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The Price equation

Andy Gardner

George Price (1922–1975; Figure 1) was an American scientist whose brief but productive career as an evolutionary theorist during the late 1960s and early 1970s is one of the most fascinating episodes in the history of the discipline. Price trained as a chemist and had worked on the Manhattan Project before becoming a science writer. Self-funded by a large insurance settlement after a botched medical operation, he relocated to London at the end of 1967 and began teaching himself the basics of evolutionary theory, working first in libraries and then at the Galton Laboratory at University College London. Bringing a fresh perspective to the discipline, Price discovered an entirely novel approach to population genetics, and the basis for a general theory of selection — the Price equation. Other accomplishments followed, but the period of discovery was cut tragically short by Price's suicide, after which his name faded into obscurity. However, the Price equation has come to underpin several key areas of evolutionary theory, and is beginning to illuminate difficult issues in other disciplines.

The Price equation
The Price equation is a simple mathematical statement about change. In its usual formulation, it describes how the average value of any character — body weight, antler size, proclivity to altruism — changes in a biological population from one generation to the next. Price denoted the individual's character value as z, its number of offspring as w, and the discrepancy between the character values of itself and its offspring as Δz, and showed that the change in the population average value of the character between parent and offspring generations is:

$$\Delta \bar{z} = \text{cov}(w/\bar{w},z) + \text{E}((w/\bar{w})\Delta z) \qquad (1)$$

where overbars denote population averages (see Box 1 for a simple derivation).

The Price equation separates the total change into two component parts. The first part is the change that can be ascribed to the action of selection, and this takes the form of a statistical covariance between individuals' character values (*z*) and their relative reproductive success ($w/\bar{w}$). For example, if individuals with larger values of the character of interest tend to have more offspring, then the covariance is positive and selection acts to increase the population average value of the character. The remainder term takes the form of an expectation (arithmetic average) describing how offspring differ from their partners, and this is denoted the change due to transmission. If offspring are identical copies of their parents, then the transmission effect is zero and selection is the only factor involved in the evolution of the character. However, offspring will often differ from their parents, perhaps because of mutation, or because their genes are recombined in a new way, or because of a change in their physical, biological or cultural environment, and in this case the transmission effect is non-zero.

The importance of the Price equation lies in its scope of application. Although it has been introduced using biological terminology, the equation applies to any group of entities that undergoes a transformation. But despite its vast generality, it does have something interesting to say. It separates and neatly packages the change due to selection versus transmission, giving an explicit definition for each effect, and in doing so it provides the basis for a general theory of selection. In a letter to a friend, Price explained that his equation describes the selection of radio stations with the turning of a dial as readily as it describes biological evolution. Sadly, this general theory of selection remains undeveloped. Nevertheless, because of its generality and simplicity, Price's equation has been used to uncover fundamental processes in evolution and, as a meta-model, it allows comparisons and contrasts to be drawn between different models and methodologies. As such, it is an important conceptual aid that has led to the discovery of unexpected connections between different bodies of theory, has settled long running controversies, and has helped to resolve semantic confusion.

Darwinism

The Price equation has most frequently been applied to biological evolution, and equation (1) appears to capture the Darwinian idea of the 'survival of the fittest'. Transmission effects aside, selection operates to favour those characters that are positively correlated with individual reproductive success. However, the modern theory of natural selection is framed in terms of changes in gene frequencies, and Price formulated this by focusing on the additive genetic component (*g*) of the character, rather than the actual phenotypic value (*z*). Discarding the genetic change due to transmission, the Price equation can be used to provide a formal statement of natural selection:

$$\Delta_s \bar{g} = \text{cov}(w/\bar{w}, g) = \beta_{w/\bar{w},g}\, \text{var}(g). \quad (2)$$

Price found it illuminating to express natural selection as a product of its component factors: the regression (slope) of relative reproductive success against the genetic value of the individual ($\beta_{w/\bar{w},g}$); and the genetic variation in the population (var(*g*)). This highlights the fact that natural selection operates when there are heritable differences between individuals with respect to some character that is correlated with reproductive success. Furthermore, because variances are never negative, any response to natural selection must be in the direction of increasing reproductive success (having the same sign as $\beta_{w/\bar{w},g}$). The Price equation thereby captures the improving effect that natural selection has on biological populations.

Darwinism is a theory of the purpose as well as the process of adaptation. Darwin argued that because natural selection causes those characters that improve individual fitness to accumulate in biological populations, organisms will correspondingly appear as if designed to maximise their fitness. This appearance of design or agency makes biology unique among the natural sciences, and is the reason why the evolutionary literature abounds with intentional language — selfishness, strategies, conflicts of interest. But the issue of this almost magical appearance
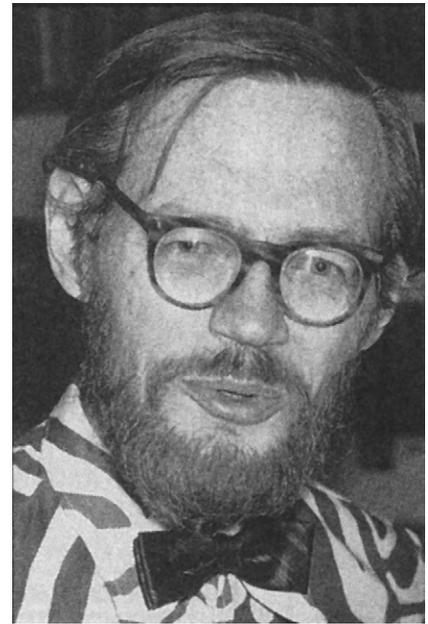

Figure 1. George R. Price.
Photograph taken in 1973. With thanks to Princeton University Press.

of agency has long been neglected by population geneticists, who have tended to obscure the role of the individual organism by focusing instead on genes and genotypes. Price's equation, in contrast, highlights the individual and its fitness, and links this to changes in gene frequency. For this reason, evolutionary theorist Alan Grafen has used the Price equation to establish mathematical links between population genetics and optimisation theory that formally justify the view of individual organisms as economic, fitness-maximising agents. In capturing both the process and purpose of adaptation, the Price equation forms the mathematical foundations of Darwinism.

Social evolution

Darwin argued that individuals should be favoured to behave in ways that improve their personal reproductive success. However, altruistic behaviour is common in the natural world, and this is difficult to reconcile with 'the survival of the fittest'. Recognising this problem, Darwin explained how certain characters could be favoured because they improve the reproductive success of one's relatives (kin selection), or else because they provide an overall benefit to the social group

Box 1.

Deriving the Price equation.

The Price equation is based on a mapping between individuals in parent and offspring generations; an example is given in the diagram below. Biological terms are used for concreteness, but the mapping applies to any groups of entities that undergo change. Each parent is assigned a unique index i, and it is mapped to w_i offspring that are given the same index; w_i can be regarded as the individual's fitness. The proportion of the parental generation that is made up of the ith parent is q_i — for example, $q_i = 1/n$ where n is the number of parents — and the proportion of the offspring generation that is made up of the offspring of the ith parent is $q_i' = q_i w_i/\bar{w}$, where $\bar{w}$ is the average fitness of all the parents. Finally, the value of some character of interest is z_i for the ith parent and the average value of this character among its offspring is $z_i' = z_i + \Delta z_i$; Δz_i can be regarded as the change in character occurring through transmission from parent to offspring. In the diagram, individuals exhibiting a character of interest (shaded) leave more offspring than individuals not exhibiting the character (unshaded). Also, whilst there is a tendency for offspring to resemble parents, this is not perfect.

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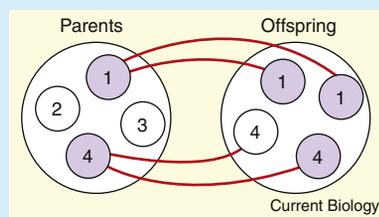
The Price equation describes the change in the average value of the character between the two generations. This is given by $\Delta\bar{z}_i = \bar{z}_i' - \bar{z}_i$, where $\bar{z}_i'$ and $\bar{z}_i$ are the averages in the offspring and parent generations, respectively. Substituting in the notation introduced above obtains:

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

and with some rearrangement this becomes:

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

The first two terms on the right-hand side represent the covariance between relative fitness and character value across individuals: $cov(w/\bar{w},z) = E((w/\bar{w})z) - E(w/\bar{w})E(z)$, where E denotes an expectation taken across the population. When character value is independent of relative fitness, $E((w/\bar{w})z) = E(w/\bar{w})E(z)$, and the covariance is zero. A positive correlation between character value and relative fitness gives a positive covariance, and a negative correlation gives a negative covariance. The third term on the right-hand side is the average character change due to transmission between parent and offspring, weighted by parental fitness, and can be rewritten as $E((w/\bar{w})\Delta z)$. This yields equation (1) in the main text — the Price equation.

(group selection). Today, Price's equation provides the formal foundation of both kin selection and group selection theories (Box 2), and has clarified that these are not competing hypotheses but rather two different ways of looking at the very same evolutionary process.

The kin selection approach, developed by W.D. Hamilton in the 1960s, takes the view that a gene can be favoured by natural selection by increasing the reproductive success of its bearer and also by increasing the reproductive success of other individuals that carry the same gene. All that matters is that the gene

propels copies of itself into future generations — where these copies come from is irrelevant. The condition by which an altruistic (or indeed, any) behaviour is favoured by selection, termed Hamilton's rule, is $rb - c > 0$, where c is the fitness cost to the actor, b is the fitness benefit to the recipient, and r is the genetic relatedness between actor and recipient. Thus, altruism is favoured provided the actor and recipient are sufficiently close relatives. The quantity $rb - c$ has been termed the 'inclusive fitness' effect of the behaviour, and describes the actor's impact on the reproductive success of all its

relatives (including itself), weighted by the genetic relatedness of each. It is the inclusive fitness rather than the personal reproductive success of the actor that is maximised by natural selection. Hamilton's rule was originally developed using a simplified population genetic model that made rather restrictive assumptions, and was long derided by population geneticists as being inexact and heuristic. However, Hamilton later provided a much neater proof of the rule using Price's equation (Box 2), clarifying the definition of terms and demonstrating the rule's generality. Many subsequent developments of kin selection theory have also used Price's equation as their underlying basis.

An alternative view of social evolution suggests that selection operating to favour one social group over another can counteract selection operating within social groups, so that behaviours giving individuals a disadvantage relative to their social partners may evolve through group selection. Such ideas were rather confused until Price, and later Hamilton, showed that the Price equation can be expanded to encompass multiple levels of selection acting simultaneously (Box 2). This allows selection at the various levels to be explicitly defined and separated, and provides the formal basis of group selection theory. Importantly, it allows the quantification of these separate forces and yields precise predictions for when group-beneficial behaviour will be favoured. It turns out that these predictions are always consistent with Hamilton's rule, $rb - c > 0$. Furthermore, because kin selection and group selection theory are both based upon the same Price equation, it is easy to show that the two approaches are mathematically exactly equivalent, and are simply alternative ways of carving up the total selection operating upon the social character. Irrespective of the approach taken, individual organisms are expected to maximise their inclusive fitness — though this result follows more easily from a kin selection analysis, as it makes the key element of relatedness more explicit.

Beyond evolutionary biology
It is historical accident that has led Price's equation to be associated with

evolutionary theory, and in the last few years the equation has begun to make an appearance within other disciplines. Biologists Troy Day and Sylvain Gandon have recently applied the Price equation to epidemiology, in the context of the evolution of parasite virulence. Here, it has been useful for conceptualising and deepening the understanding of existing theoretical results. It also provides an avenue into a better understanding of the co-evolutionary arms races of parasites and their hosts, where natural selection leads to improvement of one species, which is undone by any improvement in its enemy. The net result of these forces can be difficult to understand when they are taken together, but the Price equation provides a means of separating them so that they can be considered, and understood, in isolation.

In the ecological literature, Price's equation has provided insights into the impact of local extinctions on community productivity. There is some controversy over whether species richness *per se* is important, particularly when redundancy in function means that vacated niches can become occupied by other species that are already present in the community. Jeremy Fox has used the Price equation to separate the various causal factors that can give rise to community productivity effects, and to provide a meta-model which generalises and allows easy comparisons of the rather complicated and restrictive models that have been devised to address this problem.

What happened to Price?
Following the development of the Price equation, Price went on to make two other major contributions to evolutionary theory. The first of these was to formally prove and provide an interpretation for R.A. Fisher's fundamental theorem of natural selection, a mathematical result that had perplexed population geneticists for decades. The theorem states that the change in the mean fitness of the population under the action of natural selection is proportional to the variance in fitness, and Fisher claimed that it captured the directional, improving action of natural selection as the builder of organismal adaptations. Price explained that Fisher's theorem was a partial result,

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Box 2.

Foundations of social evolution theory.

Hamilton's rule of kin selection theory can be derived using the Price equation. From equation (2), the direction of selection acting upon a character of interest is given by least-squares the regression (slope) of relative fitness on the genetic value of the character ($\beta_{w/\bar{w},g}$). The basis of the kin selection approach is the understanding that fitness may be mediated both by genes in the focal individual (g) and also by genes in that individual's social partners (g'), and the least-squares regression can be partitioned so as to describe the partial effects of both sets of genes:

$$\beta_{w/\bar{w},g} = \beta_{w/\bar{w},g\cdot g'} + \beta_{w/\bar{w},g'\cdot g} = \beta_{g'g}$$

The partial effect of the genes in the focal individual on its own fitness, holding fixed the effect of the genes in its social partners, is $\beta_{w/\bar{w},g\cdot g'} = -c$, the personal cost of the social behaviour. The partial effect of the genes in social partners, holding fixed the effect of the focal individual's genes, is $\beta_{w/\bar{w},g'\cdot g} = b$, the benefit of being a recipient of social behaviour. Finally, the genetic association between social partners is $\beta_{g'g} = r$, the kin selection coefficient of genetic relatedness. Thus, the condition for the behaviour to be favoured ($\beta_{w/\bar{w},g} > 0$) yields Hamilton's rule: $rb - c > 0$. This derivation has taken the 'neighbour-modulated fitness' approach to kin selection, where b is interpreted as the impact of social partners upon the reproductive success of the focal individual. An alternative but equivalent approach is the inclusive fitness view, where b is interpreted as the impact of the focal individual on the reproductive success of its social partners; the two approaches always yield the same result.

The group selection approach to social evolution begins by considering that the entities in the parent and offspring populations are social groups rather than individual organisms. For clarity, we index groups $i \in I$ and individuals within groups $j \in J$. The Price equation describes the change in additive genetic value of the character as:

$$\Delta \bar{g} = \text{cov}_I(w_i/\bar{w},g_i) + \text{E}_I((w_i/\bar{w})\Delta g_i)$$

that is, a sum of group selection and group transmission effects. Note that the transmission effect from parental group i to its offspring (Δg_i) is similar in form to the change between the parent and offspring populations as a whole ($\Delta \bar{g}$). This means that we can write a lower-level Price equation to describe the change within social groups that mirrors the change within whole populations. Neglecting individual transmission effects, and substituting the lower level Price equation into the higher-level Price equation, we have:

$$\Delta \bar{g} = \text{cov}_I(w_i/\bar{w},g_i) + \text{E}_I((w_i/\bar{w})\text{cov}_J(w_{ij}/w_i,g_{ij})).$$

The right-hand side has partitioned the net selection on the trait into separate between-group selection (first term) and within-group selection (second term) components. Thus, it provides an explicit mathematical definition of group selection and shows that change in the evolutionary character is neither wholly determined by selection within groups nor selection between groups, but a mixture of both. In some situations group selection may be strong enough to overpower the effects of within group selection and allow the evolution of characters that are disfavoured within groups.

Mathematical manipulation reveals that the sum of between-group selection and within-group selection is simply $\text{cov}(w_{ij}/\bar{w},g_{ij})$, the usual individual level selection expression of equation (2) that summarises the combined effects of selection at the between and within group levels. Since this single selection covariance is the basis of Hamilton's rule, the group selection and kin selection approaches are mathematically equivalent.

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a description of the action of the natural selection effect with all other evolutionary effects stripped away, and the theorem is easily proven using the Price equation:

$$\Delta_s \bar{w} = \text{cov}(w/\bar{w},w) = \text{var}(w)/\bar{w} \qquad (3)$$

Price's final contribution was the first explicit application of game theory to evolutionary biology, in a seminal article co-authored with John Maynard Smith entitled *The Logic of Animal Conflict*. This is widely regarded as one of the most important developments of evolutionary theory, and has launched a highly successful programme of research. It is Maynard Smith who is usually attributed with this breakthrough, and

indeed he played the major role in its development. But the idea originated with Price, in an unpublished manuscript that Maynard Smith had reviewed for *Nature*. Maynard Smith later explained that "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".

Price's inability to focus on publishing his theoretical insights was due to a sudden religious experience in the summer of 1970 and a shift of priorities in his life. It is not known what in particular led Price, formerly a hardline atheist, down this avenue, although he did mention to Hamilton that a series of coincidences had forced him to conclude that God existed. He came to regard his equation as a gift from God and, taking a very literal interpretation of the New Testament, gave up science in order to dedicate his life to altruism. He sheltered the homeless in his flat, and gave away all his money and possessions to the poor and needy, and his life spiralled out of control. He became deeply depressed shortly after Christmas of 1974, and was found dead in his squatter's tenement on the 6th of January 1975. He had cut his throat with nail scissors.

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Meaningful call combinations in a non-human primate

Kate Arnold and Klaus Zuberbühler

Human speech is based on rule-governed assemblage of morphemes into more complex vocal expressions. Free-ranging putty-nosed monkeys (*Cercopithecus nictitans*) provide an interesting analogy, because males combine two loud alarm calls, 'hacks' and 'pyows', into different call series depending on external events [1]. Series consisting of 'pyows' are a common response to leopards, while 'hacks' or 'hacks' followed by 'pyows' are regularly given to crowned eagles [2,3]. Sometimes, males produce a further sequence, consisting of 1–4 'pyows' followed by 1–4 'hacks'. These 'pyow–hack' (P–H) sequences can occur alone, or they are inserted at or near the beginning of another call series. Regardless of context, P–H sequences reliably predict forthcoming group progression [4]. In playback experiments, we tested the monkeys' reactions to 'pyows', 'hacks' and P–H sequences and found that responses matched the natural conditions. Specifically, females started group progressions after hearing P–H sequences and responded appropriately to the other call series. In a second experiment, we tested artificially composed P–H sequences, and found that they were also effective in eliciting group progressions. In a third experiment, we established that group movement could only be triggered by the calls of the group's own male, not those of a stranger. We conclude that, in this primate, meaning is encoded by call sequences, not individual calls. Many birds and primates are limited by small vocal repertoires [5,6], and this constraint may have favored the evolution of such combinatorial signaling.

We designed playback experiments to investigate whether P–H sequences given by a male are causally responsible for eliciting
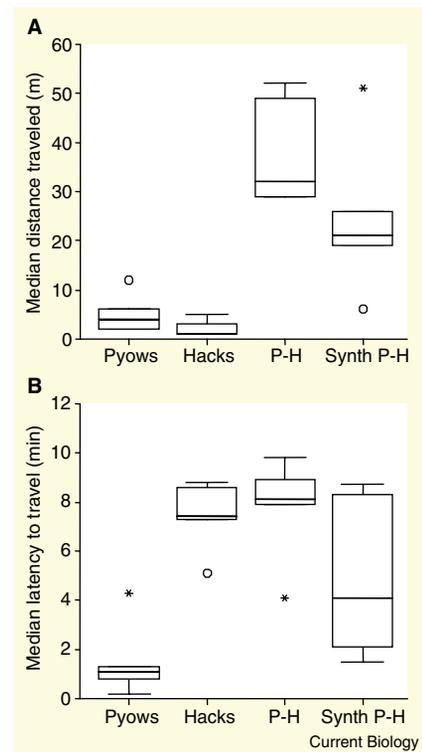
Figure 1. Median distance traveled (A) and median latency to travel (B) after hearing playbacks of different call series by the group's male: 'pyow' series, 'hack' series, natural P–H sequences (P–H), and artificially composed P–H sequences (Synth P–H).

Box plots indicate medians, inter-quartiles and ranges; outliers are indicated by open circles.

travel in individual group members. We conducted a series of playback experiments with free-ranging putty-nosed monkeys at Gashaka Gumti National Park, Nigeria. In a first experiment, we observed the behavior of the females of a habituated group in response to playbacks of natural call series of their own male. A female could serve as focal subject if she was located at the periphery of the group while the male was at the opposite side, hereby ensuring that the male's calls emanated from the correct direction. Playback trials consisted of five 'hacks', five 'pyows' or a five-call P–H sequence. Using a GPS unit, the focal female's location was marked prior to and 20 min after playback, while her behavior was monitored continuously.

Our results showed that playback of 'hack' series (usually indicating eagle presence) inhibited movement in females (median = 1.0 m) and