## Explaining cooperative groups via social niche construction

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Cooperative behaviours can be defined as those that benefit others at an apparent cost to self. How these kinds of behaviours evolve has been a topic of great interest in evolutionary biology, as the Darwinian paradigm seems to suggest that nature will be "red in tooth and claw" and that we would not expect one organism to evolve to help another. The evolution-of-cooperation literature has therefore generally been about showing how the altruism involved in these cases is only apparent (see Bergstrom 2002 for an excellent review). Consider kin selection, in which interactions are more likely to occur between related individuals. The cost of altruism to the individual is real but, having identified the correct score-keeping level as the genetic one, it turns out that the cooperative act is not costly but profitable.

More generally, successful explanations for cooperation rely on the presence of a population structure that clusters cooperators together, such that they enjoy the benefits of each others' actions. However, the question that has been left largely unaddressed is how does this structure itself evolve? If we want to really explain why organisms cooperate, then we need to explain not just their adaptation to their social environment, but how they came to live in that environment.

Recent work by Powers (2010) and Powers et al. (in press) has addressed this question. They show that social behaviour can exert indirect selection pressure on population structure-modifying traits, causing individuals to adaptively modify their population structure to support greater cooperation. Moreover, they argue that any component of selection on structure-modifying traits that is due to social behaviour must be in the direction of increased cooperation; that component of selection cannot be in favour of the conditions for greater selfishness. Powers et al. then examine the conditions under which this component of selection on population structure exists. They argue that not only can population structure drive the evolution of cooperation, as in classical models, but that the benefits of greater cooperation can in turn drive the evolution of population structure: a positive feedback process that they refer to as social niche construction (after Odling-Smee et al. 2003).

Maynard Smith and Szathmary (1995) note that most of the big unanswered questions in biology are not about how a particular behaviour is selected for at one level of organization but about the emergence of whole *new* levels of organization, e.g., the transition from single- to multi-celled organisms, or from solitary insects to eusocial colonies. Any satisfactory account of these transitions must explain how the individuals came to live in a population structure that supported high degrees of cooperation, as well as showing that cooperation is individually advantageous given that structure. The social niche construction process identified by Powers et al. can explain some of the major transitions, by showing how a new selective level can begin through evolution of individual characters, such as group size preference or dispersal tendency. The potential emergence of reliable cooperation via the co-evolution of individual cooperative and population-structuring behaviours demonstrates that groups of cooperating agents can

create an environment in which they become so "locked in" to their group identity that the group warrants redescription as an individual in its own right. Consider the move from independent protozoans, to an intermediate cooperative stage as in slime moulds, to fully multi-cellular animals. Such creation of population structures that support cooperation parallels negotiation of a social contract.

What are the philosophical implications of this perspective for understanding and explaining human social behaviour? On the one hand, it gives respectability and unique explanatory value to group-selectionist accounts. Explaining the origin of within-group cooperation and the origin of the groups themselves become part of the same project, which in turn means that we cannot understand social and cooperative behaviour in humans without understanding human population-structuring traits, e.g., living in family groups, group fission-fusion behaviours, migratory behaviours, etc.

What will the explanations we seek look like? de Pinedo and Noble (2008) have argued that the description of evolved behaviour cannot be exclusively in mechanistic terms: we need both explanations that focus on an agent's interaction with its environment, and explanations that focus on the physical or computational enabling conditions of such an interaction. In a context in which what counts as an agent is taken for granted, de Pinedo and Noble argue that both agent and sub-agent level explanations will be required. The perspective being outlined here forces an expansion of that position and reminds us that agency is not to be taken for granted; that it emerges from a lower level of organization after a history of selection brings simpler entities together in a coherent cooperative whole. The implication is that truly multilevel explanations will be necessary in the area of social behaviour. We explain the origin of the multi-cellular organism as the result of a cooperative merger of single-celled organisms, and we explain the origin of a super-organism such as an ant colony in a similar way. At each transition, the autonomous agents of the previous level become component mechanisms in the next, but no explanatory level can be entirely done away with.

A human being is an example of a multi-cellular organism with a highly developed social aspect, occupying an intermediate point between radical individual independence and total group cohesion. To fully explain human behaviour, we need to know about the cellular machinery that enables personal-level agency. But we also need to know how human machinery fits together into families, communities and nations that will, at least partially, have their own emergent goals and purposes: "partially" because we are not yet a super-organism, of course.

In conclusion, the perspective we outline suggests a view of the social contract as not at all unique to Hobbesian rational agents who have become tired of an insecure and violent lifestyle. Instead the ongoing negotiation of the social contract amongst ourselves can be seen as echoing earlier, now-successfully-concluded negotiations between the entities that became our genes and then our cells.

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