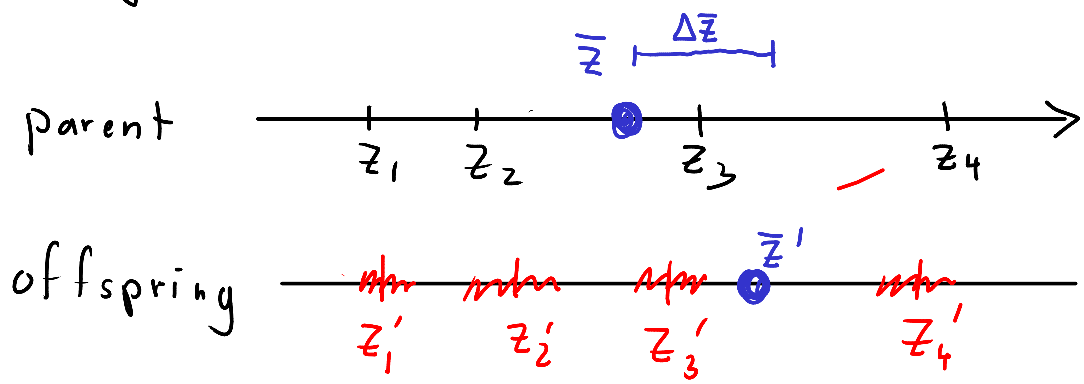
RECAP of Price equ:

group i: $n_i \to n_i'$ $\qquad W_i = \dfrac{n_i'}{n_i}$



tend. toward altruism

$$\Delta z_i = z_i' - z_i$$

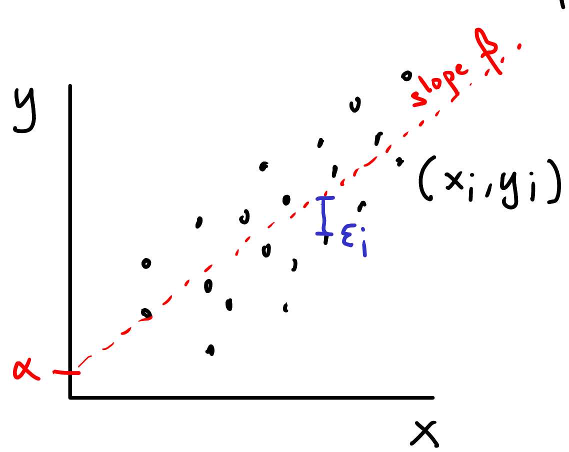
$$\Delta \bar{z} = \bar{z}' - \bar{z}$$

Price equ: $\Delta \bar{z} = \dfrac{1}{\bar{W}} \left[\operatorname{cov}(w, z) + \overline{(w \Delta z)} \right]$

"natural selection"

"transmission bias" (= 0 in usual bio cases)

interpretation: start w/ review of linear regression



best fit linear model:

$$y = \beta x + \alpha$$

error of model:

$$\varepsilon_i = \underset{\text{true}}{y_i} - \underset{\text{predicted}}{(\beta x_i + \alpha)} \quad \text{for each } i$$

minimize squared errors: $\mathcal{L} = \sum_i \varepsilon_i^2$

$$\hookrightarrow \quad \frac{\partial \mathcal{L}}{\partial \alpha} = 0 \qquad \frac{\partial \mathcal{L}}{\partial \beta} = 0$$

ANS: $\beta = \dfrac{\mathrm{cov}(x,y)}{\mathrm{var}(x)}$ $\qquad \alpha = \bar{y} - \beta \bar{x}$

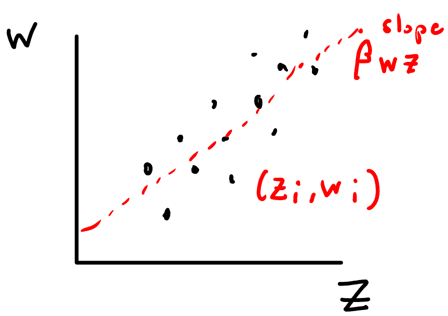
turns out: $\bar{\varepsilon} = 0 = \bar{y} - (\beta \bar{x} + \alpha) = 0$

$$\mathrm{cov}(x,\varepsilon) = \mathrm{cov}(x,y) - \beta \overbrace{\mathrm{cov}(x,x)}^{\mathrm{var}(x)} - \cancel{\mathrm{cov}(x,\alpha)}^{0}$$

$$= 0$$

Focus on bio version of Price (no trans. bias): $\qquad \mathrm{var}(z) \geqslant 0$

$$\Delta \bar{z} = \frac{1}{\bar{w}} \mathrm{cov}(w,z) = \beta_{wz} \mathrm{var}(z) \cdot \frac{1}{\bar{w}}$$



Darwin in a nutshell:

- $\mathrm{var}(z) > 0$: variation in a trait
- $\beta_{wz} > 0 \Rightarrow \Delta \bar{z} > 0$

if posit. correl. b/t trait & fitness $\Rightarrow$ natural selection will on avg. increase the trait

Special case: trait <u>is</u> fitness

$$z_i = w_i$$
$$\beta_{wz} = 1$$

$$\Delta \bar{w} = \frac{\overline{\mathrm{var}(w)}}{\bar{w}}$$

(only true if $\overline{w \Delta z} \approx 0$)

Fisher's fundamental theorem of natural select. [1930]

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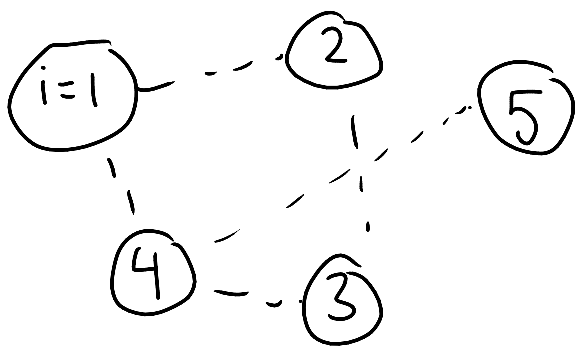
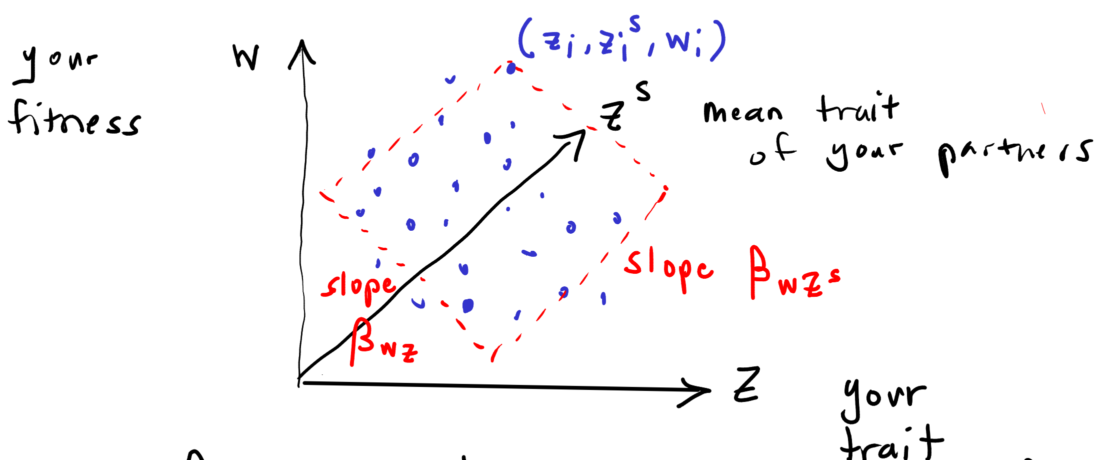
interacting groups:



z_i = trait related to social behavior (i.e. altruism)

z_i^s = mean value of z_j among all partners of group i



multi-dim. regression: fitting plane to cloud

here: $\beta_{wz} < 0$: behavior related to trait costs you fitness

$\beta_{wz^s} > 0$: behavior in partners helps you defines altruism

model: $w = \underbrace{\beta_{wz}}_{\substack{\text{slope of } w \\ \text{versus } z \\ \text{at const.} \\ z^s \,=\, \left.\frac{\partial w}{\partial z}\right|_{z^s}}} z + \underbrace{\beta_{wz^s}}_{\left.\frac{\partial w}{\partial z^s}\right|_{z}} z^s + \alpha$

for any group i; $w_i = \beta_{wz} z_i + \beta_{wz^s} z^s_i + \alpha + \underset{\substack{\uparrow \\ \text{error}}}{\varepsilon_i}$ (1)

regression: find $\beta_{wz}, \beta_{wz^s}, \alpha$ that minimize

$$\sum_i \varepsilon_i^2$$

$$\Rightarrow \quad \bar{\varepsilon} = 0 \quad \text{cov}(z, \varepsilon) = 0 \quad \text{cov}(z^s, \epsilon) = 0$$

Price equ. w/ no transm. bias:

$$\Delta \bar{z} = \frac{1}{\bar{w}} \text{cov}(w, z)$$

$$= \frac{1}{\bar{w}} \frac{1}{N} \sum_i (w_i - \bar{w})(z_i - \bar{z})$$

$\Big\}$ plug in w_i from (1)

$$= \frac{1}{\bar{w}} \Big[\beta_{wz} \, \mathrm{var}(z) + \beta_{wz^s} \, \mathrm{cov}(z^s, z) + \cancelto{0}{\mathrm{cov}(\varepsilon, z)} \Big]$$

$$= \frac{1}{\bar{w}} \Big[\beta_{wz} \, \mathrm{var}(z) + \beta_{wz^s} \, \mathrm{cov}(z^s, z) \Big]$$

$$\Rightarrow \Delta \bar{z} = \frac{\overset{\geq 0}{\mathrm{var}(z)}}{\underset{> 0}{\bar{w}}} \Big[\underbrace{\beta_{wz}}_{-c} + \underbrace{\beta_{wz^s}}_{\equiv b} \, \underbrace{\beta_{z^s z}}_{r} \Big]$$

$$\beta_{z^s z} = \frac{\mathrm{cov}(z^s, z)}{\mathrm{var}(z)}$$

= slope of linear fit of z^s vs z

$\equiv r$ measure of relatedness of your group to social partners

where c = cost of the behavior to your group

b measures benefit you get from interactions

$$\boxed{\Delta \bar{z} > 0 \text{ iff } rb > c}$$

Hamilton's rule

note of caution: β coefficients are measures of correlation, not causation