Cooperation and Construction

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New idea

"I would jump into the river to save two brothers or eight cousins".

– J.B.S. Haldane (ca. 1930)

What is inclusive fitness?

"Inclusive fitness may be imagined as the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship appropriate to the neighbours whom he affects; unit for clonal individuals, one-half for sibs, one-quarter for half-sibs, one-eighth for cousins,....and finally zero for all neighbours whose relationship can be considered negligibly small."

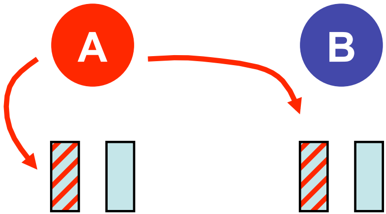
(Hamilton 1964)

What is inclusive fitness?

- Inclusive fitness effect $=$ my offspring **only due to my own actions** + $R\times$ (my relatives' offspring **only due to my own actions**)

What is the inclusive fitness effect?

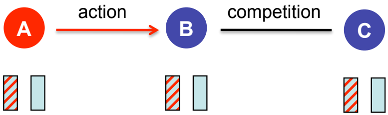
Inclusive fitness:



$$W_{IF} = \sum_j (\text{effect of actor on } j) \times R_j$$

where R_j is the relatedness of the actor to individual j.

Complication: Hidden effects



- what about competition effects?

Example: cycle

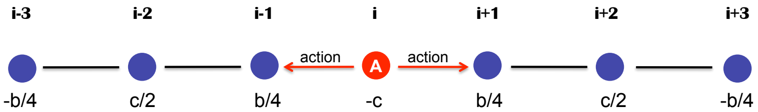
- Consider a population situated on the nodes of a cycle

- individuals interact with their neighbors and every interaction is a simplified Prisoner's Dilemma game with cost *c* and benefit *b*
- the fecundity of individual i is given by

$$f_i = 1 + \delta \text{payoff}_i$$

- evolutionary update: at every time step an individual is picked to die at random and the two neighbors compete for the empty spot proportional to fecundity.

Example: cycle with death-birth (DB) updating



$$b_i = \frac{1}{N}\left(\frac{f_i}{f_i + f_{i-2}} + \frac{f_i}{f_i + f_{i+2}}\right)$$

$$f_i = 1 + \delta(2cg_i + bg_{i-1} + bg_{i+1})$$

The expected fitness of individual i is then $w_i = 1 - d_i + b_i$ which in the limit of weak selection becomes

$$w_i = 1 + \frac{\delta}{N}\left(-cg_i - \frac{b}{4}g_{i-3} + \frac{c}{2}g_{i-2} + \frac{b}{4}g_{i-1} + \frac{b}{4}g_{i+1} + \frac{c}{4}g_{i+2} - \frac{b}{4}g_{i+3}\right)$$

Example: cycle with death-birth (DB) updating

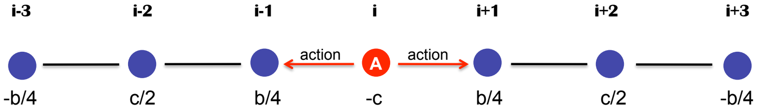
The expected fitness of individual i is then (in the limit of weak selection) given by

$$w_i = 1 + \frac{\delta}{N}\left(-cg_i - \frac{b}{4}g_{i-3} + \frac{c}{2}g_{i-2} + \frac{b}{4}g_{i-1} + \frac{b}{4}g_{i+1} + \frac{c}{4}g_{i+2} - \frac{b}{4}g_{i+3}\right)$$

The inclusive fitness effect of individual i is

$$W_{IF} = 1 + \frac{\delta}{N}\left(-c - \frac{b}{4}R_{i-3} + \frac{c}{2}R_{i-2} + \frac{b}{4}R_{i-1} + \frac{b}{4}R_{i+1} + \frac{c}{2}R_{i+2} - \frac{b}{4}R_{i+3}\right)$$

Example: cycle with death-birth (DB) updating



- notice the competition effects

A general question

- we consider a spatially-structured haploid population of fixed size N
- each individual has one of two strategies A and B
- individuals interact and accumulate payoff; reproduction is proportional to payoff
- reproduction can occur with mistakes; mutation rate u

Question: When is A favored over B in the stationary distribution of the mutation selection process?

i.e. when is $\langle x_A \rangle > 1/2$

When is A favored over B? (low mutation, weak selection)

- Let δ denote the intensity of selection. In the limit of low mutation ($u \to 0$) and weak selection ($\delta \to 0$) the condition that A is favored over B becomes

$$\left\langle \frac{\partial}{\partial \delta} \Delta x^{sel} \Big|_{\delta=0} \right\rangle_0 := \left\langle \sum_i g_i \frac{\partial}{\partial \delta} w_i \Big|_{\delta=0} \right\rangle_0 > 0$$

Connection to inclusive fitness

The question is: when can we re-write the standard low mutation condition

$$\left\langle \sum_i g_i \frac{\partial}{\partial \delta} w_i \Big|_{\delta=0} \right\rangle_0 > 0$$

as $W_{IF} > 0$ where

$$W_{IF} = \sum_j \frac{\partial}{\partial \delta} \frac{\partial w_\bullet}{\partial g_j} \Big|_{\delta=0} R_j$$

Here $\bullet$ denotes the index of the actor; eg. $w_\bullet = 1 - d_\bullet + b_\bullet$ denotes the fitness of the actor.

What is relatedness?

- relatedness is defined as relative identity by descent

$$R_{ij} = \frac{Q_{ij} - \overline{Q}}{1 - \overline{Q}}$$

where

- $Q_{ij} = \langle g_i g_j \rangle_0$ is the probability that i and j are identical by descent and
- $\overline{Q}$ is the probability that two random individuals are identical by descent.

IF is an average quantity

- in order to have relatedness be identity by descent (IBD), inclusive fitness becomes an average quantity
- unlike fitness, which is properly defined in a state

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Connection to inclusive fitness

$$\left\langle \sum_i g_i \frac{\partial}{\partial \delta} w_i \bigg|_{\delta=0} \right\rangle_0 > 0$$

$$\Downarrow ?$$

$$\sum_j \frac{\partial}{\partial \delta} \frac{\partial w_\bullet}{\partial g_j} \bigg|_{\delta=0} \langle g_\bullet g_j \rangle_0 > 0$$

- Pick a representative actor.

$$\left\langle g_\bullet \frac{\partial}{\partial \delta} w_\bullet \bigg|_{\delta=0} \right\rangle_0 > 0$$

Connection to inclusive fitness

$$\left\langle g_\bullet \frac{\partial}{\partial\delta} w_\bullet \Big|_{\delta=0} \right\rangle_0 > 0$$

$$\Downarrow ?$$

$$\sum_j \frac{\partial}{\partial\delta} \frac{\partial w_\bullet}{\partial g_j} \Big|_{\delta=0} \langle g_\bullet g_j \rangle_0 > 0$$

- Assumption (ii). The game is additive.

$$\left\langle \sum_j \frac{\partial}{\partial\delta} \frac{\partial w_\bullet}{\partial g_j} \Big|_{\delta=0} g_\bullet g_j \right\rangle_0 > 0$$

Connection to inclusive fitness

$$\sum_j \left\langle \frac{\partial}{\partial \delta} \frac{\partial w_\bullet}{\partial g_j} \Big|_{\delta=0} g_\bullet g_j \right\rangle_0 > 0$$

$$\Downarrow ?$$

$$\sum_j \frac{\partial}{\partial \delta} \frac{\partial w_\bullet}{\partial g_j} \Big|_{\delta=0} \langle g_\bullet g_j \rangle_0 > 0$$

- Assumption (iii). The population structure is ‘special’.

$$\sum_j \frac{\partial}{\partial \delta} \frac{\partial w_\bullet}{\partial g_j} \Big|_{\delta=0} \langle g_\bullet g_j \rangle_0 > 0$$

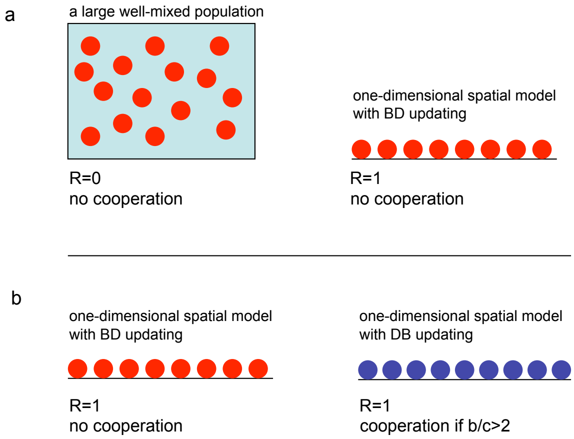
Partial Summary

- the concept of inclusive fitness can easily break down if either one of the following assumptions is not satisfied
  - weak selection
  - additive games
  - ‘special’ structures

- where IF can be defined, it yields a calculation which is **identical** to calculations that only use fitness

- many empirical studies rely exclusively on correlating relatedness with cooperative behavior

Relatedness measurements alone are inconclusive



Often correlation and not causation

Example: cooperatively breeding birds

Often high relatedness cannot trump the strong effects of competition

"Justified, rather tendentiously, by the Koranic verse *'what is the death of a prince to the loss of a province?'* [the fratricidal law] allowed sultans to execute their brothers (and nephews) to prevent power struggles."

(J. Goodwin, Lords of the Horizons: A History of the Ottoman Empire)

What is kin selection?

"Process by which traits change in frequency over evolutionary time in part because of their effects on the fitness of related individuals." – (Maynard Smith, Peter Taylor)

$\Downarrow$

effects on kin can be both negative and positive

"Natural selection favoring the spread of alleles that increase the indirect component of fitness is called kin selection." – Freeman and Herron, "Evolutionary Analysis"

$\Downarrow$

effects on kin are assumed to be positive

Conclusions

- IF (as proposed by Hamilton 1964) does not have a working definition; it is constantly being expanded to be used more widely but so far its assumptions are quite limiting. It is used by theoreticians as a different accounting technique.
- with the correct definition, kin selection does not offer a mechanism.
- relatedness and the idea of kin interactions are relevant and important to incorporate into models that accurately describe the world; however, relatedness measurements alone are inconclusive.
- in order to decide when relatedness based correlations are correct, one needs a mechanistic/conceptual model.

Next time

- The evolution of eusocial behavior
- Parallels to multicellularity of type I