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A Darwinian approach to the origin of life cycles with group properties

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ABSTRACT

A selective explanation for the evolution of multicellular organisms from unicellular ones requires knowledge of both selective pressures and factors affecting the response to selection. Understanding the response to selection is particularly challenging in the case of evolutionary transitions in individuality, because these transitions involve a shift in the very units of selection. We develop a conceptual framework in which three fundamental processes (growth, division, and splitting) are the scaffold for unicellular and multicellular life cycles alike. We (i) enumerate the possible ways in which these processes can be linked to create more complex life cycles, (ii) introduce three genes based on growth, division and splitting that, acting in concert, determine the architecture of the life cycles, and finally, (iii) study the evolution of the simplest five life cycles using a heuristic model of coupled ordinary differential equations in which mutations are allowed in the three genes. We demonstrate how changes in the regulation of three fundamental aspects of colonial form (cell size, colony size, and colony cell number) could lead unicellular life cycles to evolve into primitive multicellular life cycles with group properties. One interesting prediction of the model is that selection generally favors cycles with group level properties when intermediate body size is associated with lowest mortality. That is, a universal requirement for the evolution of group cycles in the model is that the size-mortality curve be U-shaped. Furthermore, growth must decelerate with size.

Summary

Factors influencing the early evolution of life cycles with group properties are largely undefined. A theoretical framework is provided here in which three fundamental processes (growth, division, and splitting) shape the architecture of the simplest five life cycles and their evolution. We demonstrate the critical importance of three fundamental aspects of colonial form (cell size, colony size, and colony cell number) in the transition from unicellular life to primitive multicellular life cycles. Our model reveals selection pressure for cycles with group properties when intermediate body size is associated with lowest mortality (i.e. U-shaped size-mortality relationship) and growth decelerates with colony size. This heuristic model provides a conceptual framework which could be used to further study the evolution of earliest colonial life cycles.

1. Introduction

"And what is it, then, which is immortal? Clearly not the substance, but only a definite form of activity…the cycle of material which constitutes life returns even to the same point and can always begin anew, so long as the necessary external conditions are forthcoming…the cycle of life, i.e. of division, growth by assimilation and repeated division, should [n]ever end; and this characteristic it is which I have termed immortality. It is the only true immortality to be found in Nature—a pure biological conception, and one to be carefully distinguished from the eternity of dead, that is to say, unorganized, matter". Weismann (1890)

A life cycle consists of successive states through which life passes until it returns to some initial state. Division, growth, and splitting are the minimal constituents of a life cycle, and the way these three processes are organized in time and space defines the broad outline of development–defined by Griesemer (2001) to be the acquisition of the capacity to reproduce. Division is the simplest form of reproduction, without which the life cycle will eventually go extinct as some mortality is unavoidable. It necessitates

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the production of new material, i.e. growth. Finally, some kind of a splitting process, by which the products of reproduction go their own ways and complete the cycle, is required. An important question concerns the way these three basic processes at the cellular level are assembled to produce more complex forms during the initial stages of the evolutionary transition from unicellular to multicellular life.

There is a brief multicellular state before splitting inherent in all unicellular life cycles when daughter cells have been produced by cell division and are still held together. This state is transient and represents an inevitable state through which the unicellular life cycle must pass. In most multicellular forms of life, the single-celled state tends to be transient and often restricted to single-celled propagules or gametes. Intermediate levels of complexity, by which we mean a significant contribution to the life cycle of both single-celled and colonial states, are the focus here. Such mixed life cycles must have been represented in transitional forms if the evolutionary transition to multicellularity involved small continuous steps as Darwin proposed in his explanation of the evolution of complex organs such as the human eye.

We investigate how and why simple unicellular life cycles become more complex and begin to involve colonial states and processes that operate at the cell group (i.e. multicellular) level. We investigate the conditions under which small modifications (resulting from random mutations) of unicellular life cycles could lead to the evolution of stable, more complex cycles that represent the presumed transitional forms on the way to multicellular life.

2. Materials and methods

2.1. States, transitions, and mortality

For the purpose of analytical tractability of the explicit mathematical model given below, we impose an upper limit of four-fold growth of a single cell yielding, with two divisions, four daughter cells. We consider single cells, 2-celled colonies, and 4-celled colonies and define body size (unicellular or multicellular) as total cellular volume. Since we are studying the earliest stages of evolution of colonial life cycles, we ignore the contribution of the extracellular matrix to body size. We measure size relative to the size of a single small cell given as x. We include single cells with three different sizes (1x, 2x, and 4x), 2-celled colonies in which the colonies have two different sizes (2x and 4x), and 4-celled colonies composed of 1x-sized cells (4x). A 2x cell and 2-celled colonies composed of 1x cells have the same body size in our model as they have the same total cellular volume. Likewise, a single 4x cell, 2-celled colonies composed of 2x cells, and the 4-celled colony composed of 1x cells are also assumed to have the same body size. We have a total of 6 states in the model, each defined by body size and the number of cells it contains (Fig. 1). We denote a state by the general notation NxSy, where N represents Number with x being the number of cells in the state (1 = single cell, 2 = 2-celled colony, and 4 = 4-celled colony) and S represents Size with y being the cell size (1 = 1x, 2 = 2x, and 4 = 4x). For example, N2S2 represents a 2-celled colony consisting of cells with size 2x.

During its life cycle, the organism transitions from one state to the next. We consider all possible transitions between states (Fig. 2). The parameter associated with each arrow in Fig. 2 shows the time required for the corresponding transition to take place. The three transitions that constitute a life cycle are: (i) growth, a cell or colony (uni- or multicellular) grows 2-fold in size without increasing the number of cells; (ii) division (asexual), one or two rounds of mitosis during which a single cell becomes a 2-celled (one round of mitosis) or a 4-celled (two rounds of mitosis) colony, or a 2-celled colony becomes a 4-celled colony; and (iii) splitting, the cells comprising the colony split from the colony and go their own way. We denote the transition times for growth, division, and splitting by g, d, and s, respectively. $g1$ and $g2$ are the transition times for the growth of N1S1 to N1S2 and N1S2 to N1S4, respectively. As discussed below, we ignore cooperation and other kinds of interactions among cells within groups. Consequently, we assume that being in the colony *per se* does not affect the rate of growth. Specifically, a 1x-sized cell is assumed to have the same growth rate whether it grows as an independent single cell ($g1$) or within a colony ($g3$). This means $g3 = g1$. We assume that division and splitting are significantly more rapid transitions than growth, thus $d = s = 0$. This is consistent with the fact that mitosis typically takes up only a small portion of the life cycle (Alberts et al., 1994), while growth takes longer as it requires production of new biomaterial. A group property in our model is represented by a transition that begins with and ends in a group state (red arrows in Figs. 1 and 2). There are two such transitions in the model: transition from N2S1 to N2S2 (growth as a group) and from N2S2 to N4S1 (division within the group). Transitions from a group state to a non-group state (e.g. N2S1–N1S1) do not represent a group property because the presence of group states such as N2S1 is required to form a cycle.

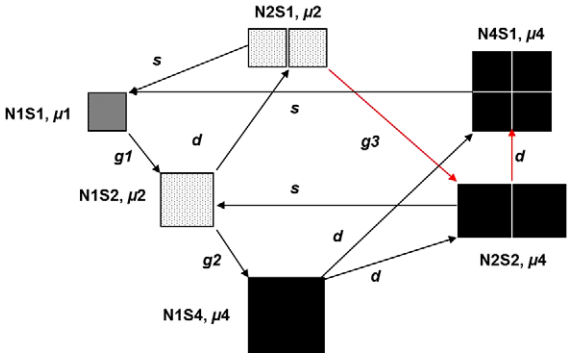

Fig. 1. The complete life cycle diagram. Six states can be identified in the model. They are represented by the general notation NxSy, where x represents the number of cells in the state (1 = single cell, 2 = 2-celled colony, and 4 = 4-celled colony) and y represents the cell size (1 = 1x, 2 = 2x, and 4 = 4x). States in the same size class are shown with the same filling pattern. Transitions (growth, division, and splitting) are indicated by arrows, and those representing a group property (beginning with and ending in a group state) are shown in red. The rates of growth, division, and splitting are denoted by g, d, and s, respectively. Mortality is shown as μ and states in the same size class have the same mortality. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Mortality (μ) is the probability of dying in a certain state before making a transition to another state and is assumed to depend strictly on body size. Hence, states with the same size are assumed to have equal mortality values. $\mu 1$, $\mu 2$, and $\mu 4$ denote the probabilities of death in 1x, 2x, and 4x states, respectively.

2.2. Genotypes

Each cycle is encoded in the model by an asexual haploid genotype. At least three genes are required to join together the basic life cycle properties of growth, division and splitting. While there are a variety of choices, the genes we have chosen are motivated by evidence involving cell cycle control in simple colonial organisms (see Discussion): c (maximum *cell* size), C (maximum *colony* size), and N (maximum colony cell number). Each gene has two possible alleles, allele 2 or 4. The cell can reach, outside of a colony, a size of 2x when $c = 2$ and 4x when $c = 4$. Similarly, the colony can reach a size of 2x when $C = 2$ and 4x when $C = 4$. The colony can have a maximum of 2 cells when $N = 2$ and 4 cells when $N = 4$; it cannot hold together more cells than determined by gene N. We identify a genotype by the triplet (c, C, N).