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Capturing the Superorganism or Reviving a Monster?

"The beauty of the dream vanished, and breathless horror and disgust filled my heart," so said Victor, a well established scientist from the upper east side of Transylvania as he witnessed life cross the threshold of the lifeless and into his newly created monster – Frankenstein!

Well, OK – maybe quoting from Mary Shelly’s Frankenstein is a bit over-the-top, but a recent article published in the *Journal of Evolutionary Biology* has made me question whether or not Andy Gardner and Alan Grafen have created a monster of their own – one that they may eventually come to regret.

In a recent article (available as a PDF [Here](#)) titled “Capturing the superorganism: a formal theory of group adaptation,” Gardner, a Royal Society University Research Fellow, and Grafen, a Professor at Oxford University widely known for his work in statistics (most memorable to me for his mathematical modeling of *Zahavian Handicaps*), define, describe and quantify group adaptation and group selection as functional modes of natural selection.

On one hand the article is innovative in that it takes steps to cleanly differentiate between often befuddled concepts, like “kin selection” versus “group selection” and various interpretations of “fitness;” it also empirically formalizes (and limits) the group adaptation theory - indeed it lifts the theory to new heights. However, on the other side of the coin, the article (antagonistically in my mind) compounds any preexisting misunderstanding of these concepts by arguing for even greater expansion of analogy.

For example, the article tediously - though accurately - makes distinctions between various measures of fitness, including inclusive fitness, relative fitness, within-group fitness, personal fitness, between-group fitness, individual fitness and indirect fitness; but then, rather than provide simplicity and clarity to this dizzying collection of measurement methodologies, the article uses them as a foundation in support of further artificial constructs – namely groups as individual units or actors in natural selection.

The superorganism enters… [As a side note, there is a good E.O. Wilson interview (audio file) at NPR’s Science Friday website from last December in which he discusses the superorganism concept and his book of the same title – [HERE](#)]

Through their delineations, Capturing the Superorganism’s authors intentionally reveal that both the individual organism and the “group” as focal points of adaptation are only ‘maximizing agent’ analogies and that
both are only intermediaries to ever fluctuating gene frequencies. Unfortunately, rather than arguing for a more reductive measure of selection, an all encompassing fitness-model or perhaps even a gene-centered perspective, they instead suggest viewing the process at a greater scale and wider focus.

Ironically, the article opens with a quote from Richard Dawkins' Extended Phenotype;

“I have characterized inclusive fitness as 'that property of an individual organism which will appear to be maximized when what is really being maximized is gene survival'... One might generalize this principle to other 'vehicles'. A group selectionist might define his own version of inclusive fitness as 'that property of a group which will appear to be maximized when what is really being maximized is gene survival'!

This excerpt, and the context in which it is constructed, clearly makes an argument against viewing the individual organism as a unit of selection and implies that any unit above that of the gene is so artificial as to be considered arbitrary. Key to this idea is the phrase "will appear to be maximized," which means that it is not truly being maximized, but rather it is a merely an extension of the gene – a vehicle. A “vehicle” is precisely what a “group” represents, a vehicle composed of multiple smaller vehicles – all of which have a gene behind the wheel.

From the abstract: “Adaptation is conventionally regarded as occurring at the level of the individual organism.”

Perhaps individual organisms are ‘conventionally regarded,’ but not accurately so... Individual organisms may be units of reproduction, but they are not replicators. Genes lay at the core of all phenotypes; morphological, behavioral, social or otherwise - is it really convenient to think of natural selection as occurring at the level of the individual organism? Most successful organisms aren’t replicated in their entirety; rather it’s the successful, or surviving, genes contained within their DNA that are passed on with an increased probability of contributing to the genome of future generations. Genes are passed on, not whole organisms; if the analogy is not “true” for individuals, why up the ante and recommend adopting a level of biological organization that is even higher than an individual?

The authors admit that the Group Maximization Analogy (GMA) does have limitations;

“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.”

According to the authors, group adaptation seems a best fit in those situations in which individual members have identical genomes (i.e. are “cloned”) or in those scenarios where competition is repressed (i.e. is “policed,” or controlled by an external agent). Wouldn’t these situations, one in which like-vehicles “strive” to move like-genes, and one in which a dominant phenotype exhibits some level of control (policing or chemical control via pheromones) over a less-dominant phenotype, also represent strong cases for a gene-centered, or an Individual Maximization Analogy?

Considering that within-group selection (i.e. genes by way of individual
organisms) is inevitable, are there any cases, or models for group-
selection that take this into account?

“We have found no formal justification for group
adaptationism in any scenario in which within-group
selection is permitted. Obviously, no real-world species will
perfectly embody the ideal of zero within-group selection.”

OK, doesn’t such a finding impair the group model as an inclusive theory?

“...we emphasize that this is not sufficient grounds for
abandoning the notion of group adaptation in evolutionary
biology.”

Why not?

“The theory of individual-level adaptation is similarly based
upon limiting assumptions, such as unbiased genetic
transmission, which are not expected to be perfectly realized
in any species; yet, it enjoys huge experimental and empirical
success.”

True, however the individual-level adaptation model is also a
“maximization analogy,” used as a tool, artificially constructed to
demonstrate, measure and communicate what in actuality is occurring at a
lower level - the level of the gene. Is that the purpose of the GMA,
simply an additional tool to be used in exhibiting the effects of genetic
frequency, and if so what is the benefit of up-scaling from the level of the
organism to that of the group, or extending the phenotype to greater
distances, bearing in mind that at the very least the individual is the unit
of reproduction and any expansion of analogy is likely to cause even
greater confusion?

“Our emphasis has been on formality and not generality –
there is much work to be carried out to establish whether
other scenarios will admit a group adaptationist view of
social evolution. In the meantime, we suggest that it is safer to
view social adaptations as occurring at the level of the
individual organism, where they function to maximize
inclusive fitness.”

Gardner et al. (2009). Capturing the superorganism: a formal theory of
group adaptation. *Journal of Evolutionary Biology* DOI: 10.1111/j.1420-
9101.2008.01681.x

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