Frank, S. A. 2002. George Price. Pages 930-931 in Encyclopedia of Evolution. M. Pagel, ed. Oxford University Press.

PRICE, GEORGE

George Price, 1922–1975, trained as a chemist, contributed to the Manhattan bomb project during World War II, and worked at various biology and engineering research positions until the mid-1960s. Throughout this period, he read widely, corresponded with many scientists on various topics, and wrote a few papers, including a scientific analysis of paranormal phenomena. Price, born in the United States, left for England in 1967 and took up the study of evolutionary genetics.

Price made three fundamental contributions to population genetics and social behavior. His first contribution was a mathematical expression of natural selection known as the Price equation. This equation shows how a character will evolve over time, depending on the character's association with fitness and the fidelity with which the character is transmitted to offspring. W. D. Hamilton (1996) used the Price equation to develop his theory of biological altruism based on kin selection. [*See* Kin Selection.] Hamilton showed that an individual actor may behave in an altruistic way toward relatives. Such altruism evolves because relatives who benefit from altruism produce offspring with genes and thus characters that are similar to the actor's. Before he met Price, Hamilton had formulated his theory in terms of Wright's correlation coefficient of relatedness between kin. [*See* Wright, Sewall.] Price's insight, embodied in the Price equation, led Hamilton to the correct measure of relatedness for kin selection, the regression coefficient of recipient on altruist. By adopting this new measure of relatedness and by using the Price equation, Hamilton developed a far more powerful expression of his altruism theory.

In his second contribution, Price developed a model for how an animal behaves when in conflict with a neighbor. The puzzle is why animals often settle fights in a ritualized way rather than inflicting serious or deadly wounds. For example, male deer often fight furiously by crashing antlers in head-on battle, but they refrain from attacking when an opponent turns away and exposes an unprotected side. Price solved this problem by recognizing that fighting is a strategic game in which the best strategy of each individual depends on the strategies of neighbors. If everyone else escalates and fights to the death, it would be best to value life over the gains of battle and yield readily in a fight. By contrast, if all opponents yield quickly against escalating aggression, then aggression would lead to victory in all battles with little risk of a serious fight. Populations therefore settle into mixtures of aggressive and yielding interactions, where frequencies of alternative strategies depend on the balance between the danger of escalated fights and the potential gain in each battle. This idea of strategic equilibrium led John Maynard Smith and George Price (1973) to develop the theory of evolutionarily stable strategies, a central theoretical concept of modern evolutionary theory. This concept has been applied to diverse problems, including the sex ratios of populations and the virulence of parasites.

Price's third contribution solved the mystery of R. A. Fisher's fundamental theorem of natural selection, perhaps the most widely quoted theorem in evolutionary genetics. Fisher claimed in 1930 that his theorem held "the supreme position among the biological sciences" and compared it with the second law of thermodynamics. Yet for forty-two years no one could understand what the theorem was about, until Price in 1972 explained the theorem and its peculiar logic. The usual interpretation of the theorem is that the rate of increase in the adaptation (mean fitness) of a population is equal to the genetic variance in fitness of that population. However, this interpretation requires special assumptions about mating, competition, and other factors. Price solved the contradiction between Fisher's claim for generality and the limited scope of the usual interpretation. Price showed that Fisher partitioned the total change in mean fitness into two components. The first is the change caused directly by natural selection, and it is this component that increases at a rate equal to the genetic variance in fitness. The second component accounts for how the changing environment, including changes caused by natural selection, often causes a reduction in fitness. Changing environment includes enhanced adaptation of parasites, predators, and competing individuals from the same species. Price showed how these parts combine into a theorem of universal scope, as Fisher originally claimed.

[*See also* Altruism; Fundamental Theorem of Natural Selection; Game Theory; Hamilton, William D.]

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— STEVEN A. FRANK