Chapter 3

★ Social evolution is all about ASSORTMENT: who interacts with who.
What payoff you get depends on who you interact with.

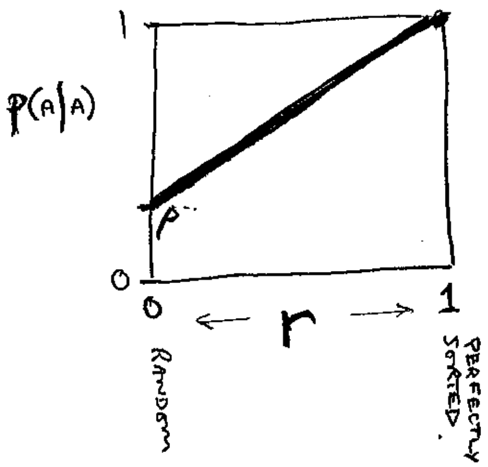
★ Last time we assumed RANDOM MIXING:

if there are 2 types: A, B, and ρ is freq. of A's,
$\text{prob}(A|A) = \rho$
$\text{prob}(B|A) = 1-\rho$.

★ But what if A's...
- tend to seek each other out?
- tend to end up in similar places?

Model with a parameter r: $\begin{cases} r = 0 & \text{is RANDOM.} \\ r = 1 & \text{is COMPLETELY SORTED (like only meets like).} \end{cases}$

(and $0 < r < 1$ interpolates between these).



$$\boxed{p(A|A) = r + (1-r)\rho}$$

& Similarly,

$$P(B|B) = r + (1-r)(1-\rho)$$

& We don't need $P(B|A)$ since it is just $1 - P(A|A)$ ....

Possible mechanisms for assortment:

- pseudo-physical, like the sorting of stones on a beach by wave action.
- kin recognition: "only cooperate with close relatives..."
- limited dispersal of offspring...?
- other ways ??...

IN THIS CASE you could think of r as "relatedness by descent".

∴ We have **probabilities** of interaction:

$P(\text{other}\,\overset{\text{with}}{}\,|\,\text{self})$

	self: A	self: B
other: A	*	*
other: B	*	*

.... and **payoffs** (expected) for each such interaction:

$V(\overset{\text{to}}{\text{self}}\,|\,\overset{\text{given}}{\text{other}})$

	other: A	other: B
self: A	*	*
self: B	*	*

So put these together to get expected fitnesses; averaged over interactions

$$W(A) = W_0 + P(A|A)\,V(A|A) + P(B|A)\,V(A|B)$$

& $$W(B) = W_0 + P(B|B)\,V(B|B) + P(A|B)\,V(B|A)$$

SOME TRIVIAL TEDIUM

an UGLY (but linear) EQUATION:

$$W(A) - W(B) = \left[r(1-\rho) + \rho\right]\left[V(A|A) - V(A|B)\right] + V(A|B)$$
$$- \left[r\rho + (1-\rho)\right]\left[V(B|B) - V(B|A)\right] - V(B|A)$$

expected fitness of A's

assortment ("relatedness")

relative frequency of A's.

if this r.h.s. > 0, A's will increase at the expense of B's.

Example:

Prisoners Dilemma

A → "C" : cooperator ; benefits another by b at cost to self of c.
We assume $b > c$ (NB. ρ is freq. of cooperators)

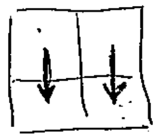
B → "D" : defector ; does nothing...

Payoff matrix ≡ V:

		other: C	other: D
self	C	$b-c$	$-c$
	D	b	0

Hawk-Dove is the same

Notice structure * is



ie. Prefer D regardless of other.

⟹ D-D is rational, but has lower payoff than C-C, hence the "dilemma".

Case 1: no assortment $(r = 0)$. Plug that, and the above payoffs into UGLY EQUATION, which becomes

$$W(C) - W(D) = -c \qquad \text{(everything else cancels!)}$$

This is negative, so D's always fitter than C's, so $\boxed{\rho \to 0}$ as expected.

Case 2: Assume $\rho \simeq 0$ (all Defectors).
At what r value does $W(C)$ become $> W(D)$?

UGLY EQTN, with $\rho = 0$, becomes

$$W(C) - W(D) = rb - c$$

∴ the tipping point is at $\boxed{r > c/b}$

"Hamilton's Rule".

["r" can be relatedness-by-descent, in a kin-selection model.
But more generally it's any assortment]

Example: $\boxed{\text{Stag Hunt}}$

(NB. ρ is freq. of Stag hunters.)

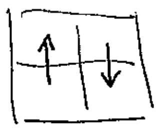
A → "S" : Stag hunter — a pair of Stag hunters get benefit s (each)
B → "H" : Hare hunter — hunts solo, hares have benefit h (to self).

We assum $s > h$

Payoffs V:

		other	
		S	H
self	S	s	0
	H	h	h

Notice structure is

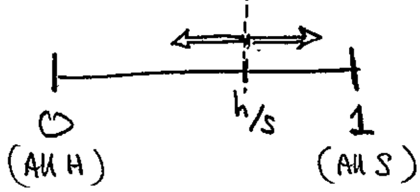


makes this a "coordination" game.

$\boxed{\text{Case 1}}$ no assortment. ($r = 0$).
UGLY EQTN becomes....

$$W(S) - W(H) = \rho s - h$$

So Stag hunters increase if their frequency $\boxed{\rho > h/s}$

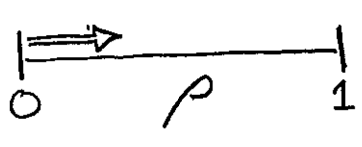


$\boxed{\text{Case 2}}$ At what r could rare Stag hunters invade?

$\rho \approx 0 \ldots$

$$W(S) - W(H) = rs - h$$

(ie) S can invade a pure H population if $\boxed{r > h/s}$



The Price Equation (simple form)

Consider allele "A", with frequency ρ.

We showed new generation has : $\rho' = \rho \dfrac{W(A)}{\bar{w}}$

average fitness of the A's in this population.

average fitness across whole populatn.

So $\Delta\rho = \rho' - \rho$

$= \rho\left(\dfrac{W(A)}{\bar{w}} - 1\right)$

or $\bar{w}\,\Delta\rho = \rho\, W(A) - \rho\,\bar{w}$.

we need 3 numbers : ρ, $W(A)$, and $\bar{w}$

In Terms Of Individuals :

Say $a_i = \begin{cases} 1 & \text{if } i^{th} \text{ individual carries the A gene.} \\ 0 & \text{otherwise.} \end{cases}$

then

$$\rho = \frac{1}{n}\sum_{i=1}^{n} a_i = \bar{a}$$

$$\bar{w} = \frac{1}{n}\sum_{i=1}^{n} w_i$$

fitness of the i^{th} individual.

and $W(A) = \dfrac{\sum_i w_i a_i}{\sum_i a_i}$ = av. fitness of those that have $a = 1$

$$\therefore \quad \bar{w}\,\Delta\rho = \frac{1}{n}\sum_i w_i a_i - \bar{w}\,\bar{a}$$

$$= E[w_i a_i] - E[w_i] * E[a_i]$$

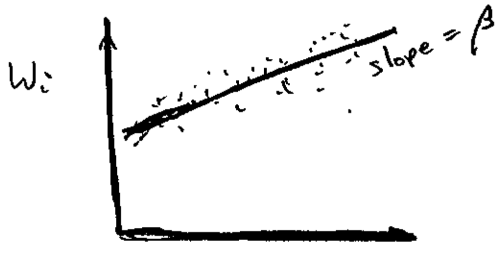
$$\bar{w}\,\Delta\rho = \text{cov}(w_i, a_i)$$

PRICE'S EQTN, true for any allele.

$$\equiv \text{var}(a_i) * \beta(w_i; a_i)$$

eg. if a_i binary this is just $\rho(1-\rho)$

Slope of the regression line relating fitness w_i to gene a_i



Key points

- sign of Δp = sign of $\beta(w_i ; a_i)$

- If our model has a function for fitness in terms of a, we can find β by differentiating the function.

  slope of w vs. a

- Example: Prisoner's dilemma.

  $x_i \in \{0,1\}$ indicator of presence of "cooperator gene".

$$w_i = w_0 + b x_j - c x_i$$

individual that gets to interacts with i^{th}.

$$\text{Slope: } \beta = \frac{dw_i}{dx_i} = b\,\frac{dx_j}{dx_i} - c$$

$$= b\left(\underbrace{\frac{\partial x_j}{\partial x_i}}_{r} \cdot \underbrace{\frac{dx_i}{dx_i}}_{1}\right) - c$$

$$= rb - c$$

$\therefore \Delta p$ +ve if $\boxed{r > c/b}$ Hamilton's Rule

Tricksy: method due to Taylor & Franks. See the book....