Levels of Selection

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Fictional self-assembly
Actual self-assembly

Summary: levels of selection

- levels of selection
- building higher levels
- a levels of selection view of the world

- genomic conflict
- group selection
Levels of selection

- I am pretending to a unity, deep inside myself, I know does not exist. I am fundamentally mixed, male with female, parent with offspring, warring segments of chromosomes that interlocked in strife millions of years ... (ago).

  W. D. Hamilton (in Narrow Roads of Gene Land, 1997)

Levels of selection

- genes → cells → individuals → kin → groups → species

from Stearns & Hoekstra 2005
Levels of selection

• uncritical ‘group selectionist’ arguments are almost universal in the scientific literature before approx. 1970
  • ‘frogs lay so many eggs to ensure the survival of the species, because tadpoles suffer extremely high rates of predation’
  • ‘wolves have ritualised displays and combats, because escalated combats would be too disadvantageous for the survival of the species’
• such arguments are pervasive in old nature documentaries, and still common in the general press and the general population, but they are usually completely unfounded
  • in most cases there is no clear evidence that these traits have evolved to the benefit of the species
• many of these traits can be shown to be optimal for the individual
  • and many traits are clearly maladaptive at the level of the species
• group selection has been shown to work under specific conditions
  • but there is an ongoing debate about how important group selection is

Levels of selection

• as a contrast to the prevailing ‘group selectionist’ mind frame Dawkins (1976) proposed the perspective of the selfish gene
  • but he did not actually claim that the other levels were unimportant
  • and by ‘gene’ Dawkins means “any portion of chromosomal material that potentially lasts for enough generations to serve as a unit of natural selection”
• **replicators** are the enduring units of replication (i.e. information)
  • replicators do not age (although the DNA ‘storage medium’ of course can)
• **vehicles** are the phenotypic effects of the replicators (i.e. matter)
  • vehicles can age and they are in fact dispensable
• natural selection cannot pick directly among the different replicators (alleles)
• instead natural selection picks among vehicles (phenotypes) created by these alleles
  • and the successful vehicles contain the (thereby) successful alleles (and other genes carried by the same vehicle)
Building higher levels

- how can selection that acts among low-level vehicles favour the evolution of higher-level vehicles?

- how does selection at one level affect the selection at levels above and below that level?

- do the lower-level processes necessarily stop once a higher level has emerged?

repulsive forces
  - e.g. close proximity leads to more resource competition

attractive forces
  - e.g. a larger size allows to escape predation

centrifugal forces
  - e.g. the allure of a ‘solitary’ existence (this may often not be possible anymore, but at the origin it probably was)

Fig. 1.1. The formation of higher-level vehicles from lower-level vehicles. A higher-level vehicle forms when the attractive inclusive fitness force (see box 1.1) for lower-level vehicles overcomes the repulsive and centrifugal inclusive fitness forces.

from Keller & Reeve 1999
Building higher levels

- the inclusive fitness concept (Hamilton’s rule) influences how cooperation between individuals can evolve

- \[ b \cdot r > c \]
  - \( b \) is fitness benefit for the recipient of a co-operative act
  - \( c \) is fitness cost for the helper for performing the co-operative act
  - \( r \) is relatedness of the recipient to the helper (a value between 0 and 1)

- the larger the relatedness, the easier this inequality is fulfilled
  - many co-operative systems have mechanisms that ensure a high relatedness
  - problems can arise if relatedness is reduced

- so co-operation more easily evolves between highly related vehicles (such as clonal cells within a body) than between unrelated vehicles (such as birds in a flock)

A levels of selection view of the world

- the origin of co-operating groups of ‘replicator-level vehicles’ essentially represents a question about the origin of life
  - possibly the earliest forms were RNA molecules that also had catalytic functions
  - as far as we currently know, life is monophyletic (since all known life is based on DNA and RNA, using essentially the same genetic code)

- the integration into higher-level vehicles may result from benefits of
  - complementation (e.g. via the formation of ‘chromosomes’)
  - compartmentalisation (e.g. via the formation of cells)
  - division of labour (e.g. via formation of cell types in multicellular vehicles)

- these earliest processes are difficult to study, because the environmental conditions are very different today
  - there originally was almost no oxygen in the atmosphere
  - there was a vast amount of time available
  - there were amazingly many different places and conditions on Earth
  - and we cannot even be certain that life originated on Earth (panspermia)
A levels of selection view of the world

• increased complexity resulted from co-operation and fusion between lower-level vehicles
  • shift from pro- to eukaryotes (via acquisition of mitochondria and chloroplasts)
  • may also explain the acquisition of other cell organelles (maybe flagella?) and similar transitions are still occurring today in the context of symbiosis
  • the benefits probably often result from complementation of functions
  • a very active field of research (which greatly benefits from genomics)

A levels of selection view of the world

• shifts from uni- to multi-cellular organisation
  • such shifts have occurred many times and can still be observed in a number of organismal groups (e.g. social bacteria, slime molds, volvocine green algae)
  • the benefits result from division of labour and large size
  • but such shifts often also lead to problems with cheating
• a very active field of research
  • facultative multi-cellularity
  • origin of the soma-germline distinction (i.e. the origin of death as a normal step in the life history or an organism)
**A levels of selection view of the world**

- *Dictyostelium discoideum*
  - usually free-living haploid amoeboid cells that divide asexually
  - when starved 10’000 to 100’000 cells will aggregate into a ‘slug’
  - the anterior 20% of the slug differentiates into a stalk (‘soma’)
  - most of the remaining cells become spores (‘germ-line’)
  - this leads to a potential for cheating

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microsatellite genotypes of slugs formed from single clones and from mixed clones

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mixtures of GFP-labelled and unlabelled clones reveal unequal distribution within the ‘slug’

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from Strassmann & al. 2000

from Santorelli & al. 2008
A levels of selection view of the world

• shifts from individual life to life in social groups
  • the frequent occurrence of eusociality in Hymenoptera may be linked to their special genetic system (haplo-diploidy)
  • this causes the workers to be more closely related to their sisters than to their own offspring

![Central American Paper Wasp (Apoica pallens) by Silas Kent](image)

A levels of selection view of the world

• shifts from individual life to life in social groups
  • part-time social groups of (generally) unrelated individuals are formed during sexual reproduction
  • $r$ is usually low between parents (that is kind of the point of sex)
  • $r$ is relatively high among the offspring, and also between the parents and the offspring (but this will depend on the level of multiple paternity)
  • the centrifugal forces are high because there may be other mating opportunities for both parents (can lead to strong conflicts)

![Collared Flycatcher (Ficedula albicollis)](image)
A levels of selection view of the world

- depending on your specific research questions a levels of selection view may not necessarily be required
- but you should decide this only after careful consideration and keep this possibility in the back of your mind
- ask yourself the following questions:
  - at which level is selection likely acting in a given interaction?
  - can there be conflicts of interest between different levels of selection?
  - which vehicle (i.e. gene, cell, mating partner) benefits from a given outcome?
  - how labile is a system? can its components function independently?
  - which traits of a given system could potentially be adaptations that enforce cooperation (i.e. policing)?
- sometimes the conflicts between levels of selection can be difficult to detect due to a balance of power
  - they often appear when two diverged populations are crossed

Genomic conflict

- selection can favour a trait at one level but select against it at another
  - when carrying mitochondria of both type A and a is advantageous at the higher level (the cells), then a selection process or a biased segregation occurring at the lower level (the organelles) can be detrimental to the fitness of higher level

Figure 9.3 Two-level selection. The left-hand column represents newly formed cells; each, for example, with two mitochondria (A and a). The middle column represents mitochondrial replication. The right-hand column represents the result of cell duplication.
- (a) No selection at lower level
- (b) lower-level selection favoring A
- (c) biased segregation favoring A.
Genomic conflict: meiotic drive

• mitosis and meiosis are thought to lead to a fair transmission of the genetic material in the parental cells (or the parental individuals) to the daughter cells (or the offspring)
• for example, during meiosis heterozygous $Aa$ individuals are expected to produce 50% $A$ gametes and 50% $a$ gametes (equal segregation or fair meiosis)
• but certain genes can cause meiotic drive (segregation distortion)

Genomic conflict: the $t$ haplotype in mice

• three ‘alleles’ occur at the $t$ complex: $T$, $t$ and +
  • but the main effects can be explained by just considering $t$ and +
• genes in the $t$ complex produce a toxic effect on + carrying sperm
  • spermatogenesis appears normal, but the + carrying sperm are non-functional
• genes in the $t$ complex also produce an antidote, which allows normal function in the $t$ carrying sperm
• $t/+ \text{ males produce } 90-100\%$ of $t$-carrying sperm at the site of fertilisation (with no apparent effect on the female gametes)
• the $t/t$ genotype is lethal, causing male-sterility or reduced viability
  • so at the level of the individual gamete, the $t$ haplotype is favoured, but at the level of the individual mouse, the + haplotype is favoured
• this does not lead to fixation, but to a stable coexistence of $t$ and +
  • given the combination of observed fitness effects of the $t$ and + haplotypes, the expected frequency of $t$ carrying mice should be about 70%
Genomic conflict: meiotic drive

- meiotic drive is probably rare
  - usually involves a system with a toxin and an antidote
  - requires that the alleles are tightly linked (maybe one reason for the evolution of recombination is to break such linkage)
  - requires that they originate together (because alone they offer no advantage)
- the processes of mitosis and meiosis might be expected to show evidence for selection against segregation distortion

Genomic conflict: male-sperm conflict

- there may be a genetic conflict between the male and his sperm
  - the father is 100% related to his sperm (although each of course only carries 50% of his alleles)
  - the sperm are on average only related to each other by 50%
  - biased transmission or provisioning of some sperm genotypes would be advantageous for those genotypes, but likely disadvantageous for the father
  - cytoplasmic bridges between the developing sperm may allow to maintain paternal diploid control over haploid sperm
Group selection

- selection may occur between groups of individuals, but
  - groups need to have a high risk of extinction
  - migration rate between groups needs to be low (or at least biased)

Group selection: the $t$ haplotype in mice revisited

- earlier, I mentioned that the expected frequency of $t$ carrying mice is about 70%, but the actually observed frequency is only 6-25%
- could selection at the group level explain this difference?

- groups often contain only 2 resident males
- so if the $t$ haplotype increases in frequency within a group, both resident males may become $t/t$ and will thus die or be sterile
- a lack of (fertile) resident males may lead to group extinction if the migration rates between groups are sufficiently low
- the $t$ carrying groups may therefore go extinct more often
Group selection: t haplotype in mice revisited

- a nice idea, but likely not true
  - wild-type males (and females) can be competitively superior
  - it is mainly selection at the individual level that maintains low t frequencies

![Bar chart](image)

**Fig. 2.** Comparison of dominant (white bars) and subordinate (black bars) status among all +/- and +/- males. Genotype has a significant effect on male dominance status. +/- males are twice as likely to be dominant as they are to be subordinate, whereas +/- males are twice as likely to be subordinate as they are dominant ($P < 0.007$).

![Graph](image)

**Fig. 3.** Survivorship of all 234 founders. Males suffered greater overall mortality than females in our enclosures. Mortality of dominant +/- males and +/- females (open symbols, hatched lines) was greater than mortality of +/- individuals (solid symbols, solid lines) over the 10-month experiments. Mortality of subordinate males did not differ among genotypes.

from Carroll & al. 2004

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Literature

• Mandatory Reading

• Suggested Reading

• Books