The evolution of a unicellular bottleneck in the life history of multicellular organisms

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JMS: All collective living involves a ‘social dilemma’

- Multi-cellular organisms are collectives of cells
- Collective living exists in virtue of opportunity for mutual advantage - economies of scale, division of labour, reduced risk of predation due to size, etc.
- But cooperation is undermined by the Tragedy of the Commons, the so-called ‘free-rider problem’
- It’s a non zero-sum game in which players are all better off if all cooperate but each is tempted to 'cheat' to do better still. But if all cheat, then all lose out.

All collective living involves a ‘social dilemma’

Cell Behavior	Level of Selection	
	Cell	Group (organism)
Defection	(+) replicate faster or survive better	(-) less functional
Cooperation	(-) replicate slowly or survive worse	(+) more functional

Figure from Michod & Roze (1999) Cooperation and Conflict in the Evolution of Individuality III

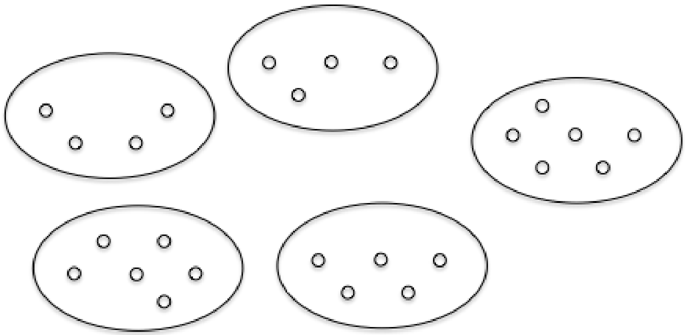
Dissolving the social dilemma

- Collective living is unstable due to the social dilemma
- Yet collective living (e.g. multicellularity) is common ...
- JMS: various life-history traits can be seen as adaptations which ameliorate the essential dilemma of collective living, so suppressing subversion of collectives from below:
    - **Genetic bottleneck**
    - Germline segregation
    - Policing mechanisms, coercion and punishment

Bottlenecks in the natural world - evolved independently

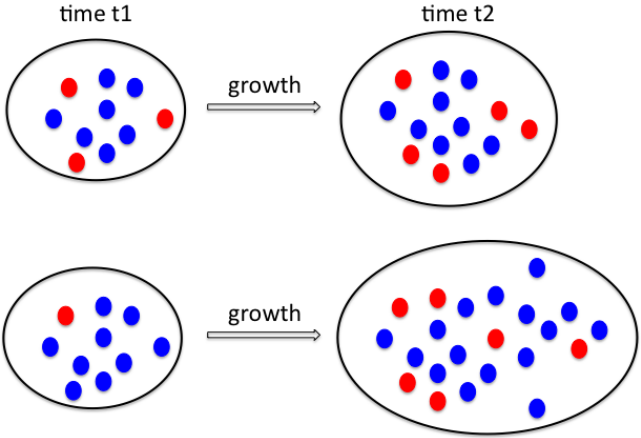
Model overview

explicit two-level population structure, with Particles nested within Collectives



Model: growth phase - particle fitness

within each collective, particles grow and compete in a public goods consumption dilemma



Two-locus coevolutionary model

- Particle trait 1: **strategy in social dilemma** (familiar)
  - Cooperate = efficient resource usage, slow growth leaving more for others (bigger collectives)
  - Defect = inefficient resource usage, rapid growth leaving less for others (smaller collectives)
  - formally an n-way Prisoners' Dilemma

- Particle trait 2: **preferred propagule size** (novel feature)

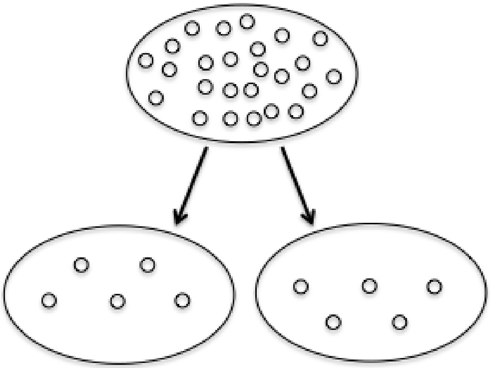
Roze & Michod's (2001) Am.Nat model is similar in some respects but crucial difference is that their bottleneck is imposed exogenously while mine in endogenous

Model: reproduction phase - collective fitness

Discrete generations. After growth is complete, collectives emit offspring collectives and then die.

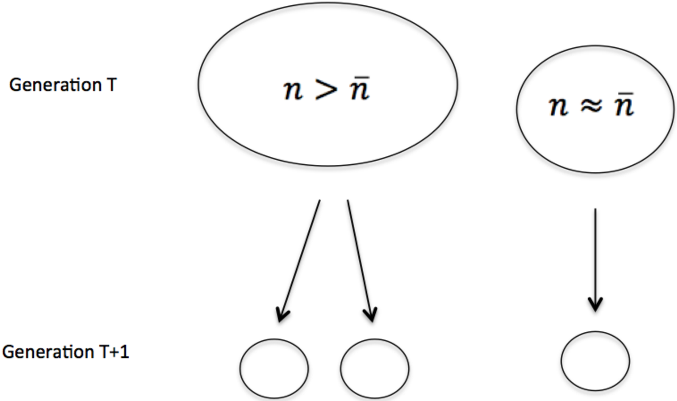
Generation T

Generation T+1



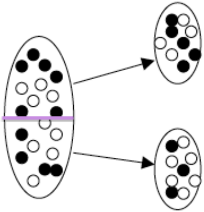
Model: collective fitness is a function of mature particle number

Collective fitness is a function of particle number at maturity

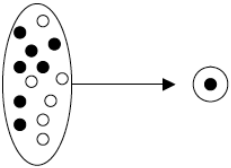


Model: propagule (offspring collective) formation

- Decide propagule size, Z: a lottery over particles in collective
- Propagule formation: select Z particles from the parent
- Propagule size trait varies from $n/2$ (max) to 1 (min)



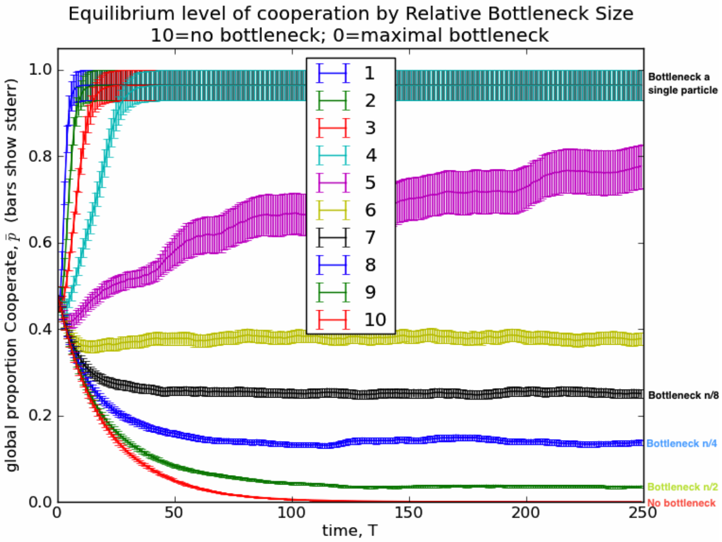
bottleneck size n/2
binary fission



bottleneck size 1
unitary propagule emission

Images adapted from Okasha (2006)

Initial test. Control variable: bottleneck size
Response variable: equilibrium level of cooperation

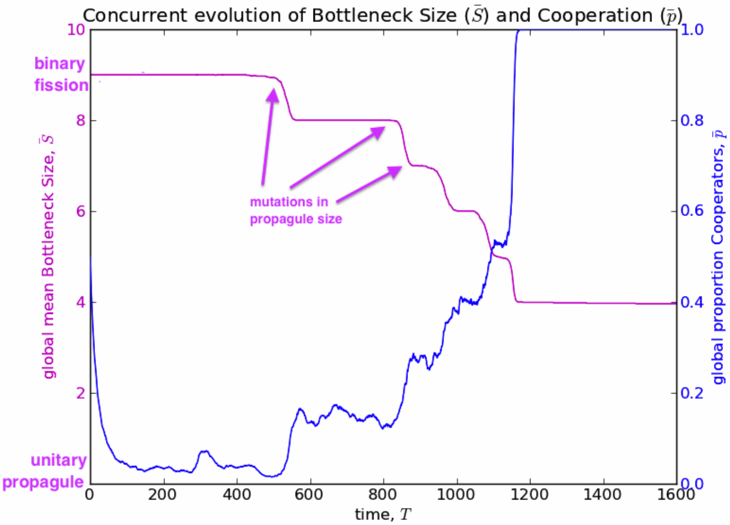


Main experiment

Main experiment: will selection push propagule downwards?

- allow mutation
- initialise particles 50% Cooperate, 50% Defect
- initialise collectives with maximum bottleneck size, $n/2$
- press ‘go’

Tighter bottleneck and higher cooperation co-evolve

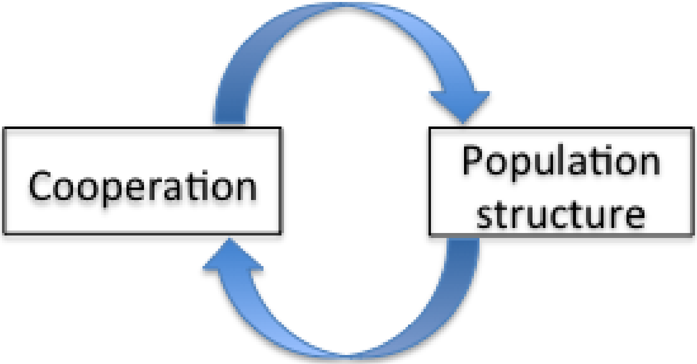


Next steps ...

- what does it really mean for fitness to be ‘exported to the higher level’?
- apply 2-level Price Equation . . .
- Particle level, measure $Cov(w_i, z_i)$ ←*built into model*
- Collective level, measure $Cov(W_k, Z_k)$ ←*emergent?*
- Expectations:
- particle-level character-fitness covariance to decrease as bottlenecking evolves (when measured over multiple generations)
- collective-level character-fitness covariance to increase as bottlenecking evolves

Discussion - many ways to think about this model

Social Niche Construction (Powers 2010) - positive feedback between population structure and cooperation provides *endogenous* explanation of evolution of cooperation-friendly population structure



Discussion - many ways to think about this model

- Godfrey-Smith: bottleneck denies Darwinian Individuality to the lower level (removes variation)
- Michod's 'export-of-fitness' view: variance in fitness is shifted from lower to higher level
- Okasha's version: shift from MLS1 to MLS2 during a major evolutionary transition
- Bourke's version: this is really kin selection; the bottleneck increases relatedness
- evolution of the parent-offspring relation

Acknowledgements

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