5 The units of selection and the gene's-eye view of evolution

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Units of selection

-> selection of **individuals** in traditional darwinian explanation

-or: selection acts at the **level** of the individual

-or: the individual as the **unit** of selection

-BUT:

-> not logically necessary:

-**hierarchy** of biological organisation

-**general principle** of natural selection (Lewontin: ‘heritable variation in fitness’)

Biological altruism

-behaviour which **costs** the individual, but **benefits** another
-*prima facie*, **hard to explain** in Darwinian terms

Darwin in *The Descent of Man*:

'he who was ready to **sacrifice** his life, as many a savage has been, rather than **betray** his comrades, would often leave **no offspring to inherit his noble nature**'

(1871, 163)

-> possible solutions:
i) not an adaptation at all
ii) a group or colony-level adaptation
iii) others?

'a **tribe** including many members who **. . .** were **always ready to give aid** to each other and **sacrifice** themselves for the **common good**, would be **victorious** over **most other tribes**; <u>and this would be natural selection</u>'

(1871, 166)

-i.e. altruism can evolve through group selection

Levels of Selection Problem

-natural selection can operate **at more than one level**
-what's **favoured** by selection at one level, may be **disfavoured** at another

-1950s and 60s: the **'good of the group' fallacy** was common
-e.g. Konrad Lorenz on animal aggression

-Wynne-Edwards did explicitly invoke group selection to (allegedly) explain *reproductive restraint* in birds

G. C. Williams's *Adaptation and Natural Selection* (1966)
-argued that group selection is **empirically implausible** (subversion from within)
-and **not needed** to explain altruism anyway

-> conceptual, as well as empirical arguments
-group selection is 'unparsimonious'
-gene as the true 'unit of selection'

-similar arguments by Maynard-Smith, Dawkins and others
-as a result, group selection fell from favour among evolutionary biologists
-recently, situation has changed somewhat

Kin Selection and Inclusive Fitness

-**alternative** explanation for altruism
-W. D. Hamilton (1963)

-basic idea: selection can favour altruism, if it's directed toward kin

-> why? because relatives share genes

-> so beneficiaries of altruism will tend to be altruists themselves

-> so altruistic behaviour can spread

-intuitively obvious, and supported by **mathematical models**

Kin Selection and Inclusive Fitness

Hamilton's rule:
altruism will spread if and only if

b > c/r

-'r' is coefficient of relationship between donor and recipient
(i.e. probability that donor and recipient share gene for altruism)

-> led to a highly successful empirical research programme
-often, Hamilton's rule leads to very precise predictions of animal behaviour

-concept of **inclusive fitness**

-> when **social interactions** are taken into account, selection won't maximise individual fitness
-instead: maximisation of **inclusive fitness**

inclusive fitness: personal fitness + sum of weighted effects on every other individual in the population; weights are determined by r

-then: i*ndividuals will act to maximise their inclusive fitness*

The Gene's Eye View of Evolution

-adaptations not for the good of organisms, or groups, but **genes**
-concept of '**selfish gene**'
-evolution as a struggle between competing gene lineages

-> arises directly from kin selection

Hamilton (1963):
'despite the principle of the 'survival of the fittest', the ultimate criterion which determines whether a gene G [that codes for a certain behaviour] will spread is not whether the behaviour is to the benefit of the behaver, but whether it is to the benefit of the gene G; and this will be the case if the average net result of the behaviour is to add to the gene-pool a handful of genes containing G in higher concentration than does the gene-pool itself'

The Gene's Eye View of Evolution

-altruism **anomalous** from organism's viewpoint, but **makes good sense** from gene's viewpoint
-a simpler alternative to inclusive fitness

-leads to '**gene's eye reasoning**'
-organismic traits as '**strategies**' designed by genes to spread in population
-heuristically very powerful

-R. Dawkins (1976) *The Selfish Gene*
-applies gene's eye reasoning across the board, not just to social behaviours

The Gene's Eye View of Evolution

Dawkins's arguments for gene's eye view

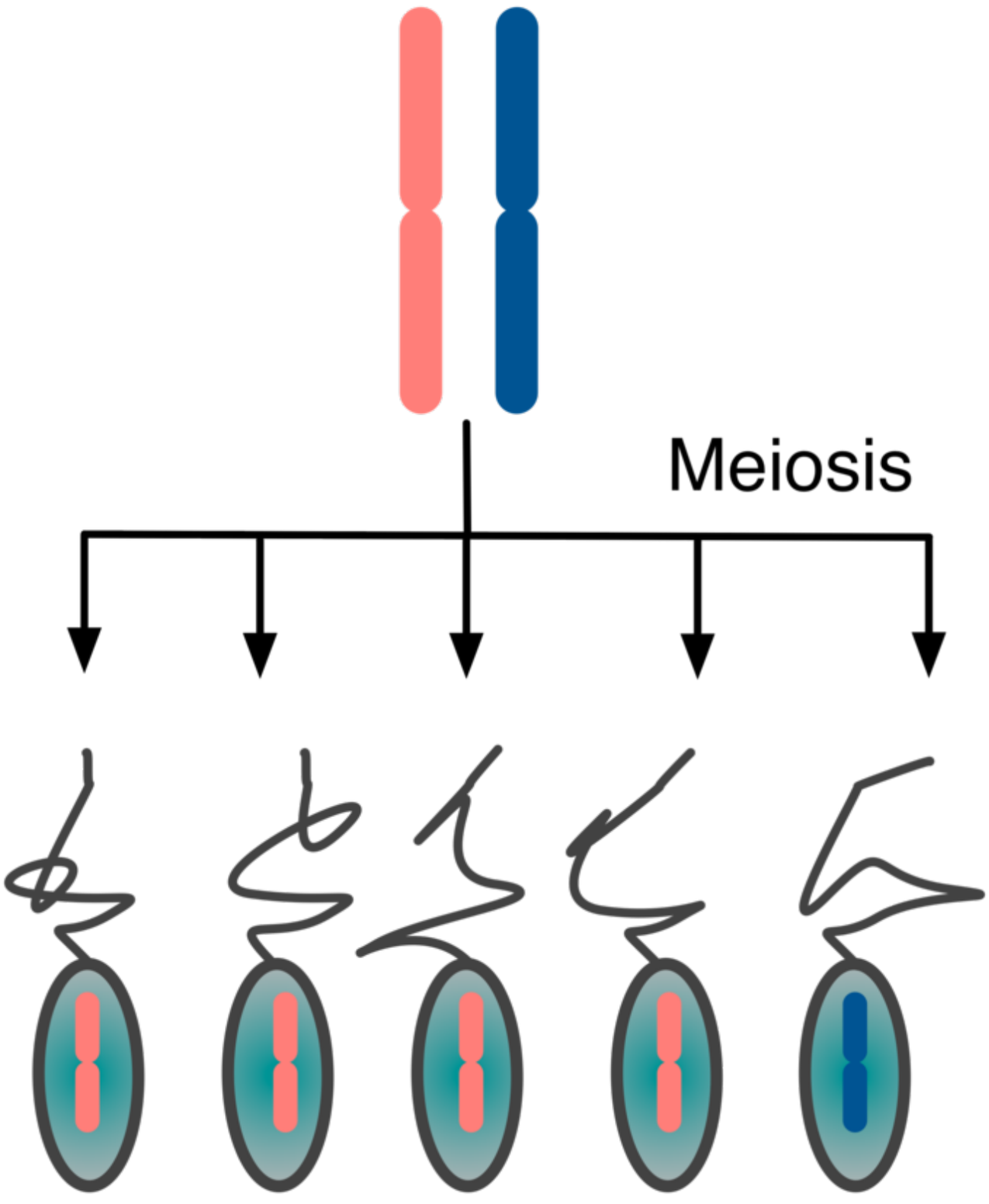
a) germ line genes are **potentially immortal**, organisms aren't
i.e. genes form lineages, organisms don't
-concept of a **replicator**
-> gene as the **ultimate beneficiary** of selection

b) accommodates empirical phenomena that organism-centred view can't
e.g. outlaw genes, meiotic drive (segregation-distorter genes)
-> **intra-genomic conflict**

c) a very general conception of evolution
-> all evolutionary change can be understood as **change in gene frequencies**

d) **heuristically** valuable
-focuses attention on questions that might otherwise go unnoticed
e.g. why are there organisms?

e) allows problem of altruism to be solved **without group selection**


Meiosis

The Gene's Eye View of Evolution

arguments against gene's eye view

a) genes aren't **directly 'visible'** to natural selection (Gould)

b) genic selectionism is committed to '**beanbag genetics**' (Gould)
-**no one-one mapping** between genes and phenotypic traits of interest

c) **book-keeping argument** (Gould and Lewontin)
-gene's eye view obscures **important causal information**

d) **context-dependence** argument
-effects of genes depend on context

e) what exactly is a gene?
-'gene' has a fairly clear meaning in molecular biology
-**less clear** in evolutionary genetics

The Gene's Eye View of Evolution

-'gene-centred' view of evolution

-> the gene as the true **unit of selection**

-> organisms are simply '**vehicles**' that genes have constructed to ensure their future propagation

-equivalent to orthodox organism-centred view or not?

-Dawkins is somewhat **unclear** on this point

-general philosophic issue of **realism vs conventionalism**

Dawkins and Hull on replicators and interactors/vehicles

-two types of entities involved in natural selection
-replicators and **interactors** (or vehicles)

-replicators: ‘entities which pass on their structure intact from one generation to another’

-interactors: ‘entities which interact as a cohesive whole with their environment’

-evolution as a sequence of **replication and environmental interaction**

-natural selection when differential replication is caused by interaction

-permits (supposed) **refinement** of units-of-selection issue:
-> what are the units which **replicate**?
-> what are the units whose **interaction** with environment causes differential replication?

answer to 1 is **genes**, to 2 is an **open empirical issue** -organisms, groups, etc.

Dawkins and Hull on replicators and interactors/vehicles

-consequences of this conceptualisation

a) no **empirical issue** at stake between genie and organismic selectionists
-> different ways of viewing the same set of facts

b) **wrong** to oppose genic selection to group selection (as Dawkins 1976 does)
-for genes are replicators, groups are interactors

c) the **empirical** issue becomes: what are the interactors?

The ‘New’ Group Selection

-Sober and Wilson (1998)
-‘groups’ need not be multi-generational, **isolated** groups
-rather, they can be ‘**trait groups**’, generated by **limited dispersal**
-new group selection avoids many of the pitfalls of the earlier group selection of 1960s
-but some say: it’s ultimately **equivalent** to kin selection

-recall question: how can altruism evolve?
-general answer: needs a special **population structure**
-> requires a **statistical tendency** for altruists to find themselves in each other’s company
[Simpson’s paradox]
-kin-selection simply a good way of getting this ‘positive assortment’
-the only way?

Major Evolutionary Transitions

- multi-level selection theory/hierarchical selection theory

-> natural selection can operate **simultaneously** at **different levels** of the biological hierarchy
-a **generalisation** of the new group selection idea
-ultimately **compatible** with the gene's eye view
-applies in particular to '**major evolutionary transitions**'
-in such transitions, free-living individuals coalesce into groups, ultimately giving rise to new, higher-level individuals

e.g.
individual replicators -> networks of replicates
genes -> chromosomes
prokaryotic cell -> eukaryotic cell
single-celled organism -> multi-celled organism
solitary organism -> colony
human society??

Major Evolutionary Transitions

-each transition requires **higher level selection** to dominate

-individuals must **co-operate**, sacrifice their **individuality**, become part of a whole

-kin selection / Hamilton's rule highly relevant

-many transitions (though not all) involve **closely related** individuals

-within-group competition must be compressed

-individual self-interest must be aligned with **group's interest**, for transition to happen

-what we call 'individuals' are in fact **groups of co-operating sub-units**

Species selection

-a **macroevolutionary** idea; cf. Eldredge and Gould (1977)
-**not** analogous to group selection/ kin selection
-key idea: selection acts on whole species, over geological time
-fittest species: ones which **survive longest/speciate fastest**
-**speciation** is the **analog** of organismic reproduction

crucial difference between group selection and species selection:
-> 'group fitness' in group selection theory means expected number of total ***individual*** **offspring**
-> 'species fitness' in species selection theory means expected number of **offspring** ***species***

-> different senses of 'fitness'

-> species selection theory is a genuine 'hierarchical expansion' of the basic Darwinian principle; in a sense, group selection theory is not

Reciprocal Altruism and Evolutionary Game Theory

-how to account for altruism towards **non con-specifics**?
-Trivers: **reciprocal altruism**
-it may pay to be altruistic, if there's the **expectation of return benefit in the future**

-also, Hamilton and Axelrod: '**tit-for-tat' strategy** in the **iterated Prisoner's Dilemma**
-more generally: use of **game-theoretic reasoning** in biology

-> lots of theory, but much less empirical support than kin selection

For further study:

-Godfrey-Smith, *Philosophy of biology*, ch. 3.3

-Sterelny, *Dawkins κατά Gould*, part 2

-Hull & Ruse, chapter 3

-Samir Okasha (2006) *Evolution and the Levels of Selection,* OUP.