Hamilton's rule:

$$r \, b > c$$

r: degree of genetic relation. b/t organisms

b: benefit to recipient

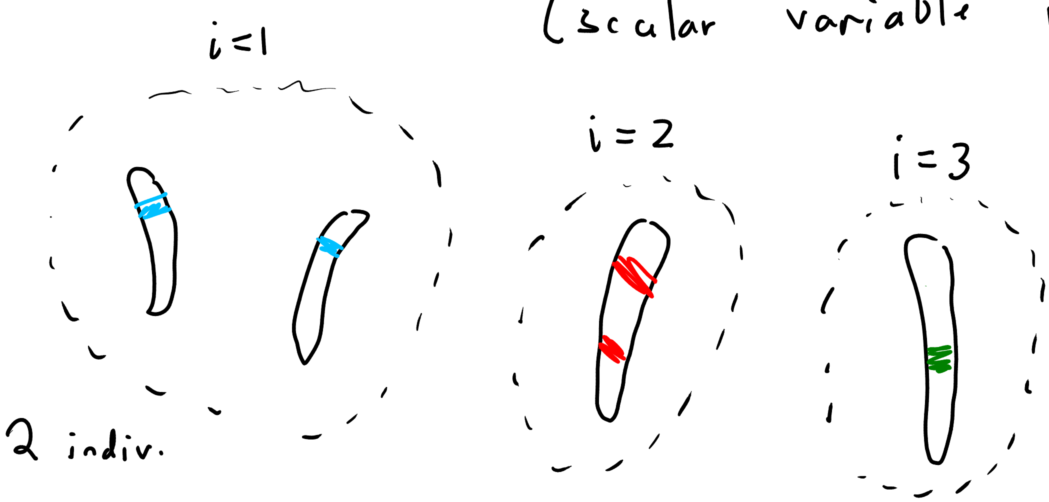
c: cost to actor

Step 1: derive Price equation

consider a population of "individuals" (gametes: eggs or sperms)

group by shared genetic trait:

z_i = trait of group i (scalar variable representing trait)



example:

single gene w/ two alleles

$z_1 = 0$ wild-type

$z_2 = 1$ mutant

z_i could reflect a larger collection of genes: $\underline{0}\ \underline{1}\ \underline{1}\ \underline{0}$

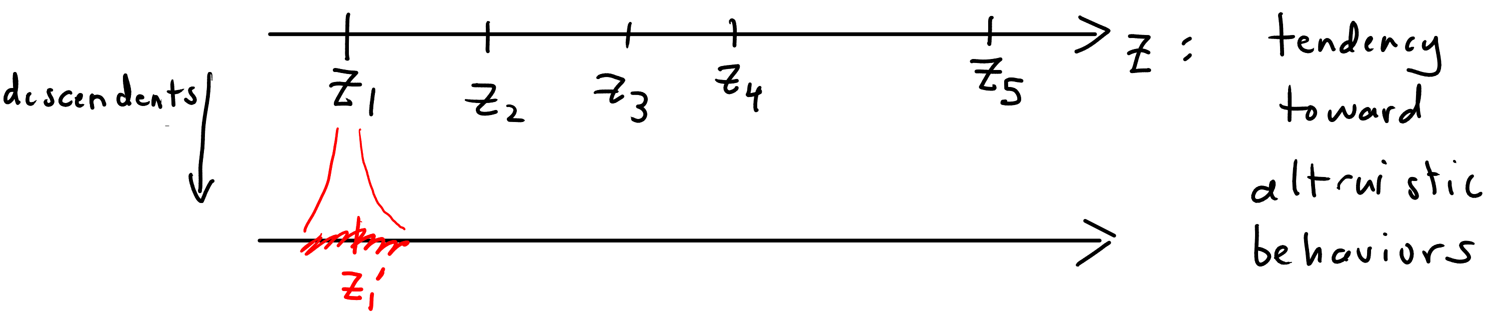
0 = WT
1 = mutant

$\Downarrow$

16 combos

$\Rightarrow$ 16 numbers (binary $\Rightarrow$ integ)

in extreme case: $z_i \to$ a number on real axis



n_i = current # of indiv. in group i

N = total population $= \sum_i n_i$

z_i' = mean value of trait among offspring of group i

n_i' = avg. # of offspring of group i in next generation

$N' = \sum_i n_i'$ total pop. in next gen.

$\Delta z_i = z_i' - z_i = \begin{cases} = 0 & \text{usual assumption: unbiased mutation + recombination} \\ \neq 0 & \text{"transmission" bias} \end{cases}$

fitness of group i : $w_i = \frac{n_i'}{n_i}$ $\qquad w_i > 1$ numbers increase, etc.

statistical definitions:

$$\left.\begin{aligned} \bar{f} &= \frac{1}{N}\sum_i n_i f_i \\ \bar{f'} &= \frac{1}{N'}\sum_i n_i' f_i' \end{aligned}\right\}$$

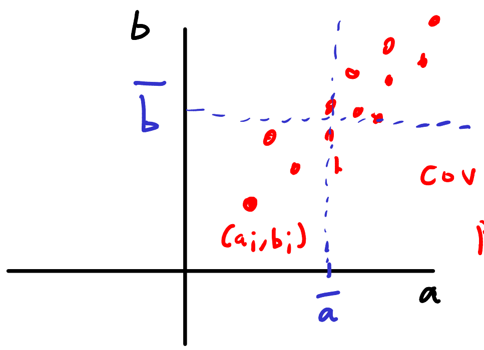
GOAL: find an equation for $\Delta\bar{z} = \bar{z}' - \bar{z}$

$$\overline{(ab)} = \frac{1}{N}\sum_i n_i a_i b_i$$

$$\text{Cov}(a,b) = \overline{(ab)} - \bar{a}\,\bar{b}$$

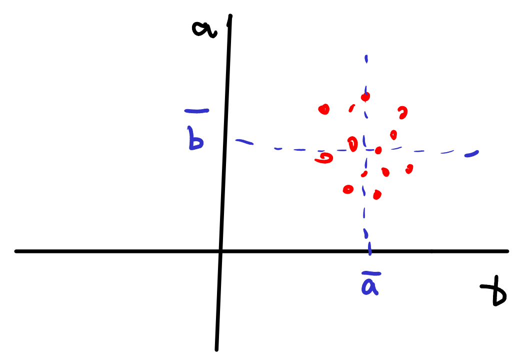
$$= \frac{1}{N}\sum_i n_i (a_i - \bar{a})(b_i - \bar{b})$$

$$\text{Var}(a) = \text{cov}(a,a) = \overline{a^2} - \bar{a}^2$$



$\text{cov}(a,b) > 0$

pos. correl. b/t a, b



$\text{cov}(a,b) \approx 0$

Some facts: (1) $\bar{w}$ mean fitness $= \frac{1}{N}\sum_i n_i w_i = \frac{1}{N}\sum_i \cancel{n_i}\frac{n_i'}{\cancel{n_i}}$

$$= \frac{N'}{N}$$

(2) $$\overline{(w\Delta z)} = \frac{1}{N}\sum_i n_i w_i \underbrace{\Delta z_i}_{z_i' - z_i}$$

$$= \frac{1}{N}\sum_i n_i w_i z_i' - \frac{1}{N}\sum_i n_i w_i z_i$$

$$= \underbrace{\frac{1}{N}\sum_i \cancel{n_i}\frac{n_i'}{\cancel{n_i}} z_i'}_{\frac{1}{N'}\cdot \underbrace{N'\frac{1}{N}}_{\bar{w} \text{ from } (1)} \sum_i n_i' z_i'} - \overline{(wz)}$$

$$\Rightarrow \quad \overline{(w\Delta z)} = \bar{w}\,\bar{z}' - \overline{(wz)} \qquad (2)$$

(3) $$\mathrm{cov}(w,z) = \overline{(wz)} - \bar{w}\,\bar{z}$$

add (2) + (3) : $$\mathrm{cov}(w,z) + \overline{(w\Delta z)}$$

$$= \bar{w}\,\bar{z}' - \bar{w}\,\bar{z}$$

$$= \bar{w}\,\Delta\bar{z}$$

$$\boxed{\Delta\bar{z} = \frac{1}{\bar{w}}\left[\mathrm{cov}(w,z) + \overline{(w\Delta z)}\right]}$$

Price equ.