THE SUPERORGANISM CONCEPT

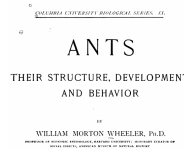
Pedro Augusto Da Pos Rodrigues
= ECOL 497S/597S =
Fall 2010

- Analogy of societies to living organisms: since the times of Plato and Thomas Aquinas (Emerson, 1932)

Weissman (1893) referring to social insects:

"The whole colony behaves as a single animal, the state is selected, not the single individuals; and the various forms behave exactly like the parts of one individual in the course of ordinary selection" (*apud* Emerson, 1932)

Wheeler (1910; 1911): social insects caste system parallels somatic and reproductive cells of an organism


COLUMBIA UNIVERSITY BIOLOGICAL SERIES. XI.

ANTS

THEIR STRUCTURE, DEVELOPMENT AND BEHAVIOR

BY

WILLIAM MORTON WHEELER, Ph.D.

REPRODUCTIVE TISSUE

"NUTRITIVE CASTE" OR GASTROVASCULAR SYSTEM

IMMUNE SYSTEM (soldiers)

COMMUNICATION = NERVOUS SYSTEM
(each individual is equivalent to neurons)

"SKELETON": nest – may exhibit symmetry and capability of regeneration. Dead constructions = shells; Bony skeleton

Photo: Alex Wild

Emerson (1932): analogy is valid at least for social insects

Biological individual: "living entity exhibiting a certain dynamic equilibrium and maintaining a relative stability in time and space"

Colony:

- Ontogeny, Coordination and Integration
- Activity gradients and Symmetry
- Chemical integration
- Nervous integration
- Rhythmic periodicity

"much of our evidences rest upon the use of analogy"

However, in the past century:

- Communities
- Ecosystems
- Symbiotic associations
- Gaia Hypothesis

How does natural selection work on these entities?

-W. D. Hamilton (1964): Kin Selection and inclusive fitness: "selection at the individual level"

-Dawkins (1976): selection at the gene-level

The death for the Superorganism concept?

D.S Wilson and Sober (1989):

"The superorganism concept fails as a grandiose theory of nature, and its death in this form is indeed a triumph of modern evolutionary biology."

"Against this background, reviving the superorganism concept might seem like bringing back Dr. Frankenstein's well-intentioned monster."

(1)Individual Selection is based on a logical contradiction *

(2) Superorganism exist in nature

(3) A formal theory can avoid excess from the past (e.g Gaia and etc) *

(4)Adaptations may evolve when individuals function as alleles *

(5)Semantics of individual selection and group selection must be corrected *

D.S Wilson and Sober (1989):

(1)Individual Selection is based on a logical contradiction
(5) Semantics of individual selection and group selection must be corrected
To 'demystify' the superorganism concept/group selection

Individual: "spatio-temporally localized entities that have reasonably sharp beginnings and endings in time" (Hull, 1980)

= atom, genes or creatures

Organism: "a form of life composed of mutually dependent parts that maintain various vital processes" (Random House dictionary, unabridged edition)

Then,

Superorganism: "collection of single creatures that together possess the functional organization implicit in the formal definition of organism."

D.S Wilson and Sober (1989):

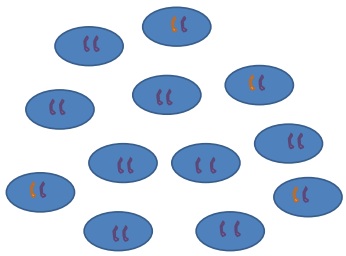
(1) Individual Selection is based on a logical contradiction

-An individual is a group of alleles: one allele may be more fit than its alternative

Therefore,

Why groups can not be functionally organized as superorganisms and its individuals acquire the status of alleles?

- An assexual insect lay eggs in stagnant water pools

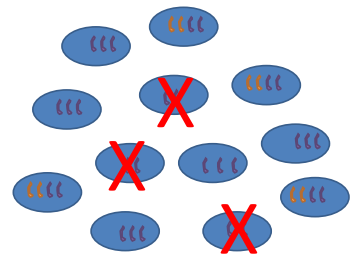


Two morphotypes develop from the eggs:

Detoxifies harmfull chemicals

- No fitness cost

- An asexual insect lay eggs in stagnant water pools



Two morphotypes develop from the eggs:

Detoxifies harmfull chemicals

- No fitness cost

- In this scenario, some groups would be favored by the presence of a different morphotype = equivalent to a different allele in a organism

D.S Wilson and Sober (1989):

Conditions for the evolution of a superorganism:

(1)Population is divided as groups

(2)Groups vary in properties that affect the number of dispersing progeny (group fitness)

(3)Variation in groups fitness is caused by underlying genetic variation that is heritable (effects of alleles or individuals are not similar to each other)

(4)No difference exist in the fitness of individuals within groups

D.S Wilson and Sober (1989):

(1)Individual Selection is based on a logical contradiction
(3) A formal theory can avoid excess from the past (e.g Gaia and etc)
(5) Semantics of individual selection and group selection must be corrected

-in real life: different traits involve costs (e.g. a "A" type individual may detoxify the water but be less fit than the alternate type of individual)

"Between unit selection vs. Within unit selection"

"When within-unit selection overwhelms between-unit selection, the unit becomes a collection of organisms without itself having the properties of an organism."

Use of this terminology prevents the contradiction of individual vs. group selection as auto-exclusive theories.

D.S Wilson and Sober (1989):

-Sex ratio -> conflict in 3 levels of selection: gene, individual and group

(A)If resource are abundant: more females, increased group productivity (between-unit selection)

(B)Within unit selection: same investment in males and females;

The example shows that sometimes there is no winner force of selection, but a compromise.

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Capturing the superorganism: a formal theory of group adaptation

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In this article, we provide a formal foundation for the group-centred view of social adaptation.

In particular, we find that there is a strong mathematical correspondence between the dynamics of gene frequency change and the GMA analogy in scenarios where groups comprise genetically identical individuals or where within-group competition is repressed. This correspondence reveals that, in such scenarios, natural selection acts to optimize group phenotypes for the purpose of group fitness maximization – i.e. group adaptation.

Capturing the superorganism: a formal theory of group adaptation

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†St John's College, University of Oxford, Oxford, UK

Contrary to D.S Wilson and Sober (1989):

defining group adaptation itself. By contrast, we emphasize that the function of individual-level adaptation is to maximize inclusive fitness and that this obtains irrespective of the relative strength of within-group vs. between-group selection. Moreover, if we want the term 'adaptation' to retain its meaning as we move from the individual to the group level, then group adaptation is not simply a response to between-group selection, but instead a rather stronger notion of group optimization – that only obtains if within-group selection is completely abolished.

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DECONSTRUCTING THE SUPERORGANISM: SOCIAL PHYSIOLOGY, GROUNDPLANS, AND SOCIOGENOMICS

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-Three kinds of societies: team-like (incipiently eusocial), factory-like like (monomorphic workers) and machine-like (physical castes)

-For team like societies, both individual and group-level selection play key roles. More advanced societies evolve mainly by group-level selection

- All of them are considered superorganisms

Eusocial insects as superorganisms

Insights from metabolic theory

James F. Gillooly[1,*] Chen Hou[2] and Michael Kaspari[3,4]
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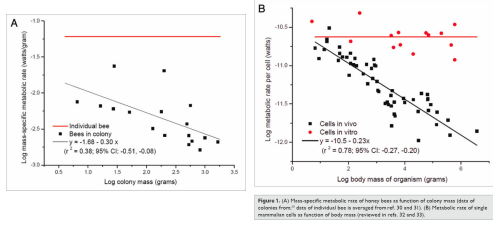

Figure 1. (A) Mass-specific metabolic rate of honey bees as function of colony mass (data of colonies from [7] data of individual bee is averaged from ref. 30 and 31). (B) Metabolic rate of single mammalian cells as function of body mass (reviewed in refs. 32 and 33).

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A Brief History of the Superorganism, Part Two

By Brandon Keim | July 11, 2007 | 10:09 am | Categories: Uncategorized

Interview with Bert Holldobler (2007)

It's as exciting as understanding the pattern of a brain. We try to understand the connections of these millions of ants that creates this caste system, complex communicaiton and foraging and territorial strategies, and it's all done by these interactions. When you look at these things, you can't avoid saying, at this stage an insect colony functions like an organism. A superorganism. And you can go forward and say, this is an extended phenotype: selection doesn't work on individual level, but on the whole colony.

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A Brief History of the Superorganism, Part Two

By Brandon Keim | July 11, 2007 | 10:09 am | Categories: Uncategorized

Interview with Bert Holldobler (2007)

> Not all ant societies are like this. They're not full superorganisms. Ed Wilson sees this for all ants; I don't. There are phylogenetically primitive ants, not so evolved as leafcutters, and they have internal friction — fights for reproduction privileges. They have superorganism traits, but I wouldn't call them true superorganisms, as there's a lot of selection going on at the individual level in the community. They haven't reached point where in-colony conflict is gone and it's now between-colony.

COMMENT Samir Okasha

7 OCTOBER 2010 | VOL 467 | NATURE |

Lastly, kin and multi-level selection are not alternative theories; they simply offer different takes on the question of how social behaviour evolved. Proponents of kin selection, for example, explain sterile workers in insect colonies by saying that the workers are helping the queen to reproduce, and thus boosting their own inclusive fitness. Proponents of multi-level selection argue that the workers are providing a benefit to the colony as a whole, thus making the colony fitter than other colonies. These explanations may seem different, but mathematical models show that they are in fact equivalent[10–12].

In summary:

-The superorganism concept was originally developed from an old analogy between common, well defined organisms and animal societies; it was not formally linked to any theory, model or explanation to its evolution

- Later, with development of modern evolutionary theory, the superorganism concept was automatically linked to group-level selection

-After publication of Hamilton's kin selection theory, the use of superorganism was heavily discouraged (superorganism=group-selection)

- The confusion with semantics (organism? Individual? Group-selection? Individual Selection? Between-selection? Within-Selection? Multi-level selection?) lead to the revival of the superorganism concept and there is still debate over the definitions of individuality and organismality for social organisms.

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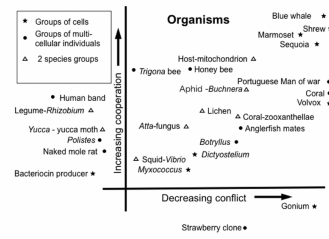
THE SOCIAL ORGANISM: CONGRESSES, PARTIES, AND COMMITTEES

Joan E. Strassmann[1,2] and David C. Queller[1]



High Cooperation and High Conflict = Societies

High Cooperation and Low Conflict= Organisms

COMMENTARY © 2010 The Author(s). *Evolution*

THE SOCIAL ORGANISM: CONGRESSES, PARTIES, AND COMMITTEES

Joan E. Strassmann[1,2] and David C. Queller[1]

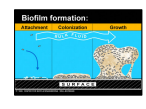
Organism	Kinship	Evolution	Example
Fraternal	yes	Kin-selection	Multicelullar organisms
Egalitarian	Not necessary	Mutualism	Eukaryotic cell

* Common interest over reproduction, in both cases

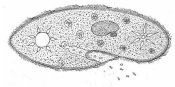
- Conflict is never totally absent, even in 'paradigm organisms' (e.g. cancer; transposable elements, etc)

- Since organisms are defined in terms of degrees of cooperation and conflict, **there is no reason to use the concept of Superorganism**

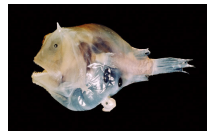
- Insect societies are in general considered as fraternal organisms, even when kinship is not as high as it can be in a haplodiploidy system (e.g. due to multiple mating). The distinction of organimaslity, in this case, would derive mainly from the level of conflicts between individuals of a colony.



Egalitarian:

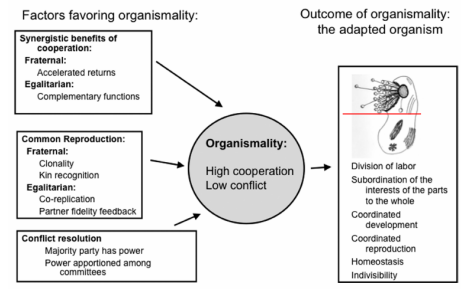


Paramecium



Anglerfish
("sexual cooperation"

Haeckel Lichenes



Congresses: (based on parliamentary concept by Leigh, 1971)

- It introduces the idea of the **power (e.g. majority)**

-Defined as the different parts of a social organism. It is further composed by parties and committees.

Parties: group of member with the same interest or coreplicons
- collective interests: allegiances
- cheaters: "mavericks", may disrupt the cooperation and, ultimately, the organism itself
- evolution of mechanisms of suppression: if committed to one party, there is nothing to loose repressing 'mavericks'

Committees: membership between parties which determine the success of future 're-elections' (reproduction).

Questions for discussion:

- Does the introduction of concepts like congresses, parties and committees bring insightful new aspects about the evolution of eusociality?

- What is the role of 'mavericks' in the evolution of cooperation?

- Should colonies be designated as organisms only when defending group selection?

-What are the advantages of considering an insect colony as an organism (or superorganism)? Is it still a valid idea?