The role of life-history tradeoffs in the evolution of cell specialization

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Overarching idea

- Question: Why does cell specialization evolve?
- Tools: Optimality models inspired by volvocine algae.

Volvocine algae

- Flagellated photosynthetic organisms ranging from unicellular *Chlamydomonas reinhardtii* to *Volvox* with 500-50000 cells.
- Distinctive cell division (palintomy) and asexual lifecycle (autocolony).
- A model system for evolution of multicellularity and evolutionary transitions of individuality.

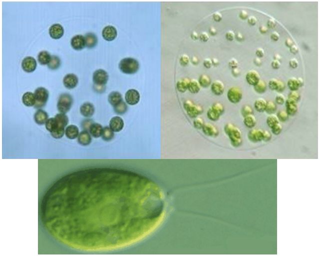


Figure 1 : Clockwise from top left: *Eudorina*, *Pleodorina*, *Chlamydomonas*.

Features of volvocine algae that can be important for modeling

- Semelparity.
- Cell number is fixed throughout life, colony grows by cells inside it growing.
- Most of the weight of a parent goes into offspring.

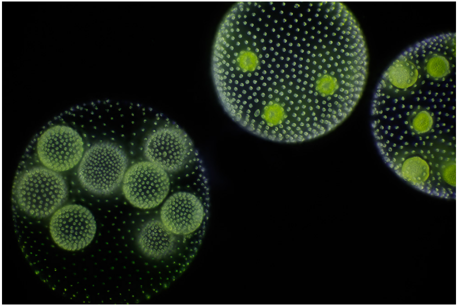


Figure 2 : *Volvox*. Picture: Frank Fox at www.mikro-foto.de.

Cell specialization

- Some species of colonial volvocine algae have cells specialized into soma (vegetative function) and germ (growth and reproduction) cells.
- Why? When is this differentiation optimal?

Michod et al.'s model of germ-soma differentiation

- We describe a model from "Life-history evolution and the origin of multicellularity" [MVS+06].
- Assume we have a colony made up of N single cells.

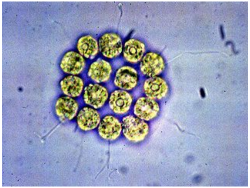
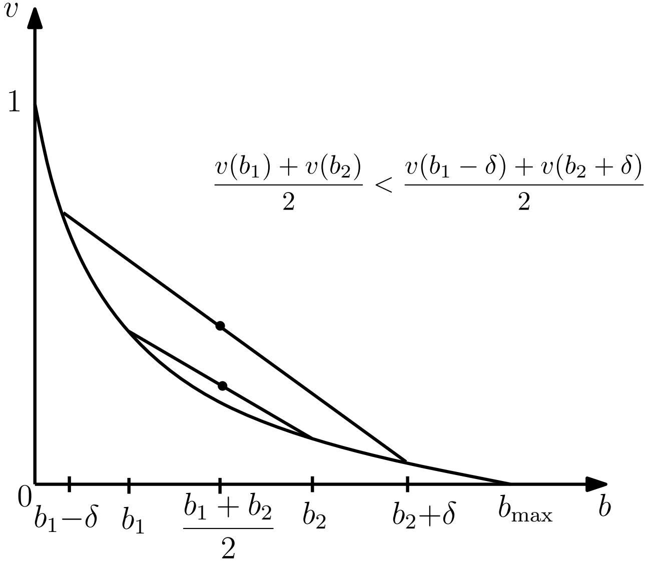


Figure 3 : *Gonium pectorale* $(N = 16)$. Picture by the EPA.

- Unicell i has fecundity b_i, viability v_i and fitness $w_i = b_i v_i$.
- The fecundity of the colony is $B = \frac{1}{N}\sum b_i$ and the viability of the colony is $V = \frac{1}{N}\sum v_i$.
- The fitness of the colony is $W = BV$.
- Since energy can be put into either reproduction or survival we assume a tradeoff between v and b at the single cell level.

Convexity explains germ-soma differentiation

Michod et al. show that if the cell-level v-b tradeoff is convex then complete germ-soma differentiation is optimal.



$$\frac{v(b_1)+v(b_2)}{2} < \frac{v(b_1-\delta)+v(b_2+\delta)}{2}$$

What are these b's and v's?

- There are at least three plausible ways to interpret b and v:
  - The literal fecundity (number of offspring if the cell survives to reproduce) and viability (probability of survival to reproduction) of the single cell.
  - The effort that the single cell puts into fecundity and viability.
  - The components of the colony fecundity and viability.
- We take the first point of view and introduce generation time, growth models and viability models to attempt to connect these results to empirically measurable traits.

First model: exponential growth and constant mortality

- Assume that a cell has a generation time t and then all the mass of the cell goes into its offspring so fecundity is $b = m(t)/m_0$.
- Assume mass m of the single cell grows exponentially so $m = m_0 e^{rt}$ and $b = e^{rt}$. Further assume that viability is $v = e^{-Mt}$.
- Notice that if r and M are fixed, then increasing t increases b and decreases v.
- If t is fixed then the v-b tradeoff must come from an r-M tradeoff.

Project goals

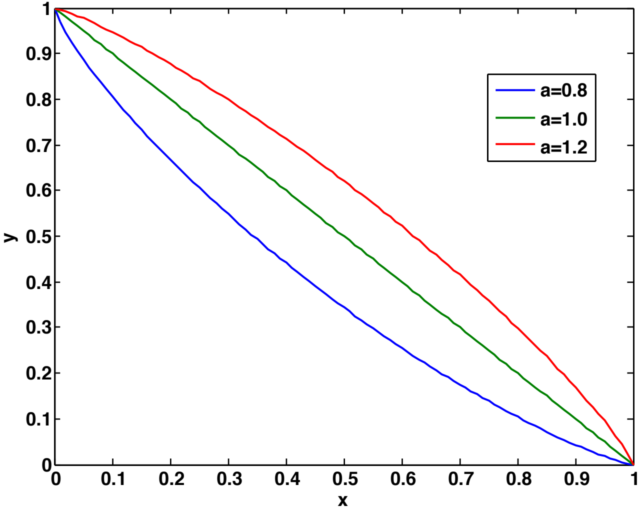
- Determine when germ-soma differentiation is optimal, depending on
  - colony generation time,
  - the family of single cell tradeoffs $v(t)$ against $b(t)$, and
  - the method of combining the traits of cells to get the fitness of the colony.

One way of combining traits of cells to get fitness of colony

- We define the fitness of a single cell to be $w = (bv)^{1/t}$. Notice $w = e^{\ln(bv)/t}$ so this is just the Malthusian parameter $r_{\text{pop}} = \ln(bv)/t$ on a different scale.
- For us, $b = e^{rt}$ and $v = e^{-Mt}$ so $w = e^{r}e^{-M}$ does not depend on t.
- For a colony with generation time T we assume all cells grow and are vulnerable for time T then average their fecundities and viabilities to get the fecundity and viability of the colony.
- Thus $W = \left(\left(\frac{1}{N} \sum_i e^{r_i T} \right) \left(\frac{1}{N} \sum_i e^{-M_i T} \right) \right)^{1/T}$.

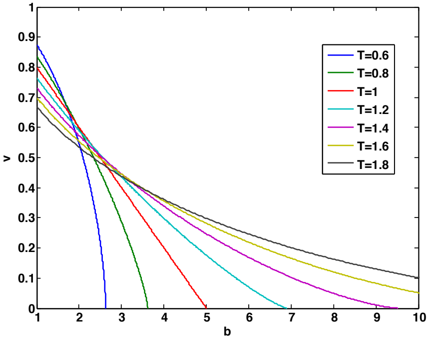
A family of functions

- First notice that $f_a(x) = (1 - x^a)^{1/a}$ is convex if $a \leq 1$ and concave if $a \geq 1$.



A family of tradeoffs

- Define $b_{\max}(t) = e^{r_{\max} t}$. Assume that
$$v(t^*) = \left(1 - \left(\frac{b(t^*)}{b_{\max}(t^*)}\right)^a\right)^{1/a}.$$
- We can then show that for any t,
$$v(t) = \left(1 - \left(\frac{b(t)}{b_{\max}(t)}\right)^{at^*/t}\right)^{t/at^*}.$$



The result

- Assume $T_{\min} \leq T \leq T_{\max}$ where $b_{\max}(T_{\min}) \geq 2$. If there is some generation time where the v vs b curve is convex then the optimal colony has complete germ-soma differentiation and generation time $T_{\max}$.
- Sketch of why:
  - Where $v(T)$ is a convex function of $b(T)$ it is optimal to completely differentiate.
  - We can calculate the fitness of a completely differentiated colony as a function of T and show it increases with T as long as $b_{\max}(T) \geq 2$.
  - Where $v(T)$ is a concave function of $b(T)$, the optimal colony has the same fitness as an undifferentiated colony for any generation time so cannot be optimal.

Second model: power function growth, fixed switching time, constant mortality

- We solve
$$\frac{dm}{dt} = rm^{3/4}, \quad m(t_{\text{fix}}) = m_0$$
to see $b = \left(1 + \frac{r}{4m_0^{1/4}}(t - t_{\text{fix}})\right)^4$. As before, take $v = e^{-Mt}$.
- Now the single cell has an optimum generation time t and growth rate r.
- What about the colony? Only partial results so far but something like the following may be true: "If t^* is the single cell optimum generation time and $v(t^*)$ is a convex function of $b(t^*)$ then with some other conditions it will be optimal to have germ-soma differentiation and increase T to some intermediate value".

Conclusion

- The original theoretical result says convex v-b tradeoff implies germ-soma differentiation is optimal.
- We are attempting to add variable generation time and explicit growth/mortality models.
- With exponential growth, constant mortality and a particular form of viability-fecundity tradeoff our results just require that *some* $v(t)$-$b(t)$ tradeoff is convex and furthermore predict that in that case generation time will increase.
- More complicated models will hopefully have the same kind of results with more realism.

The end

- Questions?
- P.S. For more volvocine algae, come to Deborah Shelton's dissertation defense tomorrow in this room at 11am.

References I

Richard E Michod, Yannick Viossat, Cristian A Solari, Mathilde Hurand, and Aurora M Nedelcu.
Life-history evolution and the origin of multicellularity.
Journal of theoretical biology, 239(2):257–272, 2006.