The Price Equation

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

Levels of selection literature...

- Price, GR. 1970. Selection and covariance. Nature 227: 520-521.
- Price, GR. 1972. Extension of covariance selection mathematics. Annals of Human Genetics 35: 485-490.
- Frank, SA. 1995. George Price's contributions to evolutionary genetics. Journal of Theoretical Biology 170: 393-400.
- Frank, SA. 1997. The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis. Evolution 51: 1712-1729. [also book]
- Wade, MJ. 1985. Soft selection, hard selection, kin selection, and group selection. American Naturalist 125: 61-73.
- Queller, DC. 1992. A general model for kin selection. Evolution 46: 376-380.

What did Price hope for?

- Very general equation of "selection" to provide broad insight into all selective processes
- "The mathematics given here applies not only to genetical selection but to selection in general. It is intended mainly for use in deriving relations and constructing theories, and to clarify understanding of selection phenomena, rather than for numerical calculation." (Price 1972)

- but here focus on evolutionary genetics

Price Equation

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

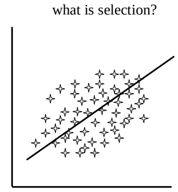
Change in mean phenotype due to selection (=differential reproductive success)

Change due to transmission bias

Selection with no transmission bias

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

$$=\beta_{wz}V_z$$



- "The covariance between fitness and character value gives the change in the character caused by differential productivity." (Frank 1997)

- Robertson (1966) Cov(w,g) "Robertson's secondary theory of natural selection", Li (1967)

If trait is fitness

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

Δw =Cov(w,w)

=Var(w)

The change in mean fitness depends on variance in fitness. This is "Fisher's fundamental theorem of natural selection".

Note that variance in fitness constrains the maximum covariance between any trait and fitness and is sometimes called the "opportunity for selection" I.

Transmission with no selection

if no variation in fitness

$$\Delta\overline{z} = E(w\Delta z)/\overline{w}$$

$$E(\Delta z) = \Sigma q_i \Delta z_i$$
$$= \Sigma q_i (z'_i - z_i)$$

difference between mean "parent" and "offspring" phenotype due to transmission bias, for example from mutation, unfair meiosis, random drift

- "The expectation term is a fitness-weighted measure of the change in character value between ancestor and descendant – a measure of the transmission fidelity of a character between parent and offspring." (Frank 1997)

Expanding to hierarchical levels

$$\overline{w}\Delta\overline{z} = Cov(w_i, z_i) + E_i(w_i \Delta z_i)$$

$$\overline{w}\Delta\overline{z} = Cov(w_i, z_i) + E_i\{Cov_j(w_{j.i}, z_{j.i}) + E_j(w_{j.i}\Delta z_{j.i})\}$$

selection between groups (i...N)

selection between individuals (j....n) within group (i...N)

transmission

Importance of different levels of selection

$$\overline{w}\Delta\overline{z} = Cov(w_i, z_i) + E_i\{Cov_j(w_{j.i}, z_{j.i}) + E_j(w_{j.i}\Delta z_{j.i})\}$$

constrained by fitness variation between groups

constrained by fitness variation between individuals