Evolutionary Psychology

www.epjournal.net – 2012. 10(1): 45-49

Book Review

Group Selection Theories are Now More Sophisticated, but are They More Predictive?

A review of Samuel Bowles and Herbert Gintis, *A Cooperative Species: Human Reciprocity and its Evolution*. Princeton University Press: Princeton, NJ, 2011, 288 pp., US\$35.00, ISBN #978-0-691-15125-0 (hardcover).

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Human beings are unique among species in their ability to cooperate in large groups of genetically unrelated individuals, and in this book, Samuel Bowles and Herbert Gintis attempt to account for the origins of this ability. The authors specialize in the use of formal models and agent-based simulations in order to precisely specify their theories of cooperation, and they often draw on studies conducted in hunter gatherer societies and in experimental economic laboratories for evidence that they find relevant to evaluating these theories. The book is a valuable review of these anthropological and economic literatures, and a thorough showcase of the authors' expert formal theorizing about how cooperation may have evolved. However, I often found myself disagreeing with the authors' focus on group selection as an explanation for human cooperation, and with their views on how well the empirical findings provide support for group selectionist theories.

The authors believe that cooperation is best explained by theories of multi-level selection. They do not overlook the individual as a vehicle of selection; their version of multi-level selection focuses on both individuals and groups. However, they do not believe that human cooperation could have evolved via individual-level adaptation alone, and they explain its evolution ultimately in terms of the survival advantages that it brought to whole groups. To me it seems premature to resort to the group selectionist aspects of this view. It's possible that a theory that combines group and individual selection will ultimately lead to a more predictive science of human cooperation than could be achieved via an individual-level adaptationist theory alone. Currently, however, it's not clear what extra predictive power we gain from evoking biological group selection.

The debate in biology about group selection is not new, of course. As unfashionable as group selection became in the decades following the publication of Williams (1966), it has been resuscitated to some extent in more recent years (e.g., Wilson and Wilson, 2007). Nevertheless, adaptationist researchers in biology and psychology continue to regard

individual-level biological adaptation as standard, and group-level biological adaptation as extraordinary, and to assume that when there is a conflict between these two levels, the individual level will prevail. The individual-level perspective has proven highly predictive and productive in human evolutionary psychology, and the same cannot be said—at least not yet—for the group-level perspective. That's why most evolutionary psychologists still agree that "adaptation should be attributed to no higher a level of organization than is demanded by the evidence" (Williams, 1966, p. v).

Does the evidence of human cooperation in groups demand a group selectionist explanation? For the most part, it's not clear that it does, because members of cooperative groups generally seem to act in ways that would have been individually-adaptive in ancestral environments (Price, 2011; Price and Johnson, 2011). Bowles and Gintis are correct, of course, to emphasize the groupishness of humans, and the vital importance of group cooperation in human ancestral environments. But contributing to group endeavors is a fundamental way in which individuals acquire resources and social status, and these are things that obviously promote individual fitness. Bowles and Gintis are also correct to focus on war as a selection pressure (they argue that it was a key force of intergroup selection), but this emphasis is equally compatible with the individual-level view; individual-level adaptationists have been interested in war since the early days of modern human behavioral biology (Alexander, 1979; Chagnon and Bugos, 1979; Symons, 1979).

The view that group selection is needed to explain most human cooperation seems inconsistent with the fact that over the past several decades, most successful research on this cooperation has theorized that it is produced by individual-level adaptations (Price, 2011; Price and Johnson, 2011). The most influential and predictive theories of group cooperation have assumed that people contribute to group efforts in order to acquire resources for themselves, and that the main obstacle to successful cooperation is that members often do better individually by contributing less, or by consuming more, than would be optimal for group success (Hardin, 1968; Olson, 1965). These theories have served as the basis for an immense body of research which has demonstrated their predictive power; a quick overview of this research follows. Individual group members tend to acquire return benefits via their cooperation, by engaging in behaviors that can be regarded as n-person reciprocity or conditional cooperation (Fischbacher, Gaechter, and Fehr, 2001; Tooby, Cosmides, and Price, 2006), competitive altruism (Hardy and Van Vugt, 2006; Roberts, 1998), and status-for-altruism transactions (Price, 2003, 2006); they free ride frequently, when they can get away with it (Fehr and Gaechter, 2000); they monitor other members' contribution levels so that they can detect and punish free riding (Ostrom, 1990; Price, 2006), and they experience more punitive sentiment towards free riders when they are more individually vulnerable to being free ridden (Price, 2005; Price, Cosmides, and Tooby, 2002); they engage in partner choice, which allows highly cooperative individuals to assort positively and thus avoid being exploited by free riders (Barclay and Willer, 2007; Page, Putterman and Unel, 2005); and they engage in more cooperation and third party punishment when they can acquire more reputational benefits from doing so, or when they detect cues that their actions are being monitored (Bateson, Nettle, and Roberts, 2006; Kurzban, DeScioli, and O'Brien, 2007; Milinski, Semmann, and Krambeck, 2002).

Bowles and Gintis' main argument for the predictive inadequacy of individual selection is based on experimental game results which demonstrate that participants continue to cooperate to some extent, even after experimenters have attempted to eliminate all individual-level benefits (e.g., by organizing a game that, because it is anonymous and one shot, rules out direct and indirect reciprocity). The main problem with this suggestion has been pointed out repeatedly (Trivers, 2004; Burnham and Johnson, 2005; Hagen and Hammerstein, 2006; Price, 2008): Experimental economic games are not ecologically valid contexts from which to draw conclusions about how humans are adapted for one-shot, "anonymous" social activity. One-shot games are easy enough to orchestrate in experimental labs, but what would the analogue be in ancestral environments? Ancestrally, no experimenter was present to enforce the one-shot nature of an interaction, so social interactions were intrinsically iterative; for instance, if you cheated somebody, he might retaliate (Trivers, 2004). There's no real reason, therefore, to expect the human mind to be adapted to a one-shot interaction context, or to process such experimental interactions as if they were truly one-shot. Further, for a behavior to be perceived as anonymous in the ancestral past, the actor would need to feel sure that no one else could consciously observe the act (e.g., she would need to be alone in the middle of the forest). This is nothing at all like the environment of an experimental lab, where you may be surrounded by other participants, you believe you are interacting with other conscious participants, and you know that your behavior is being recorded and scrutinized by researchers. Even if a participant consciously believes that his behavior is anonymous, his semi-autonomous adaptations producing his cooperative behavior may not act as if they believe this.

In sum, results from experimental economics games can be highly illuminating and useful for many purposes, but just like any kind of behavioral data, they have limitations. It is doubtful that experimental economic results actually reveal much of anything about how people are adapted for one-shot anonymous interactions, and they should not be regarded as evidence about the relevance of the individual as a vehicle of selection in ancestral environments.

I also found myself a little distracted by what seemed like moralistic overtones in the book's prose style. For instance: "The moral, generous, and civic-minded predispositions documented... in the pages that follow show that evolution can not only foster self-interest but also promote the generous and ethical behaviors that help us escape the prisoner's dilemma and avert the tragedy of the commons, and that permit us to sustain the hope for a society committed to freedom and justice for all" (p. 7). The message seems to be that "self-interest" (or more accurately, adaptations designed to promote individual fitness) could never lead to such desirable outcomes as generosity, ethical behavior, freedom, and justice; therefore, unless we want to claim that such great things are impossible or illusory, we had better accept a group selectionist view. One problem here is that all such virtues are in fact entirely compatible with individual-level theories of cooperation (e.g., reciprocal altruism, indirect reciprocity, n-person reciprocity, partner choice and positive assortment, costly signaling), and there's no good reason for suggesting otherwise. Another problem is that the language used by Bowles and Gintis seems to imply, inappropriately, a kind of moral obligation on the part of the reader to accept the group selectionist view.

In summary, the book is valuable both as a review of the anthropological and economic literatures on cooperative behavior, and as an impressive collection of formal models for how such behavior may in theory have evolved. But we have to remind ourselves that formal models are just as theoretical as verbal models. People sometimes seem to treat the output of formal models as data in and of itself, and to overlook that the data we are actually trying to predict are those describing the cooperative psychology of real humans. To the extent that any formal model allows us to make unique, accurate predictions about this psychology—under ecologically valid circumstances—it should be regarded as indispensible. For the time being, however, individual-level theories seem to outshine group selection when it comes to illuminating human biological adaptations for cooperation.

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