Adaptation and multilevel selection : the case of evolutionary transitions

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Adaptations, circa 1990:

- What means « to be an adaptation »
  - Brandon, Sober, etc., « Adaptation = result of natural selection » historical conception
  - Reeve Sherman 1993: currentist conception, an adaptation = the highest fitness phenotypic variant in a population; corollary : distinction between « origin » questions and « maintenance » questions
  -> *Issue of pluralism – is « adaptationism » univocal*?

Adaptationism controversies

Context : optimality models (Dunbas 2001, parental care by gorillas)

ESS modeling – fundamental tool for maintenance investigation – no information on the origins of the strategy set

Orzack and Sober, *Optimality and adaptation*, 1996

Dupré, *The latest on the best*, 1989

General issue : the idea of constraints

Constraints vs optimality is the problem

What limits the power of Natural Selection is named « constraints » (in the 30s, eg Fisher Wright controversies, the main issue was genetic drift)

Question : what kinds of constraint exist and how they are related ?. Main role of Evo Devo (via developmental constraints on variation) (see Maynard-Smith et al 1985)

Question #2. – what do explain constraint and selection respectively (Amundson 1996) ?

Our framework : Multilevel selection theory

Theory of Multi level selection (Damuth et Heisler 1987, 88; Sober & Wilson 1998; Dugatkin & Reeve, ; Dugatkin & Wilson 1997; Keller 1999, Kerr & Godfrey Smith 2002, Rice 2004, Okasha 2005); its role in the evolutionary transitions research program (Maynard-Smith & Szathmary 1995; Michod 1999; Michod & Nedelscu 2003)

outline

Adaptation and MLS in the context of evolutionary transitions

I. Adaptation problem in the MLS theory

II. Understanding adaptation in the context of evolutionary transitions

I. Multi level selection

- Individuals ni of types a, b, c
- Collectives Gj of individuals (G (i,j))
- Fitness differences Wi between the ni therefore between the G(i,j)
- Differential replication of ni; natural selection on ni
- *Changes in the composition and respective sizes of the Gj*

G1   G2   G3

A 6a a b6 b8 b

b b
b a a a a bb bb b

a1 a2 b1 b2 b3

A 4 a5   b4 b5
B b b b b

A a9 b10
a11 a12 a
a

B a a
B b b b b b

The « new » group selection

- Sloan Wilson and Sober (98); Wade ; Goodnight etc. (empirical / theoretical work in the late 80s, 90s)
- Reviving group selection after the Hamilton-Dawkins interpretation of group selection as kin selection

- Dugatkin & Sloan Wilson 97: role of assortive interactions (instead of genetic relatedness) in the evolution of cooperation
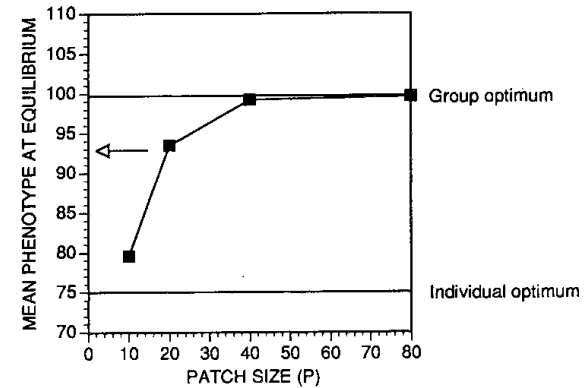

FIG. 2.—The effect of assortative interactions on the balance between levels of selection in a quantitative genetic model. Relative fitness within groups is maximized at a phenotypic value of $x = 75$, and the fitness of groups is maximized at a phenotypic value of $x = 100$. Group size is $N = 10$, and groups are formed by assortative interactions in patches of size P that are random samples of the global population, as in figure 1C. When $P = 10$, variation among groups is random, and the mean of the phenotypic distribution at equilibrium shifts slightly away from the individual optimum toward the group optimum. This represents a balance between levels of selection in which group selection is a significant but relatively minor force. Assortative interactions change the partitioning of variation within and among groups, shifting the balance in favor of group selection. For comparison, the arrow gives the balance between levels of selection in a kin selection model with interactions among full siblings.

What's new ? Idea of « *trait group* » (vs superorganism, or localized groups)

Multi level selection conceived of as resulting from both intra group and inter group competition

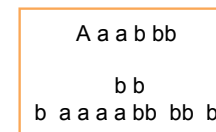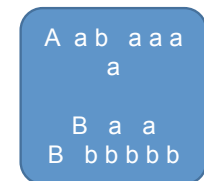This « result » can be modelled through Price's equation

$\Delta z = E[Cov^W (z^{ij}, w^{ij})] + Cov^B (Z^j, W^j)$

or through contextual analysis (Goodnight et al. 1992)

$w\Delta T = a \, Var (T) + b \, Cov (T, GP)$

(coefficients obtain by partial regression)

Both have strengths and shortcomings in some cases (Okasha 2006)

- Achievement : theoretical model of the evolution of altruism (Wilson and Sober 98): the success of altruism occurs even if the by definition they fare worst off than selfish, provided that intergroup competition is strong enough

- Sober and Wilson (98) claim: kin selection is a case of MLS (trait groups are defined through genetic relatedness)
- The superiority of kin selection as an alternative to group selection (West et al. 2007): mostly equivalent and mathematically tractable

- *General issues:*
- Relating kinds of selection : pluralism issue (Kerr and Godfrey Smith 2002 : mathematical equivalence between MLS and individual selection with fitness of individuals contextualised across groups)
- Defining trait groups (importance of population structure)
- MLS 1/ MLS 2 (Damuth and Heisler 1987) : fitness as nb of individuals in a group vs fitness as a number of offspring-groups (evolution of altruism vs species selection for ex.)
- How to define group heritability ? In which case is it necessary? (Okasha 2007)

Reeve and Höllbloder (2007) : thug of war model for the evolution of insect colonies – genetic relatedness and intergroup conflicts are two parameters of the model to understand altruistic allocation of energy in colonies. Are those variables to be interpreted realistically or pragmatically ?

$$f^* = \frac{N(n-1)(1-r)}{Nn - 1 - r(n-1) - (N-1)r'[1 + r(n-1)]}$$
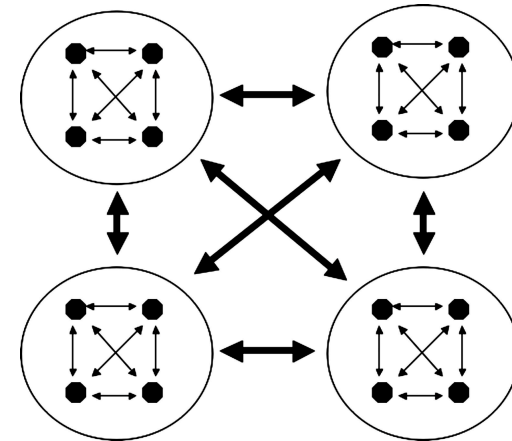
Adaptation – who is the bearer of adaptations ?

Example : is altruism an *adaptation* of the *individuals* ? And for what ? (not for something directly beneficiary to individuals)

Unlike the currentist view altruists are not the highest fitness individuals

Unlike the historical view, it does not result from selection on individuals for some benefiting effect (compare : metal tolerance in plants, Antonovics et al., 1971) -> the historical view must be refined to include various cases

Is it an adaptation of the group (*sensu* Williams 1966) ? But it's a trait of individuals

- *Problem for the historical view* : MLS separates the level where selection acts and the level to which belongs the trait seen as an adaptation.

- In the case of MLS 1, adaptations are properties of individuals (e.g. altruism) but they benefit the group (and would not have evolved by selection on individuals);

- In MLS 2 adaptations are properties of the groups (e.g. wide range) but they benefit the individuals

Concerning the meaning of adaptation in MLS2

Suppose G3 and G5 are selected. Yet the highest fitness G(i,j) are with j=2 and 4. So no selection for highest fitness individuals. But no constraints.

If we call traits of G (i,3) adaptations, we can not say « adaptation = optimality / constraints » because no constraints here (developmental, genetics, etc.)

Objection : adaptation = properties of groups; optimality (applied to groups) is achieved.

Answer : what if groups are not well defined ? What if the case is borderline between MLS 1 and MLS 2?

-> *evolutionary transitions*

II. Evolutionary transitions

- New units of fitness (Michod 1999)
- New selective regimes
- Maynard-Smith/ Szathmary (1995) : new modes of information storage and transmission (limited/unlimited heredity)

Emergence of new individuals ?

Selfish genetic elements (Burt and Trivers 2006). Two lessons:

- They are pervasive, therefore there is effective genic selection
- They are not so powerful, hence organisms and cells are buffered againts the effects of this selection. Why ? This is an evolutionary result – according to which process ?
- -> Evolutionary transitions program (unlike questions of units of selection) – the replicators do not preexist the selection process (see Griesemer 2000)

- **Transitions** : hypercycles -> genes; genes -> cells; cells->multicellular organisms; etc.
  General explanatory scheme = MLS

- « I*s the evolutionary transitions research an adaptationist research program (since it is selection all over the place)* ? » But what means « adaptation » here ?

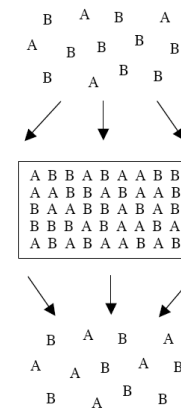Is it MLS 1 or MLS 2 ? (Okasha 2006, Michod &2006; Michod & Nedelscu 2003):

MLS1 *then* **MLS2**.

(Start : fitness of cells = number of cooperating genes within it; end: fitness of a cell= number of daughter cells)

Unlike the group selection controversies : no spatially distinct group – the group is precisely the result of the process (for ex. the cell membrane)

• At the beginning of a transition there are no groups

• Not even a trait delimiting a « trait group »

However – groups with boundaries, or even trait groups, are a special case of structured populations; the population structure can impinge in various ways on the result of natural selection (see Godfrey Smith 2007)

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     B   A  B    A
  A    B  B   B   B
     B    A   B   B
```



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  A B  B A B A A B B
  A A B B A B A A B
  B A A B B A B A B
  B B B A B A A B A
  A B A B A A B A B
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     B   A  B    A
  A    A  B   A   B
     B    A   B   B
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« Adaptive dynamics » : group selection occurs when the invasion senstivity to a mutant depends on the population structure (and not only on the fitness distribution) (Waxman Gavrilets 2005, Weitz Hartmann Levin 2005)

- Traulser Nowak 06, **"higher-level selection emerges as a by-product of individual reproduction and population structure"**

« The non-linearity inherent in hypercycles is not only a property of genes networks at this early stage in life; rather it is a general feature of evolutionary transitions. New higher levels gain their properties by virtue of interactions among lower-level units. Before the evolution of a structure come to « house » the new higher level unit (and this must come later) interactions among lower levels units are density and frequency dependent, and, therefore, there will be problems with rarity and advantages to commonness. » (Michod 1999, 35).

- Research program on transition = specifying the relevant population structure effects

In the case of transitions:

Michod : *cost of rarity / cost of commonness* (clusters vs. sparsed individuals);

That plays the role of « group selection » whereas no trait group is there yet.

Multi-level selection : not in general the addition of inter group and intra group selection, but the addition of fitness distribution's impact on differential reproduction and population structure effects.

Shortcomings of a general formulation of selection

- Levels of selection : replicators / interactors view (Hull, Brandon 1989 etc.)
- Separating both allows one to talk of selection at various possible levels
- *But here* : what is interacting is only the replicators, however it's not a process involving exclusively replicators from the beginning to the end

Transitions = a two-stages process

Stage 1: population structure effects and non linearity (MLS1 … up to MLS 2)

Stage 2 (MLS 2): creating and enforcing the new level of individuality

- « During the emergence of a new unit, population structure, local diffusion in space (Ferriere and michod 96, 95) and self structuring in space (Boerlijst and Hogeweg 1991) may facilitate the trend toward a higher level of organization, culminating in an *adaptation* that legitimizes the new unit once and for all. Examples of such adaptations include the cell membrane in the case of the transitions from genes to groups of cooperating genes, or… the germ-line or self policing functions, in the case of the transitions from cells to groups of cooperating cells, that is, multicellular organisms. » (Michod 1999, 42)

Why talk about adaptation at this stage ?

This stage 2 « adaptation » buffers the new level (the « collective ») against disruption by « individual » level selection

-> it lessens the impact of the prime for defection at low level

It institutes reliable selection against high-fitness individual variants

Which accounts for the fact that most of the time evolution of the low level individuals can be computed by considering evolution of high level individual (e.g. genic selection and organismic selection match..). A « shared fate » is instituted

Notice : this is not a question about the units of selection (individual/collective distinction is a contextualised difference). The problem stands even if the question of which are the « genuine » units of selection in nature would be solved.

Currentist definition of adaptation is inadequate:

« when birth is a non linear function of density, the adaptive features of a unit of selection are no longer sufficient to predict the outcome of natural selection. « Survival of the fittest » is false, and there is no measure of overall adaptedness » (72)

Above all, the process promotes one high level individual, so no reason to talk of a highest fitness variant (because no variants at this level)

Historical definition ? Result of selection on the individuals is not a trait of individuals themselves : cell membrane, distinction between somatic and germinal cells, etc.

Adaptation is not defined in terms of optimality facing constraints:

« Natural selection can lead to unfit individuals, *even in the absence of genetic constraints.* » (ibid 73)

-> the role usually played by constraints is played by decoupling between levels of selections : even without constraints the fittest get not fixed, because fitness-increasing and results of selection are detached

Who are the beneficiaries of this adaptation ? The specificity is that there are no preexisting replicators, they just emerge with the adaptation (cells as contemporary of cell membranes)

Yet the « components » individuals benefit from this adaptation : example of the bottleneck, at the level of multicell organisms, but which protects cells from delterious, segregation distorters, alleles

Such adaptation is the condition of further adaptations at the new level of individuality (classically defined as results of selection at this level)

« During the origin of each new kind of individual, conflict mediation is a necessary step, otherwise new adaptations at the new level cannot evolve, for there is no clearly recognizable (by selection) unit, no individuality. *The evolution of conflict mediation is necessary for adaptation at the new level.* »

Initial « adaptations » that enforce an emergent level of individuality are the conditions of following adaptations; they entail the *adaptiblity* of the structure

They can be modeled in several ways : public good, etc.

Notice that here « adaptability » means rather decrease in possible (low level) variants than in the variability of the system

Two main structures : division of labour; conflict mediation (ex. separation between somatic and reproductive cells/ cell membrane)

Multicellularity : Division of labour between cells; bottleneck as conflict mediation - Michod & Nedelscu 2003

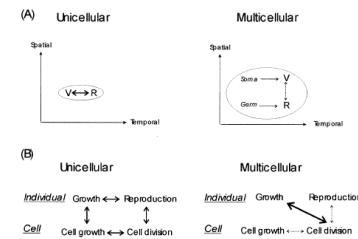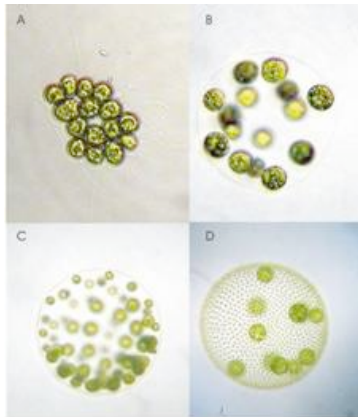Study that on volvocales (contemporary toy case)

FIG. 2. Relationships between vegetative (V) and reproductive (R) functions and spatial and temporal contexts (panel A), in unicellular *versus* multicellular individuals, and between processes and properties at the level of the cell and the individual, respectively (panel B); broken arrows denote relationships in which the two components are not necessarily dependent on one another.
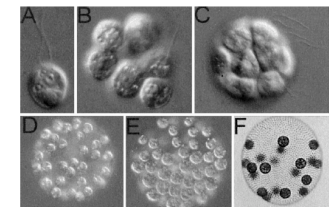

FIG. 3. The volvocine lineage. A subset of colonial volvocalean green algae that show a progressive increase in cell number, volume of extracellular matrix per cell, division of labor between somatic and reproductive cells, and proportion of vegetative cells. A: *Chlamydomonas reinhardtii*; B: *Gonium pectorale*; C: *Pandorina morum*; D: *Eudorina elegans*; E: *Pleodorina californica*; F: *Volvox carteri*. Where two cell types are present, the smaller cells are the vegetative/somatic cells, whereas the larger cells are the reproductive cells (gonidia). Images kindly provided by David L. Kirk.

Coordination and cooperation

Cooperation: it pays to defect

Coordination: each could not do without the other doing it (benefit is conditional on the other's benefiting)

The beneficiary individuals are not the same as in the cooperation case

Where is the adaptation in the case of cooperation? Of coordination ?

Example of the trade off between reproduction and viability (Buss, 1987, Michod 2006, Michod et al 2006)

Convexity as negative covariance between survival and reproduction of cells; it is self-enforcing (*the more cells, the more convexity*)

-> Motricity is an adaptation whose beneficiary is the reproductive cell. Each cell benefit of the other kind (W(a) decreases when W(b) decreases)

• « Division of labour » is a coordination feature that buffers the « multi cell » level against the prime to defection

• Thereby results of selection at the level of the cell is a property of the whole which is beneficial to both kinds of cells

Conclusion

• They rely on MLS but not exactly group selection

• They require to change the meaning of adaptation by not focusing on the optimality/ constraints debate; and not equating adaptability and variability.

• They compel to extend the historical definition of adaptation

• More generally : redefining adaptation in order to consider various research programs using MLS or non optimising strategies (neutral network of RNA Lenski, Stadler, Schuster etc.)