One-Locus Two-Allele Models With Maternal (Parental) Selection

Sergey Gavrilets

Department of Ecology and Evolutionary Biology and Department of Mathematics, University of Tennessee, Knoxville, Tennessee 37996-1610

Manuscript received March 17, 1997
Accepted for publication February 23, 1998

ABSTRACT

I formulate and study a series of simple one-locus two-allele models for maternal (parental) selection. I show that maternal (parental) selection can result in simultaneous stability of equilibria of different types. Thus, in the presence of maternal (parental) selection the outcome of population evolution can significantly depend on initial conditions. With maternal selection, genetic variability can be maintained in the population even if none of the offspring of heterozygous mothers survive. I demonstrate that interactions of maternal and paternal selection can result in stable oscillations of genotype frequencies. A necessary condition for cycling is strong selection.

MATERNAL effects refer to situations in which an individual's phenotype depends (besides other factors) on the phenotype of its mother. Well known to biologists for decades, maternal effects have been considered as a nuisance that makes interpretation of biological data more difficult and that should be removed from experiments if possible (Falconer 1989). Recent years, however, have been characterized by a growing realization that maternal effects may actually be very important in evolution (*e.g.*, Cheverud and Moore 1994; Wade and Beeman 1994; Fox and Mousseau 1996; Roosenburg 1996; Rossiter 1995, 1996; Sinervo and Doughty 1996; Wade 1996; Wolf *et al.* 1997). This realization is coming partially from theoretical models that have shown that maternal effects can result in very interesting and sometimes counterintuitive evolutionary dynamics (Cheverud 1984; Kirkpatrick and Lande 1989; Lande and Kirkpatrick 1990; Orr 1991; Ginzburg and Taneyhill 1994; Wade and Beeman 1994). The concept of maternal effects can be generalized to the concept of "kin effects" (Cheverud 1984; Cheverud and Moore 1994) incorporating the effects of any relatives on an invidivual's phenotype.

"Maternal selection" is one of various maternal effects. This notion describes situations in which an individual's fitness depends (besides other factors) on the phenotype of its mother (Kirkpatrick and Lande 1989). Most of the theoretical work on the evolutionary consequences of maternal selection has been done within a quantitative genetics framework (*e.g.*, Dickerson 1947; Villham 1963, 1972; Falconer 1965; Cheverud 1984; Kirkpatrick and Lande 1989; Lande and Price 1989; Lande and Kirkpatrick 1990). There have been only a handful of theoretical studies considering major locus effects. An extreme case of fitness that depends entirely on the mother's genotype at a single diallelic locus was considered by Wright (1969, pp. 57–59) and Nagylaki (1992). Wright (1969, pp. 148–149) and Wade and Beeman (1994) studied single-locus two-allele models in which offspring of a specific genotype with a parent of a specific genotype has a reduced fitness.

Here I consider the dynamics of a series of simple one-locus two-allele models for maternal (and paternal) selection. These models are closely related to those introduced and discussed by Wade (1996) who, however, did not consider the dynamic behavior. Although the models studied in this article probably oversimplify real situations, they may be useful in identifying different dynamic possibilities and important parameters and in training our intuition about more complex (and realistic) systems.

A MODEL FOR MATERNAL SELECTION

I consider a single randomly mating diploid population with nonoverlapping generations. I assume that fitness (viability) of an individual depends on its genotype at a single diallelic locus as well as on the genotype of its mother at this locus. Let $i = 1, 2, 3$ correspond to genotypes **AA**, **Aa** and **aa**, respectively, and let $w_{i,j}$ be the fitness of an individual with genotype i raised by a mother with genotype j. Genotype frequencies are equal in both sexes after one generation of selection and segregation. Let x, y and z be the frequencies of adults with genotypes **AA**, **Aa** and **aa**, respectively. The nine mating types and the frequencies of the corresponding matings and offspring are given in Table 1. Using this table, the adult frequencies x', y' and z' in the next generation are defined by

$$\overline{w}x' = w_{1,1}x^2 + \frac{1}{2}(w_{1,1} + w_{1,2})xy + \frac{1}{4}w_{1,2}y^2, \quad (1a)$$

Address for correspondence: Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996-1610.
E-mail: gavrila@tiem.utk.edu

TABLE 1

Mating types and offspring

Mating types		Frequency of mating	Offspring		
Female	Male		**AA**	**Aa**	**aa**
AA	**AA**	x^2	1	0	0
	Aa	xy	1/2	1/2	0
	aa	xz	0	1	0
Aa	**AA**	xy	1/2	1/2	0
	Aa	y^2	1/4	1/2	1/4
	aa	yz	0	1/2	1/2
aa	**AA**	xz	0	1	0
	Aa	yz	0	1/2	1/2
	aa	z^2	0	0	1

$$\bar{w}y' = \frac{1}{2}(w_{2,1} + w_{2,2})xy + \frac{1}{2}(w_{2,2} + w_{2,3})yz + (w_{2,1} + w_{2,3})xz + \frac{1}{2}w_{2,2}y^2, \quad (1b)$$

$$\bar{w}z' = w_{3,3}z^2 + \frac{1}{2}(w_{3,3} + w_{3,2})yz + \frac{1}{4}w_{3,2}y^2, \quad (1c)$$

where the mean fitness of the population $\bar{w}$ is such that $x' + y' + z' = 1$. If $w_{i,j} = w_i$ for all i,j, that is, if the fitness of an individual depends only on its own genotype, one has a classical model of "pure" viability selection. If $w_{ij} = w_j$ for all i,j, that is, if the fitness of an individual depends only on the genotype of its mother, one has a model of "pure" maternal selection considered by Wright (1969) and Nagylaki (1992). In both models, the system evolves to a single polymorphic equilibrium if there is overdominance ($w_2 > w_1, w_3$) and to a monomorphic state otherwise. I will be interested in the model dynamics when both individual and maternal genotypes affect individual fitness.

The dynamic system (1) has two monomorphic equilibria (1, 0, 0) and (0, 0, 1) corresponding to the fixation of genotype **AA** and **aa**, respectively. Conditions for stability of these equilibria, which can be found in a straightforward manner, are given in

Result 1 (stability of monomorphic equilibria): Monomorphic equilibrium (1, 0, 0) is locally stable if

$$w_{1,1} > \frac{1}{2}(w_{2,1} + w_{2,2}), \quad (2a)$$

and is unstable if the latter inequality is reversed. Monomorphic equilibrium (0, 0, 1) is locally stable if

$$w_{3,3} > \frac{1}{2}(w_{2,3} + w_{2,2}), \quad (2b)$$

and is unstable if the latter inequality is reversed.

Thus, a monomorphic equilibrium is stable if fitness of the homozygote having a homozygous mother is larger than the average of the fitnesses of heterozygotes having a heterozygous mother and a homozygous mother. Reversing both inequalities results in the conditions for protecting polymorphism in this model. Analysis of attractors of (1) other than the monomorphic equilibria requires additional simplifying assumptions about fitnesses w_{ij}. Some special simplifying cases are examined below.

Symmetric model for maternal selection

A standard approach for simplifying analysis of population genetic models is to introduce some symmetry in the model. In this section, I will assume that fitnesses $w_{i,j}$ are symmetric in the sense that $w_{1,1} = w_{3,3}$, $w_{1,2} = w_{3,2}$, $w_{2,1} = w_{2,3}$. This symmetric case can be described by the following fitness matrix:

	Maternal genotype		
Individual genotype	**AA**	**Aa**	**aa**
AA	α	β	—
Aa	γ	δ	γ
aa	—	β	α

where α, β, γ and δ are nonnegative. Note that neither genotype **AA** can have a mother with genotype **aa**, nor can genotype **aa** have a mother with genotype **AA**. This symmetric model implies that fitnesses of homozygotes raised by homozygous mothers are identical, fitnesses of homozygotes raised by heterozygous mothers are identical and fitnesses of heterozygotes raised by homozygous mothers are identical. The dynamic equations (1) become

$$\bar{w}x' = \alpha x^2 + \frac{1}{2}(\alpha + \beta)xy + \frac{1}{4}\beta y^2, \quad (3a)$$

$$\bar{w}y' = \frac{1}{2}(\gamma + \delta)(x + z)y + 2\gamma xz + \frac{1}{2}\delta y^2, \quad (3b)$$

$$\bar{w}z' = \alpha z^2 + \frac{1}{2}(\alpha + \beta)yz + \frac{1}{4}\beta y^2. \quad (3c)$$

In this symmetric model, the conditions for stability of monomorphic equilibria, which have been given above, simplify.

Result 1a (stability of monomorphic equilibria): Monomorphic equilibria (1, 0, 0) and (0, 0, 1) are (simultaneously) locally stable if

$$\alpha > (\gamma + \delta)/2 \quad (4)$$

and are (simultaneously) unstable if the latter inequality is reversed.

Let us consider polymorphic equilibria of Equation 3.

Results 2 (existence of a symmetric polymorphic equilibrium): There always exists a symmetric polymorphic equilibrium with $x_{\text{sym}} = z_{\text{sym}}$. The genotype frequencies at this equilibrium are $x_{\text{sym}} = u/(2u + 2)$, $y_{\text{sym}} = 1/(u + 1)$, $z_{\text{sym}} = u/(2u + 2)$, where

$$u = \frac{\alpha - \delta}{2\gamma} + \sqrt{\left(\frac{\alpha - \delta}{2\gamma}\right)^2 + \frac{\beta}{\gamma}}. \qquad (5)$$

A symmetric polymorphic equilibrium exists always but is not always stable.

Results 3 (stability of the symmetric polymorphic equilibrium): The symmetric polymorphic equilibrium is locally stable if

$$(\alpha - \gamma)u < (\delta - \alpha). \qquad (6)$$

A symmetric polymorphic equilibrium is never stable if $\alpha > \gamma,\delta$ and is always stable if $\alpha < \gamma,\delta$. Note that the former (latter) inequality guarantees the stability (instability) of the monomorphic equilibria. If $\delta > \alpha > \gamma$, then a symmetric equilibrium is stable for sufficiently small β and is unstable for sufficiently large β. If $\delta < \alpha < \gamma$, then it is stable for sufficiently large β and is unstable for sufficiently small β. It is possible that both monomorphic equilibria and a symmetric equilibrium are stable simultaneously. In this case, initial conditions determine whether polymorphism is or is not maintained in the system under consideration. On the other hand, it is possible that none of the equilibria we have considered so far are stable.

Results 4 (existence of a pair of unsymmetric polymorphic equilibria): A pair of unsymmetric polymorphic equilibria with genotype frequencies (x^*, y^*, z^*) and (z^*, y^*, x^*) exists if

$$\frac{\delta - \alpha + \beta/\alpha(\gamma - \alpha)}{\alpha - (\gamma + \delta)/2} > 2\sqrt{\beta/\alpha}. \qquad (7)$$

Here

$$y^* = \frac{2\alpha - \gamma - \delta}{(\alpha - \gamma)(1 - \beta/\alpha)},$$

and x^* and z^* are positive real solutions X to quadratic

$$X^2 - (1 - y^*)X + (\beta/4\alpha)y^{*2} = 0.$$

If $\alpha > \gamma,\delta$ or $\alpha < \gamma,\delta$, the unsymmetric polymorphic equilibria do not exist. If α is closer to δ than to γ (that is, $\Delta_1 \equiv |\alpha - \delta| < \Delta_2 \equiv |\alpha - \gamma|$), then the unsymmetric polymorphic equilibria exist for sufficiently small β/α (for $\beta/\alpha < \Delta_1/\Delta_2$). If α is closer to δ than to γ (*i.e.*, $\Delta_1 > \Delta_2$), then the unsymmetric polymorphic equilibria exist for sufficiently large β/α (for $\beta/\alpha > \Delta_1/\Delta_2$).

Can these equilibria be stable? Conditions for stability of these equilibria can be found in a straightforward manner but are rather cumbersome. These conditions simplify if $\beta = \delta = 0$, that is, if offspring of heterozygous mothers are inviable. In this case, the genotype frequencies at unsymmetric equilibria are

$$\left(0, \frac{\alpha}{\gamma - \alpha}, 1 - \frac{\alpha}{\gamma - \alpha}\right) \quad \text{and} \quad \left(1 - \frac{\alpha}{\gamma - \alpha}, \frac{\alpha}{\gamma - \alpha}, 0\right);$$

at the former, genotype **AA** has zero frequency, whereas at the latter, genotype **aa** has zero frequency.

Result 5: If $\beta = \delta = 0$, the necessary and sufficient condition for both existence and simultaneously stability of a pair of asymmetric polymorphic equilibria is $\gamma > 2\alpha$.

This somewhat conterintuitive result means that genetic variability can be maintained in the population even if none of the offspring of heterozygous mothers survive. This is a general feature of models where there is competition between sibs within a family and a feature of the maternal-effect selfish gene model of Wade and Beeman (1994).

Multiplicative model for maternal selection

Let an individual's fitness, w, be a product of two parameters, one of which, v, depends on an individual's own genotype, whereas another one, m, depends on its mother's genotype

$$w_{ij} = v_i m_j, \; i,j = 1, 2, 3. \qquad (8)$$

This is a plausible assumption if different components of fitness are important at different stages of the life cycle. In this case, the dynamic system (1) reduces to

$$\overline{w}x' = v_1\left[F_{11}x^2 + F_{12}xy + \frac{1}{4}F_{22}y^2\right], \qquad (9a)$$

$$\overline{w}y' = v_2\left[F_{12}xy + F_{23}yz + 2F_{13}xz + \frac{1}{2}F_{22}y^2\right], \qquad (9b)$$

$$\overline{w}z' = v_3\left[F_{33}z^2 + F_{23}yz + \frac{1}{4}F_{22}y^2\right], \qquad (9c)$$

where

$$F_{ij} = (m_i + m_j)/2 \qquad (10)$$

for all i,j. Equations (9) are equivalent to those describing a general one-locus two-allele model with both viability selection (characterized by v_i) and fertility differences (characterized by F_{ij}) introduced by Bodmer (1965). Equations 9 and 10 with $v_i = 1$ (no viability differences) define a model with additive fertilities, as studied by Penrose (1949). The general system (9, 10) represents a partial case of a multiplicative fertility selection model studied by Bodmer (1965). For some parameter values this system admits two simultaneously stable polymorphic equilibria.

Symmetric model for parental selection

In this section, I assume that both parents contribute to an offspring's fitness. Let $w_{i,jk}$ be the fitness of an individual with genotype i raised by a mother with genotype j and a father with genotype k ($i, j, k = 1, 2, 3$). Using Table 1, the adult frequencies x', y' and z' in the next generation are defined by

$$\overline{w}x' = w_{1,11}x^2 + \frac{1}{2}(w_{1,12} + w_{1,21})xy + \frac{1}{4}w_{1,22}y^2, \qquad (11a)$$

$$\bar{w}y' = \frac{1}{2}(w_{2,12} + w_{2,21})xy + \frac{1}{2}(w_{2,23} + w_{2,32})yz$$

$$+ (w_{2,13} + w_{2,31})xz + \frac{1}{2}w_{2,22}y^2, \qquad (11b)$$

$$\bar{w}z' = w_{3,33}z^2 + \frac{1}{2}(w_{3,32} + w_{3,23})yz + \frac{1}{4}w_{3,22}y^2. \quad (11c)$$

Let us assume that $w_{i,jk} = w_{jk}$, that is, the fitness of an individual depends only on the genotypes of its parents and does not depend on its own genotype. This is a two-parent generalization of the model introduced by Wright (1969, pp. 57–59). Let us further assume that the fitness matrix w_{jk} is symmetric and has the following form:

	Paternal genotype		
Maternal genotype	**AA**	**Aa**	**aa**
AA	α	β	γ
Aa	β	δ	β
aa	γ	β	α

where α, δ, γ and δ are nonnegative parameters. Note that the meaning of these parameters in the model considered here is completely independent of that in the previous sections. With fitnesses as above, the dynamic equations (11) can be rewritten as

$$\bar{w}x' = \alpha x^2 + \beta xy + \frac{1}{4}\delta y^2, \qquad (12a)$$

$$\bar{w}y' = \beta xy + \beta yz + 2\gamma xz + \frac{1}{2}\delta y^2, \qquad (12b)$$

$$\bar{w}z' = \alpha z^2 + \beta yz + \frac{1}{4}\delta y^2. \qquad (12c)$$

These equations are exactly the same as those analyzed by Hadeler and Liberman (1975) in the context of fertility selection models. Numerous results by these authors are applicable here. In particular, the dynamic system (12) can have two simultaneously stable polymorphic equilibria or a stable limit cycle with period two!

To illustrate this, let us assume that only offspring of heterozygous parents and of different homozygous parents are viable, and offspring of all other pairs of parents are inviable. In this case the following is true.

Result 6: Let $\alpha = \beta = 0$, δ, $\gamma > 0$. Then if $4\gamma > \delta$, the only stable equilibrium of (12) is a symmetric polymorphic equilibrium (with $x^* = z^*$). If $4\gamma < \delta$, the system does not have any stable equilibria.

In the latter case, the system cycles with period two (see Figure 1). In general, a dynamic system (12) cycles if the fitness δ of individuals with both parents heterozygous is sufficiently large relative to the fitness γ of individuals with different homozygous parents, which in turn is sufficiently larger than fitnesses α and β of other individuals.

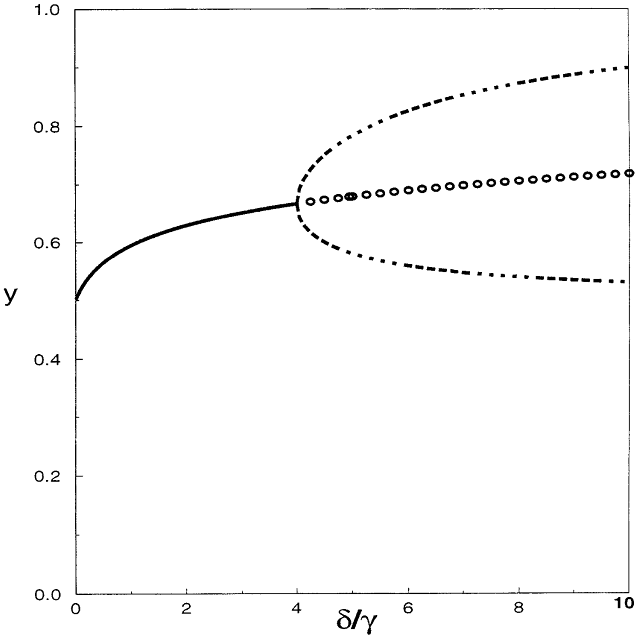

Figure 1.—The bifurcation diagram for the heterozygote frequency y in the symmetric model of parental selection (12) with $\alpha = \beta = 0$. The symmetric polymorphic is stable for $\delta/\gamma < 4$ (solid line) and is unstable for $\delta/\gamma > 4$ (circles). At $\delta/\gamma = 4$, a stable two-cycle bifurcates from the equilibrium point (dashed line). The homozygote frequencies $x = z = (1 - z)/2$.

CONCLUSIONS

Here I have studied a series of simple one-locus two-allele models for maternal (parental) selection. Srb *et al.* (1965, Chapter 11) give several examples for maternal effects that can be attributed to a single diallelic locus; see Wade (1996) for more discussion of the relevance of maternal effects controlled by a small number of loci with large effects. My results indicate similarity between dynamic behaviors under maternal selection and fertility selection. The latter is well-known to be much more complicated than the dynamics resulting from viability selection (*e.g.*, Owen 1953; Bodmer 1965; Hadeler and Liberman 1975). I have shown that maternal selection can result in a simultaneous stability of equilibria of different types. Thus, in the presence of maternal (parental) selection, the outcome of population evolution can significantly depend on initial conditions. With maternal selection, genetic variability can be maintained in a population even if none of the offspring of heterozygous mothers survive. I have demonstrated that interactions of maternal and paternal selection can result in stable oscillations of genotype frequencies. A possibility for cycling and even chaos in theoretical models incorporating maternal effects has been already demonstrated by Ginzburg and Taneyhill (1994). In Ginzburg and Taneyhill's model, cycling resulted from ecological factors. In contrast, in the model considered here cycling is brought about by genetic factors and maternal selection.

The counterintuitive results about the maintenance of variability and cycling require selection to be strong. The following two examples of very strong maternal selection are interesting in this respect. The first example (Srb *et al.* 1965, pp. 319–320) concerns Drosophila where the sex-linked recessive gene *fused* causes partial sterility as well as fusion of two longitudinal wings' veins. At least one wild-type allele of the *fused* locus must be present in either the mother or in the progeny in order for embryogenesis to proceed normally. As a result, offspring with identical genotypes may die or develop to maturity, depending on the genotype of their mother. The second example is a class of dominant lethal genetic factors called *Medea* that is widespread in natural populations of the flour beetle, *Tribolium castaneum* (Beeman *et al.* 1992). These factors cause maternal-effect lethality of all offpring not inheriting a copy of the factor [see Wade and Beeman (1994) for a theoretical study of the evolutionary dynamics of these factors]. These examples suggest that conditions necessary for complex dynamics might be satisfied at least for some biological systems.

Results and findings reported here are complementary to those obtained within the quantitative genetic framework (*e.g.*, Dickerson 1947; Villham 1963, 1972; Falconer 1965; Cheverud 1984; Kirkpatrick and Lande 1989; Lande and Price 1989; Lande and Kirkpatrick 1990). The latter typically considers an additive quantitative trait that is controlled by both direct genetic and maternal factors and that is subject to phenotypic selection. The main focus is usually on the dynamics of the mean value of the trait, whereas (constant) genetic variability is tacitly assumed to be maintained by some factors that are not considered explicitly. The major locus framework utilized here and in Wright (1969), Nagylaki (1992), and Wade and Beeman (1994) focuses on maternal effects contributing directly to fitness. This framework allows for analyzing conditions for the maintenance and dynamics of genetic variability and the existence of multiple stable equilibria. Generalization of this approach for the case of multiple alleles and loci would be very desirable.

I am grateful to MaryCarol Rossiter and Michael Wade for sharing manuscripts before publication and to reviewers for valuable comments and suggestions. This work was partially supported by National Institutes of Health grant GM-56693.

LITERATURE CITED

Beeman, R. W., K. S. Friesen and R. E. Denell, 1992 Maternal-effect selfish genes in flour beetles. Science **256:** 89–92.

Bodmer, W. F., 1965 Differential fertility in population genetics models. Genetics **51:** 411–424.

Cheverud, J. M., 1984 Evolution by kin selection: a quantitative genetic model illustrated by maternal performance in mice. Evolution **38:** 766–777.

Cheverud, J. M., and A. J. Moore, 1994 Quantitative genetics and the role of the environment provided by relatives in behavioral evolution, pp. 67–100 in *Quantitative Genetic Studies of Behavioral Evolution*, edited by C. R. B. Boake. University of Chicago Press, Chicago.

Dickerson, G. E., 1947 Composition of hog carcasses as influenced by heritable differences in rate in economy of gain. Iowa Agr. Exp. Sta. Res. Bull. **354:** 492–524.

Falconer, D. S., 1965 Maternal effects and selection response, pp. 763–774 in Proceedings of the XI International Congress on Genetics, Vol. 3, S. J. Geerts, editor. Pergamon Press, Oxford.

Falconer, D. S., 1989 *Introduction to Quantitative Genetics*. John Wiley & Sons, New York.

Fox, C. W., and T. A. Mousseau, 1996 Larval host plant affects fitness consequences of egg size variation in the seed beetle Stator Limbatus. Oecologia **107:** 541–548.

Ginzburg, L. R., and D. E. Taneyhill, 1994 Population cycles of forest Lepidoptera: a maternal effect hypothesis. J. Anim. Ecol. **63:** 79–92.

Hadeler, K. P., and U. Liberman, 1975 Selection models with fertility differences. J. Theor. Biol. **2:** 19–32.

Kirkpatrick, M., and R. Lande, 1989 The evolution of maternal characters. Evolution **43:** 485–503.

Lande, R., and T. Price, 1989 Genetic correlations and maternal effect coefficients obtained from offspring-parent regression. Genetics **122:** 915–922.

Lande, R., and M. Kirkpatrick, 1990 Selection response in traits with maternal inheritance. Genet. Res. **55:** 189–197.

Nagylaki, T., 1992 *Introduction to Theoretical Population Genetics*. Springer-Verlag, Berlin.

Orr, H. A., 1991 Is single-gene speciation possible? Evolution **45:** 764–769.

Owen, A. R. G., 1953 A genetic system admitting of two distinct stable equilibria under natural selection. Heredity **7:** 97–102.

Penrose, L. S., 1949 The meaning of "fitness" in human populations. Ann. Eugenics **14:** 301–304.

Roosenburg, W. M., 1996 Maternal condition and nest site choice—an alternative for the maintenance of environmental sex determination. American Zoologist **36:** 157–168.

Rossiter, M., 1995 Impact of life-history evolution on population dynamics: predicting the presence of maternal effects, pp. 251–275 in *Population Dynamics*, edited by N. Cappuccino and P. W. Price. Academic Press, San Diego.

Rossiter, M., 1996 Incidence and consequences of inherited environmental effects. Ann. Rev. Ecol. Syst. **27:** 451–476.

Sinervo, B., and P. Doughty, 1996 Interactive effects of offspring size and timing of reproduction on offspring reproduction—experimental, maternal, and quantitative genetic aspects. Evolution **50:** 1314–1327.

Srb, A. M., R. D. Owen and R. S. Edgar, 1965 *General Genetics*, Ed. 2. W. H. Freeman, San Francisco.

Villham, R. L., 1963 The covariance between relatives for characters composed of components contributed by related individuals. Biometrics **19:** 18–27.

Villham, R. L., 1972 The role of maternal effects in animal breeding. III. Biometrial aspects of maternal effects in animals. J. Anim. Sci. **35:** 1288–1293.

Wade, M. J., 1996 The evolutionary genetics of maternal effects. (in press)

Wade, M. J., and R. W. Beeman, 1994 The population dynamics of maternal-effect selfish genes. Genetics **138:** 1309–1314.

Wolf, J. B., E. D. Brodie III, J. M. Cheverud, A. J. Moore and M. J. Wade, 1997 Evolutionary consequences of indirect genetic effects. Trends Ecol. Evol. **13:** 64–69.

Wright, S., 1969 *Evolution and the Genetics of Populations, Vol. II. The Theory of Gene Frequencies.* The University of Chicago Press, Chicago.

Communicating editor: W. H. Li

APPENDIX

In analyzing the dynamics of Equation 3 it is convenient to use new variables $u = 2x/y$ and $v = 2z/y$, which are defined for $y \neq 0$. The dynamic equations for u and v are

$$u' = \frac{\alpha u^2 + (\alpha + \beta)u + \beta}{\gamma uv + 1/2(\gamma + \delta)(u + v) + \delta}, \quad \text{(A1a)}$$

$$v' = \frac{\alpha v^2 + (\alpha + \beta)v + \beta}{\gamma uv + 1/2(\gamma + \delta)(u + v) + \delta}. \quad \text{(A1b)}$$

Subtracting Equation A1a from Equation A1b,

$$u' - v' = \frac{\alpha + \beta + \alpha(u + v)}{\gamma uv + 1/2(\gamma + \delta)(u + v) + \delta}(u - v). \quad \text{(A2)}$$

The last equality means that at equilibrium either $u = v$, or

$$\frac{\alpha + \beta + \alpha(u + v)}{\gamma uv + 1/2(\gamma + \delta)(u + v) + \delta} = 1. \quad \text{(A3)}$$

if $v = u$, Equation A1b takes the form

$$u' = \frac{\alpha u + \beta}{\gamma u + \delta} \equiv F(u). \quad \text{(A4)}$$

It is easy to see that $F(u)$ is a monotonic function of u with no inflection points. Thus, the equation $u = F(u)$ has a single positive solution, which defines the value of u at the symmetric polymorphic equilibrium and is given in Result 2.

The symmetric equilibrium is stable with respect to symmetric perturbations (such that perturbed values of u and v are equal), if at this equilibrium

$$-1 < \frac{dF(u)}{du} < 1.$$

The latter inequality follows from the fact that the graph of $Y = F(u)$ crosses the line $Y = u$ from left to right. The former inequality can be proven after calculating dF/du and plugging in the equilibrium value of u. Thus, the symmetric equilibrium is always stable to symmetric perturbations. To analyze the stability of this equilibrium to asymmetric perturbations (such that perturbed values $u \neq v$), one needs to analyze Equation A2. This equation tells us that the equilibrium is stable if the expression in the left-hand side of Equation A3 is <1. Rewriting this condition under the assumption that both u and v are equal to the equilibrium value defined by Equation A4, one finds Equation 6, which completes the proof of Result 3.

Combining Equation A3 with Equation A2 at equilibrium, one finds that at asymmetric equilibria

$$uv = \beta/\alpha, \quad \text{(A5a)}$$

$$u + v = \frac{\delta - \alpha + \beta/\alpha(\gamma - \alpha)}{\alpha - (\gamma + \delta)/2} \equiv T. \quad \text{(A5b)}$$

Eliminating v, one finds that equilibrium values of u satisfy to a quadratic $u^2 - Tu + \beta/\alpha = 0$, which has both roots positive and real if $T > 2\sqrt{\beta/\alpha}$. The latter is the condition of existence of unsymmetric polymorphic equilibria stated in Result 4. Equilibrium values of genotype frequencies can be found by using the inverse transformation $x = u/(2 + u + v)$, $y = 2/(2 + u + v)$, $z = v/(2 + u + v)$.

If $\beta = \delta = 0$, the values of u and v at the unsymmetric equilibria are $(0, \alpha/(\gamma/2 - \alpha))$ and $(\alpha/(\gamma/2 - \alpha), 0)$. Thus, these equilibria are feasible if $\alpha < \gamma/2$. The eigenvalues of the stability matrix at these equilibria are $2\alpha/\gamma$ and $1 - 2\alpha/\gamma$. For the unsymmetric equilibria to be stable these eigenvalues should lie between -1 and 1, which is obviously the case given that the equilibria exist. This completes the proof of Result 5.

Using Equations 4 and 6 from Hadeler and Liberman (1975), one finds that if $\alpha = \beta = 0$, the only equilibrium of Equation 12 satisfies to the cubic

$$\varepsilon w^3 + w - 1 = 0, \quad \text{(A6)}$$

where $\varepsilon = \delta/\gamma$. The eigenvalue that determines stability of this equilibrium is equal to $-2\varepsilon w^3$. One can easily show that if $\varepsilon < 4$, then $\varepsilon w^3 < 1/2$ and hence the symmetric polymorphic equilibrium is stable. On the other hand, if $\varepsilon > 4$, then $\varepsilon w^3 > 1/2$ and hence the symmetric polymorphic equilibrium is unstable. This completes the proof of Result 6. Note that iterating Equation 4 from Hadeler and Liberman (1975) twice one can easily find the genotype frequencies corresponding to the two-cycle symmetric solution of Equation 12. The fact that the right-hand side of Equation 4 from Hadeler and Liberman (1975) is a monotonically decreasing function implies that this equation does not have any other periodic solutions.