues and the original eigenvectors.

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Appendix 1

Sexual dimorphism and sex-limited traits

Let the female and male characters, which may differ in number, be represented by the vectors $z_\female$ and $z_\male$ respectively, and let the corresponding selection gradient vectors be $\beta_\female$ and $\beta_\male$. The model of inheritance analogous to equation (1), allowing for both maternal and paternal (non-Mendelian) effects, is

$$
\begin{aligned}
z_\female(t+1) &= a_\female(t+1) + e_\female(t+1) + c_\female(t+1) \\
&\quad + M_\female z_\female^*(t) + F_\female z_\male^*(t), \\
z_\male(t+1) &= a_\male(t+1) + e_\male(t+1) + c_\male(t+1) \\
&\quad + M_\male z_\female^*(t) + F_\male z_\male^*(t),
\end{aligned}
\tag{A 1}
$$

in which the matrices $M_\female$ and $F_\female$ contain the coefficients of maternal and paternal effects on female offspring, whereas $M_\male$ and $F_\male$ contain the coefficients of maternal and paternal effects on male offspring. Again we assume that the population mates at random and that the Mendelian part of the inheritance is autosomal with no epistasis. By taking expectations and accounting for the sex-limited expression of the characters the following dynamical equations can be derived for the vector of mean phenotypes $\bar{z}^T = (\bar{z}_\female^T, \bar{z}_\male^T)$ in response to the selection gradient $\beta^T(t) = (\beta_\female^T(t), \beta_\male^T(t))$,

$$
\Delta\bar{z}(t) = \tfrac{1}{2}C_{az}\beta(t) + M\{\Delta\bar{z}(t-1) + P\Delta\beta(t-1)\},
\tag{A 2}
$$

in which again $C_{az} = \text{Cov}[a(t), z(t)^T] \approx G(I - \tfrac{1}{2}M^T)^{-1}$. The variance-covariance matrices of the phenotypic vector and the vector of breeding values, $a^T = (a_\female^T, a_\male^T)$, have the forms

$$
P = \begin{pmatrix} P_{\female\female} & 0 \\ 0 & P_{\male\male} \end{pmatrix} \quad \text{and} \quad G = \begin{pmatrix} G_{\female\female} & G_{\female\male} \\ G_{\female\male}^T & G_{\male\male} \end{pmatrix},
\tag{A 3}
$$

in which $P_{\female\female}$ and $P_{\male\male}$ are the phenotypic variance-covariance matrices for females and males, respectively. $G_{\female\female}$ and $G_{\male\male}$ are the corresponding additive genetic variance-covariance matrices of the female and male characters, and the ijth element of the matrix $G_{\female\male}$ is the additive genetic covariance between female trait i and male trait j. The square matrix of maternal and paternal effect coefficients is

$$
M = \begin{pmatrix} M_\female & F_\female \\ M_\male & F_\male \end{pmatrix},
\tag{A 4}
$$

and I is an identity matrix of the same size. In the absence of non-Mendelian inheritance, when $M = 0$, equation (A2) is equivalent to the usual model for the evolution of sexually dimorphic characters (Lande, 1980).

Appendix 2

Individual selection index

Given the vector of economic weights, **d**, corresponding to the character vector **z**, we wish to find the vector of relative weight coefficients **b** in the linear selection index $I = \mathbf{b}^T\mathbf{z}$ that maximizes the rate of economic improvement, $R = \mathbf{d}^T\Delta\bar{\mathbf{z}}$, in a population under a given intensity of artificial selection on the index. With maternal inheritance, text equation (4) shows that the rate of economic improvement in response to a constant direction and intensity of selection asymptotically approaches

$$R = \mathbf{d}^T\mathbf{A}i\mathbf{b}/(\mathbf{b}^T\mathbf{Pb})^{\frac{1}{2}}, \tag{A 5}$$

in which the matrix $\mathbf{A} = (\mathbf{I}-\mathbf{M})^{-1}\mathbf{C}_{az}$ is non-symmetric, $i = s_I/\sigma_I$ is the intensity of selection on the index (selection differential in units of phenotypic standard deviations), and we have used the fact that $\beta = i\mathbf{b}/(\mathbf{b}^T\mathbf{Pb})^{\frac{1}{2}}$ (Harris, 1963). Applying the gradient operator $\nabla_b^T = (\partial/\partial b_1, \partial/\partial b_2, \dots \partial/\partial b_k)$ to (A 5) gives

$$\nabla_b^T R = \mathbf{d}^T\mathbf{A}i(\mathbf{b}^T\mathbf{Pb})^{-\frac{1}{2}} - \mathbf{b}^T\mathbf{P}(\mathbf{b}^T\mathbf{Pb})^{-\frac{3}{2}}\mathbf{d}^T\mathbf{A}i\mathbf{b}. \tag{A 6}$$

With the condition for an extremum, $\nabla_b^T R = 0$, and assuming that **P** is non-singular (positive definite) this yields the solution in text equation (6),

$$\mathbf{b} = \mathbf{P}^{-1}\mathbf{A}^T\mathbf{d}, \tag{A 7}$$

from which we have omitted a scalar multiplier. Substituting the optimal solution into (A 5) gives the long-term rate of economic improvement

$$R = i(\mathbf{b}^T\mathbf{Pb})^{\frac{1}{2}}. \tag{A 8}$$

We can show that the solution in (A7) maximizes R by applying the gradient operator to (A 6) to obtain the matrix of second partial derivatives, $\mathbf{H} = \nabla_b\nabla_b^T R$. When evaluated at the extremum, using $\mathbf{A}^T\mathbf{d} = \mathbf{Pb}$, this simplifies to

$$\mathbf{H} = \{\mathbf{Pbb}^T\mathbf{P} - \mathbf{P}(\mathbf{b}^T\mathbf{Pb})\}i(\mathbf{b}^T\mathbf{Pb})^{-\frac{3}{2}}.$$

The solution maximizes R if $\mathbf{x}^T\mathbf{Hx} \leqslant 0$ for an arbitrary vector **x**, which implies

$$(\mathbf{x}^T\mathbf{Pb})^2 \leqslant (\mathbf{x}^T\mathbf{Px})(\mathbf{b}^T\mathbf{Pb}).$$

Letting $\mathbf{y} = \mathbf{P}^{\frac{1}{2}}\mathbf{x}$ and $\mathbf{v} = \mathbf{P}^{\frac{1}{2}}\mathbf{b}$ this condition becomes $(\mathbf{y}^T\mathbf{v})^2 \leqslant (\mathbf{y}^T\mathbf{y})(\mathbf{v}^T\mathbf{v})$, which is the vector form of Cauchy's inequality, the left side being smaller than the right by a factor of $\cos^2\theta$ where θ is the angle between the vectors **y** and **v**.

Appendix 3

Information from relatives

When characters of low heritability are involved, information from relatives is often incorporated into the selection criterion. We consider two cases of selection on a combination of individual and family merit, full sib families and paternal half sib families in

which each offspring has the same father but a different mother. Assume that all families are of equal size n, and that there is no sexual dimorphism. Define the vector of family mean phenotypes as $\mathbf{z}_f$ and the vector of individual deviations from the family mean as $\mathbf{z}_w$, which are statistically uncorrelated components that sum to produce the individual phenotype (Robertson, 1955). The optimal selection index, $I = \mathbf{b}_f^T\mathbf{z}_f + \mathbf{b}_w^T\mathbf{z}_w$ that maximizes the long-term rate of improvement in economic value in the population, incorporating information from relatives, has the same general form as in equation (A 7) where the vector of weight coefficients for the $2k$-dimensional trait vector $\mathbf{z}^T = (\mathbf{z}_f^T, \mathbf{z}_w^T)$, is denoted as $\mathbf{b}^T = (\mathbf{b}_f^T, \mathbf{b}_w^T)$ and **I** is the $2k$-dimensional identity matrix. Because $\mathbf{z}_f$ and $\mathbf{z}_w$ sum to produce the individual phenotype, they have equal economic value and the transpose of enlarged vector of economic value is $(\mathbf{d}^T, \mathbf{d}^T)$. By considering the matrix analog of equations (1) for the enlarged vector of characters **z** we can deduce that the enlarged matrix of maternal effect coefficients is

$$\begin{pmatrix} \mathbf{M} & \mathbf{M} \\ \mathbf{0} & \mathbf{0} \end{pmatrix} \quad \text{or} \quad \begin{pmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{M} & \mathbf{M} \end{pmatrix}, \tag{A 9}$$

for full sibs or half sibs respectively. The enlarged additive genetic covariance matrix is

$$\begin{pmatrix} r_n\mathbf{G} & \mathbf{0} \\ \mathbf{0} & (1-r_n)\mathbf{G} \end{pmatrix}, \tag{A 10}$$

in which $r_n = r + (1-r)/n$ is the additive genetic correlation between siblings in families of size n, with $r = \frac{1}{2}$ for full sibs and $r = \frac{1}{4}$ for half sibs (Falconer, 1981). The enlarged phenotypic covariance matrix for full sibs or half sibs is respectively

$$\begin{pmatrix} \mathbf{P}-(1-\frac{1}{n})(\frac{1}{2}\mathbf{G}+\mathbf{E}) & \mathbf{0} \\ \mathbf{0} & (1-\frac{1}{n})(\frac{1}{2}\mathbf{G}+\mathbf{E}) \end{pmatrix} \quad \text{or}$$

$$\begin{pmatrix} \frac{1}{4}\mathbf{G}+\frac{1}{n}(\mathbf{P}-\frac{1}{4}\mathbf{G}) & \mathbf{0} \\ \mathbf{0} & (1-\frac{1}{n})(\mathbf{P}-\frac{1}{4}\mathbf{G}) \end{pmatrix}. \tag{A 11}$$

Single character

In the case of artificial selection on a single character, using information from relatives, the bold-faced matrices in equations (A 9)–(A 11) are scalars: $\mathbf{M} = m$, $\mathbf{G} = \sigma_a^2$, $\mathbf{P} = \sigma_z^2$, $\mathbf{E} = \sigma_e^2$, $\mathbf{E}_c = \sigma_c^2$ and the enlarged **P** matrix can be simply expressed as

$$\begin{pmatrix} t_n\sigma_z^2 & 0 \\ 0 & (1-t_n)\sigma_z^2 \end{pmatrix}, \tag{A 12}$$

in which $t_n = t + (1-t)/n$ is the phenotypic correlation between siblings in families of size n (Falconer, 1981). For half sibs $t = h^2/4$ and for full sibs $t = h^2/2 + c^2 + m^2 + mh^2/(1-m/2)$, where the heritability $h^2 = \sigma_a^2/\sigma_z^2$ is the proportion of the total phenotypic variance due to additive genetic effects and $c^2 = \sigma_c^2/\sigma2_z^2$ is the proportion of the total phenotypic variance due to

common family environmental effects not including maternal effects. The optimal selection index for full sib families then has weight coefficients

$$\begin{pmatrix} b_f \\ b_w \end{pmatrix} = \frac{h^2}{(1-\frac{1}{2}m)(1-m)} \begin{pmatrix} [r_n+(1-r_n)\frac{1}{2}m]/t_n \\ (1-r_n)(1-\frac{1}{2}m)/(1-t_n) \end{pmatrix}$$

(A 13 a)

corresponding to a long-term rate of economic improvement

$$\frac{R}{\sigma_z} = \frac{h^2 i}{(1-\frac{1}{2}m)(1-m)} \left\{ \frac{[r_n+(1-r_n)\frac{1}{2}m]^2}{t_n} + \frac{(1-r_n)^2(1-\frac{1}{2}m)^2}{1-t_n} \right\}^{\frac{1}{2}}.$$

(A 13b)

The optimal selection index for half sib families has weight coefficients

$$\begin{pmatrix} b_f \\ b_w \end{pmatrix} = \frac{h^2}{(1-\frac{1}{2}m)(1-m)} \begin{pmatrix} r_n(1-\frac{1}{2}m)/t_n \\ [1-r_n(1-\frac{1}{2}m)]/(1-t_n) \end{pmatrix}$$

(A 14a)

corresponding to a long-term rate of economic improvement

$$\frac{R}{\sigma_z} = \frac{h^2 i}{(1-\frac{1}{2}m)(1-m)} \left\{ \frac{r_n^2(1-\frac{1}{2}m)^2}{t_n} + \frac{[1-r_n(1-\frac{1}{2}m)]^2}{1-t_n} \right\}^{\frac{1}{2}}.$$

(A 14b)

For a family size of one, $n = 1$, these methods reduce to individual selection which has the long-term rate of economic improvement

$$\frac{R}{\sigma_z} = \frac{h^2 i}{(1-\frac{1}{2}m)(1-m)}.$$

(A 15)

The asymptotic rates of response for a character expressed and selected only in females would be half as large as in equations (A 13b), (A 14b) and (A 15).