

# Notes on the Price Equation

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## 1 Introduction

The Price equation is a complete description of the evolutionary process. With it, we partition the change in the mean of a trait from one generation to the next into two quantities: (1) the effect of transmission and (2) the effect of selection.

## 2 The Price Equation

Price's original (1970) paper in which he develops his eponymous formula (PE) is rather terse and, unfortunately, many of the followers of Price have maintained this tradition. It is therefore useful to try to expand a bit on his derivation. His development of the PE is as follows. We will use Price's original notation (but see section 2.1 below). Let there be two populations  $P_1$  and  $P_2$ , where  $P_1$  contains all parents of  $P_2$  and  $P_2$  all the offspring of  $P_1$ . The total size of  $P_1$  is  $N$  individuals and individuals in  $P_1$  is indexed  $i = 1, 2, \dots, N$ . The zygotic ploidy is denoted  $n_z$  (e.g., a diploid organism would have  $n_z = 2$ ) and  $g_i$  denotes the dose of gene  $A$  in individual  $i$ . Let  $q_i = g_i/n_z$  be the frequency of gene  $A$  in individual  $i$  and let  $Q_1$  be the frequency of  $A$  in population  $P_1$ . Thus,

$$Q_1 = \sum_i g_i/n_z N = \sum_i n_z q_i/n_z N = \bar{q}$$

We now look at the offspring. Let  $n_G$  be the genetic ploidy of gene  $A$  (different than  $n_z$ ?) and  $z_i$  be the number of successful gametes contributed by individual  $i$ . Let  $g'_i$  be the number of  $A$  genes in the set of  $i$ 's successful gametes and  $q'_i = g'_i/z_i n_G$  be the frequency of gene  $A$  in the set of gametes (assuming that  $z_i \neq 0$ ). Let  $\Delta q_i = q'_i - q_i$  and let  $Q_2$  be the frequency of  $A$  in  $P_2$ . Price derives his equation in three lines. The first is:

$$Q_2 = \frac{\sum g'_i}{\sum z_i n_G} = \frac{\sum z_i n_G q'_i}{\sum z_i n_G} = \frac{\sum z_i q'_i}{N \bar{z}}. \quad (1)$$

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The next line is:

$$\frac{\sum z_i q'_i}{N\bar{z}} = \frac{\sum z_i q_i}{N\bar{z}} + \frac{\sum z_i \Delta q_i}{N\bar{z}} = \frac{\bar{z} \cdot \bar{q} + \text{Cov}(z, q)}{\bar{z}} + \frac{\sum z_i \Delta q_i}{N\bar{z}}. \quad (2)$$

That is, the frequency in  $P_2$  is the frequency in  $P_1$  plus the change in frequency from  $P_1$  to  $P_2$ . This clearly reduces to

$$Q_2 = \bar{q} + \frac{\text{Cov}(z, q)}{\bar{z}} + \frac{\sum z_i \Delta q_i}{N\bar{z}}. \quad (3)$$

When we difference  $Q_2$  and  $Q_1$  ( $= \Delta Q$ ), we get the familiar form of the PE:

$$\Delta Q = \frac{\text{Cov}(z, q)}{\bar{z}} + \frac{\sum z_i \Delta q_i}{N\bar{z}}, \quad (4)$$

where  $\sum z_i \Delta q_i / \mathbb{E}(z \Delta q)$ .

The only tricky part of the derivation comes in the last equality in equation 2. How do we go from  $\sum z_i q_i / N\bar{z}$  to  $\bar{z} \cdot \bar{q} + \text{Cov}(z, q) / \bar{z}$ ? This arises from a simple identity relating to covariance, namely,  $\text{Cov}(z, q) = \bar{z}\bar{q} - \bar{z} \cdot \bar{q}$ . Note that  $\sum z_i q_i / N = \bar{z}\bar{q}$  and that  $\bar{z}\bar{q} = \bar{z} \cdot \bar{q} + \text{Cov}(z, q)$ .

The first term in equation 4 is the covariance between fitness and the trait value and it represents the selection acting on the trait from the first generation to the second. The second term is the expected fitness-weighted change in the trait between generations and it represents transmission. Thus total change can be decomposed into selection and transmission. We frequently make assumptions that allow us to drop the transmission term in the PE. If the population size remains constant from  $P_1$  to  $P_2$ , for example, we can work with a reduced form of the PE which simply involved the covariance term. Price (1970, 520) notes that “if meiosis and fertilization are random with respect to gene  $A$ , the summation term at the right will be zero except for statistical sampling effects (“random drift”), and these will tend to average out to give equation 1.” The equation to which Price refers is sometimes called the reduced Price equation or the “covariance equation” and has been discovered independently by a variety of authors (Robertson 1966; Li 1967; Price 1970). Using Price’s notation, it is simply:

$$\Delta Q = \text{Cov}(z, q) / \bar{z}$$

## 2.1 On Notation

I have retained Price’s original notation in the previous section to facilitate reading the original paper (Price 1970). In many ways, his notation is unfortunate since it contradicts conventional notation in evolutionary genetics. For example, Price (1970) uses  $z_i$  to denote fitness of the  $i$ th individual, and he uses  $q_i$  to denote the breeding value of the  $i$ th individual. In evolutionary genetics  $z$  is usually reserved for the trait or breeding value and  $q$  is a population proportion (where  $q_i$  is an individual proportion in Price’s usage). The more-or-less consensus notation for the Price Equation currently writes fitness as  $w$  and the trait as  $z$ , following conventions in evolutionary genetics (Lande. 1982; Arnold and Wade 1984). The form of the PE that typically occurs in the literature (Frank 1995: 1996: 1997) is as follows:

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

The right-hand side is normalized by mean fitness,  $\bar{w}$ , which is brought to the left-hand side through multiplication for largely aesthetic reasons.

## 2.2 A Derivation Using Frank's Notation

While completely redundant, I re-derive the PE in this section using the contemporary notation typified by Frank (1996). Sometimes it is pedagogically useful to see the same derivation approached in a slightly different way.

Define  $z_i$  as the value of the trait with label  $i$  in generation  $t$ . The frequency of  $i$  in generation  $t + 1$  is  $z'_i$ . By definition,  $z'_i = z_i + \Delta z_i$ , where  $\Delta z_i$  is the change in  $z_i$  from the first generation to the next.

The frequency of trait  $i$  in generation  $t$  is  $q_i$  and the frequency of trait  $i$  in generation  $t + 1$  is  $q'_i$ . The relative frequency of trait  $i$  in the next generation will be proportional to its relative fitness:  $q'_i = q_i w_i / \bar{w}$ , where  $w_i$  is the fitness of the  $i$ th trait and  $\bar{w}$  is mean fitness.

We are interested in the change in the mean trait  $\bar{z}$ . We know, by definition, that  $\Delta z_i = z'_i - z_i$ : the change in  $z_i$  is the difference in trait  $i$  from generation  $t$  to  $t + 1$ . To get the change in the mean, we need to calculate the expected values of  $w$  and  $w'$ :

$$\Delta \bar{z} = \sum_i q'_i z'_i - \sum_i q_i z_i.$$

We substitute  $(w_i / \bar{w})(z_i + \Delta z_i)$  for  $z'_i$  and use the fact that  $(w_i / \bar{w})\Delta z_i = -z_i$  to yield:

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

The first term on the right hand side is the expected value (over  $i$ ) of  $z_i w_i / \bar{w} - z_i$ , which is the covariance between  $z$  and  $w$ . This is perhaps not obvious, so let's spell it out:

$$\begin{aligned} \sum_i q_i (w_i / \bar{w} - 1) z_i &= \sum_i q_i w_i z_i / \bar{w} - z_i \\ &= \frac{1}{\bar{w}} \sum_i q_i w_i z_i - \sum_i q_i z_i \\ &= \frac{\overline{wz}}{\bar{w}} - \bar{z} \\ &= \text{Cov}(w, z) / \bar{w} + (\bar{w} \cdot \bar{z}) / \bar{w} - \bar{z} \\ &= \text{Cov}(w, z) / \bar{w} + \bar{z} - \bar{z} = \text{Cov}(w, z) / \bar{w} \end{aligned}$$

Again, we use the identity  $\text{Cov}(z, q) = \overline{zq} - \bar{z} \cdot \bar{q}$ . This leads directly to the full Price equation as seen in most contemporary writings (e.g., Frank 1996):

$$\bar{w} \Delta \bar{z} = \text{Cov}(w, z) + \mathbb{E}(w \Delta z) \quad (5)$$

$\bar{w}$  is mean fitness, which normalizes the right side of the equation. We bring it to the left side of the equation by multiplication largely for aesthetic reasons.  $\Delta \bar{z}$  is the change in mean fitness from generation one to generation two.  $\text{Cov}(w, z)$  is the covariance between the trait and fitness  $w$ . This term represents selection. The last term is the expected change in  $z$ ,  $\mathbb{E}(w \Delta z)$ , where  $\mathbb{E}()$  represents mathematical expectation. This is the transmission part of the Price equation.

### 3 Fisher’s Fundamental Theorem: Or Is It Robertson’s Secondary Theorem?

The trait  $z$  in the Price equation can be anything. Indeed, it can be fitness itself. Using the reduced form of the Price equation (i.e., the “covariance equation”), we note the following:

$$\Delta \bar{w} = \text{Cov}(w, w) = \text{Var}(w).$$

Thus with a simple identity, we see Fisher’s famous result: change in fitness is proportional to the variance in fitness. Also, mean fitness increases. This arises because variance is, by definition, greater than or equal to zero and except in the rather outlandish case where there are no differences in the population in fitness, this inequality is strict. Turns out that this is not what Fisher meant, but that’s another story (Price 1972).

### 4 Kin Selection

Hamilton (1964) originally derived the concept of kin selection by conceiving of genetic relatedness in terms of shared alleles identical by descent (IBD). The Price equation provides an alternative means of deriving the kin selection result that makes no such assumption. Hamilton (1970) and Hamilton (1975) noted that this was, in fact, the proper way to conceive of inclusive fitness theory. One key interpretation that arises from this formulation of the problem is that what matters is the statistical association between genes and fitness regardless of how such associations come about. There is nothing particular about IBD.

Again, we use the reduced form of the Price equation to model kin selection, following Queller (1992). We are investigating the effect of an individual’s breeding value with respect to the altruistic trait on fitness. Breeding value is the sum of the additive effects of an individual’s genes.

The covariance equation is  $\bar{w}\Delta\bar{z} = \text{Cov}(w, z)$ .

Following Arnold and Wade (1984), we can write down a regression equation that predicts fitness based on the breeding values  $g$  and  $g'$ , where  $g$  is the breeding value determining the level of altruism,  $g'$  is the average breeding value of an individual’s neighbors.

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

where  $\beta_{wg \cdot g'}$  is the partial regression coefficient of an individual’s breeding value’s effect on its own fitness, given its neighbors (the cost of altruism),  $\beta_{wg' \cdot g}$  is the effect of the individual’s breeding value on the fitness of its neighbors (the benefit of altruism), and  $\epsilon$  is the error uncorrelated with either  $g$  or  $g'$ .

Substitute the regression equation into the covariance equation to get:

$$\bar{w}\Delta\bar{z} = \text{Cov}(\alpha, g) + \beta_{wg \cdot g'}\text{Cov}(g, g) + \beta_{wg' \cdot g}\text{Cov}(g, g') + \text{Cov}(\epsilon, g).$$

The first and last terms on the right-hand side are zero by definition ( $\alpha$  is a constant and  $\epsilon$  is defined as being uncorrelated with  $g$ ).  $\text{Cov}(g, g)$  is, by definition,  $\text{Var}(g)$ . We can now solve for the equilibrium condition where  $\Delta\bar{z} = 0$ , yielding the following condition:

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

The first term is the cost to the individual.  $\beta_{g',g}$  is the genetic regression definition of relatedness (Hamilton 1972), which we get when we divide both sides of the equation by  $\text{Var}(g)$ . The term  $\beta_{wg' \cdot g}$  is the benefit to the individual. We see, therefore, that the Price covariance equation yield the familiar Hamilton's rule for the evolution of altruism through kin selection (i.e.,  $c + br > 0$ ).

Re-framing the problem of altruism this way leads to a fairly profound insight, discussed above, that what matters for the evolution of altruism is the statistical association between the genes of the altruist and the genes of its beneficiaries. There is nothing special about consanguinity. As noted by numerous authors, including Hamilton (1975) himself, this provides a principled way of thinking about group selection. This is the approach taken by Bowles (2006) that I discuss in the next section. Another key insight provided by this approach is that there exists the possibility for spite, whereas such behavior could never evolve under Hamilton's original formulation. This arises because the covariance between an individual and her neighbors might be negative, making the evolution of behaviors that induce a cost in both the actor and recipient at least possible.

## 5 Bowles and Reproductive Leveling

Bowles (2006) starts with a Price Equation. While he is short with details, the model he uses is the reduced covariance-equation form. The statement about constant population size is a clue to this. The PE that he uses partitions covariance between fitness and possession of the altruism allele into the within and between group components. Following his notation, this equation is

$$\Delta p = \text{Var}(p_j) \beta_G + \mathbb{E}(\text{Var}(p_{ij})) \beta_i,$$

where  $p_j$  is the fraction of altruists in the  $j$ th deme,  $p_{ij}$  is an indicator of whether the  $i$ th individual in the  $j$ th deme is an altruist,  $\beta_G$  is the regression coefficient of average fitness within a deme on the fraction of altruists in a deme, and  $\beta_i$  is the regression of individual fitness of an individual in deme  $j$  on  $p_{ij}$  (i.e., on switching from being a non-altruist to altruist). We expect  $\beta_i$  to be negative since being altruistic is, by definition, costly within the deme. Note that a regression coefficient  $\beta_{ij} = \text{Cov}(i, j) / \text{Var}(j)$ . This is why Bowles's version of the PE includes variances and regression coefficients.

Solving this equation for  $\Delta p > 0$ , we find the following condition for the spread of altruism by inter-demic competition:

$$\frac{\text{Var}(p_j)}{\mathbb{E}(\text{Var}(p_{ij}))} > -\frac{\beta_i}{\beta_G}.$$

The left-hand side is a measure of assortativeness: do altruists tend to be clustered in particular groups? The right hand side is a ratio of the fitness effects of altruism within and between demes.

Bowles introduces two key ingredients into the model: (1) selective deme extinction and (2) reproductive leveling. The idea of reproductive leveling arises both from ethnographic observations (e.g., extensive sharing of game among hunter-gatherers) and from the fact that models without it often require the group benefit from individual altruism be enormous to offset the within-group cost. The key result is as follows. The condition in which altruists (A) increase in their share of a metapopulation is:

$$\frac{F_{ST}}{(1 - F_{ST})} > \frac{(1 - \tau)c}{\kappa 2\lambda_A} \quad (6)$$

where  $F_{ST}$  is the fraction of total genetic variance at a locus that is contained between groups,  $\tau$  is the amount of reproductive leveling within demes,  $c$  is the cost to altruists,  $\kappa$  is the likelihood of a between-deme agonistic contest, and  $\lambda_A$  is the marginal increase in deme survival from individual  $i$  becoming an altruist,  $\lambda_A = d\lambda/dp_{ij}$ , where  $\lambda$  is the probability that a deme survives a contest.  $\lambda_A$  thus represents the marginal benefit to the group of a single altruist.

The left-hand side of equation 6 measures the degree of positive assortment of altruists within demes. The right-hand side is the ratio of individual costs to the benefits for the deme. Clearly, if the degree of leveling is greater, the cost will be smaller and the inequality is more likely to apply.

## References

- Arnold, S. J. and M. J. Wade (1984). On the measurement of natural selection: Theory. *Evolution* 38(4), 709–719.
- Bowles, S. (2006). Group competition, reproductive leveling, and the evolution of human altruism. *Science* 314(5805), 1569–1572.
- Frank, S. A. (1995). George Price’s contributions to evolutionary genetics. *Journal of Theoretical Biology* 175(3), 373–388.
- Frank, S. A. (1996). *Foundation of Social Evolution*. Princeton: Princeton University Press.
- Frank, S. A. (1997). The Price equation, Fisher’s fundamental theorem, kin selection, and causal analysis. *Evolution* 51(6), 1712–1729.
- Hamilton, W. (1964). The genetical evolution of social behaviour, I, II. *Journal of Theoretical Biology* 7, 1–52.
- Hamilton, W. D. (1970). Selfish and spiteful behaviour in an evolutionary model. *Nature* 228, 1218–1220.
- Hamilton, W. D. (1972). Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and Systematics* 3, 193–232.
- Hamilton, W. D. (1975). Innate social aptitudes of man: An approach from evolutionary genetics. In R. Fox (Ed.), *Biosocial Anthropology*, pp. 133–155. New York: Wiley.

- Lande., R. A. (1982). A quantitative genetic theory of life history evolution. *Ecology* 63, 607–615.
- Li, C. (1967). Fundamental theorem of natural selection. *Nature* 214, 505–506.
- Price, G. (1970). Selection and covariance. *Nature* 227, 520–521.
- Price, G. (1972). Fisher’s ‘fundamental theorem’ made clear. *Annals of Human Genetics, London* 36, 129–140.
- Queller, D. C. (1992). Quantitative genetics, inclusive fitness, and group selection. *American Naturalist* 139(3), 540–558.
- Robertson, A. (1966). A mathematical model of the culling process in dairy cattle. *Animal Production* 8, 95–108.