Live together, die alone: Levels of selection in the transition to coloniality and sociality

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Introduction

Colonial and social organisms live in unambiguous groups. They are fairly well bounded spatially as well as very close to genetically identical. But across higher taxa, variation in the amount of integration between members of the group is high. The degree of polymorphism is also variable across taxa. Almost the full spectrum of individuation (intuitively recognized) occurs in some colonial or social groups, ranging from aggregates to what have been called superorganisms.

Although major transitions in individuality are fairly common in nature, most lack a variety of transitional forms. Metazoans evolved from single celled ancestors, but no transitional forms exist. Sponges suffer, not from being good groups of cells, but being ambiguous in the number of sponges within a sleaze (a group of sponges). Plants and fungi, like sponges, are rametous, having multiple modules that can, but don't have to, live separately.

Variation in the degree of individuality is pervasive in colonial and social animals. Most taxa that exhibit coloniality or sociality also contain solitary forms. This provides the opportunity to identify the important processes of hierarchical evolution.

It seems obvious that a division of labor among parts of a colony should be advantageous. Why don't all colonies exhibit polymophisms? The proposed mechanisms for the origin of polymorphism is basically heterochronic changes in zooid form stabilized by genetic assimilation (Harvell 1994, Bonner 2001). Primitive colonies (be they groups of cells or groups of zooids) are monomorphic, but if they have allometric growth, then differentiation can occur by heterochrony.

There is no real doubt as to the occurrence of these mechanisms, but they can't be the only explanation because then the degree of polymorphism should be correlated with lineage age. This can't be true because we know that some cnidarian lineages are quite old, and yet have no polymorphism.

Colonies like siphonophores or doliolids, where functional specialization and integration among zooids is high, have successfully made the transition from groups of zooids to individuals of a higher order. It is commonly thought that selection on the group of zooids as a whole must be strong enough to drive individuation in the face of potential opposing selection among zooids. There are a number of reasons to doubt this view. Williams (1966) argued that group selection does not occur in colonial or other aggregate organisms because the all members are genetically identical, so that providing "benefits to a genetically identical individual is to benefit oneself." For him, as well as others, group selection is–by definition–selection among groups consisting of many genotypes. Individuation involves adaptations at the group level, even if all members of the group are initially genetically identical. Anatomical differences within an organism are caused by differential gene expression, among other things that generate high expressed genetic diversity among members. It is reasonable that selection acts on the sum of the parts, the whole, rather than on each part individually. Some insights from group selection theory may then be enlightening.

In particular, the strength of group selection is strongly influenced by the initial size of the group founders, the propagule size (Wade 1978, Szathmary & Demeter 1987), exemplified during major transitions as a single celled stage in the life cycles of multicellular organisms (Maynard Smith 1988, Roze & Michod 2001, Wolpert & Szathmry 2002). The single cell stage is a results from sexual reproduction, it is a product of the germ line. Germ cells in metazoans can be specified in a number of different ways (Nieuwkoop & Sutasurya 1981, Buss 1983, 1987). The mechanism of germ cell specification has direct consequences in the number of potential reproductive zones of an organism. Germ cells originate either preformistically or epigentically. Embryos can also be derived somatically. These mechanisms of germ cell sequestration limit the reproductive contribution of the body. In effect, germ line sequestration is an adaptation for controlling propagule size.

Hypothesis

A small propagule size maximizes heritability between parent and offspring groups and is essential for effective natural selection. Internal coadaptation of zooids within colonies requires selection among colonies to be dominant over selection among parts. The degree to which the germ line is specified controls the propagule size of the offspring colony and therefore the heritability of colony-level traits.

In a population of solitary cells, every cell reproduces. In colonial organisms with group adaptations, only some proportion of the member organisms reproduce. The reproductive members are the colony-level equivalent of the organismal germ line. My proposal is that as the ratio between reproductive and non-reproductive members of a colony increases, the strength of selection at the colony level increases allowing for the evolution of complex group-level adaptations. Stated in another way, the degree of individuation of a colony is dependent on the proportion of non-reproductive members in the colony (figures 1 and 2).

Predictions of the hypothesis

This hypothesis makes a number of specific predictions. I present an annotated list of these predictions below.

- The initial differentiation of part types will be between reproductive and non-reproductive.
    - Whatever the selective advantage of aggregation is (*e.g.*, scaling issues when large size is being selected), there will be an advantage to isolating physiological activity and reproductive activity. The details will differ depending on the transition being considered, but all transitions seem to show this pattern.
- Since the mode of germ cell specification determines an organism's ability to reproduce asexually (organisms with preformative germ cells cannot), the mode of germ cell specification acts as a constraint on the style of aggregation possible. Asexual organisms, those with somatic embryogenesis or epigenetically specified germ cells, will be colonial. While organisms with preformed germ cells, being sexual, will form social aggregates.
- Related to the above is the order of differentiation of parts during astogeny. Organisms with preformative germ cells will found new colonies with reproductive propagules while reproduction can occur late in astogeny in asexual organisms.
- Development will be more complex in groups with a high non-reproductive ratio. The complexity of development can be reflected in a number of ways:
    - C-values will be inversely correlated with non-reproductive ratios.
    - The number of part-part interactions is high
    - Part form is specified by both part-part signaling and determined fate
    - Diverse μRNA content will be present in colonies with polymorphisms, even if they have low numbers of cell types.
    - Complex life cycles characterized by the interaction of multiple stages will occur only in organisms with a large non-reproductive ratio.

Metadata

- Physiological/functional Individuality
    - *Degree of connectivity.* Discrete character ranging from unconnected (ants), to essentially continuous (interzooidally budded coral zooids)

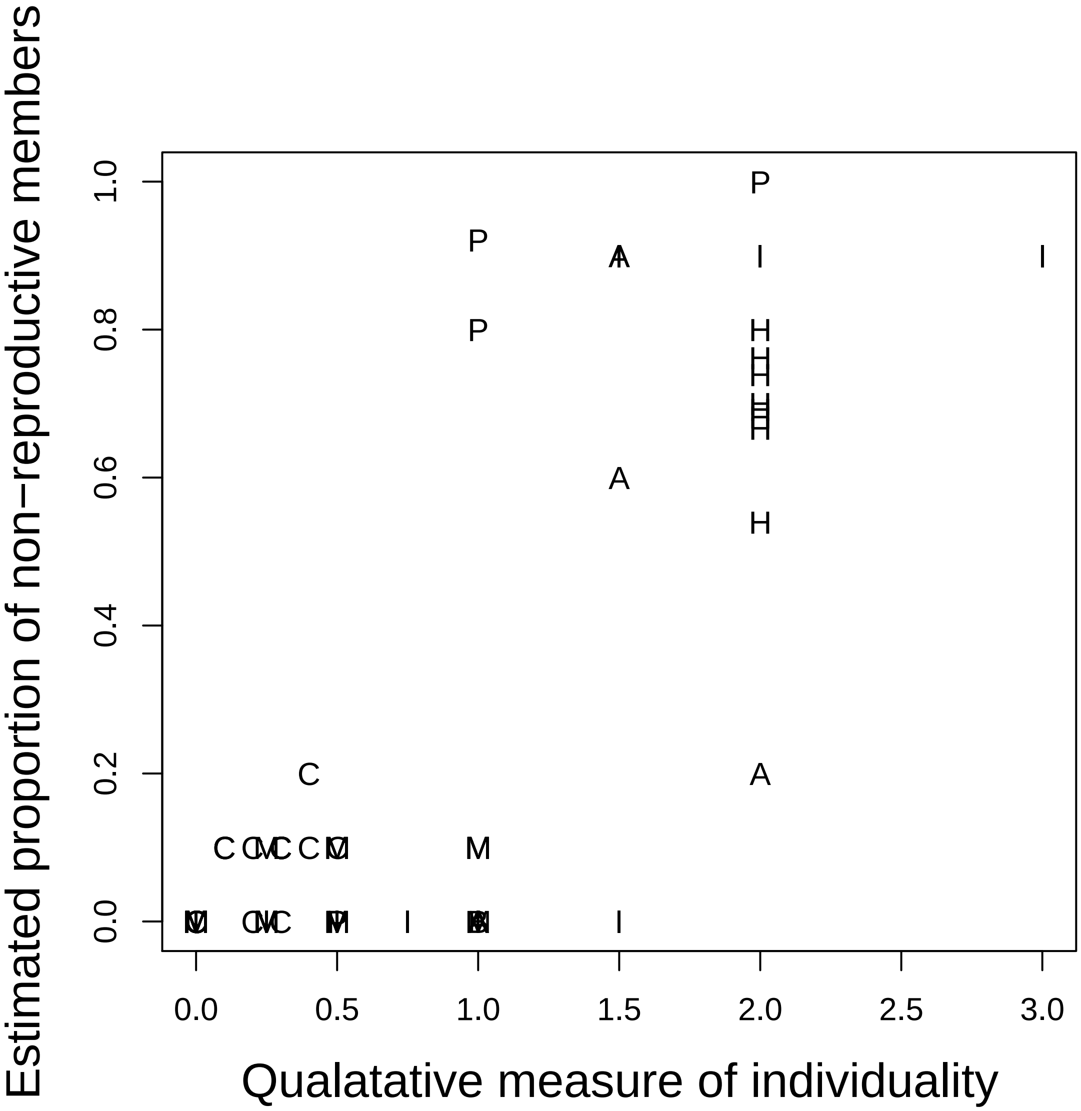

Figure 1: A qualitative assessment of the degree of individuality and non-reproductive ratio of colonial bacteria (B), protozoans (P), marine invertebrates (A), social insects (I), mammal orders (M), carnivores (C), and primitive human societies (H). A rank order individuality was given to each member of the main grouping. Data is from Wilson (1975) and Hughes (1988).

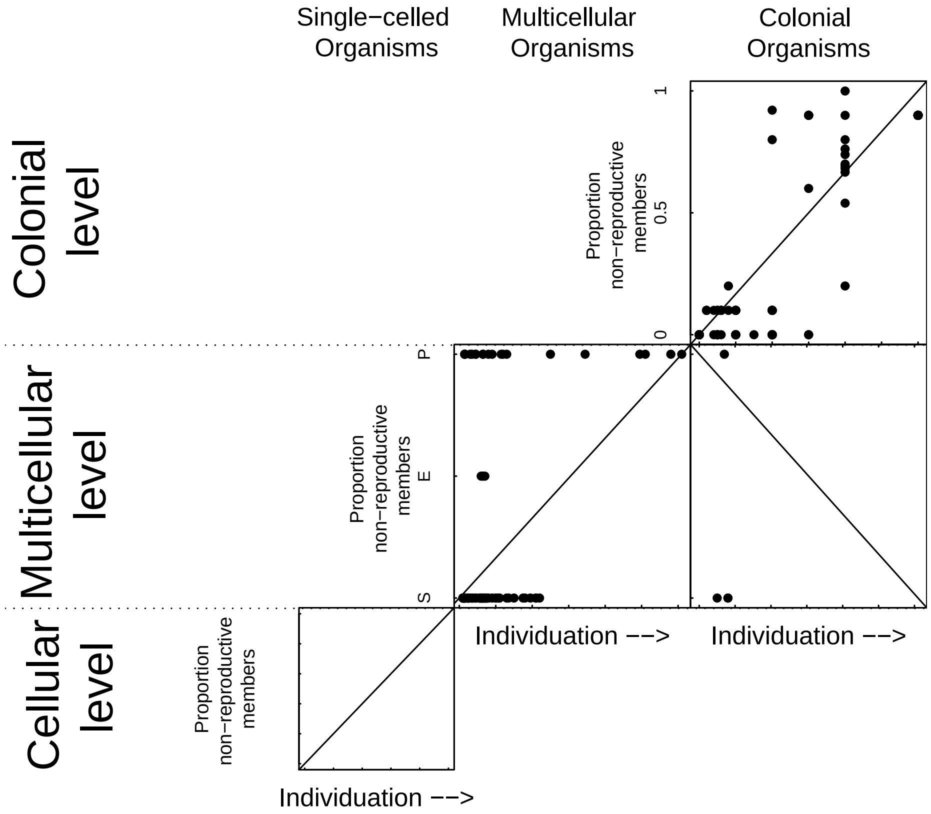

Figure 2: Previous levels of selection are not lost when a new high level emerges. The hypothesis predicts that a part of the observed complexity drain at subsumed levels can be captured in the loss of general individuality and reproductive ability of zooids within colonies. Colonial organism data is the same as in figure 1. Data for multicellular organisms is based on Buss (1983) and Bell & Mooers (1997). Individuation in this graph is represented by the number of cell types. Proportion of non-reproductive members is approximated by the mode of germ cell formation: Somatic (S), epigenetic (E), or predetermined (P). Colonial organisms are represented in the top-left panel. Directly below is the panel for the multicellular-level members of the colony. Shown here are two bryozoan species and a cestode. Individuation and the proportion of non-reproductive members are based on cell types and mode of germ cell formation.

  - *Extrazooidal parts.* Elements made by one or more zooids that occur outside zooid boundaries. These are often mineral structures, sclerites, skeletal elements, it is important to distinguish the level of extra zooidal parts. Some bryozoan skeletons, *i.e.,* the calcified vertical walls, would be extrazooidal at the zooid level, but not at the colony level. However the calacified vertical walls of dead zooid become structural in, for example, *Archemiedes.* These would be considered extrazooidal at the colony level. Other examples of extrazooidal parts are much more clear-cut. Structures that termite or ant colonies build would also count as extrazooidal parts.
  - *Astogeny/Ontogeny.* Development is the means of organismal control of its cellular constituents. Because colonial organisms are hierarchical extensions of solitary organisms, they may be constrained to modifying the existing development in the simplest possible way. Heterochronic changes in development of zooids may be a fast path to zooidal differentiation when complex complex development is lacking (*e.g.,* in cnidarians or bryozoans).
    - *Order of appearance of organs/zooids.* The developmental sequence that a predetermined set of tissues or organ systems are developed (*e.g.,* the digestive, nervous, skeletal, muscular, reproductive systems).
    - *Timing of reproductive maturation.* The rank in the above sequence of the onset of mature reproductive organs or tissues.
    - *Number of life cycle stages* In addition to differentiation by heterochrony, zooidal differentiation could occur by the aggregation of zooids of different life cycle stages. This is particularly common in hydrozoans.
  - Polymorphism
    - The number of part types at each hierarchical level: cell types, zooid types
  - Size, total number of zooids, or number of zooids per area

- Germ specification
  - Organismal level germ specification
    - *Somatic embryogenesis.* Lacks a distinct germ line. A cell lineage can function as a stem cell or give rise to gametes.
    - *Epigenetic.* A clearly differentiated germ line that appears only after other major organ systems
    - *Preformative.* Early sequestration, differentiated early often directed by maternal effects.
  - *non-Reproductive ratio.* The proportion of non-reproductive members of the aggregation. Hypothesized to be causally involved with the ability for selection to produce adaptations at the specified level of selection. Its relatively easy to

assess in cases where reproduction is severely limited like eusocial insects. There is no fixed number of reproductive members in organisms with indeterminate growth, such as bryozoans or corals. Therefore, proportions are used for all groups.

References

Bell, G. & Mooers, A. O. (1997), 'Size and complexity among multicellular organisms', *Biological Journal of the Linnean Society* **60**(3), 345–363.

Bonner, J. T. (2001), *First Signals: The Evolution of Multicellular Development*, Princeton University Press.

Buss, L. W. (1983), 'Evolution, development, and the units of selection', *Proceedings of the National Academy of Sciences* **80**(5), 1387–1391.

Buss, L. W. (1987), *The evolution of individuality*, Princeton University Press Princeton, NJ.

Harvell, C. D. (1994), 'The evolution of polymorphism in colonial invertebrates and social insects', *The Quarterly Review of Biology* **69**(2), 155–185.

Hughes, A. L. (1988), *Evolution and human kinship*, Oxford University Press New York.

Maynard Smith, J. (1988), 'Evolutionary progress and levels of selection', *Evolutionary Progress* p. 219230.

Nieuwkoop, P. D. & Sutasurya, L. A. (1981), *Primordial Germ Cells in the Invertebrates: From Epigenesis to Preformation*, Cambridge University Press.

Roze, D. & Michod, R. E. (2001), 'Mutation, multilevel selection, and the evolution of propagule size during the origin of multicellularity', *American Naturalist* **158**(6), 638–654. 499LE Times Cited:7 Cited References Count:47.

Szathmary, E. & Demeter, L. (1987), 'Group selection of early replicators and the origin of life', *J Theor Biol* **128**(4), 463–86.

Wade, M. J. (1978), 'A critical review of the models of group selection', *The Quarterly Review of Biology* **53**(2), 101–114. The efficacy of group selection is inversely related to propagule size.

Williams, G. C. (1966), *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, Princeton University Press.

Wilson, E. O. (1975), *Sociobiology: the new synthesis*, Belknap Press of Harvard University Press.

Wolpert, L. & Szathmry, E. (2002), 'Multicellularity: Evolution and the egg', *Nature* **420**, 745.