THE PRICE EQUATION: MODELLING ALTRUISM

Introduction.

• When we try to understand how evolution works, we are basically attempting to figure out how traits change in populations over time.
  – Taking that a step further, when populations change enough, we can have reproductive isolation, e.g., speciation.

• In this class, we have learned how to describe the frequency of traits are expected to change over time, but we haven’t discussed how the value of the traits themselves are expected to change over time (e.g., speed, height, “niceness”). This is really what evolution is. It incorporates frequency changes but also everything else (mutation, environment, transmission, etc.)

• We’ve alluded to this a couple times when talking about mutation and fixation, how we measure quantitative genetics (measuring phenotypic variance as a sum of genetic variance and environmental variance), and when mentioning Fisher’s Fundamental Theorem (change in mean fitness is proportional to genetic variance), but we haven’t dealt with this directly.

Goal.

• To derive a simple equation (called the Price Equation) describing the change in a trait over time as a function of the trait’s fitness.

• Give a few examples on how we can use this equation to understand the evolution of altruism and specifically kin selection.

Background on George Price.

• George Price was the biologist who derived this equation.

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• He lived a pretty sad life ending with him committing suicide in early 1975, and never really lived to see the effect of his contributions to evolution theory.

• He worked closely with W.D. Hamilton (more on him later) and John Maynard Smith and in edition to developing the Price equation, re-derived Hamilton’s Rule for kin selection (using the Price Equation) and helped introduce game theory to evolution with Maynard Smith.

• Price set out to re-derive Fisher’s Fundamental Theorem \( \bar{\omega} \bar{\Delta} \bar{z} = Var(\omega) \) and ended up with the price equation in 1970.

• His original paper only has three steps. I will try try to flesh is out and make it a little easier to understand.

**Review of covariance.**

• \( Cov(x, y) = E(xy) - E(x)E(y) \)

• Describes how one variable changes in response to another.

• when \( \uparrow x, \uparrow y, Cov(x, y) > 0 \), when \( \uparrow x, \downarrow y, Cov(x, y) < 0 \)

*Note: Price originally used different notation to make the math clearer (\( q_i = \text{fitness}, Q_i = \text{frequency} \), but it contradicts everything else we’ve done in class, so I will try to use more familiar notation (\( \omega_i = \text{fitness of group } i, q_i = \text{frequency of group } i \)).*

**Phenotypic trait values.**

• Define \( z_i \) as the trait value of some individual/group \( i \)

• Not the same as it’s fitness, \( \omega_i \)

• e.g. trait = speed, fitness = number of offspring relative to the other traits in the population

• \( q_i \) is the frequency of trait \( i \). Importantly, \( q_i' \) is *not* the frequency of that trait in the next generation, but the fraction of the descendants that are derived from ancestors with trait \( i \).

• We define fitness as \( q_i' = q_i \omega_i / \bar{\omega} \)

**Proof.**
• By definition $\Delta \bar{z} = z' - \bar{z}$

• Also by definition $\bar{z} = E(z) = \sum_i q_i z_i$

• Therefore $\Delta \bar{z} = \sum_i q'_i z'_i - \sum_i q_i z_i$
  
  i.e, the change in mean trait value $z$ from one generation to the next, is the mean trait value in one generation minus the mean trait value in the previous generation

• By using $q'_i = q_i \omega_i / \bar{\omega}$ and $z'_i = z_i + \Delta z_i$, we substitute these into the first term of the mean equation to get

\[
- \Delta \bar{z} = \sum_i q_i \omega_i / \bar{\omega} z'_i - \sum_i q_i z_i
- \Delta \bar{z} = \sum_i q_i \omega_i / \bar{\omega} z_i + \sum_i q_i \omega_i / \bar{\omega} \Delta z_i - \sum_i q_i z_i
- \Delta \bar{z} = \sum_i q_i \omega_i / \bar{\omega} z_i - \sum_i q_i z_i + \sum_i q_i \omega_i / \bar{\omega} \Delta z_i
\]

• Look at just this piece $\sum_i q_i \omega_i / \bar{\omega} z_i - \sum_i q_i z_i$
  
  Remember $Cov(x, y) = E(x, y) - E(x)E(y)$

  $= E(\omega z) / \bar{\omega} - E(\omega)E(z) / \bar{\omega} = Cov(\omega, z) / \bar{\omega}$

• Now look at the other piece $\sum_i q_i \omega_i / \bar{\omega} \Delta z_i$

  $\sum_i q_i \omega_i / \bar{\omega} \Delta z_i = E(\omega \Delta z) / \bar{\omega}$

• Put them together and get $\Delta \bar{z} = \frac{Cov(\omega, z) + E(\omega \Delta z)}{\bar{\omega}}$

  Usually written $\bar{\omega} \Delta \bar{z} = Cov(\omega, z) + E(\omega \Delta z)$

**Interpretation.**

• What does this equation mean?

• If we substitute out the fitness terms it can be a little easier to understand.

  $\Delta \bar{z} = \Sigma(\Delta q_i) z_i + \Sigma q'_i(\Delta z_i)$

• The first term is easy. It’s the change in the mean value of the trait do to natural selection. i.e., the change in the frequency of available trait values do to selection on those traits.

  The differential contribution of the ancestors to the descendant population.
• The second term is a lot harder to understand conceptually. It is the change in mean trait value due to how different descendants are from their ancestors.
  – This term incorporates everything that is not selection. Changes in the environment, mutation, differential transmission, heritability not equal to 1, etc.

• It is important to notice that we made zero assumptions on the population or the trait when deriving this. Because of that, the Price equation is a mathematical equivalence rather than a model. It holds in every case of evolution. Recently this has been big knock against the usefulness of the Price equation (by Nowak and others). Or as Steve Frank puts it, the Price equation is like John Cruyff’s quip about how to win at soccer, You always have to make sure that you score one goal more than your opponent.

• It’s usefulness comes from the fact that it provides us a mathematical framework to talk about trait change (i.e. evolution) without dealing with the messiness and assumptions of genes/alleles

**Kin Selection.**

• So how can we use the Price equation?

• Hamilton’s rule describes when an altruistic trait will evolve (e.g., prairie dogs spending time watching for predators instead of foraging for food) as a relation of the cost of the trait to the individual to the benefit to the gene.
  – i.e., The trait will be selected for if \( rB > C \). The relatedness (\( r \)) of the recipient of the altruism to the actor, times it’s benefit to the actor is greater than its cost to the actor.

• If we call \( x_a \) the population of altruistic individuals and \( x_b \) the population of beneficiaries (it is possible that \( x_a + x_b > 1 \) i.e. being an altruistic individual and a beneficiary of altruism does not have to be mutually exclusive):

• If we use the simple version of the Price Equation (i.e., only look at natural selection) we can get

\[
\frac{\text{Cov}(x_b, x_a)}{\text{Cov}(x_a, x_a)} B > C
\]
• It turns out that \( \frac{\text{Cov}(x_b, x_a)}{\text{Cov}(x_u, x_u)} \) is a measure of the probability that a benefiting and altruistic individual share genes from the same ancestor. i.e. \( r! \)

**Group Selection.**

• Group selection is harder to model, but still can be done with the Price equation
• requires a two level Price Equation were you have one Price equation with the \( z \) values representing the group level trait and another with the \( z \) values representing the individual level trait. You can then put the individual equation inside the group equation getting the two level Price Equation.
• With this model you can show the evolution of an altruistic trait that is detrimental on the individual level and beneficial at the group level.