

# THE PRICE EQUATION, FISHER'S FUNDAMENTAL THEOREM, KIN SELECTION, AND CAUSAL ANALYSIS

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**Abstract.**—A general framework is presented to unify diverse models of natural selection. This framework is based on the Price Equation, with two additional steps. First, characters are described by their multiple regression on a set of predictor variables. The most common predictors in genetics are alleles and their interactions, but any predictor may be used. The second step is to describe fitness by multiple regression on characters. Once again, characters may be chosen arbitrarily. This expanded Price Equation provides an exact description of total evolutionary change under all conditions, and for all systems of inheritance and selection. The model is first used for a new proof of Fisher's fundamental theorem of natural selection. The relations are then made clear among Fisher's theorem, Robertson's covariance theorem for quantitative genetics, the Lande-Arnold model for the causal analysis of natural selection, and Hamilton's rule for kin selection. Each of these models is a partial analysis of total evolutionary change. The Price Equation extends each model to an exact, total analysis of evolutionary change for any system of inheritance and selection. This exact analysis is used to develop an expanded Hamilton's rule for total change. The expanded rule clarifies the distinction between two types of kin selection coefficients. The first measures components of selection caused by correlated phenotypes of social partners. The second measures components of heritability via transmission by direct and indirect components of fitness.

**Key words.**—Natural selection, path analysis, population genetics, quantitative genetics.

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There are many different mathematical approaches to the study of natural selection. Each point of view provides its own key result. There is Fisher's (1958) fundamental theorem for population genetics, Robertson's (1966) covariance theorem for quantitative genetics, and Hamilton's (1964) rule for kin selection. Systems of gene-culture inheritance or arbitrary selective systems must also follow these fundamental results. However, such systems have rarely been studied in full generality and tied to the well-developed results of genetics.

One issue is that each mathematical approach tends to focus on a partial analysis of total change. Since the parts included and excluded by different approaches may differ, relationships among approaches are often obscure. This suggests that a proper framework begin with an exact, complete model for total evolutionary change. Various approaches can then be compared against this touchstone.

A second problem for a general theory is how to partition the causes of character values among predictor variables. The standard approach is to fit a regression model, describing a character by the individual contributions of various predictors (Fisher 1918, 1958). The typical predictors are alleles and interactions among alleles, but any predictor may be used. The regression approach, based on least squares analysis, has the advantages of maximizing the use of information about phenotype available in the data, and rendering additive the individual contributions of various factors.

Once a regression model has been fit for a particular character and its predictor variables, total change in the character can be partitioned into two components. The first is the direct effect of natural selection in changing the frequency of the predictor variables, for example, a change in allele frequency. The second component is the difference in the contribution

of each predictor variable in the context of the changed population, the fidelity of transmission. This partition is the central feature of Fisher's (1958) fundamental theorem of natural selection (Price 1972a; Ewens 1989), yet the properties of this partition have rarely been exploited (Frank and Slatkin 1992).

I begin with the Price Equation, which is an exact, complete description of natural selection and its evolutionary consequences. When a regression model is fit for a character using any arbitrary set of predictors, the Price Equation describes the total change in the character by analysis of the predictor variables. A natural partition follows between the two components mentioned above, frequency change of predictors caused directly by natural selection and changes in the effects of each predictor after transmission. The natural selection component can itself be partitioned into distinct causes. This partition is the familiar causal analysis of fitness by multiple regression (Lande and Arnold 1983).

I use the Price Equation to link Fisher's fundamental theorem, multiple regression models of natural selection, and kin selection. I also expand these results to arbitrary selective systems and types of inheritance. My expansion is an exact framework that uses both alleles and contextual variables to explain the evolutionary change of characters. Contextual variables include maternal effects, group-level traits, cultural beliefs, or any other factor that can explain some of the variance in character values and fitness (Heisler and Damuth 1987; Goodnight et al. 1992).

## PREDICTORS AND PARTITIONS

A brief example of predictors and partitions is useful before starting. Let  $z$  be a variable influenced by a set of predictors,  $\{x_j\}_{j=1}^n$ , where each  $x_j$  takes values of zero or one for presence or absence of some factor. Each instance of the variable,  $z_i$ ,

has among its predictors  $x_{ij}$ , a total of  $k$  factors present and  $n - k$  factors absent, thus  $\sum_{j=1}^n x_{ij} = k$ . By the standard theory of least squares we can write

$$z_i = \sum_j b_j x_{ij} + \delta_i,$$

where  $b_j$  is the partial regression of  $z$  on  $x_j$  and  $\delta_i$  is the unexplained residual. The average of  $z$  is  $\bar{z} = \sum b_j \bar{x}_j$  because we may set  $\bar{\delta} = 0$ . Each  $\bar{x}_j$  is the frequency of the  $j$ th predictor in the population. If we use primes to denote the population at a later time, then we can also write a second regression equation in which  $\bar{z}' = \sum b'_j \bar{x}'_j$ . It will be useful to have a symbol for the change in each quantity:  $\Delta \bar{z} = \bar{z}' - \bar{z}$ ,  $\Delta \bar{x}_j = \bar{x}'_j - \bar{x}_j$ , and  $\Delta b_j = b'_j - b_j$ . The change in the average value of the variable over time is

$$\begin{aligned} \Delta \bar{z} &= \sum_j b'_j \bar{x}'_j - \sum_j b_j \bar{x}_j \\ &= \sum_j (b_j + \Delta b_j)(\bar{x}_j + \Delta \bar{x}_j) - \sum_j b_j \bar{x}_j \\ &= \sum_j b_j (\Delta \bar{x}_j) + \sum_j \bar{x}'_j (\Delta b_j). \end{aligned} \quad (1)$$

This example shows the partition between two components of total change in a variable. The first component is the change in the frequency of predictors,  $b\Delta\bar{x}$ . The second component is the difference in the effect of predictors,  $\Delta b$ , in the context of the changed population,  $\bar{x}'$ . This partition is always true, but is difficult to interpret in terms of selection. For a selective analysis, it is useful to have a measure of fitness and a measure of transmission. Fitness describes differential reproductive success as a function of character values. Transmission describes the degree to which an offspring is similar to its parent.

The Price Equation is the same partition for  $\Delta \bar{z}$ , but written in a more general form and in a manner that emphasizes selection and transmission. I develop the Price Equation in the next section. I then apply Price's partition to a character that is expressed in terms of predictors and regression coefficients, yielding the partition in equation (1) written in terms of selection and transmission. A simple proof of Fisher's fundamental theorem follows immediately.

I then use the Lande-Arnold (1983) partition of selection into multiple components. That partition provides a very general theory when combined with the previous analyses. I show the power of this formalism by clarifying two aspects of Hamilton's rule of kin selection. First, the rule may be viewed as a partition of selection into social components (Queller 1992a,b). Second, the rule may be interpreted as a partition of transmission into components of heritability. Some problems can be interpreted equivalently by partition of selection or by partition of heritability. Other problems require clear separation between selection and transmission, a point that is often confused in the literature. I also develop an exact analysis of social evolution, and show that the standard approximation for kin selection is formally equivalent to one part of Fisher's fundamental theorem.

#### THE PRICE EQUATION

The Price Equation is an exact, complete description of evolutionary change under all conditions (Price 1970,

1972b). The equation provides insight into many evolutionary problems by partitioning change into meaningful components (Frank 1995).

Here is the derivation. Let there be a population (set) in which each element is labeled by an index  $i$ . The frequency of elements with index  $i$  is  $q_i$ , and each element with index  $i$  has some character,  $z_i$ . One can think of elements with a common index as forming a subpopulation that makes up a fraction  $q_i$  of the total population. No restrictions are placed on how elements may be grouped.

A second (descendant) population has frequencies  $q'_i$  and characters  $z'_i$ . The change in the average character value,  $\bar{z}$ , between the two populations is

$$\Delta \bar{z} = \sum q'_i z'_i - \sum q_i z_i. \quad (2)$$

Note that this equation applies to anything that evolves, since  $z$  may be defined in any way. For example,  $z_i$  may be the gene frequency of entities  $i$ , and thus  $\bar{z}$  is the average gene frequency in the population, or  $z_i$  may be the square of a quantitative character, so that one can study the evolution of variances of traits. Applications are not limited to population genetics. For example,  $z_i$  may be the value of resources collected by bees foraging in the  $i$ th flower patch in a region (Frank 1997), or cash flow of a business competing for market share.

Both the power and the difficulty of the Price Equation come from the unusual way it associates entities from two populations, which are typically called the ancestral and descendant populations (see Appendix A). The value of  $q'_i$  is not obtained from the frequency of elements with index  $i$  in the descendant population, but from the proportion of the descendant population that is derived from the elements with index  $i$  in the parent population. If we define the fitness of element  $i$  as  $w_i$ , the contribution to the descendant population from type  $i$  in the parent population, then  $q'_i = q_i w_i / \bar{w}$ , where  $\bar{w}$  is the mean fitness of the parent population.

The assignment of character values  $z'_i$  also uses indices of the parent population. The value of  $z'_i$  is the average character value of the descendants of index  $i$ . Specifically, for an index  $i$  in the parent population,  $z'_i$  is obtained by weighting the character value of each entity in the descendant population by the fraction of the total fitness of  $i$  that it represents (Appendix A). The change in character value for descendants of  $i$  is defined as  $\Delta z_i = z'_i - z_i$ .

Equation (2) is true with these definitions for  $q'_i$  and  $z'_i$ . We can proceed with the derivation by a few substitutions and rearrangements:

$$\begin{aligned} \Delta \bar{z} &= \sum q_i (w_i / \bar{w})(z_i + \Delta z_i) - \sum q_i z_i \\ &= \sum q_i (w_i / \bar{w} - 1) z_i + \sum q_i (w_i / \bar{w}) \Delta z_i \end{aligned}$$

using standard definitions from statistics for covariance (Cov) and expectation (E), yields the Price Equation

$$\bar{w} \Delta \bar{z} = \text{Cov}(w, z) + E(w \Delta z). \quad (3)$$

The two terms may be interpreted in a wide variety of ways because of the minimal restrictions used in the derivation (Hamilton 1975; Wade 1985; Frank 1995). One interpretation partitions total change into parts caused by selection and

transmission, respectively. The covariance between fitness and character value gives the change in the character caused by differential productivity. The expectation term is a fitness-weighted measure of the change in character value between ancestor and descendant—a measure of the transmission fidelity of a character between parent and offspring.

The Price Equation's notation and abstract description of selection may seem unfamiliar on first reading. Appendix A provides a brief tutorial that illustrates several concepts and notational conventions, particularly the unusual method of labeling descendant types. Appendix B summarizes various partitions of evolutionary change, and lists some of the symbols used throughout the paper.

## CAUSAL ANALYSIS

I describe two types of partition in this section. The first is the Lande-Arnold (1983) regression for assigning components of fitness to multiple traits. The second is Fisher's (1958) regression for assigning components of trait values to multiple predictors, which I briefly outlined in an earlier section.

These two partitions are the foundation of quantitative genetics. I make two additions to the theory. First, I obtain a simple and general proof of Fisher's fundamental theorem by using Fisher's regression for characters in the Price Equation. Second, I combine the Lande-Arnold regression for fitness with Fisher's regression for characters. The Price Equation shows precisely how these two regressions must fit together. Indeed, from the abstract perspective of the Price Equation, one can see how each partition arises naturally in a complete analysis of any kind of selective system.

### Predictors of Fitness

It is often convenient to consider explicitly the various factors that influence fitness. Multiple regression provides a useful set of tools, where one describes or estimates from data the direct effects of various predictors on fitness

$$w = \alpha + \pi z + \beta' \mathbf{y} + \epsilon \quad (4)$$

where  $\pi$  is the direct (partial regression) effect on fitness by the character under study,  $z$ , holding the other predictors  $\mathbf{y} = (y_1, \dots, y_n)^T$  constant,  $\beta' = (\beta_1, \dots, \beta_n)$  are the partial regression coefficients for the predictors,  $\mathbf{y}$ , and  $\epsilon$  is the error in prediction.

Lande and Arnold (1983) developed the analysis of selection and change in character values within generations by study of

$$\begin{aligned} \bar{w}\Delta\bar{z} &= \text{Cov}(w, z) + T \\ &= \pi \text{Cov}(z, z) + \sum_i \beta_i \text{Cov}(y_i, z) + \text{Cov}(z, \epsilon) + T \end{aligned} \quad (5)$$

where  $T$  is change during transmission (see next paragraph). This equation describes the direct effect of the character,  $z$ , on its own change, and the effect of correlated characters,  $\mathbf{y}$ , on the character  $z$ . Heisler and Damuth (1987) and Goodnight et al. (1992) noted that one is free to use any predictors,  $\mathbf{y}$ , of interest. In particular, they emphasized that characteristics

of groups can be used, allowing analysis of the direct effects of selection on group properties and the consequences for evolutionary change. I will return to this topic in a later section on kin selection.

Lande and Arnold (1983) extended their analysis to describe the response to selection, that is, the change in character values from one generation to the next. They used a partial form of heritability to transform changes within a generation into approximate changes between generations. I take the same approach, but derive my formulation of heritability with the formally abstract and precise methods of the Price Equation, by which one can see that  $T$  in equation (5) is  $E(w\Delta z)$ . This provides an exact analysis, with new insight into Fisher's fundamental theorem and kin selection.

### Predictors of Characters

The difficulty for any method of describing character change between generations is that observed character values,  $z$ , will have many causes that are not easily understood. Further, some of those causes, such as random environmental effects, will not be transmissible to the next time period, so that  $\Delta z$  in the second term of equation (3) will be erratic and difficult to understand. It would be much better if instead of working with  $z$  as the character under study we focus on those predictors of the character that can be clearly identified. It would also be useful if the transmissible properties of the predictive factors could be easily understood, so that some reasonable interpretation is possible for  $\Delta z$ .

Let a set of potential predictors be  $\mathbf{x} = (x_1, \dots, x_n)^T$ . Then any character  $z$  can be written as  $z = \mathbf{b}'\mathbf{x} + \delta$ , where the  $\mathbf{b}'$  are partial regression coefficients for the slope of the character  $z$  on each predictor,  $x$ , and  $\delta$  is the unexplained residual. The additive, or average, effect of each predictor,  $bx$ , is uncorrelated with the residual,  $\delta$ .

In genetics the standard predictors are the hereditary particles (alleles). We write the regression equation for the character  $z$  of the  $i$ th individual in the usual way as

$$z_i = \sum_j b_j x_{ij} + \delta_i = g_i + \delta_i, \quad (6)$$

where  $g_i = \sum_j b_j x_{ij}$  is called the breeding value or additive genetic value. The breeding value is the best linear fit for the set of predictors,  $\mathbf{x}_i$ , in the  $i$ th individual. Each  $x_{ij}$  is the number of copies of a particular allele  $j$ , in an individual  $i$ . If we add the reasonable constraint that the total number of alleles per individual is constant,  $\sum_j x_{ij} = k$ , then the degree of freedom "released" by this constraint can be used among the  $b$ s to specify the mean of  $z$ . Thus, we can take  $\bar{z} = \bar{g}$  and  $\bar{\delta} = 0$ .

The breeding value,  $g$ , is an important quantity in applied genetics (Falconer 1989). The best predictor of the trait in an offspring is usually  $(1/2)(g_m + g_f)$ , where  $g_m$  and  $g_f$  are genetic values of mother and father. There is, of course, nothing special about genetics in the use of best linear predictors in the Price Equation. The trait  $z$  could be corporate profits, with predictors,  $\mathbf{x}$ , of cash flow, years of experience by management, and so on.

*Price Equation Analysis of Predictors*

A slightly altered version of equation (3) will turn out to be quite useful in the following sections. First, any trait can be written as  $z = g + \delta$ , where  $g$ , the sum of the average effects, is uncorrelated with the residuals,  $\delta$ . Average trait value is  $\bar{z} = \bar{g}$ , as explained in the previous section. In the next time period  $z' = g' + \delta'$  and  $\bar{z}' = \bar{g}'$ . Thus the change in average trait value is  $\bar{z}' - \bar{z} = \Delta\bar{z} = \Delta\bar{g}$ . To study the change in average trait value we need to analyze only  $\Delta\bar{g}$ , so we can use  $z \equiv g$  in the Price Equation, yielding

$$\bar{w}\Delta\bar{z} = \bar{w}\Delta\bar{g} = \text{Cov}(w, g) + E(w\Delta g) \quad (7)$$

$$= \beta_{wg}V_g + E(w\Delta g), \quad (8)$$

where, by definition of linear regression,  $\text{Cov}(w, g)$  can be partitioned into the product of the total regression coefficient,  $\beta_{wg}$ , and the variance in trait value that can be ascribed to our set of predictors,  $V_g$ . In genetics,  $g$  is the (additive) genetic value and  $V_g$  is the genetic variance.

Robertson (1966), in a different context, derived  $\text{Cov}(w, g)$  as the change in a character caused by natural selection. This covariance result is called Robertson's secondary theorem of natural selection, and is the form used by Lande and Arnold (1983) to describe evolutionary change between generations. Robertson did not provide a summary of the remainder of total change not explained by the covariance term. Crow and Nagylaki (1976), expanding an approach developed by Kimura (1958), specified a variety of remainder terms that must be added to the covariance. They provided the remainders in the context of specific types of Mendelian genetic interactions, such as dominance, epistasis, and so on. The Price Equation has the advantages of being simple, exact, and universal, and we can see from equation (7) that, for total change, it is the term  $E(w\Delta g)$  that must be added to the covariance term (see the section below, Predictors and Additivity).

*Heritability: Variance Components and Fidelity of Transmission*

These two aspects of heritability are sometimes confused. The covariance term, when analyzed with respect to additive genotype,  $g$ , implicitly accounts for variance components

$$\begin{aligned} \text{Cov}(w, g) &= \beta_{wg}V_g \\ &= \beta_{wg}V_z(V_g/V_z) \\ &= \beta_{wg}V_zV_h, \end{aligned}$$

where  $V_z$  is the phenotypic variance in  $z$ , and  $V_h = V_g/V_z$  is the proportion of phenotypic variance accounted for by additive genotype. The ratio,  $V_h$ , often denoted by  $h^2$ , is a commonly used measure of heritability.

It may be that fitness is described only by its slope on phenotype rather than additive genotype. Thus  $w = \alpha + \beta_{wz}z + \epsilon_z$ , and

$$\begin{aligned} \text{Cov}(w, g) &= \text{Cov}(\beta_{wz}z + \epsilon_z, g) \\ &= \text{Cov}(\beta_{wz}(g + \delta) + \epsilon_z, g) \\ &= \beta_{wz}V_g + \text{Cov}(\epsilon_z, g) \\ &= \beta_{wz}V_zV_h + \text{Cov}(\epsilon_z, g), \end{aligned}$$

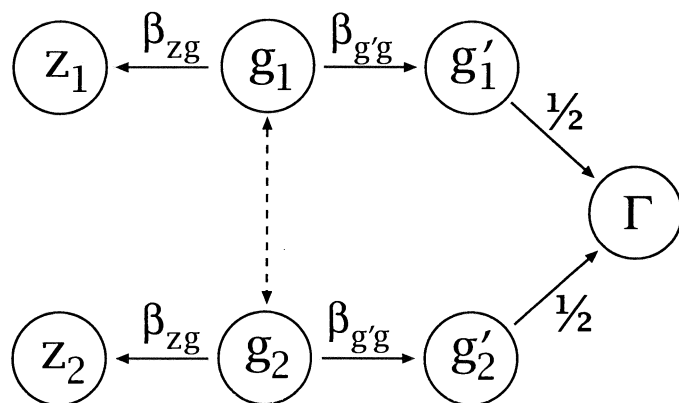


FIG. 1. Path diagram for the standard model of genetic transmission. Parental phenotype,  $z$ , is caused by genotype,  $g$ , which determines the genotypic value,  $g'$  transmitted to offspring. Each parent contributes one-half of the genotype of the offspring, so offspring genotypic value is  $\Gamma = (\frac{1}{2})(g'_1 + g'_2)$ . One measure of total heritability is the regression of parental contribution to offspring genotypic value on parental phenotype,  $\beta_{g'z}$ . The slope  $\beta_{zg}$  is normalized to one, and thus  $\beta_{g'z} = \beta_{zg}V_g/V_z = V_h$ . Therefore total heritability is the product of the fidelity of transmission and the variance ratio,  $\beta_{g'z} = \beta_{g'g}\beta_{gz} = \beta_{g'g}V_h$ . The distinction between  $\Gamma$  and  $g'$  is discussed in Appendix A. Li (1975) provides a good introduction to path analysis.

where  $\text{Cov}(\epsilon_z, g)$  is sometimes called genotype-by-environment interaction.

These standard equations of quantitative genetics do not account for how the additive, or average, effect of genotype may change between parent and offspring. In other words,  $\Delta g = g' - g$  in the  $E(w\Delta g)$  term of the Price Equation is ignored. An alternative approach from classical quantitative genetics is to measure heritability by offspring-parent phenotypic regressions. This can potentially confound two distinct factors, the proportion of phenotypic variance explained by additive genotype among the parents,  $V_h = V_g/V_z$ , and the change in the average effect of predictors between parent and offspring,  $\Delta g$ .

A clear separation between genetic variance and transmission is crucial in the causal analysis of selection. In particular, I will show later that two different kinds of kin selection coefficients have been confused because of a failure to separate between the effects of selection and the fidelity of transmission.

Separation of variance components and transmission is accomplished by starting with three basic regressions

$$\begin{aligned} w &= \alpha + \beta_{wg}g + \epsilon \\ g' &= \beta_{g'g}g + \gamma \\ z &= g + \delta, \end{aligned} \quad (9)$$

where in the last regression the slope is implicitly  $\beta_{zg} = 1$ . The fidelity of transmission,  $\beta_{g'g}$ , is illustrated in Figure 1. Using the first two regressions directly in the standard Price Equation, equation (7), yields

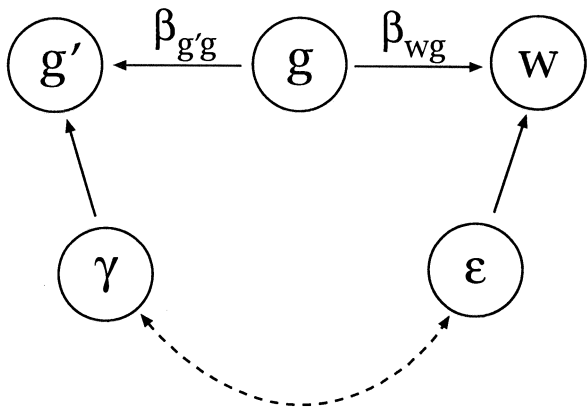


FIG. 2. Path diagram for selection and transmission. The diagram corresponds to equation (13).

$$\Delta \bar{g} = \beta_{wg} V_g \beta_{g'g} / \bar{w} + D_g + \text{Cov}(\epsilon, \gamma) / \bar{w}, \quad (10)$$

where

$$D_g = E(\Delta g) = \bar{\gamma} - (1 - \beta_{g'g}) \bar{g} \quad (11)$$

is the average difference in the effect of predictors between parent and offspring. The average is taken with respect to parental frequencies,  $q_i$ .

#### Direction of Selection

One advantage of equation (10) is that the first term on the right side combines all effects of fitness,  $w$ . This allows analysis of the evolutionary direction favored by selection according to whether this term is positive or negative. A bit of algebra and two path diagrams clarify the interpretation of this important term, which I develop in a later section on kin selection.

An alternative partition of total change can be obtained by starting with the first step in the derivation of the Price Equation, but collecting effects in a different way

$$\begin{aligned} \Delta \bar{g} &= \sum q'_i g'_i - \sum q_i g_i \\ &= \sum q_i (w_i / \bar{w}) g'_i - \bar{g} \\ &= \text{Cov}(w, g') / \bar{w} + \sum q_i (g'_i - g_i) \\ &= \beta_{wg'} V_{g'} / \bar{w} + D_{g'}. \end{aligned} \quad (12)$$

The role of fitness is entirely summarized by the term  $\beta_{wg'}$ . This regression is clarified in Figure 2, based on the regression equations in equation (9). Genotype,  $g$ , affects fitness according to  $\beta_{wg}$ , and  $g$  affects  $g'$  according to the fidelity of transmission,  $\beta_{g'g}$ . Using the standard statistical definitions of regression coefficients yields the algebraic description of the diagram in Figure 2

$$\beta_{wg'} V_{g'} = \beta_{wg} V_g \beta_{g'g} + \text{Cov}(\epsilon, \gamma). \quad (13)$$

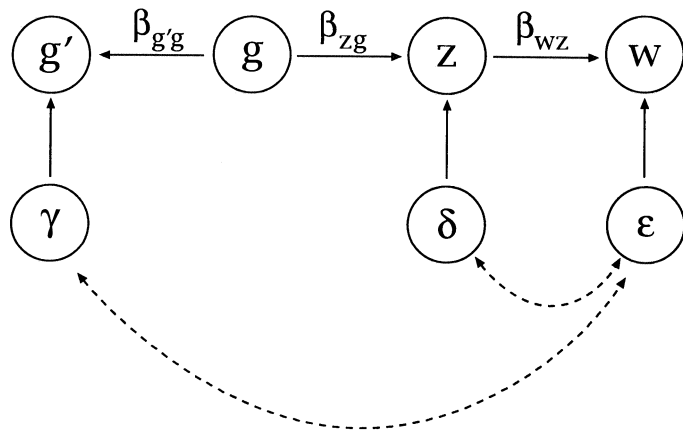


FIG. 3. Path diagram for selection and transmission, with explicit use of phenotype,  $z$ . The diagram corresponds to equation (14).

Typically, in the analysis of how selection influences the direction of evolutionary change, one ignores the error covariance,  $\text{Cov}(\epsilon, \gamma)$ . One also assumes that offspring-parent regression of genotype is greater than zero,  $\beta_{g'g} > 0$ . Thus the direction of evolutionary change caused by selection is described by  $\beta_{wg} V_g$ , as in the covariance term of the standard Price Equation. However, I will show later that keeping track of  $\beta_{g'g}$  is often crucial for successful analysis of the direction of selection.

We can also include phenotype in the causal analysis, as in Figure 3, which matches the expression

$$\beta_{wg'} V_{g'} = \beta_{wz} V_z V_h \beta_{g'g} + \text{Cov}(\epsilon, \gamma) + \text{Cov}(\epsilon, \delta). \quad (14)$$

#### Predictors and Additivity

Confusion sometimes arises about the flexibility of predictors and of the Price Equation. The method itself adds or subtracts nothing from logical relations; the method is simply notation that clarifies relations. For example, in equation (6), I partitioned a character into the average, or additive, effect of individual predictors (alleles). One could just as easily study the multiplicative effect of pairs of alleles, including dominance and epistasis, by

$$z_i = \sum_j b_j x_{ij} + \sum_j \sum_k \phi_{jk} x_{ij} x_{ik} + \delta_i = g_i + m_i + \delta_i,$$

where  $\phi_{jk}$  is the partial regression for multiplicative effects, and  $m_i$  is the total multiplicative effect of alleles. Then the analogous, exact expression for equation (7) is

$$\bar{w} \Delta \bar{z} = \bar{w} \Delta (\bar{g} + \bar{m}) = \text{Cov}(w, g + m) + E[w(\Delta g + \Delta m)].$$

Examples of the Price Equation applied to dominance and epistasis are in Frank and Slatkin (1990). That paper showed how to calculate character change during transmission by direct calculation of  $E[w(\Delta g + \Delta m)]$ . With respect to the general problem of additivity of effects, it is useful to recall the nature of least squares analysis in regression. This anal-

ysis makes additive the contribution of each factor, for example,  $g + m$ . But a factor, such as  $m$ , may be created by any functional combination of the individual predictors.

What is additivity? Unfortunately the term is used in different ways. Consider two contrasting definitions. First, one can fit a partial regression (average effect) for each predictor in any particular population. The effects of each predictor can then be added to obtain a prediction for character value. Interactions among predictors (dominance and epistasis) can also be included in the model, and these partial regression terms are also added to get a prediction. The word additivity is sometimes used to describe the relative amount of variance explained by the direct effects of the predictors versus interactions among predictors.

Second, one can compare regression models between two different populations, for example, parent and offspring generations. If the partial regression coefficients for each predictor remain constant between the two populations, then the effects are sometimes said to be additive. This may occur because the context has changed little between the two populations, or because the predictors have constant effects over very different contexts.

Constancy of the average effects implies  $E(w\Delta g) = 0$  in many genetical problems. This sometimes leads people to say that the equality requires or assumes additivity, but I find little meaning in that statement. Small changes in  $E(w\Delta g)$  simply mean that the partial regression coefficients for various predictors have remained stable, either because the context has changed little or because the coefficients remain stable over varying contexts. Constancy may occur whether the relative amount of variance explained by the direct effects of the individual predictors is low or high.

#### FISHER'S FUNDAMENTAL THEOREM

R. A. Fisher (1930) stated his famous fundamental theorem of natural selection: "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time." He claimed that this law held "the supreme position among the biological sciences" and compared it with the second law of thermodynamics. Yet for 42 years no one could understand what the theorem was about, although it was frequently misquoted and misused to support a variety of spurious arguments (Frank and Slatkin 1992; Edwards 1994). Approximations and special cases were proved, but those sharply contradicted Fisher's claim of the general and essential role of his discovery. Price (1972a) was the first to explain the theorem and its peculiar logic. Price's work, known only to a few specialists, was clarified by Ewens (1989). Yet this history leaves two important paradoxes unresolved. First, the current proofs, although following Fisher's outline, lack the elegance and generality expected of a fundamental law. Second, Price's (1970) own great contribution, the Price Equation, has a tantalizingly similar structure to the fundamental theorem, yet Price himself did not relate the two theories in any way. In this section I provide a new proof of the fundamental theorem, following directly from the Price Equation.

#### The Fundamental Theorem from the Price Equation

We can prove the fundamental theorem of natural selection directly from equation (8). The trait of interest is fitness itself,  $z \equiv w$ , and, as for other traits, we write  $w = g + \delta$ . Thus  $\beta_{wg} = 1$  and  $V_g$  is the genetic variance in fitness. Fisher was concerned with the part of the total change when the average effect of each predictor is held constant (Price 1972a; Ewens 1989). Since  $g$  is simply a sum of the average effects, holding the average effect of each predictor constant is equivalent to holding the breeding values,  $g$ , constant, thus  $E(w\Delta g) = 0$  (see next section for details). The remaining partial change is the genetic variance in fitness,  $V_g$ , thus we may write

$$\Delta_f \bar{w} = \text{Cov}(w, g) / \bar{w} = V_g / \bar{w}, \quad (15)$$

where  $\Delta_f$  emphasizes that this is a partial, fisherian change obtained by holding constant the contribution of each predictor.

Although equation (15) looks exactly like Fisher's fundamental theorem, I must add important qualifications in the next sections. But first let us review the assumptions. The Price Equation is simply a matter of labeling entities from two sets in a corresponding way. The two sets are usually called parent and offspring. With proper labeling, the covariance and expectation terms follow immediately from the statistical definitions. For any trait we can write  $z = g + \delta$ , where  $g$  is the sum of effects from a set of predictor variables, the effects obtained by minimizing the summed distances between prediction and observation. This guarantees  $g$  is uncorrelated with  $\delta$ . If we substitute into the Price Equation, the result in equation (8) follows immediately. Fisher was concerned with the part of the total change in fitness obtained when the effect of each predictor is held constant, yielding equation (15). Thus equation (15) is obtained by using the best predictors of the trait substituted for the trait itself, and holding constant the effects of the predictors.

#### The Fisher-Price-Ewens Form

We could move directly from the simple results of the previous section to a discussion of the fundamental theorem. However, the history of the fundamental theorem is long and confused. Price (1972a) and Ewens (1989) have cleared up most issues, and it is useful to connect my results to theirs. This requires a bit of tedious algebra, but it does bring out one interesting conceptual issue regarding whether the fundamental theorem is truly universal in scope, as Fisher claimed, or is in fact limited by particular assumptions. This issue concerns whether frequency change in the predictors (alleles) must be fully described by differential fitness.

In the previous section, I used  $q_i$  for the frequency of the  $i$ th unit in the population. The index  $i$  can be applied to arbitrary groupings of predictors, for example the genotype of individuals, the genotype of mating pairs, social groups of individuals, and so on. In each case  $i$  labels units with the same set of predictor values, for example, the same genotype.

The standard form of Fisher's fundamental theorem of natural selection (FTNS) is given in terms of alleles or, in my usage, in terms of the individual predictors. Population ge-

netic models assume that each particular allele can occur only at a particular locus, and each locus has  $n$  alleles. In diploid genetics,  $n = 2$ , for tetraploids or for mating pairs with two individuals forming a group,  $n = 4$ . Thus the frequency of a particular allele (predictor) is

$$r_j = \sum_i q_i x_{ij}/n,$$

where the usage of  $x_{ij}$  is established in equation (6).

Fisher described the theorem in terms of two quantities, the average effect and the average excess of an allele. The average effect is simply a standardized regression coefficient from equation (6)

$$z_i = \sum_j b_j x_{ij} + \delta_i = \bar{z} + \sum_j \alpha_j x_{ij} + \delta_i, \quad (16)$$

where  $\sum_j r_j \alpha_j = 0$  and thus the average effect,  $\alpha_j$ , of allele  $j$ , is a standardized form of the regression coefficient  $b_j$ , such that  $\alpha_j = b_j - \bar{b}$ .

The average excess in fitness is a basic part of the Price Equation. Recall that, for entities  $i$ , the frequency of descendants that come from  $i$  is  $q_i' = q_i w_i / \bar{w}$ , so that the change in frequency is

$$\Delta q_i = q_i' - q_i = q_i w_i / \bar{w} - q_i = q_i (w_i - \bar{w}) / \bar{w} = q_i A_i / \bar{w},$$

where  $A_i = w_i - \bar{w}$  is the average excess in fitness for the entity  $i$ . It is also useful to note that, for any trait,  $z$ , and any arbitrary level of indexing,  $i$ ,

$$\text{Cov}(w, z) / \bar{w} = \sum q_i (w_i - \bar{w}) z_i / \bar{w} = \sum q_i A_i z_i / \bar{w}. \quad (17)$$

The average excess of allele (predictor)  $j$  is simply the marginal excess. In standard  $n$ -ploid genetics, the marginal excess for allele  $j$  is

$$a_j = \frac{\sum_i q_i A_i x_{ij} / n}{\sum_i q_i x_{ij} / n} = \frac{\sum_i q_i A_i x_{ij} / n}{r_j} = W_j - \bar{w}, \quad (18)$$

with the marginal fitness as

$$W_j = \frac{\sum_i q_i w_i x_{ij} / n}{\sum_i q_i x_{ij} / n} = \frac{\sum_i q_i w_i x_{ij} / n}{r_j}.$$

Thus, for alleles,  $j$ , we have a similar expression as for groupings  $i$ ,

$$\Delta r_j = r_j' - r_j = r_j W_j / \bar{w} - r_j = r_j (W_j - \bar{w}) / \bar{w} = r_j a_j / \bar{w}.$$

The frequency after selection,  $r_j'$ , is the frequency determined solely by differential fitness. This quantity may or may not be equal to the true frequency in the next generation,  $R_j'$ . For example, a biased mutation process not described in the  $W$  terms may change frequencies such that  $R_j' \neq r_j'$ . Fisher simply asserted, in his proof, that  $R_j' = r_j'$ , a point to which I will return in the following section.

Fisher stated his theorem as

$$n \sum_j r_j a_j \alpha_j / \bar{w} = n \sum_j (\Delta r_j) \alpha_j = V_g / \bar{w}, \quad (19)$$

where  $n = 2$  for the diploid genetics studied by Fisher. This

allelic form is the version proved by Price (1972a) and Ewens (1989).

I now show that my very simple proof, given in the prior section as equation (15), is equivalent to Fisher's form. I operated on inclusive groupings, indexed by  $i$ , and expanding equation (15)

$$\begin{aligned} \Delta_f \bar{w} &= \text{Cov}(w, g) / \bar{w} \\ &= \sum q_i A_i g_i / \bar{w} \\ &= \sum (\Delta q_i) g_i \\ &= V_g / \bar{w}. \end{aligned} \quad (20)$$

Formal equivalence to equation (19) is easy to prove by expanding with prior definitions

$$\begin{aligned} \sum_i q_i A_i g_i &= \sum_i q_i A_i \sum_j b_j x_{ij} \\ &= \sum_j \sum_i q_i A_i x_{ij} b_j \\ &= n \sum_j r_j a_j b_j \\ &= n \sum_j r_j a_j (\alpha_j + \bar{b}) \\ &= n \sum_j r_j a_j \alpha_j. \end{aligned} \quad (21)$$

This extended analysis simply shows that we can operate equivalently at any inclusive level of indexing that is convenient for a particular problem, as implied by the simple Price Equation proof given in equation (15).

### Discussion of the Fundamental Theorem

Fisher assumed that the frequency of alleles in the next time period,  $R_j'$ , is fully determined by changes that can be ascribed to differential fitness. In particular, the frequency caused by differential fitness is, by definition,  $r_j' = r_j W_j / \bar{w}$ , and the frequency change caused by differential fitness is  $\Delta r_j = r_j a_j / \bar{w}$ . I mentioned above that other forces, such as biased mutation, may change frequency, so that  $R_j' \neq r_j'$ .

Thus it is useful to separate two results. If we follow Fisher and assume that  $R_j' = r_j'$ , then in

$$\Delta_f \bar{w} = n \sum (\Delta r_j) \alpha_j = V_g / \bar{w} \quad (22)$$

the terms  $\Delta r_j$  describe the total changes in allele frequency. If we assume that natural selection changes allele frequencies but does not directly change average effects, then the partial change in fitness caused by natural selection is the total frequency change of alleles weighted by the average effect of each allele. Ewens (1989, 1992), in particular, has emphasized this total frequency interpretation, and Fisher himself certainly discussed the theorem from this point of view.

If we insist that  $R_j' = r_j'$  must hold for the FTNS to be true, then the scope of FTNS is limited to systems in which changes in predictor (allele) frequencies are fully described by the average excess in fitness,  $a_j$ . If, on the other hand, we interpret  $\Delta_f$  in equation (22) to be the partial change in fitness caused by natural selection, then it is reasonable to define

$\Delta r_j = r_j a_j / \bar{w} = r_j (W_j - \bar{w}) / \bar{w}$  as the partial change in allele frequencies caused directly by natural selection, where natural selection is interpreted as differential fitness. Under this broader interpretation, we do not require  $R'_j = r'_j$ . This leads to a universal result, true in all circumstances: the partial increase in mean fitness caused by natural selection is equal to the genetic variance in fitness.

I call this universal result the partial frequency fundamental theorem (PFFT) to emphasize that this applies to any selective system. In the PFFT, predictor frequency changes are assumed to be partial changes caused directly by natural selection and fully described by the average excess in fitness.

To put the matter another way, for a single factor one can obtain an exact, universal result only for a partial change. It is hopeless to look for an exact, universal expression for total change when the analysis is limited to one of many factors influencing total change. For FTNS, this limitation applies both to the total change in fitness, and to the total change in frequency.

The PFFT is always true. To show the narrower, total frequency FTNS, we need only prove  $R'_j = r'_j$ . For example, Lessard and Castilloux (1995) have recently studied FTNS for a traditional fertility selection model of population genetics. This model assumes that the number of offspring produced by a couple depends on interactions between the genotypes of the mother and father. Fitness can therefore not be ascribed to any individual but must be assigned to the joint genotype of mating pairs. In the Price Equation this is handled easily by defining  $w_i$  as the fitness of the  $i$ th kind of mating pair, where each kind of pair is defined by joint genotype. Given a traditional diploid model, in which each parent has  $n = 2$ , the mating pair can be described by a tetraploid genotype,  $n = 4$ . The proof for PFFT follows immediately from the Price Equation result in equation (15), and the total frequency FTNS follows by simply showing that  $R'_j = r'_j$ , a result included in Lessard and Castilloux's proof. Lessard and Castilloux's proof is, however, much more complicated because they started from standard population genetics theory and had to derive many results particular for the fertility selection model.

I have discussed the FTNS and the algebra at length. But we were done with the proof of the universal PFFT in equation (15) after a few brief and simple steps from the standard Price Equation. The remaining discussion and algebra was required to clarify the history and relate my simple Price Equation approach to the proofs given by Fisher, Price, and Ewens. This comparison highlighted the great flexibility of the Price Equation in working with any inclusive grouping, from alleles, to individuals, to mating pairs in fertility models, to any units defined by any set of arbitrary predictors.

#### KIN SELECTION: THE DISTINCTION BETWEEN FITNESS AND TRANSMISSION

The literature on kin selection is full of discussion and controversy about the logical status of the theory. On one side, there is Hamilton's (1964, 1970) famous rule, which provides a condition for the increase of altruistic characters

$$rB - C > 0, \quad (23)$$

where  $r$  is the kin selection coefficient of relatedness between actor and recipient,  $B$  is the reproductive benefit provided to the recipient by the actor's behavior, and  $C$  is the reproductive cost to the actor for providing benefits to the recipient.

On the other side, various exceptions to Hamilton's rule have been given (reviewed by Seger 1981; Michod 1982; Grafen 1985; Queller 1992a,b). This has led either to the conclusion that equation (23) is an approximate condition that must be treated with caution, or to the conclusion that equation (23) is exact subject to a few common guidelines that apply to most of the general results of population genetics. Suggested guidelines include the assumption of weak selection, additivity of allelic effects or fitness components, ignoring meiotic drive and genetic drift, and assuming that variance component measures of heritability hold sufficiently well when selection is occurring.

Each particular guideline was obtained within the context of a special case. Here I analyze the logical status of Hamilton's rule with the exact Price Equation. I show that there exist two different forms of Hamilton's rule, each with its own distinct coefficient of relatedness (Frank, in press a,b).

The first type of Hamilton's rule arises in social groups in which participants have correlated phenotypes. This type of selection influences what is sometimes called neighbor-modulated or direct fitness. The coefficients of relatedness in this case measure phenotypic correlation among participating behavioral actors.

The second type of Hamilton's rule arises when the fitness consequences of a phenotype can be divided into distinct components. Each component must be weighted by the transmission aspect of heritability for that component. For example, a mother may have different offspring-parent regressions for sons and daughters. Her fitness through each sex must therefore be weighted by the proper offspring-parent regression to calculate the evolutionary consequences of a behavior. This type of partition by transmission components is often called inclusive fitness.

The two types of Hamilton's rule have coefficients described by statistical regressions. The similarity in the form of these coefficients often leads to the mistaken conclusion that direct and inclusive fitness models are the same process described in two different ways. The formal treatment here, following from an exact and general formulation, clearly shows the logical distinction and the proper methods of analysis. The key is a clear separation of the predictors of fitness from the predictors of character value.

#### CORRELATED PHENOTYPES AND SOCIAL COMPONENTS OF FITNESS

I show that the direct fitness form of Hamilton's rule has the same logical status as FTNS: it is an exact, partial condition for change ascribed to social selection. The partial change is obtained holding constant the average effect of predictors, a point that Queller (1992b) mentioned but did not develop. I will also derive, with the full Price Equation,



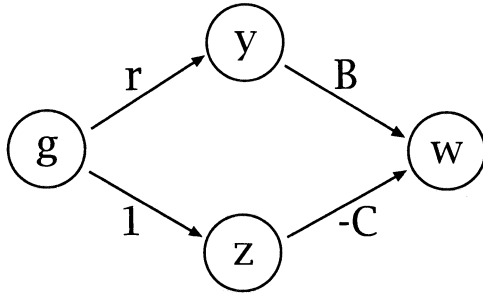


FIG. 4. Path diagram for the effect of correlated characters on fitness. The total regression of fitness on breeding value,  $\beta_{wg}$  is  $rB - C$ , which is a form of Hamilton's rule. This rule accounts only for the effect of correlated characters on fitness. In this case, the correlated character is  $y$ , the average phenotype of social partners. See Figure 5 for a partition of  $r = \beta_{yg}$  into genetic and other components.

an exact condition for total change. This total change result provides a formal, universal theorem against which Hamilton's partial result can be checked.

#### Exact-Partial and Exact-Total Models of Direct Fitness

Queller (1992a,b) developed a framework for analyzing Hamilton's rule and comparing it with standard approaches of quantitative genetics. This approach was also mentioned, but not developed, by Goodnight et al. (1992).

Queller worked with the covariance part of the Price Equation, in my notation  $\bar{w}\Delta\bar{g} = \text{Cov}(w, g)$ , dropping the second term,  $E(w\Delta g)$ . I follow his approach, but keep the expectation term and work fully with equation (3). This guarantees that, at every step, we have an exact, total result for change in character values. From this context of total change, it is much easier to be clear about the partial nature of the direct fitness rule.

We start, as before, by writing the character under study as  $z_i = g_i + \delta_i$ . For offspring derived from parental type  $i$ ,  $z'_i = g'_i + \delta'_i$ . Because  $\bar{\delta}' = \bar{\delta} = 0$ , we have  $\Delta\bar{z} = \Delta\bar{g}$ , so we can work at the level of breeding values. Following Queller

(1992a,b), and the general approach of Lande and Arnold (1983), we begin with a regression equation for fitness

$$w = \alpha + \beta_{wz \cdot y}z + \beta_{wy \cdot z}y + \epsilon,$$

where  $\alpha$  is a constant part of fitness unaffected by social interaction,  $y$  is the average phenotypic value of the local group with which an individual interacts,  $\beta_{wz \cdot y}$  is the partial regression of fitness on individual phenotype, holding group phenotypic value constant,  $\beta_{wy \cdot z}$  is the partial regression of fitness on group phenotypic value, holding individual phenotypic value constant, and  $\epsilon$  is the error term that, by least squares theory, is uncorrelated with  $y$  and  $z$ . Goodnight et al. (1992) developed a similar model, in which they emphasized that  $y$  is a contextual variable for individual fitness.

We can match this notation to standard models of kin selection (Queller 1992a,b). The direct effect of an individual's phenotype on its own fitness,  $\beta_{wz \cdot y}$ , determines the reproductive cost of the phenotype. To match the convention that cost reduces fitness, we set  $\beta_{wz \cdot y} = -C$ . The direct effect of average phenotypic value in the local group on individual fitness,  $\beta_{wy \cdot z}$ , measures the benefit of the phenotype on the fitness of neighbors, thus  $\beta_{wy \cdot z} = B$ . The fitness regression can now be written as  $w = -Cz + By + \epsilon$ . The condition for  $\Delta\bar{z}$  to increase is, from the Price Equation,  $\bar{w}\Delta\bar{g} > 0$ , thus

$$\bar{w}\Delta\bar{g} = \beta_{wg}V_g + E(w\Delta g) > 0.$$

We see from Figure 4 that

$$\beta_{wg} = \beta_{yg}\beta_{wy \cdot z} + \beta_{zg}\beta_{wz \cdot y} = rB - C,$$

where  $r = \beta_{yg}$  is a common form of the kin selection coefficient (reviewed by Seger 1981; Michod 1982; Queller 1992a). Dividing by  $V_g$  yields the condition for  $\bar{w}\Delta\bar{g} > 0$  as

$$rB - C > -\frac{E(w\Delta g)}{V_g}. \quad (24)$$

This is an exact, total result for all conditions, using any predictors for breeding value. The predictors of phenotype may include alleles, group characteristics, environmental

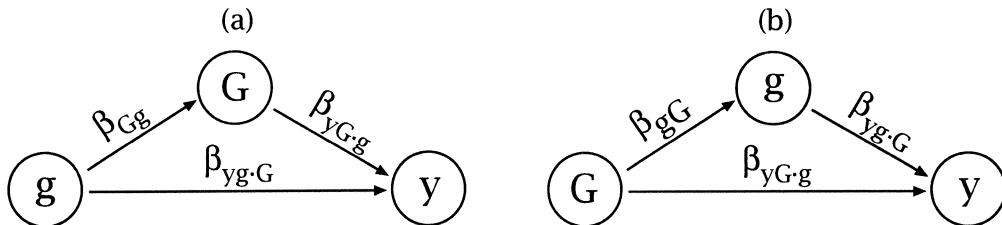


FIG. 5. Partition of the phenotypic relatedness coefficient,  $r = \beta_{yg}$ , into additive genetic and other components, where  $y$  is partner phenotype and  $g$  is recipient breeding value. (a) The diagram shows that  $\beta_{yg}$  can be partitioned as  $r = \beta_{yg} = \beta_{gG}\beta_{yG \cdot g} + \beta_{yG \cdot g}$ . (b) The slope of partner phenotype on partner breeding value is one by convention. Thus, from the diagram,  $1 = \beta_{yG} = \beta_{gG}\beta_{yG \cdot g} + \beta_{yG \cdot g}$ , which can be rearranged as  $\beta_{yG \cdot g} = 1 - \beta_{gG}\beta_{yG \cdot g}$ . Substituting this identity into the path in (a) yields  $r = \beta_{gG} + \beta_{yG \cdot g}(1 - \rho^2)$ , where  $\rho^2 = \beta_{gG}\beta_{yG \cdot g}$  is the square of the correlation coefficient between  $g$  and  $G$ . The term  $1 - \rho^2$  is the fraction of the variance in  $G$  not explained by  $g$ . The Hamilton's rule condition,  $rB - C > 0$ , is independent of whether  $r$  is caused by additive genetic correlation among partners,  $\beta_{gG}$ , or some other process that associates the phenotype of social partners with the breeding value of the recipient, summarized in  $\beta_{yG \cdot g}$ .

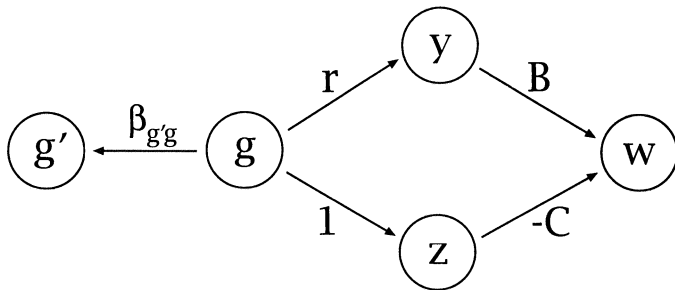


FIG. 6. Path diagram combining components of social fitness,  $rB - C$ , and the fidelity of transmission,  $\beta_{g'g}$ .

variables, cultural beliefs, and so on. If we use the Fisherian definition of partial change caused directly by natural selection, holding average effects constant, then the right side is zero and we recover the standard form of Hamilton's rule. This form of Hamilton's rule is an exact, partial result that applies to all selective systems, just as the partial frequency fundamental theorem is an exact, partial result with universal scope.

This form of Hamilton's rule is a purely phenotypic result. In particular, the components of fitness and the kin selection coefficient,  $r$ , depend only on phenotypic correlations. A frequent cause of phenotypic correlation is common ancestry and shared genotype. But the associations may just as well be between different species, and one obtains exactly the same form of the  $rB - C$  rule (Frank 1994). Figure 5 illustrates genetic and nongenetic pathways by which  $r$  is determined (see below, Partition of Kin Selection and Correlated Selection).

Equation (24) can be expressed differently by starting with the equation (12) form of the Price Equation, using equation (13), and dropping the correlation of residuals,  $\text{Cov}(\epsilon, \gamma)$ , giving

$$\begin{aligned}\Delta\bar{g} &= \beta_{wg'}V_{g'}/\bar{w} + D_g \\ &= \beta_{wg}\beta_{g'g}V_g/\bar{w} + D_g.\end{aligned}$$

The condition for  $\Delta\bar{g} > 0$  is

$$(rB - C)\beta_{g'g}/\bar{w} > \frac{-D_g}{V_g}. \quad (25)$$

This form has two advantages. First, the left side, illustrated in Figure 6, shows the distinction between phenotypic components of fitness,  $rB - C$ , and fidelity of transmission,  $\beta_{g'g}$ . Later I will develop the fidelity of transmission and show that it is a different kind of relatedness coefficient that arises frequently. The second advantage of this form is that it allows easy calculation, in which each term can be readily understood. I illustrate the use of this condition in the next section.

#### *Kin Selection of a Culturally Inherited Trait: The Rebellious Child Model*

I have mentioned that the predictors used for traits can be alleles, cultural beliefs, or other variables. Here I study the

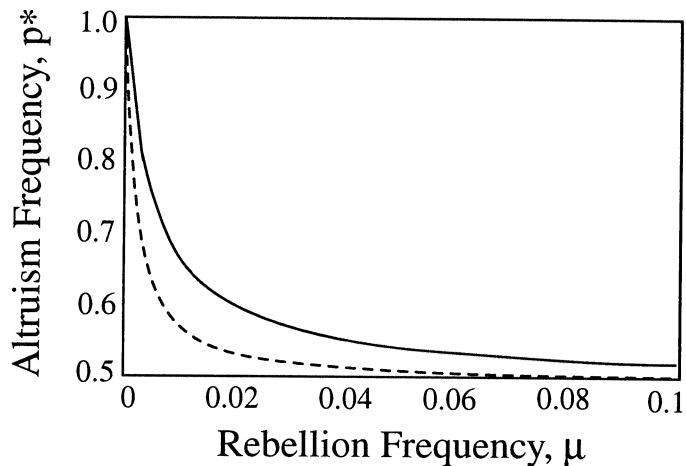


FIG. 7. The equilibrium frequency of altruism,  $p^*$  in a model of cultural inheritance. From equation (26) with  $r = 0.1$ ,  $B = 1.1$ , and  $C = 0.1$ . Solid curve,  $\alpha = 0$ , dashed curve,  $\alpha = 1$ . Note that  $r$  is treated as a parameter in the spirit of comparative statics. A fully dynamic model might define  $r$  as a function of rebellion frequency,  $\mu$ .

evolution of a culturally inherited trait for altruistic behavior. The trait is inherited directly from parent to offspring, but children are rebellious and switch to the opposite behavior from their parents with probability  $\mu$ . For simplicity, I assume that each offspring has only one parent.

Let  $p$  be the frequency of the altruistic trait. Breeding value,  $g$ , is zero or one if the trait is, respectively, absent or present in an individual. The change in average breeding value between parent and offspring,  $g' - g = \Delta g$ , is  $\mu$  if parental value,  $g$ , is zero, and  $-\mu$  if parental value is one. The general equation for fitness, from the prior section, is

$$w = \alpha - Cg + BG + \epsilon,$$

where I have taken individual phenotype as equivalent to breeding value,  $z = g$ , and group phenotype,  $y$ , as equivalent to group breeding value,  $G$ . With this setup,  $p = \bar{g} = \bar{G}$ , and  $\alpha$  is chosen so that  $\bar{\epsilon} = 0$ .

We can obtain the equilibrium frequency of the altruistic character,  $p^*$ , when the condition in equation (25) is an equality. The terms are

$$\begin{aligned}\beta_{wg} &= rB - C \\ \beta_{g'g} &= (1 - 2\mu) \\ \bar{w} &= \alpha + p(B - C) \\ D_g &= \mu(1 - 2p) \\ V_g &= p(1 - p).\end{aligned}$$

This provides all the information we need to substitute into equation (25) and solve for the equilibrium frequency of altruism. The solution is a quadratic in  $p$ . When  $\alpha = 0$ , the solution is

$$p^* = \frac{(rB - C)(1 - 2\mu) + \mu(B - C)}{(rB - C)(1 - 2\mu) + 2\mu(B - C)}. \quad (26)$$

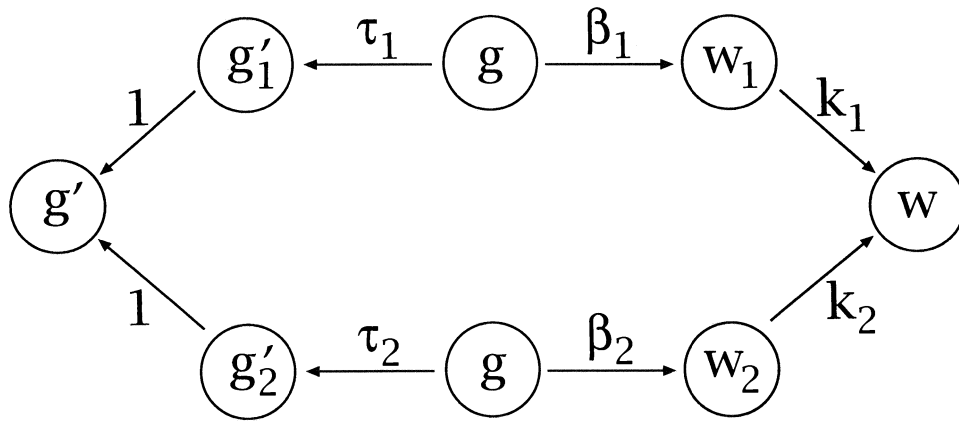


FIG. 8. Kin selection coefficients measure the components of heritability. An individual's phenotype, influenced by  $g$ , affects two different components of fitness,  $w_1$  and  $w_2$ . These fitness components have different transmission fidelities,  $\tau_1 = \beta_{g'_1g}$  and  $\tau_2 = \beta_{g'_2g}$ .

Simple numerical calculations provide values of  $p^*$  for  $\alpha \neq 0$ . Figure 7 shows how the frequency of rebellion,  $\mu$ , influences the cultural evolution of altruism. Note how quickly the frequency of altruism declines when the frequency of rebellion increases from zero.

#### GENOTYPIC COMPONENTS OF TRANSMISSION

A second type of kin selection coefficient arises when a phenotype influences different components of fitness. For example, an individual may be able to split resources between daughters and nieces, or an individual may be able to take some resources from a partner. In this case the recipients—daughters, nieces, partners—do not themselves have a phenotype. Following Hamilton (1964), we can assign the recipient fitnesses as components of the actor's inclusive fitness.

Figure 8 shows how an actor's breeding value,  $g$ , influences components of fitness and components of transmission. We can obtain the total change in a character by starting with equation (12):

$$\Delta \bar{g} = \beta_{wg} V_{g'} / \bar{w} + D_g.$$

If we assume that there is no bias in transmission,  $D_g = 0$ , and that the implicit error terms not shown in Figure 8 are uncorrelated, then from the diagram we start by writing fitness as a sum of components

$$w = \sum k_j w_j,$$

where the  $k$ s weight the components properly for reproductive value (see Taylor and Frank 1996). Then from the path diagram we obtain

$$\bar{w}(\Delta_{IF} \bar{g}) = \beta_{wg'} V_{g'} = \left( \sum k_j \beta_j \tau_j \right) V_g, \quad (27)$$

where  $\Delta_{IF}$  is the partial, inclusive fitness change in a character,  $\beta_j = \beta_{w_j g}$  is the effect of the actor's breeding value on the  $j$ th component of fitness, and  $\tau_j = \beta_{g'_j g}$  is the fidelity of transmission through the  $j$ th component. The  $\tau_j$  are a common

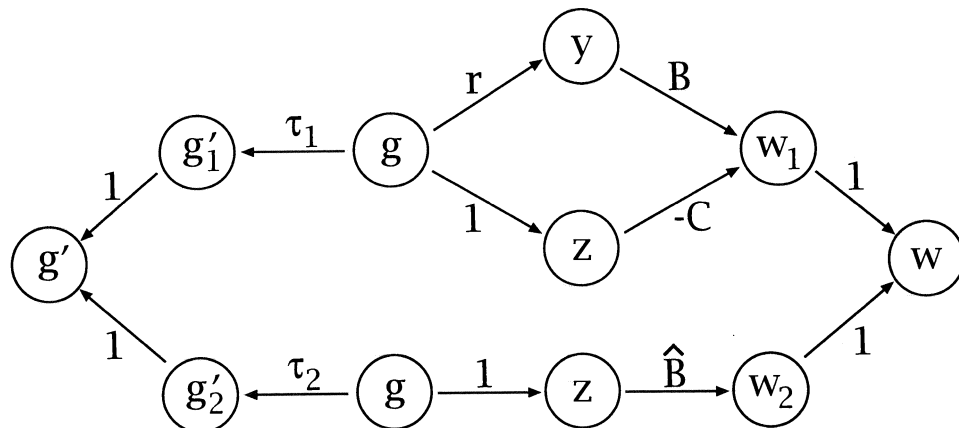


FIG. 9. A model combining correlated selection on class 1, influenced by an extrinsic phenotype,  $y$ , and the direct effect of class 1 on class 2, measured by the benefit  $\hat{B}$  caused by the class 1 character,  $z$ .

type of kin selection coefficient, the slope of recipient genotype on actor genotype. In this case  $g'_j$  measures the transmissible part of the recipient's genotype with respect to the  $j$ th fitness component.

If we ignore the reproductive value weightings, the condition for the actor genotype to increase,  $\Delta\bar{g} > 0$ , is

$$\sum \beta_j \tau_j > 0, \quad (28)$$

which is a commonly written form of Hamilton's rule. For example, suppose component one is the actor's own fitness, with  $\tau_1 = 1$ , and component two is a partner's fitness, with  $\tau_2 < 1$ , and

$$\begin{aligned} w_1 &= \alpha_1 - Cz \\ w_2 &= \alpha_2 + \hat{B}z. \end{aligned}$$

Because  $\beta_{zg} = 1$ , the condition for increase is

$$\tau_2 \hat{B} - C > 0.$$

This appears to match the  $rB - C$  rule in the prior section on phenotypes, with the phenotype correlation  $r$  of individual to social partner equivalent to the genotypic correlation,  $\tau_2$  of actor to offspring of the recipient. Under some conditions  $r$  and  $\tau$  can be made to match, but in general they measure very different aspects of evolutionary change. This can be seen by writing the actor's fitness to match the phenotypic model in the prior section

$$w_1 = \alpha_1 + By - Cz + \epsilon_1$$

and the recipient fitness as

$$w_2 = \alpha_2 + \hat{B}z + \epsilon_2.$$

The model is illustrated in Figure 9. The condition for increase is  $\sum \beta_j \tau_j > 0$ , which can be written explicitly as

$$\beta_{w_1g} \tau_1 + \beta_{w_2g} \tau_2 > 0,$$

which is, from the diagram

$$(rB - C)\tau_1 + \hat{B}\tau_2 > 0.$$

Here  $rB$  measures the effect of the correlated phenotype,  $y$ , on class 1 fitness. The phenotype  $y$  may be controlled by another species or by a different trait from the one under study. The term  $-C$  measures the effect of the class 1 phenotype,  $z$ , on its own fitness. The term  $\hat{B}$  measures the effect the class 1 phenotype,  $z$ , on the class 2 recipients that are influenced by that trait. In this case we have assigned all progeny to class 1, which is the active class. Thus  $\tau_1$  measures the heritability component, or fidelity of transmission, for the active class to its own progeny, and  $\tau_2$  measures the heritability component of the active class to class 2 progeny.

In summary,  $r$  measures the association between an actor's phenotype and a recipient's genotype within a generation. By contrast,  $\tau$  measures the association between an actor's genotype and the genotype that a recipient transmits to the next generation (Appendix B; Frank, in press a,b).

## COMPONENTS OF TRANSMISSION: RECIPIENTS VERSUS OFFSPRING

I have defined the standard measure of transmission as  $\beta_{g'_i g}$ . This is the slope of the average effects transmitted by the  $i$ th fitness component on the actor's breeding value. For example, if the  $i$ th component is the actor itself, then  $\beta_{g'_i g}$  is the slope of the actor's contribution to offspring measured in the context of the offspring generation,  $g'$ , on parent breeding value,  $g$ .

It is common in the kin selection literature to define an actor's relatedness to offspring based on the offspring's entire genotypic value rather than a particular parent's direct contribution. Thus, from Figure 1, I use parent 1's transmission coefficient as  $\beta_{g'_1, g_1}$ , whereas a common measure is the slope of the entire offspring genotypic value,  $\Gamma$ , on parental value,  $g_1$ .

The common measure is attractive because we normally think of a parent's relatedness to an outbred offspring as 0.5. But the common measure of whole offspring genotype on parent genotype can be confusing in the analysis of kin selection. For example, suppose a female actor aids her sister. The actor gains through the increased contribution to offspring by her sister. The actor also gains by the increased contribution of her sister's mates to offspring, weighted by the actor's relatedness to her sister's mates. In this case, we can either partition the actor's gain into two components—sister plus sister's mates—or we can simply measure the relatedness of the actor to the whole breeding value of her sister's offspring.

What if a female aids her brother? This may increase the brother's mating success but not change the fecundity of the brother's mates. In this case we obtain the correct weighting by measuring only the brother's direct contribution to offspring. It would be a mistake to measure the actor's relatedness to the brother's offspring.

A similar problem arises when accounting for an effect on the actor itself. For example, a fitness cost to a male may not influence his mate's fecundity. The proper measure for this cost is only through the male's direct contribution. It would be a mistake to use his relatedness to his whole offspring. By contrast, a cost to a female may influence her mate's fecundity. A proper analysis would measure her direct component plus her mate's component. In general, the valuation of offspring should always be considered as two separate fitness components, one for each parent (Frank, in press b).

## PARTITION OF KIN SELECTION AND CORRELATED SELECTION

Queller (1992a,b) provided a useful partition between the direct effects of correlated genotype and phenotype. He assumed that average effects do not change between parent and offspring,  $g' = g$ , thus his analysis is equivalent to the Fisherian definition of partial change. The previous sections expanded the analysis of selection to an exact evolutionary model, combining the partial effects of selection with the partial effects of transmission.

I follow Queller in this section to separate the direct effects of correlated genotype and phenotype. Because we assume

$g' = g$ , the condition for the increase of a trait,  $\Delta\bar{g} > 0$ , is, by the Price Equation,  $\text{Cov}(w, g) > 0$ . We had, from an earlier section, the phenotypic model of direct fitness

$$w = \alpha - Cz + By + \epsilon$$

and the condition for  $\text{Cov}(w, g) > 0$  is

$$rB - C > 0,$$

where  $r = \beta_{yg}$  is the phenotypic relatedness coefficient. A similar model, in the spirit of inclusive fitness is

$$w_1 = \alpha_1 - Cz + \epsilon_1$$

$$w_2 = \alpha_2 + Bz + \epsilon_2,$$

where the phenotype  $z$  is a property of class 1, affecting itself and the recipients in class 2. The canonical solution for this formulation, from equation (28) is  $\sum \beta_i \tau_i > 0$ , thus  $\bar{z}$  increases if  $\tau_2 B - \tau_1 C > 0$ . Because we assume  $g' = g$  in this section,  $\tau_1 = 1$  and the condition is

$$\tau_2 B - C > 0.$$

The conditions for increase match when  $r = \tau_2$ . Figure 5 shows that  $r = \beta_{Gg} + \beta_{yg \cdot G}(1 - \rho^2)$ , where  $\rho$  is the correlation coefficient between  $g$  and  $G$ . If we interpret partner genotype,  $G$ , as equivalent with a random recipient of class 2 in the inclusive fitness formulation, then  $G = g_2$  and, because we assume here that  $g' = g$ , we can write  $G = g_2'$  thus  $\beta_{Gg} = \beta_{g_2'g} = \tau_2$ , and

$$r = \tau_2 + \beta_{yg \cdot G}(1 - \rho^2).$$

The condition from the direct fitness model,  $rB - C > 0$ , can be expanded as

$$[\tau_2 + \beta_{yg \cdot G}(1 - \rho^2)]B - C > 0, \quad (29)$$

thus the purely genotypic inclusive fitness model matches the direct fitness model when  $\beta_{yg \cdot G} = 0$ . This term would be nonzero when, for example, some individuals are able to control the phenotype of their partners, or individuals are matched with partners based on a component of partner phenotype not explained by partner genotype (Frank, in press a,b).

I have described  $g$  and  $G$  as the (additive) genetic components of phenotype. This usage matches the convention of quantitative genetics, in which the only predictors of phenotype are the effects of individual alleles. But any predictors of phenotype may be used in constructing  $g$  and  $G$ , including multiplicative effects among alleles, maternal effects, functions of measurable phenotypes over any grouping of individuals, and environmental or cultural factors. The use of individual alleles is a natural choice in many cases. But one must distinguish between a useful class of applications and the essential structure of the theoretical system.

## CONCLUSIONS

The Price Equation provides a simple, exact framework to unify models of natural selection. Each individual model could, of course, be obtained by other methods. The Price Equation is nothing more or less than artful notation, showing the simple relations among seemingly disparate ideas.

Fisher (1918, 1958) made the first step in the development of general methods for the analysis of selective systems. He expressed characters by their regression on a set of predictors. The standard genetic predictors are alleles and interactions among alleles, but other predictors can be used without change in concept or notation. Fisher then partitioned the direct effect of natural selection, which causes change in predictor frequencies, and extrinsic forces that change the effect of each predictor. This led immediately to the fundamental theorem: the partial increase in fitness caused directly by natural selection equals the genetic (predictor) variance in fitness.

Hamilton (1964), interested in social selection, partitioned the components of natural selection into direct effects on the individual and direct effects on social partners. In retrospect, Hamilton's approach can be described by the regression of fitness on different predictor variables, in this case, the behavior of individuals and the behavior of social partners. Hamilton also worked with the partial increase in fitness, holding the effect of each genetic predictor constant. Thus Hamilton's rule is a type of fundamental theorem, but the object of study is a social character rather than fitness, and the causes of fitness are separated between individual and social effects.

Lande and Arnold (1983) developed the separation of different effects on fitness by a generalized multiple regression of fitness. They used approximate methods of quantitative genetics to translate the direct effect of selection, mediated by various causes, into evolutionary change between generations.

The Price Equation subsumes the particular results, by Fisher, Hamilton, Lande and Arnold, and many others, and generalizes these results to arbitrary systems of inheritance and selection. This generalization follows simply from the fact that one can choose arbitrarily the predictors of characters and the predictors of fitness. Generalized results follow immediately for Fisher's fundamental theorem, Hamilton's rule, and the Lande-Arnold method. These general results are always coupled with an exact expression for total change when the Price Equation is applied properly. Exact expressions provide a touchstone for comparison among ideas and methods of approximation. The exact expression can also be useful for solving particular problems, as shown by the rebellious child model. There I applied a modified, exact, Hamilton's rule to obtain the equilibrium frequency of altruism for a culturally inherited trait.

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## APPENDIX A

The abstract and general formulation of evolution in the Price Equation necessarily subsumes classical Mendelian genetics as a special case. But, on first encounter, the correspondence may be difficult to grasp. This appendix illustrates the relation between classical population genetics and predictors and partitions in the Price Equation. This is simply an exercise in deriving correspondences that must be true given the general proofs in the text. This analysis plays no role in the general arguments of the paper, but may be useful for readers unfamiliar with the particular definitions.

Most of the terms in the Price Equation and related models arise in the theory of quantitative genetics (see, e.g., Falconer 1989). The key terms *average excess* and *average effect* were introduced by Fisher (1930, 1941, 1958). These terms are developed in the context of Mendelian genetics in many texts and papers on population genetics (e.g., Crow and Kimura 1970; Crow and Nagylaki 1976; Ewens 1989).

The two examples below analyze a one-locus model with two alleles and dominance. The first example describes phenotypic changes caused by a change in the mating system in the absence of selection. In this case allele frequencies do not change. All phenotypic changes can be ascribed to shifts in the effect of alleles that arise from reassortment during transmission. The second example describes allele frequency change under selection. Phenotypic evolution is partitioned into the direct effects of selection on allele frequency change, and changes in allelic effects caused by the new context of genotype frequencies present after selection, reassortment, and transmission.

*Change in Mating System with No Selection*

Let there be a single locus with two alleles, *A* and *B*, with subscripts 1 and 2 used respectively for the two alleles. The main terms for this numerical example are shown in Table A1. The phenotypes, *z*, for the three genotypes show that *B* is completely dominant to *A*. The phenotypes for the three genotypes are labeled  $z_{11}$ ,  $z_{12}$ , and  $z_{22}$  for *AA*, *AB*, and *BB*, with values shown in the first line of the upper table. The upper table lists values for genotypic attributes.

The initial allele frequencies for the alleles *A* and *B* are  $r_1 = \frac{1}{4}$  and  $r_2 = \frac{3}{4}$ , shown in the upper line of the lower table. The lower table shows attributes for individual alleles. Initially, mating is random, with genotypic frequencies given by *q*. For example, the frequency of heterozygotes is  $q_{12} = 2r_1r_2 = 12/32$ .

The lower table provides three different ways to describe the effect of each allele on phenotype. The average excess is the difference between the average phenotype associated with an allele and the average phenotype for all alleles. For example; to calculate the average excess for allele *A*, each phenotype is weighted by the number of *A* alleles and the frequency of the genotype, in particular

$$a_1 = \frac{2q_{11}z_{11} + q_{12}z_{12}}{2q_{11} + q_{12}} - \bar{z} \quad (\text{A1})$$

with a similar definition for  $a_2$ .

TABLE A1. Dominance, nonrandom mating, and no selection.

	AA	AB	BB
Phenotype ( $z$ )	0	1	1
Phenotype ( $z'$ )	0	$\frac{3}{4}$	1
Phenotype ( $\hat{z}$ )	0	1	1
Frequency ( $q$ )	$\frac{2}{32}$	$\frac{12}{32}$	$\frac{18}{32}$
Frequency ( $q'$ )	$\frac{2}{32}$	$\frac{12}{32}$	$\frac{18}{32}$
Frequency ( $\hat{q}$ )	$\frac{5}{32}$	$\frac{9}{32}$	$\frac{21}{32}$
Breeding value ( $g$ )	$\frac{54}{96}$	$\frac{78}{96}$	$\frac{102}{96}$
Breeding value ( $\Gamma$ )	$\frac{21}{96}$	$\frac{61}{96}$	$\frac{101}{96}$
Breeding value ( $g'$ )	$\frac{21}{96}$	$\frac{61}{96}$	$\frac{101}{96}$
Breeding value ( $\hat{g}$ )	$\frac{21}{96}$	$\frac{61}{96}$	$\frac{101}{96}$
Marginal prediction ( $\Psi$ )	$\frac{54}{96}$	$\frac{78}{96}$	$\frac{102}{96}$
Marginal prediction ( $\hat{\Psi}$ )	$-\frac{9}{96}$	$\frac{51}{96}$	$\frac{111}{96}$
	A	B	
Frequency ( $r$ )	$\frac{1}{4}$	$\frac{3}{4}$	
Frequency ( $r'$ )	$\frac{1}{4}$	$\frac{3}{4}$	
Average excess ( $a$ )	$-\frac{36}{192}$	$\frac{12}{192}$	
Average excess ( $a'$ )	$-\frac{90}{192}$	$\frac{30}{192}$	
Average effect ( $b$ )	$\frac{54}{192}$	$\frac{102}{192}$	
Average effect ( $b'$ )	$\frac{21}{192}$	$\frac{101}{192}$	
Average effect ( $\alpha = b - \bar{b}$ )	$-\frac{36}{192}$	$\frac{12}{192}$	
Average effect ( $\alpha' = b' - \bar{b}'$ )	$-\frac{60}{192}$	$\frac{20}{192}$	

The average excess is sometimes referred to as the marginal allelic effect. One can use the marginal effects to predict the phenotypic  $z_{ij}$  as

$$\psi_{ij} = \bar{z} + a_i + a_j, \quad (\text{A2})$$

where the prediction is obtained by adding the marginal effects of the alleles. These predictions are based on two degrees of freedom because the  $a$ s are constrained by  $r_1 a_1 + r_2 a_2 = 0$ , so one is left with one degree of freedom for the mean and one degree of freedom for the  $a$ s. Marginal predictions are shown in the upper table.

Fisher (1941, 1958) noted that better prediction can be obtained by using the two degrees of freedom in a different way. One can partition the character values as

$$z_{ij} = \bar{z} + \alpha_i + \alpha_j + \delta_{ij}, \quad (\text{A3})$$

where the predicted value of the character is

$$g_{ij} = \bar{z} + \alpha_i + \alpha_j \quad (\text{A4})$$

and the distance (error) between prediction and observation is

$$\delta_{ij} = z_{ij} - g_{ij}. \quad (\text{A5})$$

The prediction,  $g$ , is the breeding value.

Fisher (1941, 1958) defined the best prediction for phenotype, using only two degrees of freedom, as the values of  $\alpha$  that minimized the Euclidean distance between all observed and predicted phenotypes. This is equivalent to finding the  $\alpha$ s that minimize the sum of the  $\delta_{ij}^2$  where the sum is weighted by the frequency of each genotype. This is the standard least squares theory of regression, with the  $\alpha$ s as regression coefficients for the partial effect of each allele.

The  $\alpha$ s are constrained such that  $r_1 \alpha_1 + r_2 \alpha_2 = 0$ , and each  $\alpha$  is a phenotypic deviation from the mean. When working with changes in the coefficients over time it is often easier to use average effects (regression coefficients) that include the contribution to the mean,  $b_i = \alpha_i + \bar{z}/2$ , thus  $g_{ij} = b_i + b_j$ .

Calculation of average effects requires minimizing the sum of squares. For this two allele system, Crow and Kimura (1970, p. 131) provide these formulas for calculation

$$\alpha_1 = \frac{(r_1 + r_2 f)z_{11} + r_2(1 - f)z_{12} - \bar{z}}{1 + f}$$

$$\alpha_2 = \frac{r_1(1 - f)z_{12} + (r_2 + r_1 f)z_{22} - \bar{z}}{1 + f}, \quad (\text{A6})$$

where  $f$ , the standard inbreeding coefficient of population genetics, can be calculated as the correlation of alleles that unite to form offspring.

These formulas allow calculation of  $g$ ,  $\alpha$ , and  $b$  in Table A1. The initial generation was formed by random mating, and the normalized values of average excess and average effect are equal,  $a = \alpha$ .

The next generation is formed by self-fertilization of all individuals. The changed variables are separated into two classes in the upper, genotypic table. The hats denote the actual value of the variables among the progeny. The primes denote offspring values according to the rules for parent-offspring assignment in the Price Equation. For most cases, the value of a primed variable for a particular genotype is the value of offspring derived from a parent of that genotype. For example, the  $AB$  genotype produces offspring of genotypes  $AA$ ,  $AB$ , and  $BB$  in a ratio of 1:2:1 under self-fertilization, so  $z'_{12} = (\frac{1}{4})z_{11} + (\frac{1}{2})z_{12} + (\frac{1}{4})z_{22}$ . The definition of  $q'$  in the Price Equation is  $q'_i = q_i w_i / \bar{w}$ . In this model fitnesses are equal for all genotypes, so  $q' = q$ .

There are two different ways to calculate the breeding value of offspring derived from a parent (see Figure 1). The actual values of offspring breeding value,  $\Gamma$ , may be used, with a calculation similar to  $z'$ . For example, under self-fertilization,  $\Gamma_{12} = (\frac{1}{4})g_{11} + (\frac{1}{2})g_{12} + (\frac{1}{4})g_{22}$ . With this definition,  $\Delta g = \Gamma - g$ . Alternatively, the breeding value transmitted by each parent,  $g'$ , can be calculated directly. In particular,  $g'_{ij} = \hat{g}_{ij} = b'_i + b'_j$  for a Mendelian model with no transmission bias. This measures the average effect of parental alleles transmitted to offspring, in which the effects are described in the context of the offspring generation. The transmitted breeding value allows one to distinguish between the effect of predictors passed from parent to offspring, and the role of reassortment of predictors in the formation of offspring.

The lower, allelic portion of Table A1 reports only primed variables. There is no distinction at the allelic (predictor) level between offspring assignments to parents (primes) and actual offspring values (hats) in most models, including this one. It is only when predictors are aggregated, such as in genotypes, that the distinctions between prime and hat offspring definitions are common.

The allele frequencies,  $r'$  do not change because there is no selection, but the genotype frequencies among offspring,  $\hat{q}$ , do change because self-fertilization causes an increase in the correlation between alleles that combine to form offspring. A standard calculation from population genetics shows that, under self-fertilization, the correlation between alleles in each generation is  $f' = (\frac{1}{2})(1 + f)$ , where the prime denotes the current generation and the unprimed variable denotes the previous generation. In this model,  $f = 0$  and  $f' = \frac{1}{2}$ . With this value, and the previous formulas, all values in Table A1 can be filled in for the offspring generation.

Note that, with nonrandom mating, average excess ( $a'$ ) and average effect ( $\alpha'$ ) differ. In this case,  $a = \alpha(1 + f)$  (Crow and Kimura 1970). The average effects provide a better estimate of phenotype in terms of minimizing the Euclidean distance between prediction and observation, indeed, it is guaranteed to be optimal in this regard. For this case, the ratio of the distances for the marginal predictions,  $\psi$ , and the breeding values,  $\hat{g}$ , is approximately 4:3.

The disadvantage of the average excess is that it confounds the independent contribution of each allele with the correlation between alleles. By contrast, Fisher emphasized that the average effect measures the expected change in phenotype when a single allele in a population is chosen randomly and transformed from one allelic state to another. Thus average effect measures change given the

TABLE A2. Dominance, random mating, and selection.

	AA	AB	BB
Fitness ( $z \equiv w$ )	0	1	1
Fitness ( $z' \equiv w'$ )	$\frac{8}{10}$	$\frac{9}{10}$	1
Fitness ( $\hat{z} \equiv \hat{w}$ )	0	1	1
Frequency ( $q$ )	$\frac{1}{16}$	$\frac{6}{16}$	$\frac{9}{16}$
Frequency ( $q'$ )	0	$\frac{9}{15}$	$\frac{9}{15}$
Frequency ( $\hat{q}$ )	$\frac{1}{25}$	$\frac{8}{25}$	$\frac{16}{25}$
Breeding value ( $g$ )	$\frac{9}{16}$	$\frac{13}{16}$	$\frac{17}{16}$
Breeding value ( $\Gamma$ )	$\frac{8}{10}$	$\frac{9}{10}$	1
Breeding value ( $g'$ )	$\frac{16}{25}$	$\frac{21}{25}$	$\frac{26}{25}$
Breeding value ( $\hat{g}$ )	$\frac{16}{25}$	$\frac{21}{25}$	$\frac{26}{25}$
Average excess ( $A$ )	$-\frac{15}{16}$	$\frac{1}{16}$	$\frac{1}{16}$
	A	B	
Frequency ( $r$ )	$\frac{1}{4}$	$\frac{3}{4}$	
Frequency ( $r'$ )	$\frac{1}{5}$	$\frac{4}{5}$	
Average effect ( $b$ )	$\frac{9}{32}$	$\frac{17}{32}$	
Average effect ( $b'$ )	$\frac{8}{25}$	$\frac{13}{25}$	
Average effect ( $\alpha = b - \bar{b}$ )	$-\frac{3}{16}$	$\frac{1}{16}$	
Average effect ( $\alpha' = b' - \bar{b}'$ )	$-\frac{4}{25}$	$\frac{1}{25}$	

current context of the population, in this case, the breeding structure,  $f$ .

Let us now consider how the Price Equation subsumes various formulations. The standard form of the equation is

$$\Delta \bar{z} = \text{Cov}(w, z)/\bar{w} + E(w\Delta z)/\bar{w}, \quad (A7)$$

which matches equation (3) after dividing each side by  $\bar{w}$ . First note that, as in equation (17)

$$\text{Cov}(w, z)/\bar{w} = \sum q_i(w_i - \bar{w})z_i/\bar{w} = \sum q_i A_i Z_i/\bar{w}, \quad (A8)$$

showing that the covariance can be written as the expected product of the average excess in fitness,  $w_i - \bar{w}$ , and the character,  $z$  (Crow

and Nagylaki 1976). In this example there is no variation in fitness, so the covariance term is zero. We are left with the identity  $\Delta \bar{z} = E(\Delta z)$ . This equality requires that  $q'_i = q_i$ , because  $\Delta \bar{z} = \sum q'_i z'_i - \sum q_i z_i$ , and  $E(\Delta z) = \sum q_i (z'_i - z_i)$ . It is a useful exercise to study this identity carefully, because the  $\Delta z$  is sometimes confusing in application.

Another point of generality, and confusion, arises from the flexible way in which  $z$  may be interpreted. It is a placeholder for any quantity consistently defined to match the derivation of the Price Equation, which puts very few restrictions on its use. I show how one may consider this term as phenotype, breeding value, or average effect.

One can calculate from Table A1 that  $\bar{z} = 15/16$  and  $\bar{z}' = 27/32$ , thus  $\Delta \bar{z} = -3/32$ . The right side is

$$E(\Delta z) = \sum q_i \Delta z_i, \quad (A9)$$

where  $\Delta z_i = z'_i - z_i$ . The term  $z_i$  is simply a measurement on the adult, for example, the adult phenotype. The term  $z'_i$  is the same measurement on all members of the offspring generation assigned to adults with index,  $i$ . From Table A1, it immediately follows that  $\sum q_i \Delta z_i = -3/32$ , and we obtain the consistent result  $\Delta \bar{z} = E(\Delta z) = -3/32$ .

We can work with breeding values instead of phenotypes by substituting  $g$  for  $z$  in the above analysis. Note that, from the definition of breeding value above,  $\bar{g} = \bar{z}$ , so  $\Delta \bar{z} = \Delta \bar{g}$ . The identity we must establish to show consistency of the Price Equation is  $\Delta \bar{z} = \Delta \bar{g} = E(\Delta g)$ , where  $\Delta g = g' - g$ . The identity is easily verified from the table and the style of calculation summarized in the previous paragraph.

We can also work directly at the allelic level with average effects. By the definition of average effect,  $\bar{z} = 2\bar{b}$ , thus  $\Delta \bar{z} = 2\Delta \bar{b} = 2E(\Delta b)$ . Calculations from Table A1 support these identities.

The ability to work alternatively with phenotype, breeding value or average effect, is an attractive feature of partitioning characters by regression analysis in the Price Equation.

Reassortment of alleles during transmission causes all change in these examples. The calculations are relatively easy because there is no selection and thus no partitioning of change into components. Also, whole offspring are assigned to a single parent because individuals self-fertilize. The following example shows how to handle the analysis when there is selection and biparental inheritance.

TABLE B1. Partitions of evolutionary change.

Change	Partition	Equation
$\bar{w}\Delta \bar{z}$	$\text{Cov}(w, z) + E(w\Delta z)$	3 <sup>a</sup>
$\bar{w}\Delta \bar{z} = \bar{w}\Delta \bar{g}$	$\pi \text{Cov}(z, z) + \sum \beta_i \text{Cov}(y_i, z) + \text{Cov}(w, \epsilon) + E(w\Delta z)$	5
	$\beta_{wg} V_g + E(w\Delta g)$	8
	$\beta_{wg} V_g \beta_{g'g} + \bar{w}D_g + \text{Cov}(\epsilon, \gamma)$	10 <sup>b</sup>
	$\beta_{wg'} V_{g'} + \bar{w}D_g$	12
	$n \text{Cov}(w, b) + nE(w\Delta b)$	30
$\bar{w}(\Delta_f \bar{g})$	$\text{Cov}(w, g) = \sum q_i A_i g_i = \sum (\Delta q_i) g_i = n \text{Cov}(w, b)$	17, 20 <sup>c</sup>
	$= n \sum r_j a_j b_j = n \sum r_j a_j \alpha_j = n \sum (\Delta r_j) \alpha_j$	19, 21
$\bar{w}\Delta \bar{g}$	$(rB - C)V_g + E(w\Delta g)$	24
	$(rB - C)\beta_{g'g} V_g + \bar{w}D_g + \text{Cov}(\epsilon, \gamma)$	25
$\bar{w}(\Delta_{IF} \bar{g})$	$\beta_{wg'} V_{g'} = (\sum k_j \beta_j \tau_j) V_g$	27 <sup>d</sup>

<sup>a</sup> Table B2 defines the notation used here.

<sup>b</sup> Note that  $D_g = E(\Delta g)$ , see Table B2.

<sup>c</sup> The Fisherian partial change applied to mean fitness is  $\Delta_f \bar{w}$ , yielding the fundamental theorem. Here  $\Delta_f$  is applied to an arbitrary character with breeding value  $g$ . This form is sometimes called Robertson's secondary theorem of natural selection.

<sup>d</sup> This equality requires that one ignore correlations among residuals (see discussion of Eq. [27] in the text) and certain causal paths (see discussion of Eq. [29] in the text).



### Selection Followed by Reassortment during Transmission

This example differs from the prior section in two ways. First, mating is random in all generations. Second, the phenotype is equivalent to fitness, so there is differential success among genotypes.

Table A2 shows the calculations for this example. The average excess of alleles is not shown because, with random mating,  $a = \alpha$ . The average excess of genotypes is given in the upper table, where  $A_i = w_i - \bar{w}$  and, as noted above, the covariance term of the Price Equation is  $\text{Cov}(w, z)/\bar{w} = \sum q_i A_i z_i / \bar{w}$ .

The calculation of primed variables is similar in principle to the previous section, but the details differ. For frequencies,  $q'_i = q_i w_i / \bar{w}$ . For phenotypes, one must take into account the kinds of offspring that each phenotype produces, which requires using the allele frequencies available among mates after selection,  $r'_1$  and  $r'_2$ . For example,  $z'_{11} = r'_1 \hat{z}_{11} + r'_2 \hat{z}_{12}$  and  $z'_{12} = [r'_1(\hat{z}_{11} + \hat{z}_{12})/2] + [r'_2(\hat{z}_{12} + \hat{z}_{22})/2]$ . Similar methods are used for  $z'_{22}$  and values of  $\Gamma$ , and  $g' = \hat{g}$ .

The net change in character value can be calculated directly from the genotype frequencies,  $q$ , yielding  $\Delta \bar{z} = 24/25 - 15/16 = 9/400$ . We can derive this total change by working with either phenotypes, breeding values or average effects, as in the prior section.

For phenotypes,  $\text{Cov}(w, z)/\bar{w} = \sum q_i A_i z_i / \bar{w} = 1/16$ . This describes the increase in the phenotype caused by selection among adults, before the adults reproduce. The second term describes changes during reassortment of alleles and transmission,  $E(w\Delta z)/\bar{w} = \sum q_i w_i \Delta z_i / \bar{w} = \sum q'_i \Delta z_i = -1/25$ . Thus total change is  $\Delta \bar{z} = 1/16 - 1/25 = 9/400$ , satisfying the consistency check for calculations on phenotypes.

The same calculation for breeding values,  $g$ , yields  $\text{Cov}(w, g)/\bar{w} = \sum q_i A_i g_i / \bar{w} = 1/40$  and  $E(w\Delta g)/\bar{w} = \sum q'_i \Delta g_i = -1/400$ , thus  $\Delta \bar{z} = 1/40 - 1/400 = 9/400$ . We can use either definition for assigning offspring breeding values to parents, with  $E(w\Delta g)/\bar{w} = \sum q'_i (\Gamma_i - g_i) = \sum q'_i (g'_i - g_i)$ . Note that breeding values change less than

phenotypes (see prior paragraph). Breeding values usually provide a better (more predictable) measure of the effect of individual alleles than obtained directly from phenotypes.

The calculation for average effects is obtained from

$$\begin{aligned} \Delta \bar{z} &= 2 \text{Cov}(W, b)/\bar{w} + 2E(W\Delta b)/\bar{w} \\ &= 2 \sum r_i a_i b_i / \bar{w} + 2 \sum r_i W_i \Delta b_i / \bar{w}, \end{aligned} \quad (\text{A10})$$

where  $\bar{z} = 2\bar{b}$ , marginal allelic fitness is  $W_i/\bar{w} = 1 + a_i/\bar{w}$  and, under random mating,  $\alpha = a$ . This partition is equivalent to the partition of breeding values. Calculations from Table A2 support this equivalence. Note that the two in these equations arises from diploidy. In the general case two is replaced by  $n$  for the number of predictors.

Many other interpretations of the Price Equation are possible. Consistency checks provide useful exercises to learn the meaning of the terms. But the consistency of the Price Equation was not in question because the original, abstract proof guarantees success for any evolutionary system that meets the limited requirements imposed in the proof.

### APPENDIX B

Many theoretical studies of natural selection develop alternative partitions of evolutionary change. Table B1 lists some of the relations among these partitions.

Table B2 summarizes the important notations of this paper. The previous appendix and tables emphasize the distinction between values assigned to parents and values that occur in the descendant population (hat versus prime variables in tables A1 and A2). Some of the notation for kin selection differs in Frank (in press a,b). I prefer the notation of the latter articles. I was constrained in the present paper by the need to relate concepts and notation across several topics: quantitative genetics, the fundamental theorem, the Price Equation, and kin selection.

TABLE B2. Important notations.

Symbol	Description
$z$	Measurable quantity, can be replaced by character value, breeding value, average effect, fitness, or any quantity
$z_i$	Measurement on the $i$ th entity, where $i$ can represent a label for any unit or grouping, such as an allele, a genotype, a family, a species, etc.
$z'_i$	Average value of $z$ in the descendant population for entities assigned to parent with value $z_i$ (see Appendix A)
$\hat{z}_i$	Value of $z_i$ in the descendant population, differs from $z'_i$ when $i$ is an aggregate grouping such as alleles in a genotype (see Appendix A)
$q_i$	Fraction of the population consisting of entities assigned index $i$
$w_i$	Fitness of entity $i$ , such that $q'_i = q_i w_i / \bar{w}$
$x_{ij}$	Predictor variable for the $j$ th character of the $i$ th entity
$b_j$	Average effect, the partial regression of a character value on a predictor variable, see Appendix A
$\alpha_j$	Normalized average effect, $b_j - \bar{b}$
$g_i$	Breeding value, the predicted value of a character $g_i = \sum_j b_j x_{ij}$
$g'_i$	Breeding value transmitted to offspring by $i$ th parental type, measured in context of offspring generation
$\Gamma_i$	Average value of $g$ in the descendant population for entities assigned to parent with value $g_i$ (for the difference between $\Gamma$ and $g'$ , see Appendix A and Fig. 1)
$\delta_i$	Difference between observed and predicted character value, $\delta_i = z_i - g_i$
$A_i$	Average excess, $z_i - \bar{z}$
$a_j$	Marginal average excess of a predictor, see equation (18) and Appendix A
$D_g$	Average difference in breeding value between parent-offspring pairs, see equation (11)
$n$	Ploidy level, the number of alleles per locus, two for diploidy
$W_j$	Marginal allelic fitness, marginal average excess in fitness for allele $j$ is $a_j = W_j - \bar{w}$
$\Delta_f \bar{w}$	Partial Fisherian change, holding constant average effects, yields the fundamental theorem when applied to average fitness, $\bar{w}$ , Robertson's secondary theorem when applied to arbitrary characters, $\bar{g}$

TABLE B2. Continued.

Symbol	Description
$\Delta_{IF} \bar{g}$	Partial inclusive fitness change, see equation (27)
$y$	Predictors of fitness in addition to $z$ , often used for phenotype of social group or social partners of an individual
$G$	Breeding value of social group or social partners of a recipient
$\epsilon$	Error in predicting fitness
$\alpha$	Intercept for fitness regression, distinguish from average effect by context, see equation (4)
$V_z$	Variance in measured character
$V_g$	Variance in breeding values, additive genetic (genotypic) variance
$V_g/V_z$	Portion of phenotypic variance explained by breeding value, a measure of heritability
$V_{g'}$	Variance in transmitted breeding values
$\beta_{wg}$	Regression coefficient of fitness on breeding value
$\beta_{wg'}$	Regression of fitness on transmitted breeding value
$\beta_{g'g}$	Regression of transmitted breeding value on parental breeding value, a measure of heritability related to offspring-parent regressions
$\beta_{wz} = B$	Fitness benefit to recipient associated with partner's phenotype $y$ , holding constant the recipient's phenotype, $z$ (partial regression)
$\beta_{wz,y} = -C$	Fitness cost to recipient associated with its own phenotype $z$ , holding constant the partner's phenotype, $y$
$\beta_{yg} = r$	Regression of partner (actor) phenotype on recipient genotype, a relatedness coefficient for fitness effects within generations
$\beta_{Gg}$	Regression of partner genotype on recipient genotype
$\beta_{yG}$	Regression of partner phenotype on recipient genotype, holding constant partner genotype, measures factors other than partner breeding value that influence $r$
$\tau_j = \beta_{g_j g}$	Relatedness coefficient for inclusive fitness, in which $g$ is an actor's breeding value and $g'_j$ is the breeding value transmitted through the actor's $j$ th fitness component; an actor's fitness component may be offspring produced by a social partner, thus $\beta_{g_j g}$ offspring-parent heritability regression in the inclusive fitness sense of assigning nondescendant progeny to a "parent"
$k_j$	Reproductive value of $j$ th fitness component