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George Price's Contributions to Evolutionary Genetics

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George Price studied evolutionary genetics for approximately seven years between 1967 and 1974. During that brief period Price made three lasting contributions to evolutionary theory; these were: (i) the Price Equation, a profound insight into the nature of selection and the basis for the modern theories of kin and group selection; (ii) the theory of games and animal behavior, based on the concept of the evolutionarily stable strategy; and (iii) the modern interpretation of Fisher's fundamental theorem of natural selection, Fisher's theorem being perhaps the most cited and least understood idea in the history of evolutionary genetics. This paper summarizes Price's contributions and briefly outlines why, toward the end of his painful intellectual journey, he chose to focus his deep humanistic feelings and sharp, analytical mind on abstract problems in evolutionary theory.

Introduction

At the age of 44, George Price quit his engineering job at IBM and took up evolutionary genetics. Price moved to the Galton Laboratories at London in 1967, where C. A. B. Smith, Weldon Professor of Biometry, provided him with space and encouragement. Price made three lasting contributions to the conceptual structure of evolutionary genetics during the brief period between 1970 and 1973. He died in 1975.

(i) Price's (1970, 1972*a*) first contribution was the Price Equation, a formal method for the hierarchical analysis of natural selection. Hamilton (1970) used this equation in his later studies to construct the foundation for modern analyses of kin selection and group selection. The equation has also been used to clarify a diverse array of conceptual issues, from quantitative genetics to the abstract properties of natural selection.

(ii) Price was the first to show that many unsolved puzzles in animal behavior could be understood by applying the logic of game theory. Price's work stimulated Maynard Smith's interest, which eventually led Maynard Smith to develop his concept of the Evolutionarily Stable Strategy (ESS; Maynard Smith & Price, 1973) and to write the classic book *Evolution and the Theory of Games* (Maynard Smith, 1982).

(iii) Price (1972*b*) was the first to crack the most obscure and misunderstood of R. A. Fisher's many oracles: the fundamental theorem of natural selection. This theorem is perhaps the most widely quoted result in evolutionary theory, yet Price demonstrated convincingly that the consensus interpretation of the theorem strongly contradicts the lessons Fisher himself drew from the theorem. Fisher stated on several occasions that the average fitness of a population is a meaningless quantity, and theories such as Wright's adaptive topography that emphasize average fitness create a strongly misleading view of evolutionary process.

Many biologists have heard of one or another of these contributions. Few people are aware that each was made by a single man. It must be unusual in the history of science for someone, without professional experience, to take up a field while in his forties and make significant contributions to the theoretical foundations of that field.

In the first sections of this paper I focus on Price's contributions to evolutionary genetics and the study of natural selection. In the final section I provide a few details about his life and the factors that motivated him to choose particular problems in evolutionary biology.

The Price Equation

> . . . a good notation has a subtlety and suggestiveness which at times make it seem almost like a live teacher. (Bertrand Russell)

The Price Equation was a new mathematical formulation for evolutionary change (Price, 1970, 1972*a*). It may seem strange that one could write down a truly new equation that describes evolution. After all, evolution is simply the change over time in some characteristics of a population. The brilliance of the Price Equation is that it adds nothing to the fundamental simplicity of evolutionary change but, by making a few minor rearrangements and changes in notation, the equation provides an easier and more natural way to reason about complex problems.

The Price Equation relies on a degree of mathematical abstraction that is rare in evolutionary genetics. Indeed, Price believed that his work was an important step toward a general theory of selection. He introduced his manuscript, "The Nature of Selection," (Price, 1995) with:

> A model that unifies all types of selection (chemical, sociological, genetical, and every other kind of selection) may open the way to develop a general 'Mathematical Theory of Selection' analogous to communication theory . . . Selection has been studied mainly in genetics, but of course there is much more to selection than just genetical selection . . . yet, despite the pervading importance of selection in science and life, there has been no abstraction and generalisation from genetical selection to obtain a general selection theory and general selection mathematics.

I begin with simple genetical applications that use a reduced form of the equation and move slowly toward the full equation. At the end of this section I discuss the general properties of the equation and the idea that there can be a theory of selection that unifies different problems such as trial-and-error learning, chemical crystallization, and linguistic evolution.

SELECTION AND COVARIANCE

The reduced form of the equation that can be used for many simple problems is

$$\bar{w}\Delta\bar{z}=\mathrm{Cov}(w,z)=\beta_{wz}V_z, \tag{1}$$

where w is fitness and z is a quantitative character. The equation shows that the change in the average value of a character, $\Delta\bar{z}$, depends on the covariance between the character and fitness or, equivalently, the regression coefficient of fitness on the character multiplied by the variance of the character. This equation was discovered independently by Robertson (1966), Li (1967) and Price (1970).

Because fitness itself is a quantitative character, one can let the character z in eqn (1) be equivalent to fitness, w. Then the regression, β_{ww}, is 1, and the variance, V_w, is the variance in fitness. Thus the equation shows that the change in mean fitness, $\Delta\bar{w}$, is proportional to the variance in fitness, V_w. The fact that the change in mean fitness depends on the variance in fitness is usually called "Fisher's fundamental theorem of natural selection," although that is not what Fisher (1958) really meant. Price himself clarified Fisher's theorem in a fascinating paper that I shall discuss later (Price, 1972*b*).

Robertson (1968) named eqn (1) the "secondary theorem of natural selection" as an extension to what is usually called Fisher's fundamental theorem. This general covariance equation has an unspecified error that can be influenced by nonlinear genetic interactions (dominance, epistasis), the mating system, meiotic drive and a variety of other factors. Crow & Nagylaki (1976) provide an elegant summary of the relationship between traditional population genetics and the covariance equation. The full Price Equation (described later) has an additional term that, together with the covariance, always provides an exact and full description for evolutionary change.

KIN SELECTION

The Price Equation has played an important role in work on kin selection (Hamilton, 1970, 1975; Wade, 1980; Seger, 1981; Uyenoyama, 1988). The equation itself cannot reduce the inherent complexity of models, but the simple covariance relationship between a character and fitness provides a compact way to see the essential features of social evolution. Recent papers have summarized the importance of Price's work in this field (Grafen, 1985; Wade, 1985; Taylor, 1988*a*, *b*, 1989; Queller, 1992*a*), so I present here only a brief example and a few historical comments.

I illustrate the problem by summarizing the first part of Queller's (1992*a*) model. I use the covariance equation, $\bar{w}\Delta\bar{g}=\mathrm{Cov}(w,g)$, where g is the breeding value that determines the level of altruism. One can write the least-squares multiple regression that predicts fitness, w, as

$$w=\alpha+g\beta_{wg\cdot g'}+g'\beta_{wg'\cdot g+\epsilon,}$$

where g' is the average g value of an individual's social neighbors, α is a constant, and ϵ is the residual which is uncorrelated with g and g'. The β are partial regression coefficients that elegantly summarize costs and benefits: $\beta_{wg\cdot g'}$ is the effect an individual's breeding value has on its own fitness in the presence of neighbors g'—the cost of altruism, and $\beta_{wg'\cdot g}$ is the effect of an individual's breeding value on the fitness of its neighbors—the benefit of altruism. Substituting into the covariance equation and solving for the condition under which $\bar{w}\Delta\bar{g} > 0$ yields Hamilton's rule

$$\beta_{wg \cdot g'} + \beta_{g'g}\beta_{wg' \cdot g} > 0,$$

where $\beta_{g'g}$ is the regression coefficient of relatedness (Hamilton, 1972). Thus Queller's model shows that the covariance equation provides a simple way to reason about the effects of relatedness on social behavior.

Hamilton (1964*a*, *b*), in his original formulation of kin selection, described genetic similarity in terms of genes identical by descent. Hamilton (1970) reformulated kin selection by explicit derivation from the Price Equation; this derivation is often regarded as the first modern theoretical treatment of inclusive fitness (Grafen, 1985). Price's covariance equation shows that what matters is not common ancestry, but statistical associations between the genotypes of donor and recipient.

One interesting consequence of treating relatedness as a statistical association is that relatedness can be negative, leading to selection for spiteful behavior. That new insight was a key point in Hamilton (1970: 1218):

> Previously I showed that the average genetical relatedness of interacting individuals is an important factor in the evolution of social adaptations. In the model, selfishness within certain limits was readily accounted for; spite [harm to self in order to harm another more] did not seem possible. But another line of reasoning shows that spite can be selected [when relatedness is negative]. Independently, using his new formulation of natural selection in a more general analysis, Dr G. R. Price reached the same conclusion.

Spite can be favored because the product of negative relatedness and a negative benefit to a recipient (harm) is positive, thus benefit multiplied by relatedness can outweigh the cost.

One possible case of spite occurs in the flour beetle *Tribolium* (Wade & Beeman, 1994). The *Medea* allele in a heterozygous mother apparently stimulates a mechanism that kills all offspring lacking a copy of the allele. There are two possible explanations for the maintenance of the *Medea* allele. First, the allele may increase its number of copies in offspring by killing competitors for limited resources. This explanation requires that destroyed zygotes are replaced with new, successful zygotes carrying the allele. In this case the allele is "selfish" because it enhances its own reproduction at the expense of a competitor.

The second possibility is that there is no replacement of killed zygotes and the number of copies of the *Medea* allele does not increase by this mechanism. *Medea* can still spread in this case because it reduces the number of copies of the alternative allele, thereby increasing its own frequency in the next generation. This is a form of spite, where the *Medea* allele uses kin recognition to destroy individuals that are negatively related to itself. Hurst (1991) has discussed spite in systems of cytoplasmic incompatibility which have properties similar to the *Medea* allele.

The original formulation of kin selection relied on the probability of identity by descent to derive the degree of relatedness (Hamilton, 1964*a*, *b*). Price's covariance equation shows that what matters is not common ancestry, but statistical associations between the genotypes of donor and recipient. Those associations often arise because individuals that live near each other tend to have common ancestors. But natural selection is indifferent to the cause of the statistical associations, and negative statistical associations favor spite. Covariance is the only proper way to think about the role of genetic relatedness in evolutionary biology. Price was the first to see this. His work provided the basis for Hamilton's (1970) reformulation of kin selection in terms of covariance, which can properly be called the modern theory of kin selection.

THE FULL EQUATION

The covariance equation provides an approximate description for evolutionary change that is useful for many applications. That equation was discovered independently by Robertson (1966), Li (1967) and Price (1970). Price's unique contribution is a more general equation that is an exact, complete description of evolutionary change under all conditions. The full equation is not just a more accurate form of the covariance equation. It adds considerable insight into many evolutionary problems by partitioning selection into meaningful components. In this section I derive the full equation, and in the following sections summarize some applications.

Here is the derivation. Let there be a population (set) where 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

$$\Delta\bar{z} = \Sigma q_i' z_i' - \Sigma q_i z_i. \qquad (2)$$

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 abundance of a particular chemical compound in galaxy i.

The queerness of the Price Equation comes from the way it associates entities from two populations, which are typically called the ancestral and descendant populations (see Fig. 1). 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 (Fig. 1). 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:

$$\Delta\bar{z} = \Sigma q_i(w_i/\bar{w})(z_i + \Delta z_i) - \Sigma q_i z_i$$

$$= \Sigma q_i(w_i/\bar{w} - 1)z_i + \Sigma q_i(w_i/\bar{w})\Delta z_i$$

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

$$\bar{w}\Delta\bar{z} = \mathrm{Cov}(w_i, z_i) + \mathrm{E}(w_i \Delta z_i). \tag{3}$$

The two terms may be thought of as changes due to selection and transmission, respectively. The covariance between fitness and character value gives the change in the character caused by differential reproductive success. The expectation term is a fitness weighted measure of the change in character values between ancestor and descendant. The full equation describes both selective changes within a generation and the response to selection (cf. Wade, 1985).

The covariance term in eqn (3) would normally be written without subscripted variables as Cov(w, z). The reason for the subscripts is additional clarity when the equation is used to expand itself:

$$\bar{w}\Delta\bar{z} = \mathrm{Cov}(w_i, z_i) + \mathrm{E}_i\{\mathrm{Cov}_j(w_{j\cdot i}, z_{j\cdot i}) + \mathrm{E}_j(w_{j\cdot i}\Delta z_{j\cdot i})\}, \tag{4}$$

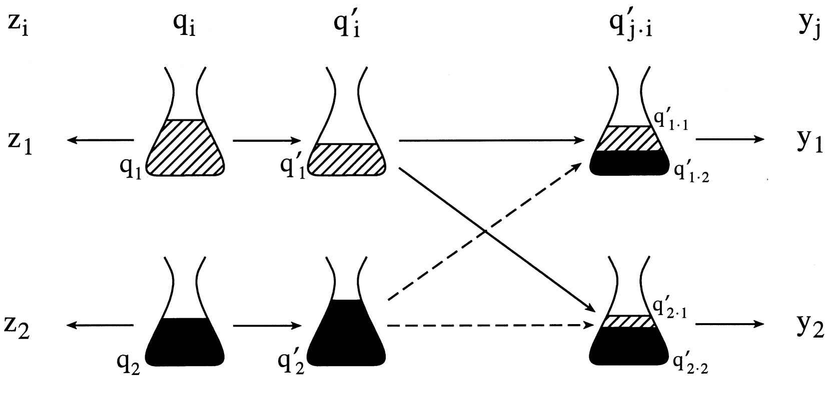

FIG. 1. Example of a selective system using the notation of the Price Equation. The initial population, the left column of beakers, is divided into subpopulations indexed by i, where q_i is the fraction of the total population in the i-th subpopulation. In this drawing, the two different kinds of transmissible material, solid and striped, are in separate subpopulations initially, but that is not necessary. Each subpopulation expresses a character value (phenotype), z_i. Any arbitrary rule can be used to assign trait values. Selection describes the changes in the quantities of the transmissible materials, where the primes on symbols denote the next time period. Thus $q_i' = q_i w_i/\bar{w}$ is the proportion of the descendant population derived from the i-th subpopulation of the initial population. The transmissible material may be redistributed to new groupings during or after the selective processes. The $q_{j\cdot i}'$ are the fractions of the i-th parental subpopulation, after selection, that end up in the j-th descendant subpopulation, thus $\Sigma_j q_{j\cdot i}' = 1$. The new mixtures in the j-th descendant subpopulations express trait values y_j according to whatever arbitrary rules are in effect. This allows full context-dependence (non-additivity) in the phenotypic expression of the transmissible material. Descendant trait values are assigned to the original subpopulations by weighting the contributions of those subpopulations, $z_i' = \Sigma_j q_{j\cdot i}' y_j$. Thus the average trait value in the descendant population is $\bar{z}' = \Sigma_i q_i' z_i'$.

where E and Cov are taken over their subscripts when there is ambiguity, and $j \cdot i$ are subsets of the group i with members that have index j. The partition of i into subgroups j is arbitrary. This recursive expansion of the E term in eqn (3) shows that transmission is itself an evolutionary event that can be partitioned into selection among subgroups and transmission of those subgroups. The expansion of the trailing expectation term can continue until no change occurs during transmission.

In later sections I shall return to the general properties of the equation itself. But first I show some simple applications in evolutionary genetics.

HIERARCHICAL ANALYSIS AND SEX RATIO

The hierarchical expansion of the Price Equation has been used to study group selection and sex ratio (Hamilton, 1979; Nunney, 1985; Frank, 1986*a*, 1987*a*). The relationship between group selection and kin selection has been a controversial aspect of this field (Wilson, 1983; Grafen, 1984; Queller, 1991, 1992*b*). Here, I give a simple derivation of the standard Local Mate Competition model (Hamilton, 1967) that shows the equivalence of kin and group selection. My derivation is somewhat more general than usual because, by using the Price Equation, any pattern of interaction among relatives (population structure) is allowed rather than the standard sib-interaction models.

Let the frequency of males produced by a mother be $r = \gamma + g\epsilon$, where g is the number of sex ratio alleles in the mother each with additive effect ϵ. The sex ratio in the neighborhood in which mating and mate competition occur is $r' = \gamma + g'\epsilon$, where g' is the average number of alleles with effect ϵ among mothers when weighted for each mother's contribution to the neighborhood.

The fitness (number of grandprogeny) of a female with g sex ratio alleles is $w_g = r(1-r')/r' + (1-r)$, and the fitness of a neighborhood with g' as its average number of sex ratios alleles is $w_{g'} = 2(1-r')$ (Hamilton, 1967).

Rewriting eqn (4) in the notation of this problem

$$\bar{w}\Delta\bar{g} = \mathrm{Cov}(w_{g'}, g') + \mathrm{E}_{g'}\{\mathrm{Cov}_g(w_g, g \cdot g')\}$$

$$= \beta_{wg'} V_{g'} + \beta_{wg.g'} \overline{V_{g \cdot g'}},$$

where $V_{g'}$ is the genotypic variance among groups and $\overline{V_{g \cdot g'}}$ is the average genotypic variance within groups. The term $\beta_{wg'}$ is the regression of fitness on group genotype, and $\beta_{wg \cdot g'}$ is the regression of fitness on individual genotype given the group genotype, g'.

The standard method to find the Evolutionarily Stable Strategy (ESS) sex ratio is to solve $(\mathrm{d}\bar{w}\Delta\bar{g}/\mathrm{d}\epsilon) = 0$ when evaluated at $\epsilon = 0$ (Hamilton, 1967; Maynard Smith 1982). This yields the solution (Hamilton, 1979)

$$r^* = (1/2)(1 - V_{g'}/V_g),$$

where $V_g = V_{g'} + \overline{V_{g \cdot g'}}$ is the total genotypic variance in the population. This form shows that a bias away from the Fisherian 1/2 occurs only when there is genetic variance among neighborhoods, $V_{g'}$. This supports the claim that group selection causes biased sex ratios in structured populations. However, one can also write

$$\frac{V_{g'}}{V_g} = \frac{\mathrm{Cov}(g', g')}{\mathrm{Cov}(g, g)} = \frac{\mathrm{Cov}(g, g')}{\mathrm{Cov}(g, g)} = \beta_{g'g},$$

where $\beta_{g'g}$ is the regression coefficient of relatedness of inclusive fitness theory. Thus the sex ratio bias is caused by a nonzero average relatedness among neighbors. The definitions of group and kin selection given here are clearly equivalent. The regression coefficient form has been particularly useful for solving sex ratio and dispersal problems with complex interactions among kin (Frank, 1986*a*, *b*, 1987*a*, *b*, *c*; Taylor, 1988*a*, *b*, 1989). In fact, the Price Equation has been the only general way to study sex ratio evolution for arbitrary population structures. Traditional population genetic methods require special, complex equations for each particular set of assumptions about how relatives interact.

DYNAMIC SUFFICIENCY

In the next few sections I describe technical aspects of the Price Equation. These issues are important for understanding the role of the Price Equation in formal evolutionary theory. Readers who are more interested in Price's contribution to particular biological problems may wish to skip ahead to the section on ESS theory.

Suppose we wish to study the evolution of a character, $\bar{z}$. We are given all of the information needed to calculate the covariance and expectation in eqn (3). Thus we know the average value, $\bar{z}$, at the start, and we can calculate the change in the average value after one time period, $\Delta\bar{z}$. There is a problem, however, if we wish to study the continued evolution of this trait through time. The Price Equation gives us back the average character value in the next time period, but not the information needed to calculate the covariance and expectation term to apply the equation again.

We cannot follow the continued evolution of $\bar{z}$ through time (Barton & Turelli, 1987) or, put another way, we lack the information to achieve dynamic sufficiency in our analysis (Lewontin, 1974). Several authors have noted this problem and have concluded that the Price Equation lacks dynamic sufficiency, whereas other methods of analysis achieve dynamic sufficiency for the same problem (Crow & Nagylaki, 1976; Grafen, 1985; Queller, 1992*a*). This is a confusing summary of the problem because it is partly true and partly false.

The true part is that one can apply the Price Equation to a problem that lacks dynamic sufficiency. It is not true, however, that dynamic sufficiency is a property that can be ascribed to the Price Equation—this equation is simply a mathematical tautology for the relationship among certain quantities of populations. Instead, dynamic sufficiency is a property of the assumptions and information provided in a particular problem, or added by additional assumptions contained within numerical techniques such as diffusion analysis or applied quantitative genetics.

The conditions under which an evolutionary system is dynamically sufficient can be seen from the Price Equation. For convenience assume $\Delta z_i = 0$ so that only the covariance term of eqn (3) need be examined. Initially we require $\bar{z}$, $\bar{w}$, and $\overline{wz}$ to calculate $\Delta\bar{z}$ because $\mathrm{Cov}(w, z) = \overline{wz} - \bar{w}\,\bar{z}$. We now have $\bar{z}$ after one time step, but to use the Price Equation again we also need $\mathrm{Cov}(w, z)$ in the next time period. This requires equations for the dynamics of $\bar{w}$ and $\overline{wz}$, which can be obtained by substituting either w or wz for z in eqn (3); recall that z can be used to represent any quantity, so we can substitute fitness, w, or the product of fitness and character value, wz, for z. If we ignore the expectation term, the dynamics of $\overline{wz}$ are given by

$$\bar{w}\Delta\overline{wz} = \mathrm{Cov}(w, wz) = \overline{w^2z} - \bar{w}\,\overline{wz}.$$

Changes in the covariance over time depend on the dynamics of $\overline{wz}$, which in turn depends on $\overline{w^2z}$, which depends on $\overline{w^3z}$, and so on. Similarly, the dynamics of $\bar{w}$ depend on $\overline{w^2}$, which depends on $\overline{w^3}$, and so on. Dynamic sufficiency requires that higher moments can be expressed in terms of the lower moments (Barton & Turelli, 1987).

PARTITIONING SELECTION AND TRANSMISSION

The full Price Equation, eqn (3), with both the covariance and expectation terms, has been used often to study the hierarchical decomposition of selection within and among groups (e.g. Price, 1972*a*; Hamilton, 1975, 1979; Wade, 1980, 1985; Arnold & Fistrup, 1982; Ohta, 1983; Frank, 1985, 1986*a*, *b*, *c*, 1987*a*, *b*, 1992, 1994*a*, *b*; Grafen, 1985; Nunney, 1985; Heisler & Damuth, 1987; Breden, 1990; see the section above on hierarchical analysis and sex ratio).

Hierarchical decomposition is clearly one important use of the equation, but the equation itself is not limited to these applications. Another interpretation of the covariance and expectation terms in eqn (3) is a partition between selection and transmission. I briefly illustrate this point with a model that balances selection among adults, the covariance term, against mutational changes that occur during transmission, the expectation term (Frank & Slatkin, 1990).

One useful aspect of the Price Equation in these mutation-selection models is that any character value can be analyzed. Instead of studying the change in a character with value z_i, we can transform the character value and study, for example, the change in the n-th power of the character, z_i^n. The Price Equation then gives the change in $\overline{z^n}$, which is the n-th non-central moment

$$\bar{w}\Delta\overline{z^n} = \mathrm{Cov}(w_i, z_i^n) + \mathrm{E}(w_i\Delta z_i^n).$$

This set of equations for the moments $\overline{z^n}$, $n = 1, 2, \ldots$, is a complete description for the evolutionary dynamics of the character z for any system of selection, mutation, mating and inheritance. The most interesting aspect of the Price Equation is the way in which mutation, non-random mating, dominance, and epistasis come into the transmission (expectation) term by changing Δz_i^n, the phenotypic differences between parent and offspring (Frank & Slatkin, 1990). At equilibrium all of the moments must be related by

$$\mathrm{Cov}(w_i, z_i^n) = -\mathrm{E}(w_i\Delta z_i^n).$$

If we normalize the population such that the equilibrium mean, $\bar{z}$, is zero, then this equilibrium equation for $n = 2$ describes how selection affects the variance. If selection is stabilizing toward the equilibrium mean of zero, then the covariance term describes the rate at which the variance is reduced because of the negative association between fitness and the squared distance of character values from the optimum. This reduction in the variance caused by selection must be balanced by the rate at which mutation adds variance to the population by increasing, relative to the optimum, the squared distance of the offspring relative to their parents. This simple equation provides easy calculation for many interesting mutation-selection problems, including nonrandom mating and nonadditive genetics (Frank & Slatkin, 1990).

The dynamics of genetic variability are difficult to study for many assumptions. The problem with these equations of mutation-selection dynamics is that the changes in each moment, $\overline{z^n}$, depend on changes in higher-order moments—the equations lack dynamic sufficiency without additional assumptions (Barton & Turelli, 1987). This lack of dynamic sufficiency is a property of mutation-selection dynamics and not of the Price Equation (see above; Frank & Slatkin, 1990). The value of the Price Equation is that, by adding nothing except clear notation, the forces that act on genetic variability are decomposed into natural components and the underlying difficulties of the analysis are made explicit. Different approaches may provide better tools for numerical calculation in some cases (Turelli & Barton, 1990).

ABSTRACT PROPERTIES

The Price Equation is a very strange mathematical relation when compared with other formalisms in evolutionary biology. The equation is much more abstract than the usual applied mathematics of evolution; it simply suggests a way to map members of one set to members of a second set. In this section I speculate about why this minimalism seems so powerful. My purpose is to call attention to what I believe is a deep problem of a purer sort than is typical in biology.

The Price Equation has been the only way to study general problems of kin interactions. Other methods require special assumptions about which relatives interact. Why is Price's simple mapping so successful for kin selection problems? Kin selection requires that one think of interactions between individuals as interactions between sets of alleles, where there is some statistical relation between the sets (relatedness). In addition, groups of individuals may interact. The consequences of group structure depend on the statistical associations within the group compared with the associations among the group means. The Price Equation provides a natural way to think about hierarchical decomposition (species, group, individual, gene) and statistical association at various hierarchical levels. Although most applications have been to groups of relatives, species-level selection (Arnold & Fistrup, 1982) and community-level selection (Frank, 1994*a*) can be studied in an elegant way.

The Price Equation also provides insight into fundamental problems such as dynamic sufficiency that require a minimal description of how selection works. In the case of mutation-selection balance a simple partition between selection among adults and mutational changes in transmission must be analyzed. This partition follows the natural separation between selection and transmission in the two terms of the equation.

There is a beauty in the equation's spareness and descriptive power. Claims for mathematical beauty rarely impress biologists, however. I have sometimes heard the question: What problems can the Price equation solve that cannot be solved by other methods? The answer is, of course, none, because the Price Equation is derived from, and is no more than, a set of notational conventions. It is a mathematical tautology.

What is the practical value of the equation? The first steps in using the equation are often quite difficult because one has to match the problem to the strange notation. This requires labeling individuals, genotypes or groups in a nonstandard way. Once the right structure is found, solving problems seems very natural both algebraically and biologically. The gain is in forcing one, right at the start, to look for the strange twist that makes the solution inevitable. The Price Equation works well because it provides nothing more than a way to fit a problem to the fundamental properties of evolutionary change. Natural selection is a statistical process, and the Price Equation forces a statistical description of problems.

THE NATURE OF SELECTION

Price recognized that his equation was a step toward a more general theory of selection. At the start of this section I quoted part of the introduction to Price's (1995) manuscript "The Nature of Selection." Here is the full text of the opening paragraph from that manuscript:

> Selection has been studied mainly in genetics, but of course there is much more to selection than just genetical selection. In psychology, for example, trial-and-error learning is simply learning by selection. In chemistry, selection operates in a recrystallisation under equilibrium conditions, with impure and irregular crystals dissolving and pure, well-formed crystals growing. In paleontology and archaeology, selection especially favours stones, pottery, and teeth, and greatly increases the frequency of mandibles among the bones of hominid skeletons. In linguistics, selection unceasingly shapes and reshapes phonetics, grammar, and vocabulary. In history we see political selection in the rise of Macedonia, Rome, and Muscovy. Similarly, economic selection in private enterprise systems causes the rise and fall of firms and products. And science itself is shaped in part by selection, with experimental tests and other criteria selecting among rival hypotheses.

Price was not the first to note the generality of selection. Karl Popper is the founder of modern philosophical analyses of learning and knowledge as extensions of the general properties of biological selection. Donald Campbell has contributed substantially to this philosophy during the past 20 years (e.g. Campbell, 1974). This work was summarized in a recent book by Plotkin (1993). The philosophical work focuses mainly on the question of whether all knowledge is necessarily the outcome of selective processes, hence the label for this work of

"Evolutionary Epistemology" coined by Campbell (1974).

Price was not particularly concerned with these philosophical questions. Instead he sought a general formulation of selection that could be applied to any problem. He hoped that a formal theory would be useful in other fields in the same way that mathematical genetics became the foundation for analyses of genetical selection. Here are the second and third paragraphs from "The Nature of Selection":

> And yet, despite the prevading importance of selection in science and life, there has been no abstraction and generalisation from genetical selection to obtain a general selection theory and general selection mathematics. Instead, particular selection problems are treated in ways appropriate to particular fields of science. Thus one might say that 'selection theory' is a theory waiting to be born—much as communication theory was fifty years ago. Probably the main lack that has been holding back any development of a general selection theory is lack of a clear concept of the general nature or meaning of 'selection'. That is what this paper is about.
>
> Let us pursue a little further the analogy with communication theory. Probably the single most important prerequisite for Shannon's famous 1948 paper on "A Mathematical Theory of Communication" was the definition of 'information' given by Hartley in 1928, for it was impossible to have a successful mathematical theory of communication without having a clear concept of the commodity 'information' that a communication system deals with. Hartley gave what he described as a "physical as contrasted with psychological" definition of *information*, which omitted all considerations of the meaningfulness of messages but measured attributes relevant to the design of communication systems. Similarly, for development of a useful mathematical theory of selection, one needs a physical rather than psychological definition of *selection*, which excludes psychological factors of preferences and decision making. It is my hope that the concept of *selection* proposed in this paper will contribute to the future development of 'selection theory' as helpfully as Hartley's concept of *information* contributed to Shannon's communication theory.

Price then describes abstract properties of selection in terms of mappings between pre-selection and post-selection sets (populations). [The full text of Price's *The Nature of Selection* is published as an accompanying paper in this issue (Price, 1995)]. In my opinion the Price Equation itself is the closest anyone has come to a general, abstract theory of selection. Price avoids formal theory in "The Nature of Selection," but clearly bases his presentation on concepts that he learned while studying the Price Equation. It remains for others to decide how much the Price Equation can aid in building a general theory of selection. I close by quoting Price's first and last paragraph from the final section of his paper.

> When Shannon's "Mathematical Theory of Communication" appeared in 1948, many scientists must have felt surprise to find that at so late a date there had still remained an opportunity to develop so fundamental a scientific area. Perhaps a similar opportunity exists today in respect to 'selection theory'. If we compare the high level of communication technology reached fifty years ago [1922] with the very disappointing results usually reached nowadays in computer simulations of evolution (for example, as described by Bossert [1967]), and if we note the degree of understanding of communication systems shown in the 1928 papers of Nyquist and Hartley and then consider that it took another twenty years before Shannon's [1948] paper appeared, we can reasonably predict that much difficult work will be required before an interesting and useful "Mathematical Theory of Selection" can be developed. The remainder of this paper contains suggestions for readers who may wish to consider working on this problem themselves . . .
>
> Consideration of questions such as these, though in terms of abstract models rather than genes or continents, should lead to deepening understanding of selection such that in time someone will have the insight to take a very large step forward like that taken by Shannon in 1948.

Game Theory and Evolutionarily Stable Strategies (ESS)

Maynard Smith (1972: vii–viii) credits George Price for introducing game theory analysis to the study of animal behavior:

> The essay on 'Game theory and the evolution of fighting' was specially written for this book. I would probably not have had the idea for this essay if I had not seen an unpublished manuscript on the evolution of fighting by Dr George Price, now working in the Galton Laboratory at University College, London. Unfortunately, Dr Price is better at having ideas than at publishing them. The best I can do therefore is to acknowledge that if there is anything in the idea, the credit should go to Dr Price and not to me.

The above quote should not be taken too literally, in that we clearly owe our current understanding of evolution and the theory of games to Maynard Smith (1982). The point is that George Price was not just another person who happened to think about evolution and game theory at the time when the field was taking shape. Rather, he was one of the first to see the theory in broad outline, and his ideas directly influenced Maynard Smith and others who developed the field. In this section I briefly summarize how ideas changed from the late 1960s to the early 1970s, and Price's role in that change. I also mention the contributions of John Price (not related), who in 1969 published the first clear description of how game theory reasoning could be used to analyze ritualized behavior.

The puzzle is why animals often settle fights in a ritualized way rather than inflicting serious or deadly wounds. Maynard Smith & Price (1973) introduce the problem with these examples:

> . . . in many snake species the males fight each other by wrestling without using their fangs. In mule deer (*Odocoileus hemionus*) the bucks fight furiously but harmlessly by crashing or pushing antlers against antlers, while they refrain from attacking when an opponent turns away, exposing the unprotected side of its body. And in the Arabian oryx (*Oryx leucoryx*) the extremely long, backward pointing horns are so inefficient for combat that in order for two males to fight they are forced to kneel down with their heads between their knees to direct their horns forward . . .
>
> The accepted explanations for the conventional nature of contests is that if no conventional methods existed, many individuals would be injured, and this would militate against the survival of the species . . . The difficulty with this type of explanation is that it appears to assume the operation of "group selection".

Although group or species level selection was no longer an acceptable explanation for behavioral evolution in the late 1960s, no one had yet formulated a successful theory of "limited war" based on individual advantage. Hamilton (1971) had recognized the problem and developed a game theory analysis to explain ritualized settlement of conflict. However, his emphasis was on the genetic relatedness of contestants and the reduced conflict that may occur among kin. Thus his explanation required that groups be sufficiently genetically differentiated to favor kin-selected altruism among group members, a condition that often does not hold.

It is not clear whether George Price or John Price was the first to develop a theory to explain ritualized settlement of conflict based on a model of individual selection. John Price laid out the problem and its solution with admirable clarity in a paper published in 1969:

> It is easy to see the advantage of yielding behaviour to the species as a whole, but what is the advantage to the individual who yields? Assuming the distribution of yielding behaviour in the population to be continuous, then it is likely that at one end of the distribution we will find individuals who do not yield at all. These non-yielders will win all their ritual agonistic encounters with yielders, and since there is clear biological advantage in being the victor in a ritual agonistic encounter, we must explain why it is that yielding behaviour has not been bred out of the population, even if it managed to get established in the first place. This is not likely to be a simple problem, but some of the reasons may be briefly summarized as follows:
>
> (1) The disadvantage of being a yielder is counterbalanced by the likely mortality when two non-yielders meet each other. Thus it is advantageous to be a yielder when everyone else is a non-yielder, and to be a non-yielder when everyone else is a yielder. This dependence of the advantage of one's phenotype on the phenotypes of the rest of the population is analogous to the situation with mimetic butterflies and tends towards the maintenance of variation in the population.

These quotes concisely summarize the main ideas of evolutionary game theory. J. S. Price wrote these lines in a paper that developed an evolutionary theory of psychological depression (see also J. S. Price, 1991). George Price had arrived at the same solution. He wrote, in a grant proposal that I describe later:

> A paper entitled "Antlers, intraspecific combat, and altruism" was accepted by *Nature* on 7 February 1969 (provided that it is shortened). This gives particular attention to the problem, recognised by Darwin (*Descent*, Chapt. 17), that deer antlers are developed at great cost to the animal and yet are highly inefficient weapons for inflicting injury on an opponent similarly armed (since branching antlers are effective shields against other branching antlers, though they would not protect against unbranched antlers projecting forward).

For some reason, Price never resubmitted the manuscript. Fortunately, John Maynard Smith, who refereed the paper for *Nature*, understood Price's insights and used them to develop evolutionary game theory into an active field of research. It would be interesting to read Price's original thoughts on this topic in his "Antlers" paper, but I have not been able to find a copy of the manuscript.

It is always difficult, in retrospect, to see the originality and insight of a simple idea. In this case frequency-dependent individual advantage explained what was, at that time, the long-standing puzzle of ritualized settlement of conflict. Fisher had, in 1930, used a frequency dependent model to explain the evolution of the sex ratio. Hamilton's (1967) sex ratio model of local mate competition extended Fisher's approach, and introduced the first modern game theory analysis of adaptation. In particular, Hamilton developed the idea of an "unbeatable strategy", which, if adopted by all members of the population, cannot be beaten by any individual using a different strategy. This provides a method for finding the frequency dependent equilibrium, where the frequency dependence is of the sort described in J. S. Price's quote above.

Although Hamilton (1967) had developed the formal analysis of behavior with the game theory methods that are still used today, he did not see the application of these ideas to the problem of ritualized behavior (Hamilton, 1971). In a recent letter

Hamilton (personal communication) wrote:

> J. S. Price is definitely quite a different person and unrelated [to George Price]. I can remember George talking about him from time to time. The Galton Lab had contacts with the Maudsley psychiatric hospital in South London and George may have visited there or come in contact with John Price or the "other Price" as he sometimes called him. It may have been reading that article by him [J. S. Price 1969] that started George thinking about whether contact was really so "ritualised" and so ultimately to his ESS idea. I myself was fairly happy with "ritualised submission" at the time as my paper in the Man and Beast Symposium shows [Hamilton 1971], and only gradually came to see under George's reiteration what he was on about, and there could be a resolution basically akin to my "unbeatable" sex ratio strategy.

The publication of Maynard Smith & Price (1973) is the end of the story as far as George Price is concerned. As Maynard Smith noted in the quote at the top of this section, Price stimulated his interested in the field (see also Maynard Smith, 1976). By 1973 Price had apparently lost interest in the subject and in publishing his work. He had turned intensely religious, and left his mark on Maynard Smith & Price (1973) by insisting that, in the Hawk–Dove game, the word "dove" not be used because of its religious significance. Thus that particular paper analyzes the Hawk–Mouse game, the only instance of that game in the literature.

Fisher's Fundamental Theorem Made Clear

Fisher's Fundamental Theorem of Natural Selection is probably the most widely quoted theorem in evolutionary genetics. Under the usual interpretation the theorem is believed to say that the rate of increase in the mean fitness of a population is equal to the population's additive genetic variance for fitness. Thus natural selection causes a continual increase in the mean fitness of a population.

This interpretation of the theorem is true only when the population mates randomly and there is no dominance or epistasis. This very limited scope contrasts sharply with Fisher's (1930, 1941, 1958) claims that his theorem is exact for all conditions, that it is similar in power to the second law of thermodynamics, and that it holds the supreme position among the biological sciences.

While most authors accepted the standard interpretation and its many exceptions, others saw the contradiction with Fisher's bold claims and tried to get at his meaning. For example, Kempthorne (1957), Crow & Kimura (1970), and Turner (1970) all saw something deeper in the theorem, but they could not fathom Fisher's derivation and meaning, and their own equations fell far short of proving a result with the generality or depth Fisher claimed. By 1970 all authors had abandoned the theorem as Fisher had intended it, except for Edwards (1967) who thought that Fisher's theorem may indeed be correct and important if only we could understand what he meant (Edwards, 1994).

Price (1972*b*) solved the problem by proving the theorem as Fisher intended. This is an entertaining paper which can still be read with ease (see also Ewens, 1989; Frank & Slatkin, 1992; Edwards, 1994). Here I briefly outline Price's key insight, speculate as to why Price succeeded where the best minds in population genetics failed, and mention where the work in this field is currently heading.

Price noted that Fisher partitioned the total change in fitness into two components. To show this I first write the total change in fitness as

$$\Delta\bar{w} = \bar{w}'|E' - \bar{w}|E, \qquad (5)$$

where primes denote one time step or instant into the future, $\bar{\mathrm{w}}|E$ is mean fitness when measured in the context of a particular environment, E, and $\Delta\bar{w}$ is the total change in fitness which everyone had assumed was the object of Fisher's analysis. However, Fisher's theorem is not concerned with the total evolutionary change, which depends at least as much on changes in the environment as it does on natural selection. Instead, Fisher partitioned the total change into

$$\Delta\bar{w} = (\bar{w}'|E - \bar{w}|E) + (\bar{w}'|E' - \bar{w}'|E).$$

Fisher called the first term the change in fitness caused by natural selection because there is a constant frame of reference, the initial environmental state E. The Fundamental Theorem states that the change in fitness caused by natural selection is equal to the additive variance in fitness. Fisher referred to the second term as the change caused by the environment, or more often, as the change caused by the deterioration of the environment, to stress that this term is often negative because natural selection increases fitness but the total change in fitness is usually close to zero. Density dependence is one simple way in which adaptive improvements in organismal efficiency must be balanced by greater competition for resources (deterioration in the biotic environment). Thus, in one model presented by Fisher (1941), "Intense selective activity is shown to be compatible with an entire absence of change in the average survival value of the population".

Price showed that the Fundamental Theorem can be proved if one adheres to Fisher's rather queer definitions. In particular, Fisher focused on the first term of eqn (5), which Ewens (1989) has called the partial change in fitness caused by natural selection. This partial change uses Fisher's measure for the average effect of a gene substitution while holding all aspects of the environment, E, constant. The environment includes the initial gene frequencies, thus evolutionary change in fitness is measured while holding gene frequencies constant. The effect of changing gene frequency on fitness appears in the second, environmental, term.

Why was Price able to see what Fisher meant where others had failed? Part of the answer is certainly Price's great ability to describe deep and general properties of natural selection with simple equations. In addition, Price may have been predisposed by his earlier work because Fisher's view depended on two properties shared with the Price Equation: a partition of total change into components and strict use of unconventional definitions.

Now that Price has shown us what Fisher really meant, we can ask whether the theorem is as deep and useful as Fisher claimed. Price's own view was that the theorem was interesting mathematically but of little practical value. Ewens (1989) echoed this view after giving a clear derivation of the theorem based on Price's paper. Perhaps the strongest case against the theorem is that Fisher himself never seemed to use it beyond developing some rather vague heuristical conclusions about how competition causes the "environment" to deteriorate (Frank & Slatkin, 1992).

The case against Fisher is not closed, however. Ewens (1992) has recently shown a relationship between the Fundamental Theorem and some fairly deep optimization principles that have been used successfully in mathematical genetics. Fisher's "average effect of a gene substitution" provides the key link between the Fundamental Theorem and the optimality principle that "of all gene frequency changes which lead to the same partial increase in mean fitness as the natural selection gene frequency changes, the natural selection values minimize a generalized distance measure between parent and daughter gene frequency values" (Ewens, 1992). This view fits nicely with Fisher's writings because Fisher repeatedly emphasized the importance of average effects in both the Fundamental Theorem and in general aspects of mathematical genetics.

What was Price trying to do?

In this section I briefly summarize what is known of Price's life. I then return to the problem of how he came to work on abstract properties of natural selection, altruism and ritualized behavior.

Although I have come across some facts about his life in the late 1960s and early 1970s from his CV (Table 1), correspondence and unpublished

TABLE 1

George Price's Curriculum Vitae in 1974

Personal Data	Age 51, divorced, U. S. citizen, admitted to permanent residence in the U.K. (work permit not needed).
Education	S.B. in chemistry, University of Chicago, 1943 Ph.D. in chemistry, University of Chicago, 1946
Employment	
1944–46	Manhattan Project (atom bomb project) research on uranium analysis at the University of Chicago.
1946–48	Instructor in chemistry at Harvard and consultant to Argonne National Laboratory.
1950–57	Research Associate in medicine, University of Minnesota, working on fluorescence microscopy, liver perfusion, etc.
1957–61	Trying to write book, NO EASY WAY, (first for Harper's, later for Doubleday) on what the United States should do about Russia and China, while supporting myself as a freelance magazine article writer and a subcontract technical writer. (The book was never finished: the world kept changing faster than I could write about it!)
1961–62	Consultant to IBM on graphic data processing.
1962–67	IBM employee in Poughkeepsie and Kingston, New York. Started as a Market Planner helping in the design phase of System/360. Final work was on mathematical optimisation carried out through simulation of private enterprise market mechanisms. Programming was in FAP (Fortran Assembly Program) on the 7094.
1967–68	Reading and writing in London on evolutionary biology, while living on savings.
1968–74	Research in mathematical genetics, on academic staff of University College London (under Professor Cedric Smith in the Department of Human Genetics and Biometry). Final position was Associate Research Fellow. The research involved much FORTRAN programming (both IBM/360 Mod 65 and CDC 6600) plus some PL/I and FORMAC. (Left because I felt that the sort of theoretical mathematical genetics I was doing wasn't very relevant to human problems, and I wanted to change to economics.)
1974	Worked June 14th to August 17th as a night office cleaner for a contract cleaning firm. (This work was undertaken for reasons having something to do with Christianity. I was considered to be slow but unusually dependable, so that after a while the supervisor did not bother to inspect my work. Left because my reason for wanting a night job no longer held.)
1975	[From a brief article in a January 15, 1975 edition of Sennet (Careers Supplement), a London student's newspaper, entitled *Jesus 'hot-line'*]: A prominent genetics researcher at University College Hospital gave up everything, including his life for his religious beliefs St. Pancras Coroner's Court was told last week. Dr. George Price gave away all his money, clothes and possessions to homeless alcoholics and left his flat in Bloomsbury to live as a squatter in Drummond Street, Kentish Town. It was there that he was found dead. A respected scientific researcher, Dr. Price was convinced that he had a "hot line to Jesus".

manuscripts, I do not have a clear impression of the man. He ended in great sadness and poverty, confident in the clarity of his mind and his insights in biology, but tormented by the feeling that he had failed to contribute in any significant way to easing human suffering. He was increasingly religious toward the end, when he gave all his money and possessions to homeless alcoholics and went to live among the poorest squatters of London. But he continued to work and write with clarity. His last plans were to take up economics, because he hoped to find in economics a better way to match his analytical power to problems of humanity.

In Price's last years he also wrote a detailed analysis of the apparent contradictions in the gospels of the New Testament. This is a subject with a long history of biblical scholarship, where the goal is to resolve contradictions about the timing of the crucifixion and resurrection of Jesus. Price's work on this subject is presented in an unpublished manuscript "The twelve days of Easter". I cannot judge the quality of his scholarship, but this paper is written with the same clarity and precision of his work in evolutionary biology.

I return now to the limited goal of understanding Price's contributions to evolutionary genetics. Specifically, why was he interested in abstract properties of natural selection? How was that interest associated with his contributions to problems of combat, altruism and game theory?

I have found only limited clues. Price wrote a thoughtful review of the relation between science and supernatural phenomena in the mid 1950s (Price, 1955, 1956). This work shows his keen analytical mind and his interest in fundamental processes. His interest here may also reflect a tension between his restless search for meaning, in terms of human interests and values, and his tenacious belief that all hypotheses must be subjected to cold, analytic scrutiny.

The next major project that I know of is his interest in the arms race and the cold war in the late 1950s (see Table 1). This interest may have set the stage for his later work on game theory and the resolution of conflict by ritualized behavior.

The hints from his pre-genetics work provide only vague clues about Price's goals in evolutionary biology. The best evidence we have comes from his own grant proposal to the Science Research Council of Great Britain. The proposal was written in 1969, after Price had spent approximately two years studying evolution. In the remainder of this section I briefly summarize the contents of that proposal. I list each of the ten topic headings in the proposal, with a concise description of the main points. Generally, I will avoid commentary; the purpose is to make available this information in the hope that someone will look more deeply into his life and his work.

GOALS AND STRATEGY

I quote the first section in full.

> The main purpose of the work is to develop improved techniques for making inferences about hominid evolution in the Pleistocene going beyond what is directly shown by fossils and artifacts. It is felt that the most fruitful way to begin is by developing (a) new mathematical treatments of evolution under conditions of complex social interactions, and (b) more simple and transparent mathematical genetics models that can provide rules-of-thumb for qualitative or semi-quantitative reasoning. One important benefit from emphasizing a mathematical approach is that this should help to protect against biasing effects of emotional prejudices about human nature and human ancestry. Also, a mathematical approach gives an advantage in exposition; to cite Haldane: when one is faced with a difficulty or controversy in science, "an ounce of algebra is worth of a ton of verbal argument" (obituary by Maynard Smith, *Nature*, 206, 239 (1965)).
>
> As these mathematical tools become available, they will be applied to specific problems of human evolution—though in the early stages of work, emphasis will be on development rather than application. In addition, since it is likely that much of the mathematical work will also have broad applicability to evolutionary biology (especially in relation to social animals), it is planned to apply the mathematical models to some ethological problems.

AN EXAMPLE

Price introduces the idea of evolutionary stability of behavior in the context of alternative hypotheses about the mating system of Pleistocene humans.

As I discussed in the earlier section on Evolutionarily Stable Strategies, Price's genetical approach to the evolutionary stability of behavioral systems was a novel way to think about the problem. Price summarized the approach in this way:

> We now concentrate attention on behaviour. A system of behaviour that is close to a selective maximum will be called a *genetically optimal* behaviour system ("optimal" in the sense of maximizing the frequency of an individual's genes in the next few generations of the local population). For a genetically optimal behaviour system to be stable, the main requirement is that children should tend to behave like their parents. Even though we have little knowledge of how cultural and genetical inheritance interacted in Pleistocene hominids, let us assume that this condition of parent-child resemblance held. Then a sudden large saltation in behaviour was comparatively improbable during that period (though such have occurred in historical times), and small changes moving away from the peak tended to be corrected against because they were disadvantageous.

The point is that we can reject any hypothesis for a mating system if it does not satisfy the condition of being locally stable against invasion by slightly different individual behaviors. Price also noticed that all the complexities of genetic and cultural inheritance may often be reduced to the issue of parent–offspring correlation when one is trying to analyze the evolutionary stability of a behavioral system.

Price then suggested two alternative hypotheses about Pleistocene mating systems to illustrate his method of reasoning. These alternatives were not meant to be a list of plausible hypotheses, but were presented to "save space" in the context of a grant proposal.

System I is one of total cooperation, with promiscuous, non-competitive mating and cooperative rearing of the young. Price concluded that: "This will be a genetically optimal system under the condition that any deficiency in cooperation is retaliated against by physical punishment and/or withholding benefits. Then an individual would increase his or her fitness both by cooperating with others and thereby avoiding punishment, and by helping to punish others who are deficient in cooperation and thereby causing them to cooperate."

System II is one of group cooperation principally in hunting by adult males, and of individual or family action in most other behaviours. Cooperation in group hunting was maintained by reciprocal exchange of food among males and punishment of significant non-cooperation, as in System I. After hunting spoils were divided among men, the distribution of food to women and children was a matter of individual choice by each man.

Price concluded, after further commentary, that System II is probably near to the truth, with each male usually having a single wife. This justifies, later in the proposal, the need to study more fully sexual selection in monogamous mating systems.

MATHEMATICAL WORK NEEDED

Price provided in this section an outline of theoretical work needed to create a foundation for evolutionary analyses of human behavior. Most of the important theoretical advances in the study of social behavior are foreshadowed here. A complete grasp of the fundamental problems listed here remains well beyond current understanding. I quote the section in full.

> From the example [of human mating systems] it can be seen that mathematical understanding of several types of biological phenomena would be useful. First, since early man presumably lived in groups, and because of the importance of understanding the relative significance of individual and group selection in human descent, better understanding of group selection would be desirable. (Even merely for the purpose of rejecting group selection as an explanatory mechanism, it would be helpful to understand it better. But it seems likely that group selection should not be entirely rejected as a factor in human evolution.) A second need is to work out details of reciprocity and punishment systems that make it individually advantageous to act in group- and species-benefiting ways, by means of transfers of benefit and harm among individuals on a basis of degree of cooperation. A third need is better understanding of nepotism effects, assortative mating, and other behaviour involving transfer of benefit or harm among individuals on a basis of degree of genetical similarity. A fourth need is investigation of the mathematics of sexual selection under the postulated conditions of individual families with permanent mating. A fifth need is work on the interactions of cultural and genetical inheritance—since the period under consideration was one of major cultural advances. A sixth need is better understanding of conditions for stability in evolutionary trends. A seventh need is simple mathematical models relating to such basic matters as the speed of evolutionary changes.
>
> These needs lead to the specific plans to be discussed in the sections that follow.

GROUP SELECTION DEPENDENT ON RANDOM DRIFT

This is standard population genetics. Price cites Kimura, Wright and others on drift-migration dynamics.

OTHER POSSIBLE GROUP SELECTION MECHANISMS

Price noted that a different kind of group selection from that traditionally studied by population geneticists may be important in evolutionary studies of behavior. He cited Hamilton's analysis of meiotic drive of the Y against the X. A gene enhancing drive of the Y spreads in the population, but causes an excess of males and a decline in the population size because females become rare. Thus selection against drive occurs at the group level. He also mentioned different systems of territoriality that could be genetically stable (roughly, an ESS) within populations but that would have different consequences for the success of the group. If the observed state corresponds to the stable state with higher group productivity, then Price suggested that group selection may partly explain the observed pattern.

SYSTEMS OF INTRASPECIFIC COOPERATION AND LIMITED COMBAT

Here Price talks about his work that eventually led to the theory of Evolutionarily Stable Strategies (ESS, see above). First he noted that cooperative behavior can be maintained if group members tend to punish uncooperative individuals, thereby making cooperative behaviour individually advantageous. He then discussed his paper that addressed apparently group-benefiting behaviors in terms of individual advantage:

> A paper entitled "Antlers, intraspecific combat, and altruism" was accepted by *Nature* on 7 February 1969 (provided that it is shortened). This gives particular attention to the problem, recognised by Darwin (*Descent*, Chapt. 17), that deer antlers are developed at great cost to the animal and yet are highly inefficient weapons for inflicting injury on an opponent similarly armed (since branching antlers are effective shields against other branching antlers, though they would not protect against unbranched antlers projecting forward). Also the paper gives briefer treatment to several other problems, such as the remarkable cooperative behaviour of the African hunting dogs.

Price then mentioned some references from anthropology and sociology, and that his specific theory has much in common with game theory models of limited war strategy. (The *Nature* paper was never published. See the section above on EVOLUTIONARILY STABLE STRATEGIES.)

SEXUAL SELECTION UNDER MONOGAMOUS MATINGS BY MUTUAL CHOICE

Price followed Darwin in citing the probable importance of sexual selection in human evolution. Issues concern "attractiveness", "fashion", and the relation between resources (e.g. food) and the genetical evolution of the mating system. But Price was mainly concerned with showing, formally, how sexual selection could have affected the evolution of humans because, as Price states, "Many critics, beginning with Wallace even before the *Descent* was finished (letter to Darwin, 29 May 1864), have questioned whether sexual selection could occur under known or assumed conditions of primitive human life."

Price described in some detail how he planned to study a formal model of sexual selection. His model had characters for behavior or anatomy, preferences for the opposite sex, a paternal rating for each male based on his character values, and a maternal rating for each female based on her character values. Ratings are based on utilitarian characters rather than those that merely affect appearance. He recognized the importance of sex-limited expression, suggesting an example model with characters that vary in their expression in males and females.

SEXUAL SELECTION—ADVANCED STRATEGY

Price noted that his previous model, in which preferences are rigidly related to characters, would probably lead to a Fisher runaway process. But Fisher's process runs away only in its intermediate stages. It is slow when getting started and toward the end when natural selection begins effectively to slow sexual selection (Price cites O'Donald's 1969 simulations).

These rate changes in character evolution suggested to Price that females might compare old and young males to determine which traits are changing most rapidly and, therefore, are most strongly correlated with fitness. If females chose the most rapidly changing traits in this way, they would be preferring what is coming into fashion, a strategy similar to economic speculation.

I don't know of any work that has followed this line of thought, and probably for good reason. The idea may work formally, but whether females could actually assess rate of character change in a useful way seems doubtful.

EXTENSIONS OF BASIC SELECTION MATHEMATICS

The work Price eventually published on the Price Equation and Fisher's fundamental theorem are described in full detail.

OTHER PROBLEMS

I quote the final paragraphs in full.

> This completes the discussion of contemplated projects where plans are sufficiently well-formulated to permit detailed explanation. Other areas where it is hoped to accomplish something useful include the problem of the interaction of cultural and genetical inheritance (which on page 4 was treated in a quite crude, inadequate way). Also it is hoped that the investigations of social interaction effects may lead to the finding of very broad generalizations. For example, the cases discussed where individual selection decreases group fitness are closely and deeply analogous to economic effects recently discussed by Hardin in a paper entitled "The tragedy of the commons" (*Science*, 162, 1243 (1968)); and the same general types of mechanisms can be used in biological systems and in human economic systems to make it advantageous to the individual (in a genetical sense or in an economic sense) to act in a way that benefits the group. It is hoped that other parallels between economics and genetics can be found.
>
> To sum up: The general plan of the work is that mathematical tools will be developed specifically in order to handle problems of human evolution, but when developed they will be applied to both human and animal evolution problems. Initially emphasis will be on developing the tools; later it will increasingly be on applying them.

Conclusions

George Price had original, fundamental insights into evolutionary biology. The Price Equation had a direct and profound influence on W. D. Hamilton's work on kin selection and on the subsequent theoretical development of social evolution. Price was the first to see that ritualized behavior, game theory and evolutionary genetics belonged together in a coherent vision of behavioral evolution. Price's vision started Maynard Smith's work on evolution and the theory of games, which is among the most influential developments of the past few decades.

These past achievements are sufficient reasons to study Price's life and work. But my own curiosity about Price's work is kept alive by the Price Equation. In evolutionary genetics, the equation continues to provide fresh insight into many difficult problems. And the future may show that this rich and poorly understood equation is indeed the key to a broader theory of selection that transcends population genetics.

W. D. Hamilton has, over the past 15 years, helped me in many ways to understand more about evolutionary genetics and about George Price. Warren Ewens changed this paper from a vague idea to an actual manuscript by his steady encouragement and his insight into the esoteric details of Fisher's fundamental theorem. Jon Seger made characteristically insightful suggestions for revision. I received helpful comments from N. H. Barton, R. M. Bush, J. F. Crow, T. Nusbaum, M. Ridley, P. D. Taylor and M. J. Wade. I owe special thanks to L. D. Hurst for his editorial assistance and for his infective enthusiasm about George Price.

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