Biological markets explain human ultrasociality

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Abstract: The evidence Gowdy & Krall (G&K) provide is more consistent with a biological markets explanation of human ultrasociality than a group selection explanation. Specifically, large-scale societies provide a better biological market for cooperation than do small-scale societies, allowing individuals to increase their fitness. Importantly, many of the quality-of-life costs G&K discuss (e.g., patriarchy) are not fitness costs.

Many of the costs Gowdy & Krall (G&K) describe for individuals in agricultural groups (e.g., patriarchy) are not *fitness* costs. Instead, they are *quality-of-life* costs. The authors themselves demonstrate the distinction between fitness and quality-of-life costs quite nicely when they observe that: "Women in agricultural societies had many more offspring than hunter-gatherer women, but their lives were shorter and arguably less satisfying" (target article, Note 27).

Separating fitness costs from quality-of-life costs is important because only fitness costs matter for natural selection: Individual-level selection will favor individuals who have more offspring over those who have fewer offspring, even if the individuals who have more offspring also have shorter and less satisfying lives. By conflating fitness costs and quality-of-life costs, G&K overestimate the evolutionary costliness to an individual of living in an agricultural group. This overestimation leads to the (incorrect) conclusion that the costs to individuals often outweigh the benefits. This conclusion leads to the (incorrect) inferences that individual-level selection is insufficient to account for human ultrasociality, and that group-level selection must be involved.

Although group selection is not involved in human ultrasociality, we do agree with G&K that agriculture and human ultrasociality are related. As G&K note while invoking Adam Smith, there are "efficiencies inherent in expanding the division of labor" (sect. 3.2, para. 5). Thus, individuals in societies with more division of labor have access to more resources than individuals in societies with less division of labor.

To this picture, we add that the additional resources are disproportionately available to the individuals who are trusted as the best cooperators. Using a common metaphor in biology, individuals compete with each other in a "biological market" to be chosen as trustworthy interaction partners: although selfish behavior may lead to higher short-term rewards, a good moral reputation can lead to higher long-term rewards from continued collaborations (André & Baumard 2011; Noë & Hammerstein 1994). In this way, the pressure exerted by the existence of partner-choice can promote high levels of prosocial behavior (Barclay 2013; Debove et al. 2015). In sum, the extreme division of labor in agricultural societies provides new opportunities for cooperative individuals to engage in more productive collaborations and to trade for mutual individual benefit.

According to our biological markets account, large-scale societies spread *not* because they contain individuals whose prosocial behaviors entail sacrificing their own welfare for the benefit of the group, but because they contain individuals whose prosocial behaviors entail access to cooperative opportunities that increase their *own* fitness. Thus, individuals in large-scale societies have higher average fitness (Diamond 1997). This process has been described as a form of "cultural group selection" in which a group has higher fitness because each *individual* has higher expected fitness (Henrich 2004). However, to avoid confusion, the phrase "group selection," with its typical implication that individuals take costs to promote group welfare, is best avoided (e.g., Pinker 2012).

One of the reasons a group selection account of the switch to agriculture may be attractive is that some individuals in agricultural societies have lower fitness than they would have in a small-scale society. An agricultural group with a relatively large number of individuals having no offspring and some individuals having very many offspring invites the hypothesis that the worse-off

individuals are sacrificing their welfare for the group. However, our biological markets account is compatible with some individuals in a large-scale society having low reproductive success. Given that average fitness is higher in large-scale societies, this situation would come about when there is higher *variability* in the fitness of individuals (for an overview of "reproductive skew" across many species, see Clutton-Brock 1998). Higher variability in reproductive success makes living in an agricultural society a high-risk but potentially high-reward situation, with an overall higher expected fitness for each individual. Those individuals who end up with lower reproductive success do not have a prosocial adaptation that causes them to sacrifice for the group – they simply ended up at the losing side of the high-risk–high-reward spectrum.

Regarding autonomy, our biological markets account is the reverse of what G&K describe: Whereas they characterize the specializations pursued by individuals in an agricultural society as disadvantageous losses of autonomy, we characterize opportunities to pursue specializations as advantageous gains in collaborative opportunities. The number of ways in which a person can "make a living" is vastly larger in large-scale societies than in small-scale societies. Note that this explanation is specific to the human switch to agriculture: Whereas it is the case that behaviorally flexible humans have more options for engaging in productive (fitness-increasing) activities when in an agricultural society, insects with morphologically defined roles do have less autonomy than individuals without such specialization.

Furthermore, as societies increase in size, the relatively higher division of labor first associated with the switch to agriculture can become further intensified from a positive impact of societal structure on moral psychology. Humans begin with a moral psychology that is particularly focused on maintaining fair relationships for collaborations (Baumard & Sheskin 2015), a feature not present in even our closest evolutionary relatives (e.g., Sheskin & Santos 2012). Once large-scale societies emerge, the benefits available from cooperative activities increase, and so the value of a cooperative reputation increases (Delton et al. 2010). Finally, as societies grow and individuals gain more wealth and therefore long-term security, individuals are free to focus more on the best long-term strategies (such as moral behavior to support cooperative interactions) rather than on short-term strategies that maximize immediate payoffs (Baumard et al. 2015; Nettle et al. 2011; Sherman et al. 2013).

In sum, the evolutionarily relevant costs of living in an agricultural group are lower than G&K expect (because only fitness costs should be included in the calculation), and the fitness benefits of living in an agricultural group are higher than G&K expect (because more division of labor is associated with greater returns from a better biological market for cooperation). The individual-level benefits of living in a large-scale society with an advanced biological market for cooperative partners explain the spread of agriculture and ultrasociality.