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GROUP SELECTION ?

Preliminaries :

★ Wynne-Edwards book — many bird behaviours functioned to prevent over-population. "Good of the species" ...

★ Hamilton, Price, Dawkins et al. objected.

"selfish gene"

★ Who is right?

We want to formalise the argument.

"Unto Others"
SOBER & WILSON.

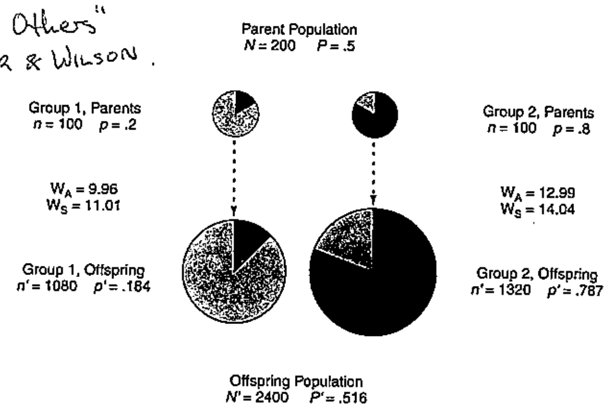


Figure 1.1. The evolution of altruistic and selfish types in an asexual population that is divided into two groups of size $n = 100$ (smaller circles). The altruistic type (black) makes up 20 percent of group 1 and 80 percent of group 2. In the offspring generation, the altruists decline in frequency within each group (the size of the black "slice" grows smaller), but the group with more altruists grows larger (to a population of 1,320) than the group with fewer altruists (1,080). As a result, altruists increase in frequency in the *global* population of 2,400 offspring. Adding the progeny from the two groups is biologically justified only if the groups periodically merge and re-form or otherwise compete in the formation of new groups.

★ RECAP : $\bar{w}\,\Delta p$ is what we are interested in

mean fitness

change (over time) in the overall frequency of a trait.

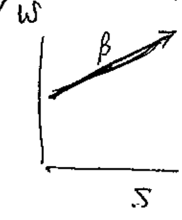
some trait.

$$\bar{w}\Delta p = \mathrm{Cov}(w, s)$$

$$= \mathrm{Var}(s)\ \beta\,(w \text{ on } s)$$

If fraction p carry the s gene, then this is $p(1-p)$

slope of graph :

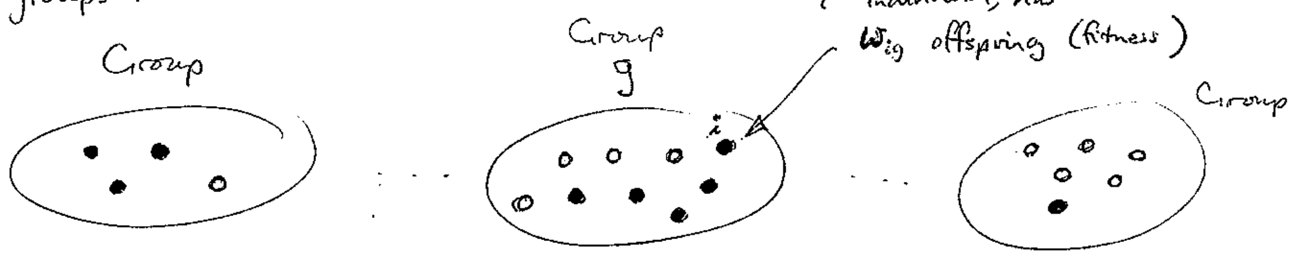


NOMENCLATURE :

Consider a trait $s = 0$ or 1. (eg: $s=1$ could be a "cooperator", for example).

$s=0 \rightarrow \bullet \qquad s=1 \rightarrow \circ$

Population in groups :



n_g individuals.
Fraction p_g have $s=1$.
Average fitness:

$$w_g = \frac{1}{n_g}\sum_i w_{ig}$$

N individuals
Fraction p have $s=1$
Average fitness : $\bar{w}$

Will p go up ?

$$p' = \sum_g p_g' \frac{\overset{= n_g w_g}{n_g'}}{\underset{= N\bar{w}}{N'}} = \sum_g p_g' \frac{n_g w_g}{N\bar{w}}$$

$$\text{so...} \quad \bar{w}\, p' = \sum_g p_g' \frac{w_g n_g}{N}$$

$$\bar{w} = \sum_g w_g \frac{n_g}{N}$$

$$\text{so} \quad \bar{w}\,\Delta p = \bar{w}\,p' - \bar{w}\,p$$

$$= \sum_g p_g' \frac{w_g n_g}{N} - \sum_g p \frac{w_g n_g}{N}$$

$$= \sum_g (p_g' - p_g) \frac{w_g n_g}{N} + \sum_g (p_g - p) \frac{w_g n_g}{N}$$

this just adds a p_g term and simultaneously takes it away

$$\boxed{\bar{w}\,\Delta p = E[\,w_g \Delta p_g\,] + \mathrm{Cov}(w_g, p_g)}$$

GENERAL FORM OF PRICE'S EQTN

Do groups with high p_g do better?

$\boxed{\text{General form of Price Equation}}$:

$$\bar{w}\,\Delta p = E\left[w_g\,\Delta p_g\right] + \mathrm{Cov}(w_g, p_g)$$

$\boxed{\text{Simplest case}}$: Suppose each "group" only contains 1 individual ...

$$\rightarrow \bar{w}\,\Delta p = \cancel{E\left[w_i\,\Delta p_i\right]} + \mathrm{Cov}(w_i, p_i)$$

(zero! no meiotic drive, and low mutation rate)

$$= \mathrm{Cov}(w_i, p_i)$$

AS WE HAVE SEEN BEFORE.

$\boxed{\text{Groups case}}$: Use the above (simplest case) to subsitute in for the 1st term (general case).

$$\rightarrow \bar{w}\,\Delta p = \underset{\text{over groups}}{E}\left[\underset{\text{in group}}{\mathrm{Cov}}(w_{ig}, p_{ig})\right] + \underset{\text{across groups}}{\mathrm{Cov}}(w_g, p_g)$$

$\boxed{p_{ig} \equiv s}$

Recall: can always re-write a covariance as a variance times a regression coefficient (ie. slope of a graph ...)

$$\mathrm{cov}(x, y) = \mathrm{var}(x)\,\beta(y \text{ on } x)$$

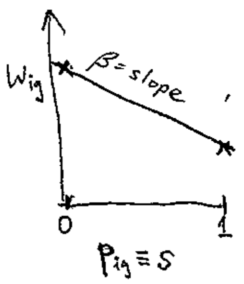
"slope of graph".

So :

$$\bar{w}\,\Delta p = \underset{\text{over groups}}{E}\left[\underset{\text{within a group}}{\mathrm{Var}}(p_{ig})\,\beta(w_{ig} \text{ on } p_{ig})\right] + \mathrm{Var}(p_g)\,\beta(w_g \text{ on } p_g)$$

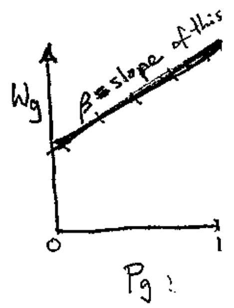
VARIATION WITHIN GROUPS $\equiv p_g(1-p_g)$

SELECTION WITHIN GROUPS



VARIATION BETWEEN GROUPS $\equiv r\,p(1-p)$

SELECTION BETWEEN GROUPS



Think of as an "accounting system" that makes groups explicit. Before, we just averaged across individuals. Here, we first average across individuals within each group, and then across all the groups. Both should give the same result!

Example of use of Price Equation: evolution of altruism.

<u>Prisoner's dilemma</u>: if a fraction p_g of a group are cooperators $(s=1)$ and $\therefore$ $1-p_g$ are $s=0$ (defectors)

Fitness of cooperator is $b p_g - c$

cost of own cooperating.

benefits from others cooperating

" " defector is $b p_g$

so $\boxed{\beta(w_{ig} \text{ on } p_{ig}) = -c}$

Average Fitness of group g is $w_g = (b-c)p_g$

so $\boxed{\beta(w_g \text{ on } p_g) = b-c}$

$$\bar{w}\Delta p = -c \underbrace{\mathop{E}_{\substack{\text{over}\\\text{groups}}}\left[p_g(1-p_g)\right]}_{?} + r\,p(1-p)(b-c)$$

if $r=0$, this is $p(1-p)$

if $r=1$, it is <u>zero</u>.

Interpolating:

$(1-r)\,p(1-p)$

$\vdots$

$$= p(1-p)(rb-c)$$

So $\boxed{\Delta p > 0 \text{ if } r > c/b}$ "Hamilton's Rule".

Exercise: do the same but for Stag Hunt instead of Prisoner's Dilemma.