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NEWS AND COMMENTARY

Evolutionary theory
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Is group selection necessary to explain social adaptations in microorganisms?

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The concept of altruism serving an evolutionary purpose has been maligned, but a newly proposed model might provide fresh support for the selfless gene rather than the celebrated selfish gene: but is it realistic?

Altruistic traits – those that seem to harm individuals who possess them but benefit the population – are common. They can be found among microorganisms as well as in higher animals, including man. Wynne-Edwards (1962) suggested that, in the long run, altruistic traits benefit their bearers indirectly by ensuring the survival of the population. He suggested that populations that include altruists survive, while others become extinct. Maynard-Smith (1964) termed this selection process 'group selection' (GS). However, he also pointed out that GS is vulnerable to invading social parasites that do not invest in the welfare of the population. His conclusion was that GS requires a population structure that might not be found in the real world.

A model proposed recently by Werfel and Bar-Yam (2004) supports the original ideas of Wynne-Edwards. The model simulates the evolution of breeding restraint, which is a form of altruism. Altruists restrain their breeding in response to signals given by crowded individuals. The authors claim that their model can explain the evolution of altruism across the board, from cooperation between cell components to that between humans. If their model actually reflected the real world, their findings would constitute a breakthrough. Unfortunately, the assumptions of the Werfel and Bar-Yam model do not fit the real world.

The model simulates a system of consumers and hosts (that is, predators and prey) interacting over 100 000 generations within a grid of 250 × 250 cells, representing territories. Some of the cells contain hosts with consumers, others contain only hosts, and the rest are empty. However, some of the assumptions of the model are unrealistic.

Firstly, the model does not allow consumers (predators) to move into or pass through cells occupied by other consumers. The authors consider this assumption as crucial to their model. However, in the real world, individual consumers do not respect occupied territories (equivalent to the cells in the model). When short of food or breeding opportunities, consumers will try to take over their neighbours' territories or pass through them to breed wherever they can find hosts (food).

Secondly, in the Werfel and Bar-Yam model, consumers signal to other consumers that they are being crowded, and altruistic receivers respond by restraining their reproduction. In the model, all consumers are considered equal. But in real life, individuals are not equal. Dominants might signal to subordinates to stop breeding; subordinates might then stop breeding, but not in order to help their population survive. They will stop breeding either because they are unable to breed, or because they might otherwise be killed or punished by the dominant individuals.

Lastly, according to the model, the host is not allowed to evolve. Unrestrained selfish consumers exterminate their hosts and consequently perish. In the real world, hosts survive only because they evolve anti-predator adaptations – not because the consumers (predators) restrain their reproduction. Consumers usually co-evolve with their hosts and cannot exterminate them. Hosts might even form coalitions with their consumers by subsidizing the less virulent consumer individuals in order to fight the more virulent ones (Zahavi and Zahavi, 1997). Such coalitions (symbiosis) of hosts and less virulent consumers evolve by simple individual selection.

Long-term observations of birds, mammals, and other higher organisms have not encountered populations in which GS seems to operate (Zahavi and Zahavi, 1997; Clutton-Brock, 2002).

On the other hand, as a rule, microbiologists studying social behaviour and signalling of microorganisms interpret their results as models of GS (Shapiro, 1998; Bassler, 2002). Does natural selection, then, evolve social adaptations and signalling in microorganisms in a way different from that in multicellular organisms?

Werfel and Bar-Yam refer to slime molds (*Dictyostelium discoideum*), a unicellular organism whose social behaviour is comparatively well known, as having a social system that conforms to their model. Under stress, slime mold amoebae collaborate to form spores, creating a slug, a multicellular community. Signals produced by the sporulating amoebae inhibit spore formation in about one-fifth of the population. The inhibited amoebae develop into stalk cells that help the sporulating individuals to survive. This would seem to be a perfect example corroborating the model.

However, an up-to-date review on the slime molds (Kaushik and Nanjundiah, 2003) permits the construction of a model of slime mold social evolution based on individual selection arguments.

The fate of an individual amoeba is to a large extent determined by its phenotypic qualities. High-quality amoebae sporulate and low-quality amoebae form the stalk that carries the spores. One of the signals secreted by the sporulating amoebae is DIF-1, a harmful chemical that interferes with the functioning of the mitochondria.

To interpret the phenomenon by individual selection, I suggest that each of the sporulating amoebae invests in the production of DIF-1 in order to protect itself from predation. Many low-quality amoebae are unable to form spores in the presence of DIF-1. They form the stalk while undergoing an active cell death (ACD) (Arnoult *et al*, 2001). In this process, the DNA of the cells is condensed and fragmented in a process similar to the programmed cell death (PCD) of multicellular organisms.

I suggest that some of the fragmented DNA has a chance to transfect the germinating spores of the survivors. Hence, ACD might be an alternative strategy for reproduction. Amoebae that cannot survive as spores try to pass at least some of their DNA to future generations. This is a strategy that stands a very small chance of success. But a small chance is better than none at all. Natural selection can exploit such minute chances to select for the

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complex social mechanisms exhibited in slime molds and other organisms. In summary, it is possible to suggest that slime molds evolved social and signalling behaviour through Individual Selection.

GS models provide the researcher with the comforting suggestion that traits that seem to harm their bearers might have evolved for the sake of the group. However, such models are superfluous once traits are explained by the direct advantage they afford their bearers. Moreover, there is a major benefit that arises when one formulates hypotheses based on Individual Selection to explain particular cases of apparent altruism: such hypotheses stimulate a search for missing mechanisms that might otherwise remain unexplored.

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Further Reading suggested by the Editor

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