The evolution of altruism: Two ways in which selfishness generates Superorganisms

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Darwin openly worried about the evolution of extreme altruism in the eusocial insects, as it seemed to pose a serious problem for his natural selection theory. So profound is the level of costly cooperation in advanced eusocial colonies of ants, bees, and wasps, that the biologists Wheeler [1] and Emerson [2] viewed such societies as virtual "superorganisms," in which the highly altruistic workers were akin to somatic cells and the queen comparable to the gonads of a single organism. Any successful evolutionary theory of altruism must be capable of explaining the evolution of anything resembling a superorganism, defined broadly here as a group of organisms organized into a higher-level unit that develops and behaves much like an individual organism by exhibiting extensive internal cooperation.

A first challenge is to characterize exactly what is meant by the phrase "a higher-level unit that behaves *much like* a higher-level organism". Fortunately, modern evolutionary biology can provide a precise metric for this notion: A higher-level unit can be usefully viewed as a "superorganism" to the degree that its subunits behave and interact so as to appear to maximize the group's reproductive output at the expense of each subunit's share of that total output. This criterion can even be made quantitative and empirically measurable by asking what fraction of a subunit's energy or time budget is allocated to increasing the overall group reproductive output at the expense of its share of that output. Note that, under this conception, the biological universe is no longer dichomotized into "superorganisms" versus "non-superorganisms" but rather the "superorganismness" of a group is seen as being described by a point along a continuum ranging from the complete lack of to a perfect overlap in the genetic interests of the interacting component individuals.

How could a group of organisms possibly evolve to the upper extreme of the superorganism continuum? This is the empirically fruitful question that has occupied theoretical evolutionary biologists for several decades. The answer usually given is that *kinship* provides the key: Positive genetic relatedness among interacting individuals can promote superorganism evolution through kin selection because the genes promoting intra-group cooperation are indirectly promoting copies of themselves by aiding relatives, which tend to possess copies of those same genes [3]. Indeed, all of the most spectacular examples of "superorganismic" insect societies such as honey bee, termite and ant societies involve groups of kin, usually daughter workers helping their mother queens [4,5].

It is now overwhelmingly accepted that genetic relatedness is a key factor predisposing the evolution of altruism, but it is less widely understood that high relatedness between workers and breeding females does not necessarily remove the incentive for worker selfishness. For example, in almost all Hymenoptera (ants bees and wasps), workers are more closely related to their potential sons than to the queen's sons (i.e., their brothers). This raises the question of why workers do not fall into an all-out tug-of-war over male production instead of altruistically channeling resources to the queen for the production of brothers.

Some new evolutionary mechanism is needed to suppress such worker selfishness.

Perhaps counter-intuitively, the two such selfishness-suppressing mechanisms that have begun to receive both theoretical and empirical attention are those involving other kinds of genetic selfishness! The first focuses on *policing* and the second focuses on *competition among colonies*.

The policing mechanism works like this: Although workers are more closely related to sons than brothers, they are less closely related to other workers' sons than to brothers if the mother queen on average mated with more than two fathers, as is the case with the honey bee, for example [6]. In this case, workers should police against male-egg production by other workers. Indeed, workers colonies eat the eggs of other workers but not those of the queen [6]. This means that the worker's selfish avenues for reproduction are shut down, funneling their efforts toward queen helping and presumably propelling the society forward along the superorganism continuum.

The policing model for cooperation enforcement still has two problems. First, it does not explain why queens initially dominate egg production. Why don't workers collect resources and then just use them to reproduce personally instead of transferring them to the queen for reproduction? Second, since policing itself is costly, does policing really yield a net increase in colony output or just decrease it further? The existing worker policing models don't allow for the co-evolution of policing and selfishness, so they can't really resolve the latter question.

I shall first present a policing model based on "tug-of-war" game theory that shows the net result of policing is indeed a dramatic gain in colony output, i.e., a shift of the society to the upper extreme of the super-organism continuum. This occurs because two genetically selfish acts, stealing from the queen and policing against such stealing, turn out to be almost mutually annihilating. Moreover, the model explains why queens initially receive resources from the workers instead of hoarding them for personal reproduction. Quite unexpectedly, the model also serves as an explanation for (1) cooperation among cells of multi-cellular organisms having early gamete determination and (2) cooperation among non-relatives contributing resources to an equally divided community pot.

The policing model for the promotion of superorganisms is attractive, but not completely general, because in many insect societies (those in which queens have an effective male mating frequency less than two), workers are *not* more closely related to brothers than to other workers' sons (nephews). What shuts down worker selfishness in these societies, as worker reproduction tends to be very infrequent?

A recent idea in the social insect research world is that superorganisms can evolve through inter-group competition. In particular, two-tiered tug-of-war game theory shows that resource competition between groups can greatly increase a society's degree of "superorganismness" by favoring the suppression of any within-group selfishness that would compromise a group's ability to compete with other groups [7], and fierce inter-group competition for food and high-quality nest sites may lie behind the evolution of the highly elaborated patterns of cooperation and communication within ant societies [8]. Other ecological factors also facilitate superorganism evolution, such as those favoring joint protection from predation and or exchange of information in uncertain foraging environments; in both cases, overly selfish individuals investing too much energy in increasing their relative protection within a group or their relative share of the group's resources may excessively reduce the group's overall ability to deter a predator or find widely scattered food. Such ecological factors in concert with high genetic relatedness appear to underlie the evolution of the high superorganismness in the termite-like eusocial mammal, the naked mole-rat [9].

In sum, within-group policing and inter-group competition, each a manifestation of genetic selfishness, appear to be critical to shutting down avenues for personal reproduction within insect societies and predisposing the evolutionary appearance of superorganisms (and, indeed, actual organisms!) under certain conditions. It seems likely that these are unifying principles not only for social insect evolution but for all social animals including humans and even multicellular organisms and genes within genomes.

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