Even so, available evidence does not support the assertion that the "good of the group" took precedence over individual preferences in agricultural societies. G&K's scenario implicitly assumes agriculture is a collective activity that requires grouplevel coordination on tasks performed for the good of the group. Yet archeological evidence shows that early agriculture was done in small plots belonging to a household who stored their production (except meat) privately, even in very large settlements like Çatalhöyük (Bogaard et al. 2009). Evolutionary models further suggest that agriculture coevolved with individual property rights that made it beneficial for individuals to invest in intense cultivation (Bowles & Choi 2013). We think that individual incentives responding to economic institutions, as Adam Smith observed, is a more plausible explanation for task specialization than the group subjugating individuals to act against their own will.

These examples demonstrate that individualist models already capture much of what G&K desire to explain: how rational choices on the part of individuals can accumulate over time to produce undesirable economic and social conditions. Individual fitness benefits are compatible with poor living conditions, and individualist models express this reality better than MLS2.

Ultrasociality without group selection: Possible, reasonable, and likely

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Abstract: It is uncontroversial that humans are extremely social, and that cultures have changed over time. But, the evidence shows that much of the social psychology underlying these phenomena (1) predates the agricultural transition, and (2) is not the result of group selection. Instead, this psychology appears intricately designed to capture social gains when possible in our complex ancestral social ecology.

Like others before them, Gowdy & Krall (G&K) marvel at human sociality. On the one hand, humans cooperate in ways like some other animals on the planet. On the other, humans are unrivalled in the complexity and scale of the societies we build. How should we explain these similarities and differences? The authors suggest that the defining aspects of human sociality are derived from selective forces operating on the group level during the agricultural transition. They point to similarities with other agricultural and social animals and to historical trends to support their argument. Unfortunately, their premises are mistaken and their conclusion false. They have missed the agricultural trees for the forest.

While leaf cutter ants and humans both practice agriculture and create complex societies, the psychological mechanisms that underlie those abstractly similar behaviors are devastatingly different. Seeing this requires stepping beyond the math models of multilevel selection and engaging with the real cognitive problems involved in actually behaving successfully in a complex social environment. While leaf cutter ant society and agriculture are complicated, they are nowhere near the scale and complexity of human society. This difference in outcome exposes the difference in cognitive processing problem each species must solve. Appreciating the complexity of the cognitive processing problems that humans solve so deftly and intuitively to create and participate in societies of billions forces your attention to the questions of what cognitive mechanisms could solve these problems, and how and when they evolved.

G&K grant that hunter-gatherer populations possessed certain preconditions for the shift to ultrasociality when the economic

forces of agriculture took hold. Yet, they ascribe the similarities of otherwise independent cultures to convergent evolution by group selection. This is not the only theory available to explain these data, and without any consideration of alternative theories, it is entirely premature to conclude this theory is correct. Let us consider one alternative now.

Decades of research in evolutionary psychology reveal that the human mind contains a rich social psychology for small-scale group living, including specialized mechanisms for: inferring kinship and cooperating with kin; estimating the value of resources to the self and others; apprehending opportunities for mutual gains in trade; inferring opportunities to exploit and be exploited; perceiving, building, and maintaining coalitions and alliances; identifying free riders on collective actions; achieving and managing coordination; and on, and on, and on (e.g., Cosmides & Tooby 1989; Delton et al. 2012; Krasnow et al. 2015; Kurzban & Neuberg 2005; Lieberman et al. 2007; Thomas et al. 2014; Tooby & Cosmides 1996). Whenever we've looked, this psychology is not unique to the agricultural or industrialized world, but rather appears to be universal in our species (e.g., Sugiyama et al. 2002). This universality should not be surprising when the ancestral social ecology is considered. The social world of our hunting and gathering ancestors was complex, presenting many complicated adaptive problems that the mechanisms above and other adaptations are solutions to. This fact alone - that much of the human social psychological architecture is reliably developing even in the absence of an agricultural context - presents a sizable and likely fatal barrier to G&K's argument.

Further, because environments have always being variable, it should be expected that these mechanisms can be facultatively responsive or otherwise calibratable by relevant environmental parameters (Tooby & Cosmides 1990). This inference has two important implications. First, it gives the expectation that different human cultures in different ecological circumstances will have different norms, behaviors, and social patterns despite having universal cognitive mechanisms. Second, because the ecology can be changed over time by the organisms that occupy it (who can change themselves in response), it is expected that even independent populations that discover a common agricultural niche in parallel will evidence similar evoked cultures. In other words, a clear alternative to the authors' view is simply that human psychology operating in a given ecology, plus time for cultural change are sufficient factors to account for the major patterns of human ultrasociality. It is possible that this alternative is not correct, but G&K do nothing to consider even this most basic alternative hypothesis.

Why are G&K motivated to pursue a group selection (or multilevel selection) argument in the first place? The authors argue that many of the behaviors humans engaged in on the way to and since agriculture appear to degrade our quality of life. They point out the many hazards that emerge as people congregate into larger communities and cities. The point of this detail is for the authors to counterpoint these apparent individual-level costs with group-wide benefits in terms of production, economies of scale, and intergroup competition. G&K use this pattern of costs and benefits to motivate their group selection argument. However, this analysis is fundamentally flawed. The currency of natural selection is reproductive fitness. Selection does not operate on quality of life. Selection can shape motivational mechanisms in the service of reproductive fitness that may attend to facets of quality of life, but only to the extent that those facets reliably predicted reproductive fitness over ancestral environments. If the motivational machinery of agricultural humans pushed them into cities that degraded their quality of life, this by itself is no evidence of group selection in action. Our motivational machinery for diet choice pushes us towards Big Macs and heart attacks, but this is similarly no evidence of group selection in action. You don't need group selection for individuals to act suboptimally; therefore, evidence of suboptimal performance is not evidence for group selection.

Humans are remarkably social; this is not controversial. Multilevel selection is a coherent way of understanding evolution; this is not controversial. Human culture has changed over time and the agricultural revolution marked a major transition in our history; this is not controversial. However, the data do not support the argument that multilevel selection operating on competing post-agricultural groups is responsible for human ultrasociality.

Social insects, merely a "fun house" mirror of human social evolution

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Abstract: Social insects show us very little about the evolution of complex human society. As more relevant literature demonstrates, ultrasociality is a cause rather than an effect of human social evolution.

Yes, it is an obvious example of convergent evolution that some species of insects domesticate fungi and aphids and have, as a consequence, large populations, ecological dominance, a complex division of labour, and diminished individual autonomy. However, no, these analogous traits do not "provide fruitful insights into the evolution of complex human society" as Gowdy & Krall (G&K) claim they do (see target article Abstract). This statement is puzzling, especially when the authors end their paper (sect. 6, para. 7) with a quote from E. O. Wilson (2014), the acknowledged expert on insect societies, that we can learn nothing worth imitating from them. G&K conclude nevertheless that these insect societies provide "a mirror" for understanding the problems posed by our own reliance on surplus production. But, as Wilson says a bit later on in the same book, this sort of reasoning, is "a bit of a stretch" (Wilson 2014, p. 100).

The problem with the analogies presented here is that they do nothing more than illustrate the general point that very different organisms may develop more or less similar solutions to the contingencies of life. It is valuable to demonstrate that evolution can be repeatable, but that lesson is of little use in explaining specific evolutionary developments or issues, when the organisms concerned are as fundamentally different as ants, termites, and humans. Comparisons of shared (homologous) and derived characteristics among closely related species would be far more relevant and instructive for understanding the issues at hand.

The target article's treatment of the concept of ultrasociality is particularly unfortunate in this regard. Ultrasociality is certainly a crucial aspect of the evolution of complex human societies, and it is fair to say that it is inconsistently defined. G&K use this ambiguity to adopt a rather a priori definition (one that suits leaf cutter ants) that limits ultrasociality to agricultural societies with a full-time division of labour. Aside from privileging leaf cutter societies, this obviates the possibility of comparing human sociality with that of chimps, and draws an excessive dichotomy between human foragers and agriculturalists. The subsequent, rather simplistic account of the evolution of complex societies recapitulates, but adds nothing new, to the work of anthropologists writing in the 1970s (e.g., the article's citation of Carneiro 1970). It is clear from that work that the domestication of plants and animals is a necessary but not sufficient cause of the development of stratified state societies. Warfare, itself a complex political process, and environmental factors, are necessary to turn the tribal gardening we still see in parts of the Amazon and New Guinea, accompanied as it is by little social stratification, into the productive basis of states, empires, and the world system. A convincing argument has been made that the entire process of increasing human social scale is driven by the machinations of elites. Their efforts to expand control over people, power, and resources is what leads to transformations of the scale of human society. The development of states and empires is "embedded in the contingencies of culture, nature and history" (Bodley 2003). Surplus production and agriculture is part of that mix (again a necessary but not sufficient condition), not a simple causal variable.

A useful, convincing, and productive discussion of ultrasociality and human evolution has been provided by Tomasello (2014). He, interestingly, also discusses insect societies and human cooperation but notes that such comparisons are only "somewhat analogous." In contrast to the genetic mechanisms at work for insects "human ultrasociality ... is based in some special psychological mechanisms" (Tomasello 2014, p. 187). These were discovered by means of a series of experiments that compared young children and chimps. Presented with a number of tasks that require collaboration to obtain desired food, the chimps responded competitively to establish dominance, whereas the children typically helped each other and divided the food equally even when they were unrelated. This concern with fairness and the development of "shared intentionality" could be ascertained in children as young as nine months of age.

In a further parallel G&K, Tomasello traces the development of shared intentionality in humans to food getting. He opines that our shared intentions, norms, shame, and guilt were an outgrowth of the need for human foragers to hunt and gather in groups. "This conceptual organization is foundational for everything from bidirectional linguistic conventions to social institutions with ... publicly created joint goals and individual roles that can be filled by anyone" (Tomasello 2014, p. 189).

Anthropologists have expended a great deal of time and energy analysing such small-scale societies. One of the few accepted generalisations of social and cultural anthropology is that hunter-gatherers and tribal people use kinship as an organising principle of society. As Chapais (2008) demonstrates, there is a "deep structure" to human social organisation. Bipedalism, pair bonding, and a sexual division of labour accompanied our species' move to its ecological niche. Bilateral kin recognition, exogamy, paternal recognition, female exchange, affinal relations, links between different local groups, and tribal organization likely developed when we split from our nearest primate relatives (Chapais 2008, pp. 303–308). A product of material conditions – of early human foragers rather than farmers - human ultrasociality is a cause, rather than a result, of the development of complex human society. Let's build on the efforts on scholars such as Bodley, Tomasello, and Chapais, and leave the ants to myrmecologists.

Ultrasociality and the sexual divisions of labor

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Abstract: The ultrasociality thesis proposes that the same "mechanistic evolutionary forces" may be at work in the evolution of insect eusociality and human ultrasociality in relation to agriculture. Wide variation in the reproductive division of labor among differing highly social phyla points to a resemblance of outcomes arising from very different selective environments and possibly different forces.

Gowdy & Krall (G&K) propose that the origins of ant eusociality and human ultrasociality are fundamentally economic, necessitated by the demands of agriculture, which led to striking divisions of labor. Among these tasks are those based on sex and reproduction,