Evolution
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Book Review

George Price, the Price equation, and cultural group selection

Oren Harman. *The Price of Altruism: George Price and the Search for the Origins of Kindness*. New York: Norton; 2010. ISBN: 9780393067781, 464 pages, $27.95.

> "If you are faced by a difficulty or a controversy in science, an ounce of algebra is worth a ton of verbal argument."
> —attributed to J. B. S. Haldane (Maynard Smith, 1965)

The problem of cooperation is central to the evolutionary and social sciences. Altruism so bothered Darwin that he thought it 'fatal to the whole theory' of evolution by natural selection. In the 1960s and 1970s, sociobiology overcame Darwin's 'special difficulty,' laying down a solid theoretical foundation on which to build a theory of social evolution. This foundation includes Hamilton's reformulation of natural selection as a force that maximizes "inclusive fitness" rather than individual fitness, George Williams' expository evisceration of old-school group selection, Robert Trivers' explanation of cooperation between unrelated individuals with the theory of reciprocity, and John Maynard Smith's application of game theory to the study of animal behavior. Sadly, too few of us include George Price in this august company. Many students of sociobiology have never even heard of George Price. This is a tragedy. He deserves our admiration. If nothing else, he left us with the Price equation, a powerful lens through which we can understand social evolution, resolving many of the debates that plague our field.

Oren Harman has set out to right this wrong. In *The Price of Altruism*, Harman pieces together the wonderful life and tragic death of George Price, polymath extraordinaire. The book is well-researched, readable and thoroughly enjoyable.

I recommend this book to anyone studying the evolution of cooperation. Harman offers an accessible introduction to Price's scientific contributions. In addition, Harman pairs each chapter of Price's life before his foray into evolutionary theory with a chapter on the scientific history of the problem of cooperation, from the time of Darwin right up until the sociobiological revolution of the 1960s. These chapters provide a succinct summary with biographical sketches and scientific contributions of Kropotkin, Huxley, Haldane, Fisher, Veblen, von Neumann, Keynes, Hamilton, Williams, Maynard Smith and more.

1. Price's life

George Price graduated from the University of Chicago in 1943 with a degree in chemistry. He stayed on for the next few years, earning a doctorate in chemistry while working on the Manhattan Project, pioneering a method to detect trace amounts of uranium exposure. He then taught chemistry at Harvard for a couple of years, worked on transistor research at Bell Labs, worked on medical research at the University of Minnesota, wrote (but never published) a book on the Cold War, published a pair of papers in *Science* criticizing research on ESP (Price, 1955, 1956), invented (but never credited for) computer-aided design, and worked as a consultant for IBM. During this time, he also found the time to correspond with several Nobel laureates from several different fields. Although possessing a remarkable intellect, Price never stuck with any project long enough to earn the respect from others he so desperately craved. Harman describes this period of Price's life as a "hustle." The science seemed to have been secondary. Price was looking for one great discovery to make his mark.

In 1967, Price moved to London to research evolutionary genetics, abandoning his wife and two children. Without a formal appointment, Price spent most of his time reading in libraries, coming up with the question: Why family? He wrote to his daughter, Kathleen, explaining how his big article was going to be on the evolutionary origin of the family. He explained that, in most mammals, males just mate with females, providing no child care. In humans, the dominant pattern is for males to invest heavily in their offspring, and Price wanted to know why. Price did not seem bothered by the fact that he was an absentee father.

In the span of a few years, Price went on to make three significant contributions to evolutionary genetics (Frank, 1995): Price (1972a) explained what Fisher actually meant with his Fundamental Theorem of Natural Selection, clearing up decades of confusion; along with Maynard Smith, Price developed the field of evolutionary game theory (Smith and Price, 1973); Price derived the equation bearing his name (Price, 1970, 1972b), to which I will return. These contributions would constitute an exceptional career. To think that Price accomplished so much in the span of about five years without any formal training is remarkable.

A grant proposal from 1969 lays out what Price wanted to work on next. To improve techniques "for making inferences about hominid evolution in the Pleistocene going beyond

what is directly shown by fossils and artifacts" (Frank, 1995, p. 385), Price thought we needed a better understanding of nepotism, group selection, reciprocity and punishment systems, assortative mating, the mathematics of sexual selection, the interaction of cultural and genetic inheritance, and the rate of the evolutionary process.

2. The Price equation

The Price equation is a general description of evolutionary change, applying to any mode of transmission, including genetics, learning, and culture. For derivations and explanations, see Frank (1988), Okasha (2006), and McElreath and Boyd (2007). Here is the full form of the Price equation:

$$\overline{w}\Delta\overline{z} = Cov(w_i, z_i) + E(w_i \Delta z_i) \qquad (1)$$

Fitness is denoted by w and the evolving trait, which could be anything from height to the level of altruism, by z. The bars above the letters on the left-hand side of Eq. (1) denote average values in the population and the delta symbol denotes the change in the average trait value ($\overline{z}$) in one generation. The i subscript indexes different individuals in the population. So, the average fitness of the population multiplied by the change in the average value of the trait in one generation (i.e., evolution) is equal to the sum of two terms, a covariance and an expectation. The covariance term measures the statistical association between fitness and trait value, and can be thought of as the evolutionary change due to selection. The expectation term is a fitness-weighted measure of the change in trait value between ancestor and descendant, and can be thought of as the change due to transmission. In standard Mendelian genetics, the net effect of transmission is zero (i.e., transmission is unbiased) and so this term drops out. When modeling processes such as meiotic drive or biased cultural transmission, this expectation may be nonzero (i.e., transmission itself results in evolutionary change).

The Price equation is a useful tool both to study the evolutionary process and to understand it. For example, we can use the Price equation to derive Darwin's postulates (as formulated by Lewontin, 1970). If we set the expectation in Eq. (1) to zero (i.e., no transmission bias), we can rewrite the Price equation this way:

$$\Delta\overline{z} = h \cdot Var(z_i) \cdot \beta(w_i, z_i) \qquad (2)$$

(For the details of this derivation, see Okasha, 2006, pp. 34–39, and the references therein.) The left-hand side of Eq. (2) represents the change in the average trait value in the population (i.e., evolution). This will be nonzero when each of the three terms on the right-hand side are nonzero. For there to be evolution by natural selection, there must be phenotypic variation (i.e., $Var(z_i) \neq 0$), there must be differential fitness (i.e., $\beta(\omega_i, z_i) \neq 0$, where $\beta(\omega_i, z_i)$ is the

regression of relative fitness on the trait value), and fitness must be heritable (i.e., $h \neq 0$, where h is heritability).

Using the Price equation, Hamilton (1964a, 1964b) reworked his theory of inclusive fitness, resulting in the modern theory (Hamilton, 1970, 1975). In his original formulation, Hamilton (1964a, 1964b) had described genetic similarity in terms of genes identical by descent. Some saw this theory of "kin selection" as an alternative to "group selection." In his re-formulation, Hamilton (1975, pp. 140–141) demonstrated that inclusive fitness and group selection were equivalent and thought "kinship should be considered just one way of getting positive regression on genotype in the recipient and that it is this positive regression that is vitally necessary for altruism." Queller (1992) presents a general derivation of kin selection using the Price equation and solves for the condition under which selection favors the spread of altruism (i.e., $\overline{w}\Delta\overline{g} > 0$, where g represents the genotype determining the level of altruism), yielding a general form of Hamilton's rule:

$$\beta(w, g \mid g') + \beta(g', g) \cdot \beta(w, g' \mid g) > 0 \qquad (3)$$

In this formulation, $\beta(w, g \mid g')$ and $\beta(w, g' \mid g)$ are partial regression coefficients. $\beta(w, g \mid g')$ represents the cost of altruism ($-c$ in Hamilton's rule), the effect an individual's genotype has on its own fitness in the presence of neighbors of genotype g'. $\beta(w, g' \mid g)$ represents the benefit of altruism (b in Hamilton's rule), the effect of an individual's genotype on the fitness of its neighbors. $\beta(g', g)$ is the regression coefficient of relatedness (related to the r in Hamilton's rule). Using the Price equation to derive Hamilton's rule, we see that common ancestry is not what really matters for the evolution of altruism; what matters is the statistical association between the genotypes of donor and recipient. With this statistical definition, relatedness can even be negative, resulting in the evolution of spite (Hamilton, 1970). Substituting $-c$ for $\beta(w, g \mid g')$ and b for $\beta(w, g' \mid g)$ and assuming weak selection, we recover the familiar form of Hamilton's rule (i.e., $rb > c$; for a detailed derivation with explanation, see McElreath and Boyd, 2007, Chapter 3).

Next, let us turn to group selection. If you carefully inspect Eq. (1), you will notice that the term on the left-hand side of the equality ($\overline{w}\Delta\overline{z}$) looks a lot like the term inside of the expectation operator on the right-hand side ($w_i \Delta z_i$). If we are considering the evolution of some trait, the expectation term on the right-hand side of Eq. (1) can be thought of as the effect of transmission bias. If we think about evolution across different levels of biological hierarchy (e.g., individuals and groups), transmission bias at one level will look like selection at a lower level. We can therefore expand the Price equation to consider evolution at different levels, resulting in:

$$\overline{w}\Delta\overline{z} = Var(z_g) \cdot \beta(w_g, z_g) + E\left[Var(z_{ig}) \cdot \beta(w_{ig}, z_{ig})\right] \qquad (4)$$

In this formulation, the subscript g indexes different groups and i indexes different individuals within groups.

This formulation of the Price equation captures the tension between selection at different levels, the multilevel perspective (Sober and Wilson, 1998). $\mathrm{Var}(z_g)$ represents the variation in the trait between groups and $\mathrm{Var}(z_{ig})$ represents the variation in the trait within a group. $\beta(w_g, z_g)$ is the regression of group fitness on trait value of the group and $\beta(w_{ig}, z_{ig})$ is the regression of individual fitness on the trait value of the individual.

If selection is to favor altruistic behavior (where altruism is formally defined as $\beta(w_{ig}, z_{ig}) < 0$ and $\beta(w_g, z_g) > 0$), the between-group component—$\mathrm{Var}(z_g) \cdot \beta(w_g, z_g)$—must be larger than the within-group component—$E[\mathrm{Var}(z_{ig}) \cdot \beta(w_{ig}, z_{ig})]$. This means that the variation between groups—$\mathrm{Var}(z_g)$—must be sufficiently large compared to the variation within groups—$\mathrm{Var}(z_{ig})$. Setting aside clonal organisms and eusocial insects, in the realm of genetical evolution, because migration erodes between-group variation, between-group selection for altruism in large groups will be weak compared with within-group selection against it.

The Price equation provides a formal link between kin selection and group selection. By starting with the same equation and deriving one expression for inclusive fitness (an individualist perspective) and one for group selection (a multilevel perspective), we can see that the two approaches are mathematically equivalent, alternative ways of seeing the same evolutionary process. Put another way, arguments about whether some particular social behavior is the result of kin selection or group selection are about terminology, not facts. For any particular situation, one perspective may be more useful than the other. Kerr and Godfrey-Smith (2002) go so far as to recommend "gestalt switching," in which the researcher switches between the two perspectives. They argue that each perspective makes some facts vivid and obscures others. Looking at the same process through both lenses may reveal more of the picture.

I want to conclude this discussion by offering a few insights on how the Price equation can address a debate in our field, the role of cultural group selection in explaining the evolution of cooperation (for a lengthier discussion, see Henrich, 2004; McElreath and Boyd, 2007, chapter 6).

First, since the Price equation is completely general, we can use it to understand cultural evolution as naturally as genetic evolution. Advocates for group selection in humans are (mostly) considering cultural, not genetic, evolution (e.g., Boyd and Richerson, 2009a). With culture, transmission mechanisms like conformity and prestige-bias homogenize groups (i.e., $\mathrm{Var}(z_{ig}) \approx 0$), resulting in stable between-group variation (i.e., $\mathrm{Var}(z_g) > 0$), providing the fuel necessary for cultural group selection. Other processes can amplify this effect. For example, sanctioning systems, including punishment and reputation, demand normative behavior from group members and different groups may settle on different norms of behavior. Costly signaling has a similar effect: different social groups may value different kinds of signals (e.g., competitive altruism in one group, conspicuous consumption in another).

Second, cultural group selection models are not usually about altruism (e.g., Boyd and Richerson, 1990, 2002). Instead, they model social interactions such as coordination games, battle of the sexes games, stag hunt games, and reputation-based reciprocity games. These situations are common in social life and result in multiple stable equilibria (i.e., different social groups settle on different norms). Put another way, within-group selection favors whatever is common. When this is true, knowing within-group fitness effects is not enough (averaged across groups, $\beta(w_{ig}, z_{ig}) \approx 0$); between-group selection determines the direction of social evolution and can favor the spread of group-beneficial norms (i.e., $\beta(w_g, z_g) > 0$). This is one of the key misunderstandings in the cultural group selection debate. For many, group selection and altruism have become inextricably linked. There is more to group selection than altruism.

Third, formulating social evolution in a multilevel perspective forces us to think carefully about the kinds of mechanisms that may give rise to between-group selection. When most people think of cultural group selection, they envision warfare between groups (e.g., Boyd, Gintis, Bowles and Richerson, 2003). There are other mechanisms that can give rise to group selection, including group extinction or dissolution (Boyd and Richerson, 1990), imitation across groups (Boyd and Richerson, 2002) and selective migration (Boyd and Richerson, 2009b).

With the cultural group selection hypothesis in mind, reconsider Darwin's description of human social evolution: "It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another…and this would be natural selection" (Darwin, 1871).

The point I want to make is this: Individualist and multilevel perspectives are formally equivalent. If you study the evolution of cooperation, your research can be understood from either perspective. Adopting a group selection perspective may result in new insights. For example, mechanisms such as reputation and costly signaling can lead to multiple-stable equilibria and so a theory of equilibrium selection is necessary to understand the evolution of norms. On the other hand, an individualist perspective is fully justified and has already led to many insights. For example, social exchange poses the adaptive problem of cheater detection, which is more naturally analyzed in terms of costs and benefits to individuals.

3. Price's death

Around 1970, Price, a lifelong atheist, had his first conversion to Christianity. Seeing coincidences everywhere, he thought there must be something more going on, leading him to a careful study of the gospels. He noted many

contradictions and put forth his own version of events in an unpublished manuscript, *The Twelve Days of Easter*. He eventually abandoned biblical scholarship and had a second conversion. If his mind did not get him any closer to God, maybe his heart would. Price embarked on a project of radical altruism, spending much of his time helping London's downtrodden in any way that he could, from lending money, to cleaning someone's apartment, to offering up his house.

Harman speculates that Price's equation may have played some role in his second conversion. Around this time, Price wrote letters to his daughters telling them what a terrible father he'd been. If he could not redeem himself, his quest for the roots of altruism may have been an attempt to redeem us all. What he found may have deeply upset him. The Price equation shows how the evolution of altruism and the 'struggle for existence' are two faces of the same evolutionary process: Altruism at one level implies competition at a higher level. Price could not accept such a world. He set out to live a life that would prove his equation wrong.

This is, of course, speculation. We will never know what drove Price. In 1975, he took his own life, cutting through his carotid artery with a pair of scissors and bleeding out. There was a small memorial service held for Price. Hamilton and Maynard Smith were in attendance. Price was buried in an unmarked grave in St. Pancras' Cemetery. If not in life, at least in death, Price is finally starting to win the accolades he so richly deserves. More importantly, he left us with a powerful way of understanding social evolution.

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