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Modeling evolution

- What is evolution?
  - Change in gene frequencies between generations

- How can we model change in gene frequencies?
  - Continuous time -> replicator dynamic
  - Discrete time -> Price’s equation

Replicator dynamics

At any time t, the proportion of players playing a particular strategy, s_i is p_i^t. There are *n* possible strategies.

And the payoff (fitness) of playing a strategy, s_i is $w_i^t = w_i(p^t)$ where $p^t = (p_1, \ldots, p_n)$

Rank strategies so that $w_1^t < w_2^t < \cdots < w_n^t$

Replicator dynamics

Assume that in every time period *dt*, each agent gains information about the payoff to another randomly chosen agent with probability $\alpha dt > 0$.

The player switches strategies (from s_i to s_j), depending on the payoff of the other agent as follows:

$$p_{ij}^t = \begin{cases} \beta\left(w_j^t - w_i^t\right) & \text{for } w_j^t > w_i^t \\ 0 & \text{for } w_j^t \leq w_i^t \end{cases}$$

Where β is sufficiently small that $p_{ij}^t \leq 1$for all i,j.

Replicator dynamics

$$E\left(p_i^{t+dt}\right) = p_i^t - \alpha dt\, p_i^t \sum_{j=i+1}^{n} p_j^t \beta\left(w_j^t - w_i^t\right) + \sum_{j=1}^{i} \alpha dt\, p_i^t p_j^t \beta\left(w_i^t - w_j^t\right)$$

Some individuals switch from s_i to better performing s_j

Some individuals switch from s_j to better performing s_i

Replicator dynamics

$$E\left(p_i^{t+dt}\right) = p_i^t - \alpha dt\, p_i^t \sum_{j=i+1}^{n} p_j^t \beta\left(w_j^t - w_i^t\right) + \sum_{j=1}^{i} \alpha dt\, p_i^t p_j^t \beta\left(w_i^t - w_j^t\right)$$

$$E\left(p_i^{t+dt}\right) = p_i^t + \alpha dt\, p_i^t \sum_{j=1}^{n} p_j^t \beta\left(w_i^t - w_j^t\right)$$

$$E\left(p_i^{t+dt}\right) = p_i^t + \alpha dt\, p_i^t \beta(w_i^t - \overline{w}^t)$$

Replicator dynamics

$$E\left(p_i^{t+dt}\right) = p_i^t + \alpha dt\, p_i^t \beta\left(w_i^t - \overline{w}^t\right)$$

Subtract p_i^t from both sides, divide by *dt* and take the limit as *dt* →0

$$\dot{p}_i^t = \alpha\beta\, p_i^t\left(w_i^t - \overline{w}^t\right)$$

Because $\alpha\beta$ does not affect stability or trajectories of the dynamical system, generally assume $\alpha\beta = 1$

A (continuous) replicator dynamic equation

$$\dot{p}_i = p_i(w_i - \bar{w})$$

p_i is proportion of all alleles that are of type i

w_i is the payoff to an individual of phenotype i

$\bar{w}$ is the population mean payoff

Note that we have made no assumptions about genetics or even about the mechanism of inheritance

Price's equation – modeling change in phenotypes and genotypes between generations

- Let p_i the proportion of individuals of a particular phenotype z_i
- Assume that proportion of next generation that descends from z_i is the relative fitness of z_i

$$p_i^{'} = p_i \left(\frac{w_i}{\overline{w}}\right)$$

- Assume that the phenotype of the descendants of z_i is z'_i

$$z_i^{'} = z_i + \Delta z_i$$

Price's equation

- Change in expected phenotype from one generation to the next:

$$\Delta\bar{z} = \sum p_i' z_i' - \sum p_i z_i$$

$$\Delta\bar{z} = \sum p_i \left(\frac{w_i}{\bar{w}}\right)(z_i + \Delta z_i) - \sum p_i z_i$$

Which rearranges to

$$\Delta\bar{z} = \sum p_i \left(\frac{w_i}{\bar{w}} - 1\right) z_i + \sum p_i \left(\frac{w_i}{\bar{w}}\right) \Delta z_i$$

$$\Delta\bar{z} = \sum p_i \left(\frac{w_i}{\overline{w}} - 1\right) z_i + \sum p_i \left(\frac{w_i}{\overline{w}}\right) \Delta z_i$$

$$\overline{w}\Delta\bar{z} = \sum p_i (w_i - \overline{w}) z_i + \sum p_i w_i \Delta z_i$$

$$\overline{w}\Delta\bar{z} = \sum p_i w_i z_i - \overline{w} \sum p_i z_i + \sum p_i w_i \Delta z_i$$

$$\overline{w}\Delta\bar{z} = E(wz) - \overline{w}E(z) + E(w\Delta z)$$

$$Cov(w, z) \stackrel{\text{def}}{=} E(wz) - E(w)E(z)$$

Price's equation

- Therefore, using standard statistical definitions, we can write this as:

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

More Price's equation

Phenotype = genotype + residual (often random environmental effects)

$$z_i = g_i + \delta_i$$

Remember that evolutionary biologists are interested in the change in phenotype due to changes in gene frequencies, i.e., Δg

Assume the average effect of δ is 0 for any particular genotype (remember, it is the residual) and no correlation between genotype and environment

More Price's equation

Then, $z_i = g_i$ and $z'_i = g'_i$ because $\delta_i = 0$ and $\delta'_i = 0$

$$\overline{w}\Delta\bar{z} = \overline{w}\Delta\bar{g} = Cov(w, g) + E(w\Delta g)$$

Price's equation

$$\overline{w}\Delta\bar{g} = Cov(w, g)$$

Fitness, w, includes some component that is not correlated with the phenotype in question, α, plus some component that is correlated with the phenotype in question as well as an error term

$$w = \alpha + \beta_{wz}z + \varepsilon$$

β_{wz} is the "selection gradient" on z = the slope of the regression of fitness on phenotype, z

Price's equation

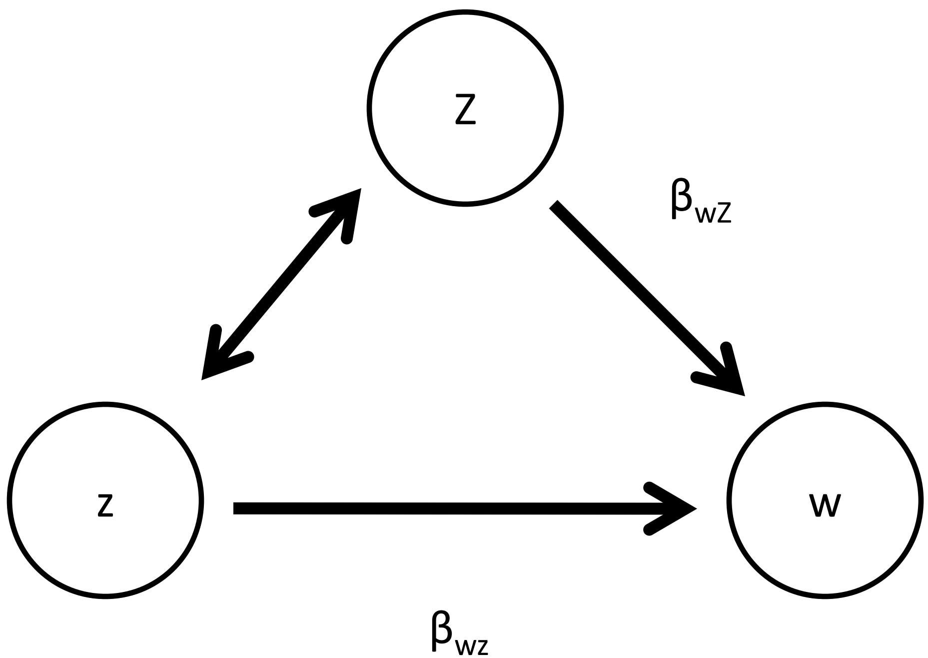
$$\bar{w}\Delta\bar{g} = Cov(w, g)$$

$$\bar{w}\Delta\bar{g} = Cov\,(\alpha, g) + \beta_{wz}Cov(g, g) + Cov(\varepsilon, g)$$

$$\bar{w}\Delta\bar{g} = \beta_{wz}V_g$$

V_g is the 'additive genetic variance' in the trait, g

Adding social selection



Partitioning variance

$$\overline{w}\Delta\bar{z} = Cov(w, z)$$

$$w = \alpha + \beta_{wz}z + \beta_{wZ}Z + \varepsilon$$

$$\overline{w}\Delta\bar{z} = Cov(w, z) = Cov(\alpha + \beta_{wz}z + \beta_{wZ}Z + \varepsilon, z)$$

$$= \beta_z V_g + \beta_{wZ}Cov(Z, z) + Cov(\varepsilon, z)$$

$$\overline{w}\Delta\bar{z} = \beta_{wz}V_g + \beta_{wZ}Cov(Z, z)$$

Price's equation and costly cooperation

- Assume that cooperative behavior is costly to an individual…

$$\beta_{wz} < 0$$

$$= - C$$

- Assume that receiving that same behavior is beneficial to an individual…

$$\beta_{wZ} > 0$$

$$= B$$

$$\overline{w}\Delta\bar{z} = -CV_g + BCov(Z,z)$$

We want to know if there is positive selection on cooperation i.e., if $\Delta z > 0$

$$\overline{w}\Delta\bar{z} = -CV_g + BCov(Z, z)$$

We want to know if there is positive selection on cooperation i.e., if $\Delta z > 0$

$$0 < -CV_g + BCov(Z, z)$$

$$C < B\frac{Cov(Z, z)}{V_g}$$

Assume that phenotype of social partners can be fully described by

$$Z = G + D$$

Where G is the 'breeding value' or genotype of social partners and D is the uncorrelated residual

$$Cov(Z, z) = Cov(G, g)$$

Conditions for the evolution of costly cooperative trait:

$$C < B\frac{Cov(G, g)}{V_g}$$

$$\frac{Cov(G,g)}{V_g} = r$$

Hamilton's rule

$$C < rB$$

What is r?

- A measure of the statistical association between actors and recipients

$$r = Cov(G,g)/Cov(g,g)$$

- The most common definition of *r* is that it is a measure of <u>relatedness</u>
  - The probability that two individuals share an allele as a result of recent, common descent

- But *r* can be any statistical association between genotypes of individuals