process called simulated annealing, which has a schedule for reducing the amount of diversity over time.

Fisher's Theorem and the Price Equation

A good place to begin thinking about variation and search is Fisher (1930) theorem of natural selection. This theorem relates the rate of increase in fitness of an organism to its genetic variance. An example reveals the logic of Fisher's theorem. In this example, I'll assume two populations of sixty turtles each. These turtles vary in their speed. In the first population (Pop1), twenty turtles have a top speed of three miles per hour (mph), twenty have a top speed of four mph, and twenty have a stop speed of five mph. In the second population (Pop2), the speeds have greater variance, with twelve turtles each topping out at speeds between two and six miles per hour. For the moment, I equate fitness with top speed so that average fitness in each population equals four. To simplify the presentation, I let N_s be the number of turtles with a top speed of s miles per hour.

Pop1: $N_3 = 20$, $N_4 = 20$, and $N_5 = 20$

Pop2: $N_2 = 12$, $N_3 = 12$, $N_4 = 12$ $N_5 = 12$, and $N_6 = 12$

To explain the dynamics, I return to the *replicator equation*:

$$p_i^{t+1} = p_i^t \, \frac{\pi_i}{\bar{\pi}^t}$$

This equation gives the proportion of type i at time $t + 1$, p_i^{t+1} as a function of the proportion at time t, p_i^t and the ratio of the fitness of that type, π_i relative to the average fitness at time t, $\bar{\pi}^t$. Here, there will be two differences between how we interpret the earlier replicator equation and this one. Previously, the i''s indexed distinct types: *e.g.*, turtles, frogs, bees, etc.... Here, they denote variants within the same type: turtles. Second, here we're using numbers, not proportions, so the rule will be written as:

$$N_i^{t+1} = N_i^t \, \frac{\pi_i}{\bar{\pi}^t}$$

where the $N's$ denote numbers instead of proportions. In this equation, the number of turtles with a top speed of 3mph in the first population will equal the number of turtles with that top speed times the ratio of their fitness to average fitness, or 20 times 3/4, which equals fifteen. Similar calculations show that the populations in the next generation look as follows:

Pop1: $N_3 = 15$, $N_4 = 20$, and $N_5 = 25$, **Average Speed:** $4\frac{1}{6}$

Pop2: $N_2 = 6$, $N_3 = 9$, $N_4 = 12$ $N_5 = 15$, and $N_6 = 18$, **Average Speed:** $4\frac{1}{3}$

Pop2, which had higher variance in speeds, ends up with a higher fitness in the next period. This example can be generalized into Fisher's theorem, which is most easily derived as a special case of the *Price Equation.* The Price Equation applies to a population of entities. These could be beetles, sunflowers, or auto companies. These entities differ in the amount of some characteristic that they possess. In other words, they exhibit variation along this characteristic.

It's possible to partition the population into sets that have the same amount of the characteristic. For example, everyone in set i would have the same speed or the same height. Given that partitioning, the Price Equation characterizes the change in average fitness, exploiting the fact that the proportions in a set are given by the replicator equation. The Price Equation shows how the amount of the characteristic in set i in the next time period can change due to crossover and mutation. Thus, the offspring of the turtles with speed five mph might not have an average speed of five miles per hour. The Price Equation captures these changes as well as the changes in fitness that result from replication to give the total change in the amount of the characteristic.[1]

[1] This derivation follows the excellent characterization of the Price Theorem by Frank (1997).

Fisher's Theorem and the Price Equation

Partition a population of size N into K sets so that the members of set i all have the same amount z_i of some attribute θ. Let p_i denote the proportion of the population in set i. It follows that the expected amount of the attribute equals $\bar{z} = \sum_{i=1}^{K} p_i z_i$. Let π_i denote the fitness of the members of set i and $\bar{\pi}$ denote average fitness. Finally, let Δz_i denote the change in the amount of attribute θ among the descendants of the members of set i. The change in the average amount of the attribute θ than is given by the following equation:

$$\Delta\bar{z} = \sum_{i=1}^{K}[p_i \frac{\pi_i}{\bar{\pi}}(z_i + \Delta z_i) - p_i z_i]$$

Rearranging terms gives:

$$\bar{\pi}\Delta\bar{z} = \sum_{i=1}^{K}[p_i \pi_i z_i - \bar{\pi} p_i z_i \;+\; p_i \pi_i \Delta z_i] \;=\; \sum_{i=1}^{K}[p_i \pi_i z_i] - \bar{\pi}\bar{z} + E[\pi \Delta z]$$

This yields the **Price Equation:**

$$\bar{\pi}\Delta\bar{z} = Cov[\pi, z] + E[\pi\Delta z]$$

Where, $Cov[\pi, z]$ equals the covariance of π and z. In the special case, where the characteristic θ is fitness ($z = \pi$), if we ignore changes in fitness due to mutations so that $\Delta z = 0$, we get **Fisher's Fundamental Theorem:**

$$\bar{\pi}\Delta\bar{\pi} = Var[\pi]$$

Which says that the change in fitness ($\Delta\bar{\pi}$) equals the variance.

The first term in the Price Equation states that the change in the average fitness depends on the covariance of the attribute θ (recall this is what z measures) and fitness.[2] This makes intuitive sense. More variance implies more high fitness offspring (that get produced with higher probability) and more low fitness offspring (that get produced with lower probability). The second term captures the change in the levels of the attribute within each set (the Δz_i terms). The Price Equation tells us exactly how much of an attribute will exist in the population in the next period. If we let the attribute equal fitness itself, then we get Fisher's theorem.

The idea that fitness increases with variance proves useful as a departure point for thinking about variation as a form of search. We can make this logic more formal (Weitzman 1979). Suppose that you're moving to a new town or city and you have an afternoon to

[2]In the statement of the Price Equation, $Cov[x, y]$ equals the covariance of the random variables x and y.