

# The economic origins of ultrasociality

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**Abstract:** Ultrasociality refers to the social organization of a few species, including humans and some social insects, having a complex division of labor, city-states, and an almost exclusive dependence on agriculture for subsistence. We argue that the driving forces in the evolution of these ultrasocial societies were economic. With the agricultural transition, species could directly produce their own food and this was such a competitive advantage that those species now dominate the planet. Once underway, this transition was propelled by the selection of within-species groups that could best capture the advantages of (1) actively managing the inputs to food production, (2) a more complex division of labor, and (3) increasing returns to larger scale and larger group size. Together these factors reoriented productive life and radically altered the structure of these societies. Once agriculture began, populations expanded as these economic drivers opened up new opportunities for the exploitation of resources and the active management of inputs to food production. With intensified group-level competition, larger populations and intensive resource exploitation became competitive advantages, and the “social conquest of Earth” was underway. Ultrasocial species came to dominate the earth’s ecosystems. Ultrasociality also brought a loss of autonomy for individuals within the group. We argue that exploring the common causes and consequences of ultrasociality in humans and the social insects that adopted agriculture can provide fruitful insights into the evolution of complex human society.

**Keywords:** agricultural transition; division of labor; major evolutionary transitions; multilevel selection; surplus production; totipotency; ultrasociality

*But the mere fact that organisms and societies evolve by various selective mechanisms is not the whole (superorganism) story, for it does not tell us the fundamental reasons that ants and termites live social rather than solitary lives. Those reasons are to be found in economics—in the science that concerns itself with how resources are utilized and allocated.*

— Michael Ghiselin (2009, pp. 243–44)

## 1. Introduction

With the widespread adoption of agriculture some 10,000 years ago, human societies took on some important characteristics shared with social insects—ants and termites in particular—that also engage in the production of their own food. These characteristics represented a sharp break in the evolutionary history of these lineages and led to two important outcomes: (1) Ecosystem domination as a product of a dramatic increase in population size and much more intensive resource exploitation; and (2) the suppression of individual autonomy as the group itself became the focus of economic organization. The evolution of agriculture in fungus-growing ants and termites, and in human societies, is an example of convergent evolution—the independent evolution of similar characteristics in species not closely related. In terms of genetics, ants, humans, and termites could hardly be more different. Yet, in all three lineages similar patterns of economic organization emerge

through similar selection pressures. We use the term *ultrasociality* to refer to these lineages, and we address the question of its origin through the fundamental question of evolutionary biology: “Where did something come from and what were the selection pressures that favored its spread?” (Blute 2010, p. 13). We follow Campbell (and Darwin) in insisting that the evolution of human ultrasociality is a consequence of some of the same mechanistic (i.e., not consciously directed) evolutionary forces that govern other species. Foley (2008, p. 164) calls the adoption of agriculture by ants and humans a case of “convergent selection.” In the struggle to survive, agricultural ants and agricultural humans face similar problems and selection tends to favor similar solutions. We fully recognize that the details of ultrasociality in humans play out in ways that are mediated by human intentionality and cultural norms.

### 1.1. What is ultrasociality?

There is no general agreement in the use of the term *ultrasociality*, partly due to the lack of consensus in the biological and social sciences in classifying social behavior. The many definitions of ultrasociality are conflicting, even among the same authors. For example, Campbell sometimes classifies ants, humans, and termites as ultrasocial (Campbell 1982) but other times refers to ultrasociality as

large-scale cooperation among unrelated individuals (Campbell 1983; see also Turchin 2013). This seems to restrict ultrasociality to humans, but remarkable examples of non-kin altruistic behavior in non-human populations are being documented, for example, the recent discovery of cooperative brood raising by two different species of spiders (Grinsted et al. 2012). E. O. Wilson (1975), although he does not use the term *ultrasocial*, considers humans to be one of the four pinnacles of social evolution, along with colonial invertebrates, social insects, and non-human mammals. Richerson and Boyd (1998) use the term *ultrasocial* to describe humans after agriculture, but do not include social insects in their definition. Following Wilson and Hölldobler (2005, p. 13368), we reserve the term *eusocial* to refer to social insects and a handful of other species having an advanced level of colonial existence and a sharp division between sterile and reproductive castes.<sup>1</sup>

We begin with Campbell's (1982, p. 160) definition of *ultrasociality*:

Ultrasociality refers to the most social of animal organizations, with full time division of labor, specialists who gather no food but are fed by others, effective sharing of information about sources of food and danger, self-sacrificial effort in collective defense. This level has been achieved by ants, termites and humans in several scattered archaic city-states.

We confine our discussion of ultrasociality to human, ant, and termite societies that actively manage food produc-

tion.<sup>2</sup> The extent of differentiation, collaboration, and cohesion of agricultural social species place them in a qualitatively different category. This demarcation is, of course, somewhat arbitrary, and we recognize the antecedents of both managed agriculture and the specific characteristics of ultrasocial societies. We argue that the change from foraging wild plants and animals to the active management of agricultural crops was a particularly powerful impetus for the human transition to ultrasociality.<sup>3</sup> To clarify our use of this term, by our classification leafcutter (attine) ants would be both eusocial and ultrasocial. Complex human societies with agriculture would be ultrasocial but not eusocial. Human hunter-gatherer bands are not ultrasocial, although the antecedents of ultrasociality are clearly present in these societies, as we discuss below. A striking difference between insects and humans is the presence of non-reproductive castes in the former.<sup>4</sup> We recognize that the term *ultrasocial* is controversial, but we insist that human and insect societies that practice managed agriculture are fundamentally different from the small-scale foraging societies from which they evolved.

## 1.2. Agriculture and ultrasociality

Mueller et al. (2005, p. 564) list the defining features of agriculture as: (1) habitual planting, (2) cultivation, (3) harvesting, and (4) nutritional dependency on the crop (obligate in insects and effectively obligate in humans). The active cultivation of crops calls forth a similar configuration of production in dissimilar species. The production of crops is a physical process entailing similar kinds of economic efficiencies. The prime examples of agricultural insect societies are the attine ants of the New World tropics (comprising about 200 different species) and the fungus-growing termites of the Old World tropics (comprising more than 300 species). All of the existing species of fungus-growing ants and termites apparently arose from a single common ancestor for each line (Aanen & Boomsma 2006; Mueller & Gerardo 2002). Old World termite agriculture arose between 24 and 34 million years ago, and New World ant agriculture appeared about 50 million years ago. These two independently evolved insect agricultural systems and human agricultural systems are examples of *mutualistic symbiosis*, that is, reciprocally beneficial relationships between genetically distant species. Aanen and Boomsma (2006, p. R1014) write of the agricultural transition in fungus-growing ants and termites: "No secondary reversals to the ancestral life style are known in either group, which suggests that the transitions to farming were as drastically innovative and irreversible as when humans made this step about 10,000 years ago."

Humans made the transition to agriculture in perhaps seven or eight regions of the world at various times after the beginning of the Holocene some 12,000 years ago. Each case was different in terms of the kinds of plants that were domesticated and the kinds of complex societies that evolved. All of them radically altered their surrounding ecosystems compared to the earlier hunter-gatherer presence. Those agricultural transitions that evolved complex state societies showed a remarkable similarity. The convergent evolution of state societies after agriculture is nothing short of astonishing. Wright (2004, pp. 50–51) describes

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the results of parallel evolution from hunter-gatherers to civilization in Europe and the Americas:

What took place in the early 1500s was truly exceptional, something that had never happened before and never will again. Two cultural experiments, running in isolation for 15,000 years or more, at last came face to face. Amazingly, after all that time, each could recognize the other's institutions. When Cortés landed in Mexico he found roads, canals, cities, palaces, schools, law courts, markets, irrigation works, kings, priests, temples, peasants, artisans, armies, astronomers, merchants, sports, theatre, art, music, and books. High civilization, differing in detail but alike in essentials, had evolved independently on both sides of the earth.

In broad outline, the same cultural patterns and institutions also evolved in the Indus Valley, the Far East, and the Middle East. This suggests the existence of some common underlying forces driving the evolution of human ultrasociality—the transformation of hunter-gatherers into agriculturalists—that transcend human intentionality and the specific characteristics of pre-agricultural cultures (Gowdy & Krall 2014).

### 1.3. Evolutionary convergence driven by the economics of production

A key evolutionary innovation that led to ultrasociality was a change in the economic organization of production, namely, the move from foraging-for-livelihood to managed agriculture (Gowdy & Krall 2013; 2014). Ultrasociality, as expressed in the active management of crops, is a reconfiguration of society around a cohesive and internalized dynamic of intensive resource exploitation and, where environmental conditions permit, expansion. The active management of the supply of food offers a species the opportunity for expansion and engages interconnected and mutually reinforcing economic drivers that give a common structure and dynamic to agricultural societies. These include: (1) actively managing inputs to food production, (2) capturing the advantages of a complex division of labor, and (3) capturing the competitive advantages of larger scale and larger group size. Selection pressures favored groups with the potential to reconfigure themselves to take advantage of economic efficiencies associated with agriculture. The new group dynamic was not simply a larger aggregation of individuals that comprised the group. The economic organization of the group itself more rigidly defined the role of individuals within it and came to constitute a cohesive whole with a unique evolutionary dynamic. In this transition, economic life was restructured in similar ways in very dissimilar species. Although ultrasociality is a well-established field of study, to date the importance of the evolution of the economic configuration of ultrasociality has not been adequately explored.

### 1.4. The consequences of ultrasociality

The consequences of the ultrasocial transformation are strikingly similar in human and social insect societies. The first similarity is the dominance of the world's ecosystems by ultrasocial species, what Wilson (2012) refers to as “the social conquest of Earth.” In only a few thousand years, humans made the transition from being just another large mammal living within the confines of local ecosystems, to a species dominating the planet's biophysical

systems. Similarly, social insects dominate the ecosystems within which they occur. One of the most complex social insects, leaf cutter ants, live in large cities of millions of individuals devoted to a single purpose – the cultivation of a specific kind of fungus that feeds the entire colony (Hölldobler & Wilson 2011).

A second similarity is the reduction in individual autonomy that occurs with the differentiation of individuals around agricultural production. Members of ultrasocial societies become profoundly interdependent and a large proportion of the day-to-day lives of individuals is spent in specialized productive activities. In this sense individual autonomy is suppressed for the good of the ultrasocial agricultural group. In ultrasocial ant societies, compared to non-ultrasocial ants, individuals have less flexibility in the tasks they perform, they have a limited repertoire of tasks compared to all of those present in the group, and they apparently have a loss of individual intelligence (Anderson & McShea 2001). Although less extreme than with social insects, a loss of individual autonomy is also seen in human societies after the adoption of agriculture. With the advent of large-scale agriculture, individuals were designated to a more narrowly defined role in the material reproduction of society. They were born into distinct and rigid castes that determined their life trajectories and occupations. The subjugation of human individuals is, of course, mediated by culture and, unlike insects, humans often resist this subjugation. Ant and termite castes are based on different phenotypes, while the human division into castes and occupational classes is based on culture, customs, and social institutions.<sup>5</sup>

It is difficult to appreciate the enormity of the break with the past that ultrasociality represents. Biologists rightly note that population explosions are common as new species move into new territories with exploitable resources, thereby increasing their biotic potential. Populations rise and fall regularly, sometimes dramatically, as resources wax and wane. But ultrasociality is unique – it is characterized by an expansion of biotic potential, which is more than simply moving into a new geographic area with a new source of food. Rather, it is the active harnessing of the inputs to food production and a reconfiguration of the group in order to do so. Ultrasocial species are configured to actively produce and expand their food supply rather than wait for nature to provide it. With the onset of ultrasociality, economic factors emerged and coalesced in such a way that the social/economic development of the diverse species that practiced it shared a similar group pattern and dynamic – a new mode of production that gave them a decisive evolutionary advantage.

In the following sections, we first discuss the general characteristics of the major evolutionary transition to ultrasociality with agriculture in the context of current controversies about multilevel selection (MLS) (section 2). Section 3 is a general discussion of ultrasociality in terms of the radical changes in human and insect societies, focusing in on the common economic drivers behind ultrasocial transitions. Section 4 focuses specifically on the human agricultural transition. In section 5 we discuss the social consequences of ultrasociality – ecosystem domination and the suppression of individual autonomy. We end in section 6 with some reflections on the implications of the ultrasocial transition for current human society.

## 2. Ultrasociality and multilevel selection

Ultrasociality is both extremely rare and extremely successful. It is difficult to explain in terms of individual selection. Why should individuals sacrifice their own interests for the good of the group? A growing number of authors argue that traditional explanations – kin selection and reciprocal altruism – cannot adequately account for the numerous examples of cooperation among unrelated individuals and even unrelated species (Grinsted et al. 2012; Nowak et al. 2010).<sup>6</sup> These traditional explanations are challenged to explain the extreme interdependence and coordination that occurs with agriculture. It is problematic (in the case of humans) to make the claim that the extreme cooperation among individuals to the point of loss of individual autonomy is connected to the survival of genes over generations. Multilevel selection (MLS) is especially important in expanding the currency of evolution beyond the gene to include economic configuration. This is essential when it is clear that the economic configuration of diverse species around agriculture looks the same and clearly gives each species a competitive advantage. MLS theory argues that the basic principles of Darwinian evolution – variation, selection, and retention – operate at different levels. Darwinism can be generalized to explain the evolution of genes, individual organisms, or groups of organisms. MLS provides a framework to understand why ants, termites, and humans developed similarly as groups once they began the transition to agriculture and how this created evolutionary paths that led these diverse species in similar directions. Unraveling the commonality of the evolutionary processes that bring diverse species to a similar place allows us to use MLS to examine the importance of economic drivers operating at the group level as a different currency of evolution. We are not discounting the importance of the play of evolution on the gene; we are simply adding another element to the complex matrix of evolution.

### 2.1. Multilevel selection and group-level traits

Despite some resistance to MLS, there is a growing interest in applying the concept more broadly to include human social evolution (Boehm 1997; 1999; 2012; Boyd & Richerson 2002; Gowdy & Krall 2013; 2014; Hodgson & Knudsen 2010; Reeve 2000; Richerson & Boyd 2005; Smaldino 2014; Turchin 2013; van den Bergh & Gowdy 2009; Wilson 1997; Wilson & Gowdy 2013; 2015). Boyd and Richerson (2002) argue that social learning in humans leads to gene-culture coevolution and selection for group-level traits. Social scientists and biologists have acknowledged the importance of the coevolution of genes and culture (Richerson & Boyd 2005; Wilson 1997). Smaldino (2014) has explored the emergence of group-level traits through, among other things, evolutionary competition between groups. Caporael (1997) and Caporael and Garvey (2014) use the concept of “core configuration” – the scaffolding of smaller to larger social and economic units – to examine the emergence of group-level traits. The group selection approach has been fruitfully applied to the evolution of cooperation (Sober & Wilson 1998), the evolution of state societies (Spencer 2010), and the role of warfare in early agricultural societies (Choi & Bowles 2007; Turchin 2006a). Campbell (1982, p. 161)

provides guidance as to how group selection works in human societies:

Much hypothesized cultural evolution must achieve a kind of “group selection” precluded among vertebrates at the purely biological level and achieved by invertebrates only through caste sterility. The models of cultural evolution of Boyd & Richerson (1980) help here. Non-linear, multiple-social-parent transmission, with a majority amplifying effect, pushes face-to-face groups to internal unanimity in the absence of selection. This provides the raw material of within group homogeneity and group-to-group heterogeneity prerequisite for group selection. Such selection would come through differential group success, differential growth, conquest with cultural imposition, voluntary attraction of converts, imitation, etc.

While it is clear that culture can promote homogeneity and cohesion within groups, it leaves ambiguous the common evolutionary process at work for both humans and insects. One cannot reasonably argue that insects have culture in the way that humans do. The explanation for homogeneity and cohesiveness of the insect colony is usually attributed to genetic relatedness, while that of humans is most often attributed to culture. A more complete parsing of the MLS literature with regard to the common evolutionary matrix at work for both social insects and humans who become ultrasocial is warranted.

### 2.2. MLS1 and MLS2

The multilevel selection literature divides selection into two types: multilevel selection 1 (MLS1) and multilevel selection 2 (MLS2). As described by Okasha (2006), MLS1 is a case where certain traits (such as altruism, to use D. S. Wilson’s trait group example) may decrease individual fitness but enhance the competitiveness of groups that practice it. Therefore, groups having many altruists have a competitive advantage over groups that have few, and altruism gets reproduced (Okasha 2006, p. 178). Altruism is an individual (particle) level trait, but the group dynamic enhances the probability that it will be reproduced. With MLS1, natural selection still operates at the individual level and also at a group level, but both levels of selection work on “a single evolutionary parameter” – in this case, altruism (Okasha 2006, p. 178). With MLS1, altruism is still an advantage to the individual because, by enhancing group survival, it also enhances individual survival.<sup>7</sup> Most examples of group selection in the literature fall into the MLS1 category – “traits that can be easily measured in individuals but require group selection to evolve because they are locally disadvantageous” (D. S. Wilson 2010, section XIX).<sup>8</sup>

### 2.3. Emergent characteristics in humans and social insects

The evolutionary picture becomes more complicated when the play of selection at the group level is not on a single trait but on a cluster of emergent characteristics that define the group and make it a whole. Okasha (2006, p. 178) says it succinctly: “In MLS2, individuals and groups are both ‘focal’ units, and the two levels of selection contribute to different evolutionary changes, measured in different currencies.” According to Okasha (2006, p. 112): “Emergent characters are often complex, adaptive features of collectives, which it is hard to imagine evolving except by selection at the collective level.” Okasha (2006, pp. 229–230) accepts

the standard view of MLS2 but points out that it applies only to the later stages of an evolutionary transition (after the collective units have formed and are replicating). In the early transitional stages, cooperation must spread among the particles so that they will eventually give up their individuality and form discrete collectives. Thus, the “emergent characters” present difficulties for multilevel selection because it is a chicken-and-egg problem. This is described by Okasha (2006, p. 113) in reference to work by Williams (1992) and Sober and Wilson (1998): “the emergent character requirement conflates product with process.” This may be true, but it does not constitute an intractable problem if sufficient attention is paid to both process and product, that is, the emergence and configuration of the group-level trait. MLS2 needs to capture the process that forms an altered group that then has sufficient cohesion and force to become a focal point of selection. The process must account for the emergent characteristics which configure the group that then becomes a unit of selection.

The commonality in the structure and dynamic of ant, human, and termite societies that develop large-scale agriculture is not merely coincidental. MLS2 does not sufficiently sort through the process/product problem and it delineates the fitness criteria as successful collectives producing more offspring collectives. This does not capture a basic attribute of the fitness of a food producing group, namely, its internal expansionary dynamic. Fitness is not simply that more new colonies form. It is that any single colony can grow to an enormous size.<sup>9</sup> With agriculture the collective is extended over generations. Some ultrasocial social insects develop new collectives from existing collectives when a queen flies away and starts a new nest. The cumulative effect is different for humans who do not start new colonies with the same ease and sharp delineation as agricultural insects. Again, we argue that, although the details of expansion may differ between humans and social insects, the economic drivers of that expansion are similar.

Smaldino has expanded the discussion of group selection with his refinement of MLS2. His discussion helps guide our thinking about the common evolutionary story of insect and human ultrasociality. The group is defined by Smaldino as the emergence of group-level traits that “involve organized collections of differentiated individuals” (Smaldino 2014, p. 243). These within-group traits constitute between-group differences that become the focus of selection. Smaldino is clear: “In order to explain group-level traits, the emergence of differences among individuals within a single group, and the subsequent organization of those differentiated individuals and their coordinated behavior must be accounted for” (2014, p. 249). In this framework we must identify the commonalities in both the process of differentiation and the commonalities in the reconfiguration of that differentiation into a whole if we are to explain the common structure and dynamic of societies of ants, humans, and termites. The configuration of the whole then defines its group-level trait and the unit of selection.<sup>10</sup>

Smaldino (2014, p. 248) specifically discusses the homogeneity of the group using the example of social ants. Collaboration among workers, soldiers, drones, and queens is promoted through genetic relatedness and the colony becomes an extended phenotype of the queen. The

conclusion is that differentiation within the colony comes about through environmental stimuli that trigger phenotypic differences and cohesion is largely a matter of genetic relatedness, although positive assortment through group structure may also play a role. Smaldino contrasts this to the situation found in humans where between-group differences, and within-group cohesiveness, are “triggered culturally rather than genetically requiring different explanations for their emergence and evolution.” Differentiation and cohesion are culturally mediated, but placing too much emphasis on the different mechanisms in social insects and humans that bring about differentiation and cohesion is a diversion from identifying the commonality among these diverse lineages. The organization of agricultural production promotes a more elaborate differentiation of individuals (division of labor). In a sense it does not matter how species attain differentiation as long as they do so. In all cases the extensive division of labor around the active management of food production creates a profound interdependence. The extreme differentiation of occupations brings about a much greater cohesion and co-dependence in production and rewrites the boundaries between the individual and the group.

### 3. Agriculture and the economic drivers of ultrasociality

The common evolutionary story of ultrasociality, that is, the emergence of group-level traits leading to agricultural societies can be understood as a matter of economic organization. The importance of economic organization has been noted but has not been developed in a systematic way. With control of the production of food, there came a tremendous potential to expand the subsistence base, thereby expanding the potential for population growth.<sup>11</sup> In the transition to agriculture, a common recipe or program took hold and led very different species in the same direction. Human and insect agricultural societies exhibit both a complex interdependence and a dynamic of expansion.<sup>12</sup> When these lineages started managing food production, some basic economic laws gave them such an evolutionary advantage that they came to dominate the planet. We separate our discussion of economic drivers for purposes of highlighting them, but we acknowledge that in reality they are mutually reinforcing and intertwined. For example, the division of labor is both a characteristic of ultrasocial systems and a pre-adaptation that enabled ultrasociality. The division of labor and economies of scale are intimately connected.

#### 3.1. Actively harnessing the inputs to food production

With agriculture it was possible for humans, ants, and termites to interject themselves directly into the food production process. Humans could actively capture solar energy in crops that replaced other vegetation and tap into stocks of agricultural inputs like fertile soil and water for irrigation. The economist Georgescu-Roegen (1976) pointed out that stocks of inputs like the nutrients in fertile soil have an advantage over flows because they can be used at any rate and can therefore make possible a larger and more complex production process (Georgescu-Roegen 1976).<sup>13</sup> More energy and other resources can be directed to food

production. E. O. Wilson (1987) points out the importance to ant agriculture of tapping into resource stocks:

What unusual or unique biological traits have enabled the ants to remain abundant and relatively unchallenged morphologically for over 50 million years? The answer appears to be that the ants were the first group of predatory eusocial insects to both live and forage primarily in the soil and rotting vegetation on the ground. (E. O. Wilson 1987, p.6)

This gave them an almost unlimited supply of nutrients to support their agriculture. Hölldobler and Wilson (2011, pp. 2–3) write: “The leafcutter ants are partly comparable in their achievement to that of human agriculturalists. And they have attained a breakthrough of organic evolution: by using fresh vegetation on which to grow their crops, they have tapped into a virtually unlimited food source.” Perhaps forest floor vegetation is not technically a stock, but it essentially amounts to a stock for ant agriculturalists. Attine ants commandeer vegetation away from species that would otherwise use it.

Tainter et al. (2006, p. 52), in discussing energy transformations in complex societies, argue that the evolution of ant agriculture shows two major resource transitions. The first was the adoption of agriculture itself – based on actively growing fungus on high-quality insect droppings. This transition was highly successful, but the size of the colonies was limited by the scarcity of quality insect droppings. The second transition was a shift from collecting droppings to growing fungus on much more abundant leaves and other organic material. Each step in ant social evolution not only paved the way for the next step, but also came with increasing complexity and regimentation of ant society, which itself enhanced the ability to tap into the stock.

### 3.2. The complex division of labor

An important economic driver of ultrasociality and its evolution is the expansion and sharpening of the division of labor. Both biologists and economists have extensively studied the division of labor. Biologists have identified the benefits of division of labor in social insects (Beshers & Fewell 2001; Franks 1987; Oster & Wilson 1978; Wilson 1971). Hölldobler and Wilson (2009, Ch. 5) give numerous examples describing its advantages. In the case of ants, the number of total tasks increases with the total number of ants sampled in a colony (Hölldobler & Wilson 2009, p. 125). Holbrook et al. (2011) and Hölldobler and Wilson (2009) found that the division of labor (the number of distinct roles) increases with colony size, although it is hard to separate cause and effect. Phenotypic variation enables ants to differentiate according to their productive role or their role in supporting productive activity (as in defense).

It should be acknowledged that the division of labor is common in the animal world and is not by itself a distinguishing characteristic of ultrasociality. For example, a division of labor based on care of the young is common among animals. It spontaneously appears in normally solitary queen ants when the queens are forced to associate (Fewell & Page 1999) and similarly in normally solitary bees. Solitary sweat bees alternately dig nesting holes and guard the nest. When two are put together, one will specialize in excavation and the other will guard the nest entrance, resulting in efficiency gains in both tasks. According to Holbrook et al. (2009, p. 301), “Paired individuals performed

more per capita guarding, and pairs collectively excavated deeper nests than single bees – potential early advantages of social nesting in halictine bees.” Even in a simple society of two individuals there is an advantage to a larger scale (from one to two), permitting a division of labor. The spontaneous appearance of the division of labor in these simple cases is remarkable and may hold keys to its development in ultrasocial societies. But the extent of the division of labor in ultrasocial species is unique in its complexity and interdependence.

The active management of agricultural crops is a particularly powerful impetus for a more complex division of labor. Consider the differences between a eusocial honeybee colony and an ultrasocial attine ant colony. Honeybees survive by foraging for pollen from plants but they do not actively manage the sources of pollen. Honeybees have a division of labor, for example, cleaning, feeding the brood, receiving the nectar, foraging, and defense, depending on the age of the individual bees (age polyethism). Yet, there are only three physical castes: workers, drones, and queens. Workers are of only one physical type. Some attine ants, by contrast, have many castes who actively manage the production of various species of fungi which feed the colony. Castes are based partially on size, which “coarse-tunes” rather than “fine-tunes” the phenotypes to perform a wide variety of tasks (Oster & Wilson 1978). Ants within each size caste can perform a number of further-refined, highly specialized tasks. For example, there is a caste of tiny attine ants whose job it is to ride atop the much larger leaf carriers and defend them from attacks by parasitic flies (Hölldobler & Wilson 2011). Large soldier ants have jaws so specialized for defense that they cannot feed themselves. There are even “untouchable” ants whose job it is to remove wastes and pathogens from the fungal gardens. The point is that the active management of food production, and the defense of food surpluses, calls forth a much more complex division of labor requiring many more tasks and a much greater degree of coordination than does mere foraging. Ferguson-Gow et al. (2014) found a significant positive relationship between the complexity of agriculture systems in attine ants (from lower attines to leafcutters) and complexity of the division of labor.

Another factor facilitating the division of labor under agriculture is mutualism. The fungi that ants and termites live on could not survive without active management by the ant colony. This requires complex tasks including using antibodies to control the bacteria that attack the fungus (Aanen & Boomsma 2006; Mueller & Gerardo 2002). It is true that flowers are pollinated by (non-agricultural) honeybees, but there exist other pollinators and the plants could survive without the presence of honeybees (as they are now doing in many areas because of honeybee die-off).

The advantages of a division of labor are a central tenet of economic theory. They were recognized by Adam Smith in *The Wealth of Nations* (1776/1937, Book 1), where he presented his well-known pin factory example of the role of the division of labor in rationalizing the production process. One person working alone, he wrote, could scarcely make one pin a day. But when the enterprise is divided into several sub-tasks, productivity increases dramatically.

One man draws out the wire, another straightens it, a third cuts it, a fourth points it, a fifth grinds it at the top for receiving the head; to make the head requires two or three distinct

operations; to put it on, is a peculiar business, to whiten the pins is another; it is even a trade by itself to put them into the paper. ... I have seen a small manufactory of this kind where ten men only were employed.... Those ten persons ... could make among them upwards of forty-eight thousand pins in a day. (Smith 1776/1937, Book 1, pp. 2–3)

Smith also pointed out that the division of labor is limited by the extent of the market. The larger the market, the more specialization is possible, which enlarges the market still more in a kind of “virtuous circle.” Although he was writing about market capitalism, Smith was onto something more fundamental in the sense that he clearly saw that there is a system at play that places a premium on capturing the efficiencies inherent in expanding the division of labor.

Active intervention in food production called for a more extensive and interdependent division of labor in humans as well as social insects. In hunting and gathering societies the division of labor was relatively simple, primarily based on gender. A more interdependent and extensive division of labor began to take form in pre-agricultural societies with the harvesting of wild grains. There were more kinds of tasks to perform. Access to the good stands of wild wheat was essential, and it is likely that defense became more important in order to lay claim to a prime spot. As the active cultivation of crops increased, so did the necessity for coordination of production in planning, preparing the soil, planting, cultivating, harvesting, processing, storing, and distributing the agricultural output. As well, reproductive rates increased in humans, so there was more work to be done in birthing and child rearing. Women’s roles became more narrowly circumscribed around these activities. Thus, agriculture expanded the division of labor and increased the interdependence between people for day-to-day sustenance.

The division of labor in humans does not entail the same phenotypic (morphological) differentiation as in ants and termites because humans have greater recourse to cultural, institutional, and technological extensions of themselves. But occupational differentiation in humans is also made possible to some extent by genotype-phenotype plasticity. Human brain plasticity allows for a remarkable degree of differentiation in terms of the ability of individuals to adapt to different cultures and behavioral patterns (Frith & Frith 2010; Wexler 2006). This is not to say that specific instances of occupational differentiation are genetically determined, but brain development plasticity gives humans the flexibility to perform a variety of functions. The extent of the detailed division of labor becomes so great in ants and in humans that individuals become tied to a very narrow productive role in society. This creates an interdependence that secures and strengthens the group as a self-referential entity.

### 3.3. Increasing returns and the competitive advantage of larger group size

Larger group size may also be more metabolically efficient because of economies of scale in energy use. Hou et al. (2010) and Shik et al. (2012) demonstrate this in their studies of ant colonies and use Kleiber’s Law (the rate at which an organism processes energy increases at a rate that is approximately equal to the  $\frac{3}{4}$  power of that organism’s body mass) as the explanation. Larger colonies have lower rates of per capita energy use (Bruce & Burd

2012). But there seems to be an upper limit on leaf cutter ant colony size due to the fact that colonies will eventually reach a limit where the returns to increasing foraging territory is not profitable (Bruce & Burd 2012).

Among the many tasks that developed with agriculture, defense was one that gave an advantage to larger group size. In human agricultural societies, because of the need to lay claim to property and because of the time lag between planting and harvesting, there was a need to defend property. Although defense may have been necessary even while harvesting wild grain, it took on added importance with the investment in managed agriculture. Human societies that were larger and better able to organize warfare, and develop war-making innovations, out-competed others and expanded rapidly (Matthew & Boyd 2011; Turchin 2006a). Eventually, warfare became prevalent as larger-scale state societies began to form. As Larsen (2006, p. 17) puts it: “The record strongly suggests that population size increases associated with food production provided conditions conducive to the rise of organized warfare and increased mortality due to violence.”

There are other advantages to larger size and scale. Unlike solitary insects, social insects can perform a number of tasks *in parallel* as opposed to *in sequence*, an advantage described in Adam Smith’s pin factory example. As Georgescu-Roegen (1965) pointed out for the human economy, if the scale of operation is large enough, idle factors of production can be eliminated and thus larger-scale systems can entail a more efficient and productive use of resources as long as they are abundant enough to support the larger scale. Also, time is not lost in moving from one task to another. An ultrasocial society can also take advantage of a spatial distribution of labor, allowing for more risk taking in foraging than would be possible for individuals acting alone.<sup>14</sup> In general, larger scale and the division of labor are mutually reinforcing. A larger scale of operation can also take advantage of a spatial distribution of labor, again allowing for more risk taking in foraging than would be possible for individuals acting alone. Also, with a larger scale of operation, individuals can specialize and become more proficient in their tasks.

Human hunter-gatherers lived off the flows of nature – from the solar energy directly captured by living plants and indirectly present in the flow of animals feeding on those plants. They had limited control over these subsistence flows. If hunter-gatherers, like any large carnivores, took too many animals or harvested too many wild plants, this resulted in immediate shortages; thus, resource management became necessary and this tended to keep human societies in ecological balance. These societies also had leveling mechanisms to promote an egalitarian distribution of wealth and power. With the adoption of agriculture, human society and the relationship between humans and the natural world changed dramatically.

## 4. Agriculture and the human transition to ultrasociality

Anatomically modern humans appeared in Africa about 200,000 years ago. Thus, for more than 95% of human history we lived as hunter-gatherers in small, mobile groups. Judging from studies of present-day and historical hunter-gatherer societies, these groups were highly

cooperative and egalitarian, and they lived within the confines of local ecosystems (Boehm 1997; 2012; Gowdy 1998; Lee 1968; 1984/2013; Pennisi 2014; Ryan & Jethá 2010). Quite suddenly, within just a few thousand years, the vast majority of *Homo sapiens* were members of populous agricultural societies with complex economies, technologies, and social organization. With the advent of ultrasociality, the human population exploded from around 6 million 10,000 years ago to more than 200 million by the beginning of the Common Era (CE) 2,000 years ago (Biraben 2003; Bocquet-Appel 2011; Cox et al. 2009).<sup>15</sup> At the same time, the role of the individual in human society changed radically. With agriculture, there was a loss of individual autonomy, rigid social hierarchies were firmly established, and there was a general decline in the well-being of the average person (Diamond 1987; Lambert 2009; Larsen 2006). This raises the question of individual choice in the agricultural transition. Why would people accept the significant costs of poorer nutrition, shorter life-spans, and the diseases that came with sedentary existence and dense settlements? The adoption of agriculture most likely was not a choice, but rather a gradual, cumulative process perhaps imperceptible within the lifetime of a single individual. There were likely marginal payoffs that propelled society toward further embracing agriculture. Yet, certainly, humans could not have anticipated where agriculture would lead them—to hierarchy, regimentation of productive life, ecological degradation, patriarchy, slavery, and poor health. Once in place, the growth in population it facilitates can then only be supported by sustained agriculture.<sup>16</sup> Humans did not consciously choose agriculture.<sup>17</sup> This again underscores the difficulty in understanding transitions themselves rather than before and after characteristics (Okasha 2006).

A basic question raised here is whether human cultural evolution is the result of conscious choice or the blind unfolding of natural laws? There are really two questions. The first is whether human agents act purposefully in pursuing chosen ends. The answer to this must certainly be “yes.” But the more interesting question is whether or not the cumulative outcome of individually chosen activities can be explained as the result of human design (see Vanberg 2014). We argue that for some of the most important cultural transitions in human history (agriculture, civilization, market capitalism), the answer is no. Choices small in scale and time—even choices that are perfectly rational from the point of view of an individual acting at a point in time—can lead inexorably to outcomes that are not only unanticipated but also actually detrimental to the individual. The economist Alfred Kahn (1966) calls this “the tyranny of small decisions.” As we have argued above, the transition to agriculture took place through a series of incremental decisions made by innumerable individuals over thousands of years. The outcome of these decisions was a number of hierarchical agricultural civilizations within which the average individual was worse off.

#### 4.1. The origins of human agriculture

There is no consensus as to the origins of agriculture. Price and Bar-Yosef (2011, p. S168) summarize: “There is as yet no single accepted theory for the origins of agriculture, rather, there is a series of ideas and suggestions that do not quite resolve the questions.” Our intention here is

not to provide the definitive explanation for this transition (which likely varied from place to place; see McCorrison & Hole 1991), but rather, to offer in broad outline a plausible story for the transition from hunting and gathering to settled agriculture and the concomitant social and environmental consequences. Agriculture gave our species the ability to control and expand its supply of food, and this was an evolutionary advantage (as measured by total population), even though it apparently made the average individual worse off. According to Larsen (2006, p. 12), “Although agriculture provided the economic basis for the rise of states and development of civilizations, the change in diet and acquisition of food resulted in a decline in quality of life for most human populations in the last 10,000 years.” The archeological record substantiates Larson’s claim. After agriculture, humans became shorter and suffered from more debilitating diseases, from leprosy to arthritis to tooth decay, than their hunter-gatherer counterparts (Cohen & Crane-Kramer 2007; Lambert 2009). It is only in the last 150 years or so that longevity once again reached that of the Upper Pleistocene. The average human life-span in 1900 was about 30 years, and for Upper Pleistocene hunter-gatherers it was probably about 33 years.<sup>18</sup> Only in the last century or so has the well-being of the majority of humanity improved dramatically. It remains to be seen whether or not these improvements can be maintained. Care must be taken not to see the achievements of the very recent past as representative of the consequences of the agricultural transition.

Humans had extensive knowledge of wild plants long before the adoption of agriculture (Cohen 1977; Zvelebil & Rowley-Conwy 1986), so there must have been some experimentation with planting during our lengthy hunter-gatherer history. Flannery (1968) observed: “We know of no human group on Earth so primitive that they are ignorant of the connection between plants and the seeds from which they grow.” Yet understanding and observing and collecting wild plants is one thing, while domestication is another. What pushed humans to adopt agriculture? Convincing arguments have been made that the Holocene provided a period of climate stability that was necessary for successful agriculture. Richerson et al. (2001) have demonstrated that the possibilities for agriculture were severely limited before the Holocene because of unpredictable climate fluctuations. There were several periods of warming after the evolution of modern humans but none except the Holocene led to agriculture. Climate data indicate that prior to the Holocene, changes in temperature as great as 8°C occurred over time spans as short as two centuries (see Bowles & Choi 2012, supporting online material, p. 4). Ice core and pollen records indicate that centuries-scale abrupt climate events occurred regularly during the Pleistocene and that it was not until the Holocene that a protracted period of warming occurred. In the Late Pleistocene, plant productivity was low because of reduced CO<sub>2</sub> levels (about 180 ppm, compared to 250 ppm at the beginning of the Holocene (Shakun et al. 2012). Beerling (1999) estimates that the total amount of stored organic land carbon was 33% to 60% lower in the Late Pleistocene compared to the Holocene.

One popular argument is that population pressure drove the adoption of agriculture (Binford 1968; Cohen 1977). But others have pointed out that there is little evidence for population pressure in the areas where agriculture



first appeared (Price & Bar-Yosef 2011). However, the Holocene warming may be related to population pressures in some areas. McCorriston and Hole (1991, p. 49) noted that the effect of the Holocene warming in the Levant was to prolong summer aridity and that this would have affected the availability of agricultural inputs. This likely affected the availability of viable locations for groups of humans. The drier climate also put more pressure on access to water and probably concentrated human and animal populations in areas with ample water. The population picture is further complicated by the fact that even incipient agriculture may have resulted in a more sedentary life, which in turn increased fertility rates. Even the gradual and marginal use of wild grains might have altered population dynamics if it made people more sedentary and more fertile, thus creating a positive feedback path reinforcing the need for more agriculture as pressure on wild food sources and hunting became more challenging.

#### 4.2. A plausible story of the human agricultural transition

A plausible scenario of the human agricultural transition can be sketched out (Gowdy & Krall 2014). Mobile hunter-gatherers moved through places where wild grains thrived, and these grains provided a significant portion of hunter-gatherer diets. As the climate warmed and became more stable, wild grains became more reliable and more important as a food source. People began to sow wild seeds to enhance grain growth, and they began to store the grain they collected. As they sowed, they also selected for desirable characteristics. Storage, especially amenable to annual grains, was a good subsistence strategy since there was variability in production from year to year. This enhanced and concentrated food supply led to a more concentrated population. Perhaps a portion of the population began to stay behind in the seasonal migrations in order to manage the wild crops. Selective planting and harvesting of crop varieties eventually led to managed agriculture and populations more and more dependent on intentional food production.<sup>19</sup>

This plausible story fits with what we know of the agricultural transition in the Levant (which includes parts of modern Palestine, Syria, Israel, and Jordan) beginning around 10,000–12,500 years ago (Bar-Yosef 1998, p. 162; McCorriston & Hole 2000b).<sup>20</sup> The Levant is the area of the world where the advent of agriculture is the best documented. A key feature of the Holocene warming in the Near East was that it created conditions favorable to the development of annual grains. The climate of the Levant became more stable and seasonal differences became greater. Around 10,000 years ago the pre-agricultural Natufians began to rely more heavily on wild grains like wheat and barley (McCorriston & Hole 2000a; 2000b). McCorriston and Hole (1991, p. 61) claim: “In our view, the wild annual plants had never been available in densities comparable to those of the Early Holocene when seasonality reached unprecedented extremes and favored annual over perennial adaptation.” Annuals have an advantage in places with enhanced seasonality, especially where there are hot, dry summers and strong seasonal rainfall variation. Annuals store their reproductive ability in seeds which can wait (sometimes years) for rain to germinate. Annuals also have unique characteristics that may allow rapid coevolution to develop between humans and plants (Cox 2009).

Annual grains can also be stored, and so a greater reliance on them meant a greater capacity to secure a surplus. Evidence exists for food storage at about 11,000 years ago, about 1,000 years before domestication and large-scale settlements, in the form of purposely built granaries (Kuijt & Finlayson 2009).

One mutation of wild wheat that would have been important was non-shattering, a mutation that allows for seeds to hang on and not fall to the ground as quickly. This is apparently a rare mutation but might have been noticed by those seed gatherers who were accessing wild stands of early wheat varieties. The time period for harvesting wild wheat was short—three days to a week before shattering occurs depending on weather conditions. After seeds shatter, they must be harvested from the ground, which is more time consuming. If people reached a stand of wild wheat after shattering had taken place, the only seeds still standing would have been the mutants, which would have been noticed. Also, using a sickle would have been a particularly good technology for non-shattering seeds. In this way mutations in wheat interfaced with human intervention to create a selection bias for non-shattering seeds or any other trait that was noticeable and desirable.

Domestication of grains may have initially been unintentional in the sense that wild varieties would have been eliminated and replaced more systematically with plants that required human intervention (Bar-Yosef 1998, p. 167). With cultivation, there gradually developed a specialized active management of grains where control of production was more concentrated within human groups (Flannery 1968; McCorriston & Hole 2000b; Rindos 1984). Active management also required more complex and integrated tasks (in both humans and insects), and thus there is a connection (mutualism) between the characteristics of the crops and the species managing the crops.

As the climate improved and stabilized during the Holocene, wild grains such as *triticum monococcum*, a wheat-like grass, became more plentiful. Evidence suggests that the Natufians intensively harvested wild cereals using sickles (Bar-Yosef 1998, pp. 164–65). There is also evidence of heavy wear of teeth, presumably due to consuming coarsely ground cereals (Smith 1972, pp. 236–37). To reiterate, annuals might have been increasingly abundant and amenable to the climate conditions of the Holocene. Hunting did not cease as the use of wild grains increased, but there was likely a shift in hunting strategies and the importance of hunting in the diet. Hunting may have become less reliable as the climate change of the Holocene would have changed the range and concentrations of wild animals (McCorriston & Hole 1991).

Some mention should be made of the effect of the Younger Dryas—a sudden cooler and drier period occurring between 12,800 and 11,500 years ago—on the cultures of the Near East. Belfer-Cohen and Bar-Yosef (2000) argue that it was the stress of the Younger Dryas that pushed the adoption of agriculture. But others point out that there is no evidence for more intensive resource use or food stress in the late Natufian (Munro 2003). In fact, during this period the population densities and settlement patterns of early Natufian culture reverted back to pre-Natufian levels. It may be that the Younger Dryas interrupted the transition to agriculture rather than encouraged it.

The Natufians were followed by the fully agricultural cultures of the Neolithic, referred to as Pre-Pottery Neolithic

A (PPN-A). PPN-A sites are much larger than the Natufian sites, with storage bins for grains, ceremonial structures, and a rich lithic industry. The best known PPN-A settlement is Jericho (about 10,000 years ago), thought to be the world's first known town, with a population of about 2,000–3,000 people. The Jericho site shows the first known domesticated cereals: emmer wheat and two-row hulled barley (McCorriston & Hole 1991, p. 51). Storage technology is found abundantly in the Pre-Pottery Neolithic. Makarewicz (2012, p. 217) writes: “The Pre-Pottery Neolithic A marks a major shift in human approaches to subsistence from plant gathering to the consistent practice of plant cultivation, where wild plant resources were augmented by a more predictable food source in the form of managed plants, particularly cereals and legumes.” Eventually the point was reached where the human population in the Levant could not survive without the grains, and the grains could not survive without human intervention.

#### 4.3. Managing crop production: The economic drivers kick in

The active management of crops fundamentally altered human economic organization. Like our ant and termite distant relatives, humans began to actively engage in the primary production of their food supply. Economic life was no longer a matter of living off the day-to-day flows from nature. It now involved a direct intervention into food production.<sup>21</sup> Many species use social organization to get food, as in cooperative hunting, for example. But direct intervention in producing food is categorically different, and the economics of production take center stage.

First of all, actively producing food requires a more complex and interdependent division of labor. This increase in complexity had its beginnings in the harvesting of wild stands of grains. Harvesting must move quickly, or most of the grain may be lost. Protecting access to the good stands of wild grain was essential. The reward was a greater control over food supply for the group as a whole, but the repercussions if things failed were formidable. As long as storage was possible, production of surplus was an insurance against lean times.

A second feature of emergent agricultural society is an impetus to expand because of the productive advantage of larger group size. More food allows expansion, and expansion captures the efficiencies of a greater division of labor and economies of scale. Also, many tasks are required that do not directly contribute to food production itself. Those who directly produce food must provide for those not actively engaged in agricultural production. Part of the dynamics of agriculture is the phenomenon of increased reproductive rates caused by sedentary life. Increased reproductive rates also provided one of the most important resources for successful agriculture, a large supply of laborers. But for a time at least, this requires some investment in nonproductive individuals, that is, young children who cannot yet work. The result is again that those engaged in the direct provisioning of food must produce enough to feed more nonproductive individuals. Greater population creates a greater need for agricultural output, and greater agricultural output creates a greater need for population.

Turchin (2013) points to increasing returns to scale in warfare as a major driver of ultrasociality. Turchin et al.

(2013) argue that agriculture increased the payoff for aggression, which, in turn, necessitated more food production to feed the expanding military. Groups with more soldiers eliminated or absorbed smaller groups. Warfare has been suggested as a key to the development of state societies (Carneiro 1970; Tilly 1992; Turchin 2006a). By contrast, a strong case has been made that warfare did not exist in hunter-gatherer societies (Culotta 2013). Violence certainly existed in these societies, but most lethal events resulted from personal disputes (Fry & Söderberg 2013).

Finally, the ecological consequences of annual grain agriculture may have also encouraged the expansionary dynamic. Annuals had a greater capacity for seed production, and the rewards of active management were greater, but they also had a greater potential for ecological damage, especially soil erosion and soil disturbance during planting (Cox 2009). Expansion was also one way out of the ecological problems caused by grain agriculture, although in the long run they exacerbated the ecological problems as agriculture expanded into forested areas and deforestation brought down silt.

#### 4.4. Surplus and hierarchy

Surplus production was perhaps initially a response to the favorable climate of the Holocene in the Near East, but surplus production and expansion increasingly became necessary to accommodate population growth, the growth of the proportion of nonproductive individuals, and the problems of seasonal variation, and to counter the ecological degradation of grain agriculture. Because of the premium placed on maximizing output, it was important to control production and maximize the output of individual laborers. During key periods such as planting and harvesting, work was necessarily intensive and repetitive. The regimentation of work and the productive benefits of a division of labor and attendant economies of scale promoted the success of agriculture but also increased the bureaucracy necessary to manage the complexity, the distribution of surplus, and the associated ecological problems. In this environment, relying on stored surpluses to carry societies over seasonal periods of low production made maximizing surplus production in any given year all the more critical. It also increased the stakes associated with management of production and with dissemination of the surplus.

With storage of surplus, complex technology, and the ability to physically control food surplus also came hierarchical societies. Control itself took on added importance, moving society increasingly in the direction of hierarchy and property. Year-round storage also meant that early farmers could settle in larger groups throughout the year, and gave society the flexibility to support specializations like craftspersons, administrators, warriors, and religious leaders (McCorriston & Hole 2000b). The need for efficiency and control set up a more mechanistic and interdependent configuration of production and distribution. The survival of the society depended on the payback from the management of production. Those at the top benefitted from pushing the envelope of agriculture intensification. The successful production of agricultural surplus expanded the material and cultural possibilities of society. But the fact that most individuals had no other option to secure the material necessities of their lives other than to participate in

directly producing food placed the human propensity to cooperate at the disposal of both direct and indirect coercion.

Antecedents to hierarchical organization exist in non-agricultural societies, which gives credence to the importance of the management of surplus and the active control of production in the creation of hierarchy. Woodburn (1982) distinguished between “immediate return” and “delayed return” hunter-gatherer societies, with the latter possessing a more elaborate technology (capital) such as nets and boats, and showing some evidence of social stratification. In delayed return hunter-gatherer societies, people have rights over valued assets of various kinds. A commonly given example of a hierarchical culture without agriculture is that of the original inhabitants the northwest coast of North America. A village on Keatley Creek in northwest Canada was occupied between 2,500–1,100 years ago by hunter-gatherers who lived on the abundant seasonal salmon runs. The village consisted of more than 115 pit houses and other structures with log and earth roofs. The peak population of the village was about 1,500 people. Evidence indicates wide disparities in living standards, which may have originated in unequal access to prime fishing grounds (Prentiss 2012; Pringle 2014). Richerson et al. (2001) point out that the transition from the beginning of agriculture to the development of state societies took around 2,000 years. Thus, a dynamic that started out modestly and benignly locked early agriculturalists into a perhaps irreversible process that led to hierarchical state societies.

## 5. The consequences of ultrasociality

Ultrasociality had two striking consequences for humans and insects. The first is the domination by ultrasocial species of the ecosystems in which they occur in terms of both sheer numbers and in the way those ecosystems are organized to meet the requirements of ultrasocial societies. The second is the loss of individual autonomy in these societies. In this section, we begin by discussing the similarities in these two evolutionary outcomes in insects and humans. We go on to discuss the perhaps even more interesting dissimilarities due to the differences in genetic (insect) and social (human) evolution, and in the fact that humans, compared to ants and termites, have only very recently started down the path to ultrasociality.

### 5.1. The social conquest of Earth: Ecosystem domination, sustainability, and collapse

Ultrasociality evolved in only a handful of species, yet those species dominate the ecosystems within which they occur and indeed the entire planet (Wilson 2012). Sanderson et al. (2002) calculated that over 80% of the global terrestrial biosphere is under direct human influence. Astonishingly, the total dry weight human biomass (about 125 million metric tons) is over 12 times the weight of all other vertebrates combined (Smil 2013). Social insects also dominate their ecosystems to an amazing degree. In a survey of a patch of rainforest in the Brazilian Amazon, social insects comprised about 30% of the entire animal biomass and 75% of the insect biomass (Fittkau & Klinge 1973; Wilson 2008, p. 6). Wilson (2012, pp. 116–17) “crudely” estimates the total number of ants to be  $10^{16}$ ,

or 10 thousand trillion. If one ant weighs one-millionth of the weight of a human, the total weight of the world’s ants is about the same as the total weight of all humans. In subtropical and tropical ecosystems, termites can make up as much as 95% of the soil insect biomass (King et al. 2013; Korb 2007, p. R998).

Ants, in effect, have re-engineered the ecosystems they are a part of. Folgarait (1998) discusses some of the major functional roles of ants, including soil modification through physical and chemical changes, changes in nutrient and energy fluxes, and changes in vegetation. Other species have coevolved to accommodate themselves to the presence of the numerically dominant ant and termite colonies. By contrast, humans after agriculture have had a predominantly negative impact on ecosystems and biodiversity.<sup>22</sup>

The archeological and historical record of early agricultural societies is characterized by rapid expansion, followed by collapse and social disintegration (Diamond 2005; Weiss & Bradley 2001; Weiss et al. 1993). Examples include the Akkadian empire, Old Kingdom Egypt, the Classic Maya, and the Harappan of the Indus valley. These civilizations disintegrated because of a variety of factors, including the loss of soil fertility, erosion from reliance on annual plants, soil salinization, water mismanagement, and the inability to withstand prolonged droughts. Climate change in particular is increasingly accepted as a driver of past societal collapse and disruption (Rosen & Rivera-Collazo 2012; Weiss & Bradley 2001). The basic problem is that ultrasocial societies are expansionary, that is, they have a constitutional proclivity to expand; and because of their tremendous interdependence, they are particularly difficult to disengage before they reach the point of collapse either due to ecological limits (that might be exacerbated by climate change) or due to internal conflicts between classes, in the case of humans, regarding the distribution and use of surplus.

Of course, social insects have had tens of millions of years of evolutionary trial and error to hone sustainable cultures. It is quite possible that the early history of ultrasocial ants and termites is also littered with unsuccessful experiments with agriculture. Can humans learn something about sustainability from insect farmers? Aanen and Boomsma (2006, p. R1016) write:

The farming insect societies had tens of millions of years of natural selection to solve many of the challenges that are also well known to human farmers. They have conveyor belt substrate processing, produce their own pesticides and antibiotics, and practice active waste management. Neither the ants nor the termites, however, have been able to overcome the fundamental laws of host-symbiont conflicts, which imply that only monoculture farming is evolutionarily stable. Our own farming practices evolved culturally by frequent exchange of crops, learning and copying innovative practices. The problem is that, on the larger scale that we apply today, many of these practices are unlikely to be sustainable, even on an ecological time scale.

Ants and termites have practiced monoculture successfully for tens of millions of years, while the short history of human management of a few crops shows a pattern of recurring instability (Benckiser 2010). One reason social insects have achieved sustainable agriculture is that their agricultural practices have more successfully harnessed the benefits of mutualism – the advantages of cooperation between ants and termites and the fungus they raise and

feed on. Our mutualism around annuals is more ecologically problematic due to soil erosion, pest control, and a number of other challenges. Cooperation between unrelated agents can have great benefits, but there is always tension between the benefits of cooperation and the benefits of defecting – the classic Prisoner’s Dilemma (Trivers 1971). Social insects have largely overcome Prisoner’s Dilemma-type reproductive conflicts by developing mutualism because one-to-one cooperation is more stable (easier to enforce) than cooperation among several agents. Ant feces provide critical nutrients (especially nitrogen) without which the fungus could not survive. Not only is mutualism between agriculturalists and their crops taken to the point where one could not survive without the other (as with humans), but in ants it is taken to the point where their physical bodies have adapted to the physical needs of the fungus. Foster and Wenseleers (2006) show that three key factors are important to mutualism evolution: (1) high benefit-to-cost ratio, (2) high within-species relatedness, and (3) high between-species fidelity. The economic drivers behind the success of managed agriculture likely raised the benefit-to-cost ratio of mutualism.

Regarding sustainability, an important difference between human and insect societies is social instability. Unlike insect societies, human groups are characterized by recurrent and sometimes calamitous within-group conflicts. Georgescu-Roegen, following Lotka, attributes this to the difference between “endosomatic” and “exosomatic” organs (Georgescu-Roegen 1977a; Lotka 1925/1956). The occupations of social insects are determined in large part by their phenotypes – for example, door keeper ants have large heads (endosomatic) which serve no other purpose than to block the entrance holes to the colony. Humans, by contrast, depend on the objects of material culture (exosomatic), which can be appropriated according to cultural rules that may or may not be accepted. An ant is born to be a soldier; a human is not. There is no biological reason for one human to be homeless and another a billionaire.

## 5.2. The loss of individual autonomy in ultrasocial societies

Another basic feature of ultrasociality is the subjugation of the individual for the evolutionary success of the group. Subjugation can be understood partly as an artifact of the division of labor in agricultural societies. An important commonality in human and ant division of labor in ultrasocial agricultural systems is that *individual* behavioral complexity and flexibility are in general not as great compared to those societies relying on hunting and gathering. The behavior of individuals, in the context of an elaborate division of labor, is simpler in ultrasocial societies even as the society grows more complex. In the case of ants, increasing social complexity is not associated with increasing individual behavioral complexity (Holbrook et al. 2011). Adam Smith (1776/1937, p. 734) recognized the danger for humans of labor specialization and the mental toil on individuals who endlessly perform the same tasks:

The man whose whole life is spent in performing a few simple operations, of which the effects are perhaps always the same, or very nearly the same, has no occasion to exert his understanding or to exercise his invention in finding out expedients for removing difficulties which never occur. He naturally loses, therefore,

the habit of such exertion, and generally becomes as stupid and ignorant as it is possible for a human creature to become.

Commenting directly on Smith’s observation, Moffett (2010), in reference to ants, writes: “This deficiency can be observed for large ant societies as well, in which specialized workers are incapable of accomplishing much without the cooperation of nestmates” (p. 70). Likewise, Anderson and McShea (2001) found that “individuals of highly social ant species are less complex than individuals from simple ant species” (p. 211). They found that individual ants in more complex ant societies with a high degree of division of labor exhibit “low individual competence” and “low individual complexity.”

Increasing social complexity in ants is associated with a loss of brain size. Riveros et al. (2012) tested the association between brain size and sociality across 18 species of fungus-growing ants and found that increased colony size was associated with decreased relative brain size.<sup>23</sup> With agriculture, human brain size began to decrease dramatically. According to Hawks (2011), the decrease in brain size during the last 10,000 years is nearly 36 times the rate of *increase* during the previous 800,000 years. There is an important distinction between the “social brain” and “social intelligence” and “collective intelligence.” We fully agree with the “social brain” hypothesis that human intelligence evolved to facilitate within-group cooperation, empathy, and mind reading (Frith & Frith 2010; Wexler 2006). Collective intelligence, on the other hand, refers to the ability of groups to solve complex problems far beyond the capabilities of any individual within the group. Collective intelligence can increase while individual intelligence declines.

Individual simplicity may be an advantage in collective decision making. In fact, the standard economic model of extreme rationality may apply more to ant colonies than to humans. For example, a number of experiments show that humans are susceptible to the fallacy of irrelevant alternatives. A choice between alternatives A (a fully paid 10-day vacation to Paris) and B (a fully paid 10-day vacation to Rome) should not be influenced by the inclusion of an irrelevant unrelated choice C (a paid vacation to your least favorite nearby city). Humans are consistently susceptible to this fallacy (Ariely 2008), but ants are not. Edwards and Pratt (2009), in an experiment involving the choice of an ant colony between nesting sites, showed that the colonies are not influenced by irrelevant alternatives. They surmise: “We suggest that immunity from irrationality in this case may result from the ants’ decentralized decision mechanism. A colony’s choice does not depend on the site comparison by individuals, but instead self-organizes from the interactions of multiple ants, most of which are aware of only a single site” (Edwards & Pratt 2009, p. 3655). In some species of ants, the colony solves very complex problems of economic organization, and in fact it may outperform humans (Edwards & Pratt (2009). Collectively, ants have developed complex strategies to manage agricultural production. Like humans, they have developed a number of herbicides to control weed molds that attack the fungus they rely on, they have elaborate manuring regimes that maximize harvests, and cultivars are shared between distantly related ant colonies (Mueller et al. 1998).

The social insects demonstrate that collective intelligence can be quite impressive without a corresponding

level of individual intelligence. Off-loading of tasks in complex human societies is one explanation given for the decline in human brain size after the Pleistocene (Geary & Bailey 2009). People may not have to be as smart to stay alive. Cognitive scientist David Geary refers to this as the “idiocracy theory” after the 2006 film *Idiocracy* (McAuliffe 2010). Geary and Bailey (2009) and Mithen (2007), among others, argue that the complex material culture that came with agriculture allowed humans to offload some cognitive requirements, allowing the energy-expensive human brain to decrease in size.<sup>24</sup> Off-loading individual intelligence to the “environment,” “technology,” or the “social brain” is not necessarily a good thing from the point of view of an individual human. Social intelligence increased, but individual intelligence may have declined (see Barrett et al. 2007). This hypothesis fits nicely with our point that a major consequence of ultrasociality is a loss of individual autonomy and, possibly, cognitive capabilities. According to Mithen (2007, p. 705), even the social brain may have deteriorated with agriculture and civilization:

This development [sociality and social intelligence] has nothing to do with *Homo habilis* or handaxes, bipedalism or brain size. It is the origin of farming at, or soon after, 10,000 years ago. It is only with the economic basis that farming provides that writing, mathematics and digital technology could be invented, and it is these that effectively define the nature of our cognition today. The brain is important, of course, but it now plays a mere supporting role to a cognitive system that is primarily located in materials entirely outside the body—books, computers, paintings, digital stores of data and so forth. There are, of course, our capacities for empathy, mind reading and social interaction that no digital computer is ever likely to replace. But I doubt if these today are very different to those of our early human ancestors living several million years ago (Mithen 1996). Indeed, if anything, I suspect they have deteriorated through lack of use as we have become dependent on material items as the source of information.

A basic categorical mistake is to conflate the collective accomplishments of civilization with the understandings and intelligence of the average human—as in “we” formulated the theory of relativity, or “we” put a man on the moon. Scientific understanding of the origins of the universe and our species, the works of Shakespeare and Mozart, space exploration, and so on, are equated with human intelligence even though most people on the planet are unfamiliar and little affected by these achievements.

Intelligence, both social and collective, may be related to group size. Dunbar (1993, p. 681) suggests that cognitive constraints imply a consistent group size for effective human communities: “There is a species-specific upper limit to group size that is set by purely cognitive constraints.” Effective group size is limited by the maximum number of individuals with whom a person (or animal) can maintain social relationships by personal contact. For humans this maximum number is somewhere around 150–200 individuals. Naroll (1956) presented evidence for a “critical threshold at a maximum settlement size of 500, beyond which social cohesion can be maintained only if there is an appropriate number of authoritarian officials” (quoted in Dunbar 1993, p. 687). The size of the neocortex increases with group size—but only up to a point.<sup>25</sup> Dunbar’s argument does not contradict the

evidence that human brain size, and by implication cognitive ability, decreased after agriculture.

### 5.3 Control without hierarchy<sup>26</sup>

Ultrasociality channeled the existing propensity to cooperate in a new direction (Gowdy & Krall 2014). For example, sociality, caring for others, and cooperation with non-kin are defining characteristics of the human species (Frith & Frith 2010). These traits not only made it possible for humans to flourish and survive the extreme environmental changes of the Pleistocene, but also they fostered sustainable use of environmental resources and equalitarian social arrangements (Boehm 1997; Pennisi 2014). In non-ultrasocial groups, these traits worked both for the benefit of the group and for individuals within the group. Small-scale human societies have developed myriad forms of social organization to minimize group conflicts and to ensure that one individual or one small group of individuals cannot dominate (Boehm 1997; Wilson et al. 2013). Woodburn (1982, p. 438) writes of immediate return (simple technology and material culture) hunter-gatherers:

Without seeking permission, obtaining instruction, or being recognized as qualified (except by sex) individuals in these societies can set about obtaining their own requirements as they think fit. They need considerable knowledge and skill but this is freely available to all who are of the appropriate sex and is not, in general, transmitted by formal (or even informal) instruction: rather it is learnt by participation and emulation. In most, but not all, of these societies neither kinship status nor age is used as a qualification to obtain access to particular hunting and gathering skills or equipment.

But sociality and cooperation take on a different character with ultrasociality. Cooperation and coordination of activities in ultrasocial societies subjugate the individual to further the needs of the ultrasocial entity. The emergence of ultrasociality leads directly to a loss of autonomy at the individual level because autonomy interferes with the coordinated functioning of the group (Anderson & McShea 2001, p. 219). There is general recognition that selfish behavior can subvert the common good. In evolutionary terms, adaptation at any given level in the MLS hierarchy tends to be undermined by what happens at lower levels (Wilson 2013). What is not generally recognized is that what is good for the higher level may be not be good for entities at the lower level. For humans, the most social of human activities is the reproduction of material life, but the productive configuration of society changed with the active management of crops. In a sense cooperation was co-opted with agriculture and rigidly structured around narrowly defined productive roles (Gowdy & Krall 2013). With human ultrasociality the terms “prosocial” and “contrasocial” lose definition. When food production becomes the organizing principle of a society, the “good of the group” becomes “the good of the ultrasocial entity,” not the good of the average member of the group. What is good for the higher-level entity may be bad for individuals at the lower level. Of course, “good” and “bad” are human value judgments that cannot be applied to ant societies.

When the evolutionary leap to ultrasociality is made, individual survival (and by extension to humans, individual well-being) becomes secondary to the survival of the group as an evolutionary entity. The selective “pull” of the group over the individual becomes greater with

increasing complexity. In an ultrasocial system, there is no reason why *specific individuals* should be more likely to survive. Like cells in a body or bees in a hive, particles are there to serve the collective. In ants and termites, serving the collective has implications for reproductive fitness. In the most extreme examples, there are sterile castes. In humans, the implications are different because sacrifice for the group is not expressed reproductively.<sup>27</sup> Rather, it is measured in the extreme interdependency that delineates and reduces individual life to the role that enables the system itself to be reproduced. When the group begins to take on a life of its own and actively begins to shape its environment,<sup>28</sup> individuals are expendable. The group is the organism subject to the imperative to survive. Bees sting to defend the nest, thereby sacrificing themselves for the good of the group. In some species of ants, soldiers have such large mandibles that they cannot feed themselves. Individuals are expendable for the good of the group.<sup>29</sup>

In both ultrasocial human and insect societies there is a loss of *totipotency*, defined as “the potential, throughout life, to express the full behavioural repertoire of the population (even if never actually expressed)” (Crespi & Yanega 1995, p. 110). The term is meant to capture the range of behavior in a society (occupations, for example) compared to the range of behaviors available to a particular individual. It has been noted that workers in complex insect societies tend to be less totipotent (Anderson & McShea 2001). Studies of social insects and colonial marine invertebrates (reef shrimp) show a negative correlation between colony size and totipotency (Burkhardt 1998). In humans, the loss of totipotency is more complex. It is expressed in the more extreme specialization that attends ultrasocial social organization, but it is also expressed by the fact that for the majority of humans, agricultural life became narrowly focused around a single economic purpose.

Interestingly, Adam Smith (1776/1937, p. 735) also discussed the loss of what might be called human totipotency in complex societies as compared to what he called “barbarous” societies:

Though in a rude society there is a good deal of variety in the occupations of every individual, there is not a great deal in those of the whole society. Every man does, or is capable of doing, almost every thing which any other man does, or is capable of doing. Every man has a considerable degree of knowledge, ingenuity, and invention: but scarce any man has a great degree. The degree, however, which is commonly possessed, is generally sufficient for conducting the whole simple business of the society. In a civilized state, on the contrary, though there is little variety in the occupations of the greater part of individuals, there is an almost infinite variety in those of the whole society.

Agriculture entailed an altered organization of economic life that changed the relationships among individuals within the group and the relationship of both the individual and the group to the biophysical world. Once in place, the economic factors driving efficiency in production gave a competitive advantage for those species that could best capture them. The evolution of state societies was reinforced by a process of “downward causation” (Campbell 1974; Sperry 1969). Campbell (1974, p. 180) writes: “Where natural selection operates through life and death at a higher level of organization, the laws of the higher-level selective system determine in part the distribution of lower-level events

and substances.... All processes at the lower levels of a hierarchy are restrained by and act in conformity to the laws of higher levels.” Those societies having group traits most favorable to surplus production outcompeted other groups. The needs of the higher-level entity began to mold the behavior, organization, and functions of lower-level entities. Some possible consequences of this for present human societies are discussed in the next section.

## 6. Summary and final speculations

We argue that with the widespread adoption of agriculture as the basis for human and insect societies, a transition was made to ultrasociality and that this transition was propelled by economic forces. With the transition, the group begins to function as a single organism and coalesces around the active management of the food supply. With this transition an altogether different group dynamic takes hold; an economic revolution becomes an evolutionary force of extraordinary proportions.

To summarize:

1. The shift from hunting and gathering to agriculture was a major evolutionary transition to ultrasociality. The active management of food production is a transformational change in the configuration of productive life that propels greater interdependence and expansion.

2. Agriculture harnessed the driving forces of a complex division of labor, increasing returns to larger group size, and the intensification of resource use by tapping into stocks of productive inputs; and this encouraged growth and accumulation. Group selection favored those societies that were larger, more specialized, and more aggressive in resource exploitation.

3. Major bioeconomic characteristics common to insect and human agriculturalists are: a population explosion, the dominance of ecosystems, and the subjugation of individuals to the group and its dynamic.

4. Ultrasociality sets into motion processes of self-reinforcing downward causation so that lower levels in the system are at the service of the higher-level collective. In the post-agricultural human economy, economic institutions, political systems, religions, and other moral systems have fallen in line to promote the goal of producing economic surplus.

5. Evolutionary systems cannot see ahead. The ultrasocial system cannot see whether it is locked into an unsustainable resource use pattern. The system works as a mechanical evolutionary process and will not self-correct until negative feedbacks begin to curtail surplus production. Early agricultural societies were characterized by overshoot and collapse of local ecosystems. In recent history, negative feedbacks affecting the human economy – for example, from climate change, biodiversity loss, and fossil fuel exhaustion – have so far been minimal. Forces driving the exploitation of nature and of human labor will continue to work to keep economic output flowing.

These observations have important implications for two current human predicaments – the accelerating degradation of the earth’s ecosystems and the generation of inequality. The general message from human ultrasociality is negative – the human enterprise is driven by a mechanical evolutionary process working against individual well-being and environmental sustainability. Humans have also evolved to be a cooperative species. But compassion and

cooperation at the individual or even community level may not be sufficient to alter the growing imbalance between humans and the rest of the earth. Indeed, to address the imbalance it may be necessary to fundamentally change the mode of production on a larger scale. This will require changing the dynamic of expansion and the extensive interdependency of labor that is now characterized by extreme inequality. What seems clear from our analysis is that unless the expansionary tendency of the system can be controlled, it will likely continue to grow. If this happens, it is likely that the earth's life support systems will be destabilized in irrevocable ways (Barnosky et al. 2012; Pimm et al. 2014; Steffen et al. 2011). It would be well to concentrate on all of the benefits that might ensue if we successfully change the structural dynamic of this system.

Changing the expansionary dynamic of the system will not be an easy task. The extent of the scaffolding of ultrasociality in our current market society is remarkable. In this economic world, human societies have come to look more and more like colonies of ultrasocial ants. A new light is thrown on the idea of the competitive market as an "invisible hand" and Smith's notion that humans have a natural propensity to "truck, barter and exchange." An invisible hand is at work, but it is very different from the benign, bottom-up conception of Adam Smith that individual self-interest will lead to the common good (Gowdy & Krall 2013; Wilson & Gowdy 2015). The propensity toward markets is the result of the invisible algorithms that have evolved through the play of natural selection on the group rather than an innate predisposition to create markets. Dominant religious, political, and institutional "cosmologies" (Gowdy et al. 2013; Sahlin 1996) reinforce the drive for production of surplus and a "leave the system alone" approach to public policy. Examples abound, of course, of societies resisting the worst aspects of the world economic order. Resistance has no analytical equivalent in ants (except perhaps attempts by workers to reproduce), but it is central to the human story.

Evidence is accumulating that our day of reckoning with our ultrasocial evolutionary legacy will soon arrive (Barnosky et al. 2012; Steffen et al. 2011). Ant and termite supercolonies are finely tuned entities that evolved over tens of millions of years to be dominant but sustainable players in the ecosystems in which they occur. Humans are not ants or termites. Our very recent ultrasocial legacy is imperfect – it is far from being efficient and stable. Insects do not face the problems of unemployment and occupational discontent, nor are they disrupted by volatile financial markets or the problems associated with capital accumulation and the class conflict it engenders. The imperfect human ultrasocial system creates openings for change not presented to ants and termites. Perhaps the important question is how to tap these opportunities to gain control of the human ultrasocial system so that our species may once again have a sustainable and equitable way of life.

The human economy has now evolved into one worldwide socioeconomic system, the global market economy – interdependent, highly complex, and driven by economic forces of capital accumulation and the profit motive. If human society becomes a single entity, there is no "selection" pressure. For example, now there seems to be no currently viable competing economic alternatives to market capitalism. The ultrasocial entity, whether ant or human,

is a finely tuned and interlocked system defined by growth and accumulation, and by the extreme material interdependence of its members. The ability of individuals to alter such systems is problematic. It is hard for us to see this control over our lives because we are so embedded in the system and because the control is invisible.

Can we resist leaving a valuable productive resource like fossil fuel in the ground any more than an ant can resist exploiting a pile of sugar? The answer may be "no." Unless present global trends quickly reverse themselves, the human experiment with ultrasociality will likely end disastrously. Unlike the cases in the past where civilizations collapsed and the survivors moved on to other places, with a global overshoot and collapse surviving humans will have no place to go. E. O. Wilson (2014, p. 95) writes, "Nothing at all can be learned from ants that our species should even consider imitating." The social insects are instructive, not as positive models of efficiency, but as a mirror showing the negative consequences of social organization based on the economics of surplus production. We evolved economic structures similar to ants and termites because the same general evolutionary forces drove our economic organization along similar paths. "Human nature" did not cause the dilemmas of inequality and environmental unsustainability. Humans are not naturally rapacious, hierarchical, and competitive any more than they are cooperative and egalitarian. Solving the daunting problems we face requires structural changes in the human economy, not merely changing individual values.

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#### NOTES

1. To add to the confusion, Wilson (2012) recently classified humans as eusocial: "*Homo sapiens* is what biologists call 'eusocial,' meaning group members containing multiple generations and prone to perform altruistic acts as part of their division of labor" (p. 16).

2. Mueller et al. (2005) include ambrosia beetles as having complex agriculture. We do not include them because little is known about their social behavior, such as their task-partitioning activities (Mueller et al. 2005, p. 575).

3. Precisely defining ultrasociality is difficult partly because of the ambiguity of the transition from "non-ultrasociality" to "ultrasociality." There also exist innumerable gradations from cooperative societies to supercolonies (see the discussion in Moffett 2012). Also, cause and effect can be difficult to disentangle. So "managed agriculture" can be both an impetus for the evolution of ultrasociality and a characteristic of full-blown ultrasocial societies. Turchin (2013, p. 62) writes of the stages of ultrasociality: "Thus, it is perhaps best to think of multiple transitions instead of a single one."

4. However, as a reviewer pointed out, a human variation on "non-reproductive" castes is the grandmother hypothesis (Hawks 2003; Williams 1957). Humans are unique among primates in that females live for an unusually long time after menopause. It is hypothesized that postmenopausal women contribute knowledge and skills, including child-rearing, that enhance the fitness of the group.

5. But see Cochran and Harpending (2009), who argue that the development of agriculture greatly accelerated the rate of human biological evolution.

6. Turchin (2013, p. 70) writes: “Although other approaches are certainly possible, I believe that the most fruitful avenue of resolving the puzzle of ultrasociality is provided by the theoretical framework of cultural group (or, better, multilevel) selection.”

7. Technically, the fitness of an altruist in a group of altruists is higher than the fitness of a non-altruist within a group of non-altruists. A non-altruist could still have an advantage in a group of altruists.

8. This level of selection might be used to describe the nature of the group-individual trade-off in hunter-gatherer societies (see the essays in Gowdy 1998). Individuals are altruistic because this enhances the survival of their group, and thus their own survival. The fitness of the group can be characterized by the average fitness of its members (Michod 2005, p. 970). Moreover, each individual within hunter-gatherer societies is important for the well-being of the group. For example, in small hunter-gatherer bands the loss of an individual hunter or gatherer represents a significant loss to the group. The good of the individual is clearly integrated with the good of other individuals in the group.

9. One “supercolony” of Argentine ants in California possibly contains a trillion individuals (Moffett 2012, p. 925). We should point out that deciding which ants depend on agriculture is not an easy matter. Argentine ants manage scale insects whose droppings (honeydew) provide about 70% of the ants’ diet, but they are also opportunistic foragers.

10. We recognize that the claim that group-level traits are units of selection is controversial. See Santana and Weisberg’s (2014) commentary on Smaldino (2014). But we believe that “strong” group-level traits are a legitimate focus of analysis. See Smaldino’s reply (2014, pp. 282–83) and the excellent commentaries on the group selection controversy by Wilson (2010) and Lloyd (2012).

11. This potential is obviously limited if resources are limited in a particular place. The expansion of human agriculture, for example, was limited in Papua New Guinea because of topography and the reliance on root and tree crops rather than cereals (Diamond 1997, p. 148).

12. In terms of the increase in size and complexity, human and insect societies differ. Insect ultrasocial species expand their territories by duplicating colonies. So that, past a certain point, total growth of numbers comes from duplicating identical modules without an increase in the social complexity of individual models. Human institutions such as markets and trade call forth increases in complexity as total populations increase.

13. Georgescu-Roegen is best known for his work on the dependence of industrial societies on stocks of scarce and finite fossil fuels, but he also wrote extensively about the unsustainable use of fertile soil.

14. This is striking in the eusocial mammal, the naked mole rat. Colonies of these animals survive by foraging for a kind of tuber scarce in the deserts where they live. One mole rat searching alone would likely starve before a tuber was found. But when one mole rat finds a tuber, it makes a call to attract the others, who can live for weeks on the find (Judd & Sherman 1996).

15. Hunter-gatherers expanded into new areas (like North America), which significantly increased the total human population before agriculture, but this is not the same as the unprecedented population explosion in limited areas that characterized the agricultural transition. Surprisingly, claims are made that the human population explosion after agriculture is not unique (Caspermeyer 2013). It is certainly true that there were periods before the Neolithic where the human population expanded. But a closer examination reveals that these early expansions were not unusual and not of the same order of magnitude as the population explosion after agriculture.

16. Mueller and Gerardo (2002, p. 15428) write of fungus-growing insects: “Evolutionary reversal back to a nonfungus-farming lifestyle has apparently not occurred in any of the nine known, independently evolved farmer lineages (one termite, one ant, and seven beetle lineages). This supports the view,

formulated first for humans (Diamond 1997) that the transition to agricultural existence is a drastic and possibly irreversible change that greatly constrains subsequent evolution.”

17. The attitude of recent hunter-gatherers to agriculture is instructive. When a !Kung man was asked why he did not grow crops, he replied, “Why should we plant when there are so many mongongo nuts in the world” (quoted in Lee 1968).

18. The Upper Pleistocene number is based on the Kaplan et al. (2000) estimate for contemporary hunter-gatherers. Life expectancy estimates are notoriously difficult to compare because of differences in infant mortality, the effects of wars and epidemics, and so on.

19. The phenomenon of step-by-step evolutionary lock-in has been much discussed. See, for example, Nanay’s (2005) discussion of cumulative evolution and Tennie et al.’s (2009) concept of the ratchet effect.

20. We do not claim that the transition to settled agriculture in the Levant is a universal story. Agriculture arose several times after the beginning of the Holocene, in different climates and with different plant ancestors. Nevertheless, the transition in the Levant, from the earlier hunter-gatherer Kebaran to the pre-agricultural Natufian to the later fully agriculturalist Pre-Pottery Neolithic, is the most well-documented agricultural transition and it is consistent with the story we outline here.

21. It is true this interjection can happen indirectly without agriculture, as is the case with the intentional use of fire to change habitat. But even here the interjection is limited and the organizational demands do not extend over time.

22. We do not mean to imply that pre-agriculture hunter-gatherers were innately more ethical in their use of the environment. Their cultures were sustainable because they had to be, since they lived directly off of the day-to-day flows from nature. Grayson and Meltzer (2003) argue that the hunter-gatherer overkill hypothesis is not supported by evidence and that it represents a convenient “evil human nature” worldview supported both by environmentalists and those who advocate the exploitation of nature.

23. The brain of leafcutter ants is remarkably large, accounting for 15% of their body mass compared to 2% for humans (Seid et al. 2011). Darwin (1871) noted that “the brain of the ant is one of the most marvelous atoms of matter in the world, perhaps more marvelous than the brain of man” (quoted in Weislo 2012, p. 1419).

24. The relationship between human brain size and intelligence is controversial. But in a meta-analysis of the relationship between *in vitro* brain volume and intelligence, McDaniel (2005, p. 337) concluded: “For all ages and sex groups, it is clear that brain volume is positively correlated with intelligence.”

25. In their commentary on Dunbar’s paper, Falk and Dudek (1993) point out that a number of factors, including total brain size, can be correlated with larger group size. They also argue that there is nothing remarkable about the size of the human neocortex compared to other apes.

26. This phrase is taken from Gordon (2007).

27. A reviewer pointed out that in human societies, unlike insect societies, human reproduction remains at the level of the individual organism. But for women, enhanced reproduction more narrowly defined their lives. Women in agricultural societies had many more offspring than hunter-gatherer women, but their lives were shorter and arguably less satisfying. Women have been fighting for many generations not to be narrowly defined by their reproductive roles.

28. There exists a large amount of literature on niche construction, a process whereby organisms selectively modify their environments and influence evolution (Laland & Brown 2006; Laland et al. 2001). Examples abound in nature, from beaver dams to nests and burrows. In ants, humans, and termites, niche construction certainly accelerated with agriculture resulting in city-states for these species (Campbell 1982).

29. Some ants live only a few hours, although the colony can persist for years. The loss of individuality is taken to extremes in ant societies that function as superorganisms. Flannery (2009, p. 2) writes:



In explaining what a superorganism is, Hölldobler and Wilson draw up a useful set of “functional parallels” between an organism (such as ourselves) and the superorganism that is an ant colony. The individual ants, they say, function like cells in our body, an observation that’s given more piquancy when we realize that, like many of our cells, individual ants are extremely short-lived. Depending on the species, between 1 and 10 percent of the entire worker population of a colony dies each day, and in some species nearly half of the ants that forage outside of the nest die each day.

We do not suggest that humans have become ants in a colony, but we may have taken that evolutionary path.

## Open Peer Commentary

### Differentiation of individual selves facilitates group-level benefits of ultrasociality

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**Abstract:** Gowdy & Krall’s target article complements our recent theorizing on group behavior. In our comment, we elucidate complementary aspects of the two theories and highlight the importance of differentiation of selves for human groups to reap the benefits of ultrasociality. We propose that achieving optimal group outcomes depends on the differentiation of individual selves.

Social scientists have long struggled with the question of whether groups are more or less than the sum of their parts (Le Bon 1895/1960; Smith 1776/1991). That is, do people perform worse in groups than alone, or do groups enable outcomes superior to those that could be achieved by individuals? We read Gowdy & Krall’s (henceforth G&K) target article with great interest because their theory bears directly on that question. Our theorizing has focused on how division of labor and other phenomena (related to ultrasociality) affect group outcomes (Baumeister et al. 2016). In our comment we aim to elucidate complementary aspects of the two theories and to highlight the importance of differentiating between selves in order for human groups to reap the benefits ultrasociality.

We proposed that group activity can be divided into two heuristic steps. In the first step, individuals seek acceptance into the group because of the benefits that group membership confers. This first step of group activity emphasizes how group members are the same. Individuals at this step are motivated to maintain cohesion and shared group identity. Group identification may motivate members to work hard on behalf of the group.

The second step is role differentiation. This stage of group activity focuses on how members of the group differ from one another. At this stage, individuals cement their acceptance by performing unique roles or functions for the group. Role differentiation in turn enables the group to operate in complex, organized systems with interlocking roles, thereby improving group performance and making more benefits available to the group.

Our review found that differentiation of selves led to better group outcomes while reducing group pathologies (e.g., social loafing,

failure to pool information). Conversely, blending individuals into the group lowered the quality of group performance. Differentiation of individual selves improves group outcomes by promoting accountability, evaluation, responsibility, and independent judgment.

G&K’s proposal that the agricultural transition prompted the evolution of ultrasociality complements our two-stage model of group activity. In particular, they argue that food cultivation led to a more complex division of labor. They also note that specialization and division of labor are well suited to larger, as opposed to smaller groups. We concur. Division of labor necessarily involves differentiation of roles and thus of the individual selves who perform the roles. The agricultural transition may have prompted human groups to move from step 1 (achieving acceptance) to step 2 (achieving role differentiation). Furthermore, the increase in biotic potential linked to division of labor in food cultivation provides an example of how role differentiation enables social systems to function better and increase benefits.

Ultrasociality is associated with group-level benefits, but a potential downside, according to G&K, is the loss of individual autonomy. They argue that ultrasociality leads to increased interdependence and specialization in a narrowly defined role. This converges with our point that in the second step in our model, individual identification makes people more susceptible to control by the group (thus reducing autonomy to some degree). Role differentiation allows groups to easily identify contributions of each member and distribute punishments or rewards accordingly. Individual members who do not perform their role adequately may be sanctioned by the group to elicit cooperation.

G&K also argue that ultrasociality is what led humans and other social animals to dominate against competitors. Here again, we agree, and we think a key component of this process in humans was the development of differentiated selves. That is, the complex social systems associated with ultrasociality may have facilitated the development of increasingly well-defined selves, enabling groups to work together more efficiently (including on the battlefield, where group dominance has often been enacted).

Efforts to locate a specific brain area associated with the self have failed, suggesting that the self may be a social rather than physical reality. Humans learn to operate selves to fit roles within society. As G&K point out, the human brain can choose to adopt any of a variety of different roles. The specific role that is adopted likely depends on the needs of the group. These differentiated selves in turn enable the group-level benefits associated with ultrasociality.

In summary, we find much to admire in G&K’s analysis of the origins of ultrasociality. Their contribution enriches our own theorizing about how human selfhood may have developed to facilitate group success. The evolution of ultrasocial economic systems in humans, which greatly expanded population size, may have created the need for differentiated selves. Differentiated selves in turn facilitate improved group-level outcomes via system gain.

### “If it looks like a duck...” – why humans need to focus on different approaches than insects if we are to become efficiently and effectively ultrasocial

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**Abstract:** The parallels between the agricultural successes of ultrasocial insects and those of humans are interesting and potentially important. There are a number of important caveats, however, including the

relative complexities of insect reproduction, their more rigidly determined altricial patterns of social behaviour, the roles of post-reproductive group members, and differences in the known factors involved in ultrasocietal collapse.

“If it looks like a duck, and quacks like a duck, we have at least to consider the possibility that we have a small aquatic bird of the family *Anatidae* on our hands.”

— Douglas Adams (1987, p. 270)

“What characterizes the living world is both its diversity and its underlying unity.”

— François Jacob (1977, p. 1164)

Ultrasocial group cooperative “strategies” maximise reproductive success. These include division of labour, generational overlap, and cooperative care of offspring (Wilson 2012). They have been described in some insects (Nowak et al. 2010); primates, including man (see Alberts et al. 2013; Foster & Ratnieks 2005); ungulates (Loison et al. 1999; Shannon et al. 2013); and various cetaceans (see McAuliffe & Whitehead 2005).

Gowdy & Krall (G&K) provide a scholarly review the economies of scale, efficiency, and reproductive fitness conferred and the resulting efficiencies of production and resource use. These economic drivers are important to the success of human ultrasocieties, but with an associated loss of individual autonomy.

I agree that the support of larger social groups requires efficient production and utilisation of nutrition, which then enable some members to engage in other activities, but I am not convinced that strict parallels are robust or informative. Explanations in behavioural evolution too often need to draw on studies of easily accessible species, are inconsistently evidence-based, and frequently invoke *post hoc ergo propter hoc* argument.

The success of ultrasocial insects relies on a diversity of factors: their exosymbiotic approach to agriculture (see Benckiser 2010); collective parasite defence (Cremer et al. 2007); and often the adjustment of colony size and behaviour to resource or climate change through polyandric genetic mechanisms (Oldroyd & Fewell 2007), which guide simple iterative patterns of genetically controlled altricial behaviour. The insect transition from family to ultrasocial living appears to be under genetic control (Kapheim et al. 2015).

A number of catastrophic changes to ultrasocial insect colonies are well-documented: Colony collapse disorder (CCD) is one example of overdetermined social implosion (Kribs-Zaleta & Mitchell 2014; Oldroyd 2007). The devastation of South African honeybee colonies through automictic thelytoky provides another (Martin et al. 2002; Rabeling & Kronauer 2013). Whether such events are infrequent or common is difficult to determine. Ultrasocial insect groups seem more vulnerable and less rapidly adaptable to genetic anomaly than their human equivalents.

In humans, the transition from hunter-gatherer groups to ultrasocial agrarian societies was driven by diverse invention: improvements in irrigation (see Ng et al. 2015), fertiliser use (Bogaard et al. 2013), insect control (see Berenbaum 1995), and plant and animal domestication (Gepts et al. 2012; Larson & Fuller 2014; Zohary et al. 2012).

Human catastrophe has resulted more typically from serendipity and lack of foresight for events ranging from natural disasters (Whyte 2008), problems with irrigation (see Stone 2006), food distribution and storage (Silver 2012), and disruption by intraspecies conflict (Turchin 2006).

Much human behaviour is inherently variable, transient, and eclectic in “content” (for example, in our cognitive and mechanical abilities; ethical and moral values; language use; and literary, musical, and artistic skills; see, e.g., Tomasello 2014). Early attempts at maintaining ultrasocieties frequently struggled or collapsed through lack of planning or adequate knowledge (see Fraser & Rimas 2010).

Eusocial insect success depends on fixed altricial behaviour. Human success depends on application of more arbitrary acquired skills through an extended period of behavioural neoteny, with

eclectic and varied results. Fritz Haber’s discoveries of both artificial fertiliser and poison gas and Alfred Nobel’s introduction of nitroglycerin and the Nobel prize may, *in toto*, have had little effect on human success.

The only example to date of human behaviour affecting the genetic makeup of a population is Genghis Khan (see Zerjal et al. 2003). Our behavioural flexibility stems from our individual capacity for rapid learning in our early family environment, and its co-construction with our caregivers over an extended period of neoteny. This process of intersubjectivity shapes our ability to predict, relate to, and empathise with the behaviour of those around us (Aitken 2008). We are beginning to understand the neurobiologies of these complex intrapersonal processes (see Dumas et al. 2010; McCall & Singer 2012; Schilbach 2015).

A feature of human groups is the high proportion of post-menopausal and post-andropausal members. *Ceteris paribus*, this should reduce reproductive fitness and has perplexed evolutionary biologists (Medawar 1952). The various post-reproductive roles of contributing to labour, sharing care of the young, and imparting context-specific trans-generational “herd memory” help maximise reproductive fitness and largely addresses the issue (see Croft et al. 2015). Recent changes to family structure and age demographics in many human ultrasocieties have disconnected post-reproduction individuals from these roles, with as yet untested but potentially deleterious consequences for economic fitness and ultimately for species survival.

Our understanding of mammalian senescence is still scant (see Brinton 2012). Some ungulates seem to show differential post-reproductive survival, but few have been studied (see Loison et al. 1999). In other ultrasocial mammals, knowledge or experiential learning histories are important and can be hugely disrupted by the loss of post-reproductive individuals (McComb et al. 2011; Shannon et al. 2013).

There has been even less research on insect senescence (see Uematsu et al. 2013). In many groups, roles are partitioned and fertility can change (Amdam & Page 2005). Neurophysiological change can be age-independent and some are even reversible (Seehuus et al. 2006). Lifespan can be extended by as much as 10-fold as a result of external stress (see Omholt & Amdam 2004).

The minutiae of insect and mammalian ultrasocietal success differ. Face-valid similarity may not reflect equivalent origins or likely consequences (see Feynman 1974). Common to terrestrial ultrasocieties are advanced nutritional support and economies of scale.

Human success stems from the capacity to both learn rapidly from as well as mould our environments. These capacities enable us to adapt to our immediate social milieu and ensure our adaptive fit to our culture. Our major weaknesses are engaging in intraspecies aggression and the massive growth in our post-reproductive populations.

As Shakespeare wrote in *The Merchant of Venice*, “All that glitters is not gold” (*Merchant of Venice*, Act II, Scene vii).

## Autonomy in ants and humans

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**Abstract:** Drawing lessons regarding the consequences of ultrasociality in ants and humans depends crucially on recognizing differences as well as similarities in the way that species are social. We focus on Gowdy & Krall’s use of the concept of autonomy to explicate essential differences in the ways in which ants and humans are social.

Gowdy & Krall (G&K) suggest that, “exploring the common causes and consequences of ultrasociality in humans and the social insects that adopted agriculture can provide fruitful insights into the evolution of complex human society” (target article, Abstract). They highlight the similarities between ant and human populations at the macro-level, and end by speculating about the implications of agriculture and ultrasociality for the predicaments humans currently confront: “the accelerating degradation of the earth’s ecosystems and the generation of inequality” (sect. 6, para. 3). In drawing implications from this comparison it is vital to be aware of the essential differences between ants and humans.

One way to explicate the radical differences between ants and humans is to unpack G&K’s assumptions about autonomy. They claim that, “a major consequence of ultrasociality is a loss of individual autonomy” (sect. 5.2, para. 4). However, the human notion of autonomy does not have a clear application to an ant’s way of life. Whether solitary species of bees have more autonomy in the sense of independence and freedom compared to those species living in hives is far from clear. In the case of humans, rather than autonomy being *lost* through human sociality, we suggest that humans develop as persons with the potential for autonomy through developing within a human social life.

Human infants are born relatively helpless and are therefore dependent on their caregivers for their needs, none of which can be *intentionally* communicated by the infant initially. However, by developing within this heavily scaffolded ecological niche, infants are able to gradually master increasingly complex forms of communication due to their burgeoning ability to anticipate others’ responses to their actions (Carpendale et al. 2013a). That is, they become aware of the meaning that their actions convey to others (Mead 1934). This step is not necessary, or indeed even possible, for social insects. As human infants learn the rudiments of language, they can begin to use these communicative skills as tools for thinking, giving them the ability to consider alternative strategies rather than blindly reacting to the events occurring around them (Canfield 1995).

Many species are social to some extent, but their ways of being social can differ radically. For example, although both human behavior (Canfield 1995) and ant behavior (Gordon 2010) can be understood through an appeal to “patterns of interaction,” it is precisely humans’ ability to gradually learn and then *consider* these interactive patterns, along with the effect that their actions can have within them, that separates the human notion of autonomy from that of ants. It is within this intelligent interaction with the world and other people that we can see the origins of autonomy in human beings. Human intelligence involves increasing flexibility in responding, and the ability to select among alternative strategies, and in this sense an increase in autonomy. According to a socio-genetic view of development, intelligence develops within social relations, beginning with communicative development in infancy before extending into the development of language, social understanding, and moral development (Carpendale et al. 2013b; Carpendale & Lewis 2015).

In sum, it is important to be cautious about comparing ant and human behavior. Although ants could be described as waging wars, capturing slaves, and dying in defense of their nests, they are not given medals. Applying the human notion of sacrificing one’s life for others does not apply to an ant’s way of life. Individual ants do not have the capacity to anticipate the (potential) effects of their (potential) actions, whereas this ability is central to both the development and continued realization of human autonomy. We applaud G&K’s attempt to grapple with the predicament humans face, but we suggest that responding to it is better served by understanding the crucial differences between ants and humans. G&K seem to conceptualize autonomy as individual choice and implicitly contrast it with compulsory conformity, but for humans, unlike ants, another form of social relations is possible among equals based on mutual respect. Humans do not just conform to rules imposed by authority; they also may choose to

live by obligations to others adopted through cooperation among equals (Carpendale 2009; Piaget 1932/1965). One factor leading to the predicaments we currently face may actually be autonomy and self-interest. The human way of being social results in flexibility and intelligence, as well as the ability to engage in discussion, such as the current debate about divestment and the need to leave three quarters of the remaining fossil fuels in the ground.

## The convergent and divergent evolution of social-behavioral economics

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**Abstract:** Human hunter-gatherers share a suite of traits with social insects, which demonstrates convergent social evolution of these taxa prior to agriculture. Humans differ from social insects in that their divisions of labor are more competitive than cooperative. Resulting higher within-group competition in humans has been alleviated by religion and culturally imposed monogamy, both of which also find parallels among social insects.

The eminent evolutionary biologist William D. Hamilton once told me a new hypothesis he had developed: that some ants had religion, of a sort. His idea was that unicoloniality, the development of massive super-colonies spanning hundreds of kilometers where every ant was accepted as colony-mate by every other, was caused by infection with a virus that caused them to lose their ability to recognize kin. The virus would benefit through increased spread, and the ants could benefit from enhanced large-scale cooperation among themselves. Everyone wins – except of course ants that are uninfected.

Hamilton’s hypothesis may be more metaphor than reality, but it raises intriguing questions about similarities between humans and social insects. Years later, I wrote an article entitled “The Insectan Apes” (Crespi 2014), which drew together the evidence regarding convergences between humans and social insects that may help explain their shared, spectacular ecological and evolutionary successes. Most of the similarities apply to human hunter-gatherer groups, within which we have spent most of our evolutionary history, and many are economic. They include: (1) life in cooperative groups with unique identities (semiochemicals or culture); (2) central place foraging; (3) extensive food sharing within groups; (4) highly diversified, and high-quality, foods; (5) divisions of labor, including extensive non-maternal care; (6) increased reproduction by females; relative to ancestral forms; (7) collective, cooperative decision making within groups; and (8) the group itself becoming a basic, necessary, social-ecological resource that enhances survival and reproduction.

What these remarkable similarities show is that human groups were behaviorally, ecologically, and economically similar to social insects well before the spread of agriculture. During the agricultural revolutions of humans and social insects, as described by Gowdy & Krall (G&K), further similarities ensued: Both groups developed larger colony sizes, with more-extensive divisions of labor and interdependencies among workers. These convergences indicate that humans and social insects have shared a broadly overlapping suite of selective pressures for millennia, especially with regard to colony-level selection, which corresponds, in humans, to selection among different cultural groups (Aunger & Greenland 2014; Crespi 2014; Keesebir 2012).

Ant religions aside, humans are also divergent from social insects in several fundamental ways that must temper comparisons. First,

as noted by G&K, human agriculture led to decreased food sharing, and reduced collectivity in decisions, due in large part to hierarchies of power and wealth. The key difference here is that social-insect divisions of labor, especially in large-colony forms like ants and termites with agriculture, are *virtually purely cooperative*; by contrast, human divisions of labor are driven predominantly by *competition*. Social insects cooperate due to coincidence of genetic interest between workers and the queen, through whom all colony members reproduce (Alexander et al. 1991). This social-insect economy thus resembles a utopian mix of Marxism and monarchy, with minimal or no incentives, or ability, to engage in selfish reproductive cheating. Where such cheating is possible, it is normally suppressed by policing: For example, in honeybees, if a worker lays an egg, it will almost invariably be eaten by other workers, who gain (as does the colony) by such “moral” behavior. It is only when human groups are threatened from outside, by culturally different groups, that their interests so strongly converge.

Competitive divisions of labor, unlike cooperative divisions of labor in ants and termites, lead directly to inequalities in resources and reproduction, as exemplified by the unbridled reproductive extremes of early city-state rulers (e.g., Betzig 2014). But such inequalities are themselves inequitable, applying more to male than female humans. Herein we find a second key divergence of humans from social insects: Insect queens can evolve greatly increased fecundity by making many, tiny juveniles that are reared by workers, but humans, as mammals, are severely constrained in reproductive potential. Human females have evolved higher fecundity than other great apes, mainly through a halving of inter-birth interval combined with alloparental care (Crespi 2014), but it pales in comparison to ant or termite queens; human juveniles also appear much more expensive to rear than juveniles of other apes.

Reproduction by all females precludes human reproductive division of labor, and indeed, human groups almost certainly benefit at the cultural group level from high fecundity of their female members (Crespi 2014). But competitive reproduction among females as well as males, like competitive divisions of labor, decreases the potential for cooperation within groups. Moreover, human groups exhibit much lower within-group relatedness than do social insects, and relatedness among interactants drops precipitously with agriculture-driven increases in group sizes. What is an insectan ape to do?

Enter culture, our human-evolutionary trump card, and re-enter religion. Primary effects of religious cognition, behavior, and institutions include the generation of psychological kinship, the unification of within-group interests, and the establishment of moral codes to suppress cheating (Aunger & Greenland 2014; Crespi & Summers 2014). With the emergence of agriculture, human groups increased greatly in size, and religions and gods also got big, as monotheistic, highly moralizing religions supplanted their predecessors (Norenzayan 2013). After agriculture, human nation-states, and monotheistic religions became well established, humans also began to adopt a new cultural means of suppressing inequalities: socially imposed monogamy (Alexander 1987).

What is interesting about religion, and imposed restriction of reproduction, is that they represent forms of prosocial, social-insectan adaptation. The first is a marker and driver for group unity, cooperation, altruism, large-scale “kinship,” and colony membership, just like a colony odor in ants, termites, or bees. The second is a reproductive leveler, that reduces competition within both families and human cultural groups (Bowles 2006; Henrich et al. 2012), like policing in social insects; human families also thus become more similar to the enlarged nuclear-family structure that typifies insect sociality (Alexander et al. 1991).

How many human social ills can further be alleviated by emulating the ants and termites underfoot? G&K are to be applauded for their synthesis of economics with social behavior and human history. We are fortunate to differ from social insects in this final key trait: the ability to think, create, plan, and lead, and thus determine our fates.

## The continuing evolution of ultrasocial economic organization

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**Abstract:** Ultrasociality, as expressed in agricultural, monetary, and fossil fuel economies, has spurred exponential growth in population and in resource use that now threaten civilization. These threats take the form of prisoner’s dilemmas. Avoiding collapse requires more cooperative economic organization that must be informed by knowledge of human behavior and cultural evolution. The evolution of a cooperative information economy is one possibility.

Gowdy & Krall’s (G&K’s) insights into the impact of agriculture on economic organization help explain humanity’s current crises of ecological degradation and growing inequality. Their work also contributes to the scientific understanding of human behavior, cultural evolution, and economic organization that will be required to develop an economic system capable of addressing these crises. I would suggest, however, that fossil fuel use and monetary exchange have taken human ultrasociality and economic organization in new directions. The emergence of an information economy may do the same, and it could possibly facilitate the re-emergence of more egalitarian and cooperative forms of economic organization.

The modern capitalist economy emerged not with the transition to agriculture, but rather, simultaneously with our ability to tap fossil fuel stocks (Farley 2010). The fossil fuel economy has taken division of labor, group size, growth, accumulation, and environmental domination to unprecedented extremes. The result is natural resource depletion, accumulating waste emissions, degradation of life-sustaining ecosystem services, overpopulation, and other existential threats to civilization.

Our current environmental challenges can all be characterized as prisoner’s dilemmas: The best outcome for the individual is selfish behavior, regardless of what others do, but the best outcome for society is cooperation. The individual gains the benefits of excessive resource extraction or pollution, but shares the costs with society as a whole, and the costs imposed by any single individual are negligible. If others extract or pollute too much, each individual would be foolish not to, and if others refrain from doing so, the individual can free-ride on their efforts. Prisoner’s dilemmas can be solved only through cooperation (Axelrod 1984; Nowak & Highfield 2011; Sober & Wilson 1998).

The modern economy is dominated by monetary exchange. Lea and Webley (2006) hypothesize that money, acting like a drug, has parasitized and corrupted the human instinct for reciprocal altruism. Simply priming individuals to think about money makes them less likely to offer help to others, solicit help, pursue social interaction, or behave ethically (Kouchaki et al. 2013; Vohs et al. 2006; 2008). Policies designed to appeal to self-interest, such as monetary rewards or punishments for certain behaviors, reduce the individual’s motivations to act for the public good (Bowles 2008). Almost the inverse of ultrasociality, mainstream economic theory (MET) assumes self-regarding, individualistic behavior and methodological individualism. All social phenomena are analyzed as the result of individual actions. MET prioritizes individual freedom, and pursues the libertarian goal of satisfying unchanging, subjective individual preferences. In practice, simply studying MET appears to increase free-riding, selfish behavior, and even corruption (Cipriani et al. 2009; Frank & Schulze 2000; Frank et al. 1993; Kirchgässner 2005; Marwell & Ames 1981; Wang et al. 2011). Modern monetary capitalism may prove incapable of solving prisoner’s dilemmas.

Humans, however, are obviously capable of cooperation and altruism as well as competition and selfishness. Multilevel selection

(MLS) offers a convincing theoretical explanation of why both types of behavior evolved. Though markets may promote selfish behavior, other institutions exist that stimulate voluntary cooperation and altruism (Axelrod 1984; Bowles & Gintis 2004; Boyd et al. 2003; Fehr & Fischbacher 2002; Fehr & Gächter 2000; Gächter 2007; Gintis 2000; Gintis et al. 2005). While MLS theory suggests that stimulating cooperation between groups can be difficult (Sober & Wilson 1998; Wilson 2007), ultrasocial species can share group identity for populations of hundreds of millions. It may be possible to evolve institutions that promote group cooperation on the scale necessary to solve our most serious global challenges. However, a single culture that strived for sustainability by reducing fossil energy use would be at the mercy of those that did not.

Many types of ultrasocial economic organization may coevolve with cultural and technological change. A monetary fossil fuel economy is very different from a pre-monetary agricultural one. Our ultrasocial species may now be transitioning to an information economy. All economic production requires information as well as natural resources and energy. Solving the problems of resource scarcity, waste emissions, and ecological degradation will almost certainly require technological breakthroughs, perhaps on the scale of agriculture and fossil fuels. Solar energy must be one of these technologies. Unlike fossil fuels, solar energy is not depleted through use, while the information required to capture it actually improves through use. Freely sharing information therefore facilitates technological advance. Once a useful technology exists, especially for a green technology, its value is maximized when all are free to use it (Farley & Perkins 2013). Market economies, however, have created intellectual property rights to incentivize the private production of knowledge. But scientists competing for a new patent will not share information, and they will unnecessarily replicate research efforts, raising the costs of technological innovation. Once an innovation exists, charging royalties reduces use, and hence societal benefits: For example, if royalties drive the price of clean energy too high, industries may continue to burn coal to the detriment of all. An information economy is more efficient when organized around cooperative provision and open access rather than competition and price rationing (Benkler 2002; Farley & Kubiszewski 2015; Kubiszewski et al. 2010).

Speaking speculatively, any country could potentially initiate the transition to a new type of ultrasocial economic organization by sharing its green technologies with others on the condition that all further improvements would also be shared. The legal structure for this, copy-lefting, already exists (Mustonen 2003). Generosity stimulates reciprocity. Countries might begin cooperating to protect the environment instead of competing for a larger share of dwindling ecological capacity. Non-cooperators could be penalized with high trade tariffs and economic sanctions. Reciprocity for generous acts and punishment for non-cooperation increase cooperation (Nowak & Highfield 2011). The Internet is already democratizing access to information, contributing to the foundation of this new and potentially more cooperative form of social organization. Whether economic organization follows this or another path, G&K's insights into the ultrasocial nature of our current economy may help us nudge cultural evolution in a more sustainable direction.

## Human and ant social behavior should be compared in a very careful way to draw valid parallels

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**Abstract:** Gowdy & Krall provide an interesting discussion of evolutionary origins and consequences of ultrasociality. However, some of their statements concerning various features of ant and human social behavior do not adequately reflect present knowledge about the discussed issues, which include, among others, polyethism, cultural information transfer, within-group conflicts and resistance in ant societies, and reproductive division of labor in humans.

Gowdy & Krall (G&K) provide an interesting discussion of evolutionary origins and consequences of ultrasociality, an advanced form of social behavior that evolved independently in both social insects and humans. Their reflections are thought-provoking, but some statements concerning various features of ant and human social behavior do not reflect adequately the present knowledge about the discussed issues.

The discussion of the role of agriculture in the evolution of ultrasocial behavior in both social insects and humans is focused on cultivation of crops such as fungi (ants and termites) and cereals (humans). However, agriculture also involves domestication of animals. Animal husbandry plays a very important role in many human and ant societies. Numerous ants rear "cattle" (such as aphids, coccids [i.e., scale insects], and treehoppers) and use their secretions as an important source of food. They construct shelters for their "cattle," transport them, and protect them against predators. Like humans, ants also sometimes eat their "cattle" to obtain proteinic food (Hölldobler & Wilson 1990).

G&K discuss food storage largely in terms of storage of produced surplus, although they mention the evidence for pre-domestication granaries in the Jordan Valley (Kuijt & Finlayson 2009). There exists further evidence showing that food and/or water storage preceded the advent of agriculture in both humans and ants. Bushmen hunter-gatherers from Kalahari store water in emptied ostrich eggshells, and the tradition of using such containers is at least 60,000 years old (Texier et al. 2010). Harvester ants do not culture plants, but forage for seeds and store them in underground granaries. Honeypot ants may act as "living larders" and store liquid food in their distended abdomens (Hölldobler & Wilson 1990).

G&K extensively discuss morphological adaptations of ants to various functions fulfilled by them within the framework of the division of labor among the members of the same colony. Yet, in the vast majority of ant species (including some ultrasocial ones) workers are monomorphic and worker behavioral specialization is based on other factors than morphology – in particular on worker age and/or degree of physiological maturation (the so-called temporal polyethism) (Hölldobler & Wilson 1990; 2009). Interestingly, temporal polyethism also seems to play an important role in the organization of human societies. In the traditional Brahmin culture of India, each man had to pass through four successive life stages: Brahmacharya (student), Grihastha (married householder), Vanaprastha (hermit), and Sannyasa (wandering ascetic). Similarly, the Vestals of the ancient Rome had to pass through three stages (training, service, and training others) during their 30-year service at the Temple of Vesta.

According to G&K, ultrasocial ants and humans dominate the earth's ecosystems. However, raiding and domination inflicted by raiding robbers are known not only in humans, but also in ants. Army ants, the best known nomadic ants employing group raiding, form huge societies characterized by sophisticated caste polyethism (division of labor based on morphological differences) (Hölldobler & Wilson 1990). This implies that among the ants neither dominance in the ecosystem, nor advanced division of labor are strictly correlated with the ultrasociality.

G&K also lay stress on the limited longevity of ant workers. However, ant workers may live up to several years (Godzińska et al. 1999; Hölldobler & Wilson 1990), and they play an important role in the cultural transfer of information between older and younger nestmates. It's hard to disagree with G&K's statement that "one cannot reasonably argue that insects have culture in the way that humans do" (sect. 2.1, para. 2). However, cultural transfer of information seems to exist also in

ants. According to Rosengren and his colleagues (Rosengren 1977; Rosengren & Fortelius 1986), red wood ants of the genus *Formica* form the so-called topographic traditions. The information about the localization of aggregations of aphids is stored throughout the winter in the brains of older workers. In the spring these “veterans” transmit that information to unexperienced young foragers, the “novices,” by guiding them to the places where the aphids will briefly appear.

G&K state that, in contrast to humans, the social life of insects is based on the reproductive division of labor (sterile and/or less fertile individuals take care of the offspring of more fertile ones), although non-reproducing individuals (namely, post-menopausal grandmothers) exist in human societies, too. However, these non-reproducing society members may also include young females (e.g., virgin priests and warriors, but also prostitutes, who may bear children but refuse to rear them) and males (e.g., eunuchs, celibate priests, unmarried slaves, servants, and soldiers). Ultrasociality and social organization based on city-states certainly promoted the role of these non-reproducing individuals in the overall organization of human societies, enhancing the similarities between advanced human and insect societies.

In section 2.3 (para. 4), G&K mention Smaldino’s (2014) statement that “an ant colony represents the extended phenotype of the queen.” However, they do not point out that such a view is oversimplified, as ant colonies are often polygynous (contain numerous queens). Consequently, relatedness between nestmates is frequently very low, sometimes even close to zero. Nevertheless, ants from such colonies can successfully cooperate (Hamilton 1987). However, conversely to what was stated by G&K in section 5.1 (para. 4), important within-group conflicts do exist also in insect societies. Members of the same colony compete mostly for the access to reproduction (Heinze et al. 1994; Hölldobler & Wilson 1990; 2009). Ant workers are not completely sterile: they may reproduce by parthenogenesis and produce males from unfertilized haploid eggs and sometimes also females from unfertilized diploid eggs (Hölldobler & Wilson 1990). Various forms of worker resistance against reproductive dominance of the queen lend support to the statement of G&K that “resistance has no analytical equivalent in ants (except perhaps attempts by workers to reproduce)” (sect. 6, para. 4). However, ant resistance may take yet other forms. In particular, enslaved ants may successfully rebel against their social parasites. Various forms of slave resistance include physical aggression against adult slave-makers, devouring of slave-maker’s brood, attempts to reproduce in the slave-maker’s colony, and slave emancipation (Czechowski & Godzińska 2015).

In conclusion, all of these examples of not strictly adequate statements demonstrate that ant and human social behavior should be compared in a painstakingly careful way in order to draw entirely valid parallels.

## On the effectiveness of multilevel selection

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**Abstract:** Experimental studies of group selection show that higher levels of selection act on indirect genetic effects, making the response to group and community selection qualitatively different from that of individual selection. This suggests that multilevel selection plays a key role in the evolution of supersocial societies. Experiments showing the effectiveness of community selection indicate that we should consider the possibility that selection among communities may be important in the evolution of supersocial species.

One of the key elements of Gowdy & Krall’s (G&K’s) model of ultrasociality is the idea that group selection plays a central role in its evolution. I would like to expand on their discussion of multilevel selection, and to argue that agriculture, whether by humans or social insects, has likely involved multi-species community selection as well as single-species group selection.

First off, it is important to recognize that group selection and community selection work. This was first demonstrated in Wade’s (1977) landmark study on group selection in *Tribolium* flour beetles. Since that time, there have been numerous studies demonstrating the effectiveness of group selection (reviewed in Goodnight & Stevens 1997), and multilevel selection has become an important tool for animal breeding (e.g., Wade et al. 2010). There has also been one study showing group selection acting in human populations (Moorad 2013). Finally, there are several studies showing a response community selection in two species communities (Goodnight 1990a; 1990b) and in soil and aquatic microbial communities (Swenson et al. 2000a; 2000b).

One surprising thing about group selection experiments is how effective they are. For example, Muir (1996), using group selection to increase egg production in chickens, observed a 160% increase in egg production in the selected lines. The cause of the effectiveness of group selection is known to be primarily due to indirect genetic effects (IGEs) (Bijma & Wade 2008). IGEs are defined as phenotypic effects in one individual due to genes in another individual. Muir’s chickens provide a good example of how these work. In his experiment, Muir, rather than selecting on the chickens that produced the most eggs, selected on the cages that produced the most eggs. Chickens are famous for having a pecking order; the most aggressive chickens get the majority of the food and lay the most eggs. The more subservient chickens get less food, lay fewer eggs, and get harassed by more dominant chickens, although they generally do survive if they can run away. In cages, however, the subservient chickens cannot run away, and they often get pecked to death. Individual selection will favor the most aggressive chickens, because they lay more eggs, resulting in more antagonistic interactions, and heightened mortality of subordinate chickens.

Muir, however, by selecting on the productivity of the cage favored those groups of chickens in which food was more equally shared, there was less mortality, and overall more eggs were laid. This illustrates the importance of IGEs in multilevel selection. Group and community selection can act on IGEs and bring about adaptations that are qualitatively different from adaptations that can evolve by individual selection. In the chicken example, individual selection can only act on direct genetic effects – thus, it will favor chickens that more aggressively dominate resources, regardless of its effects on other individuals. Group selection, however, will favor groups of chickens that overall lay the most eggs. Selection for greater overall egg production favors less aggressive chickens, which ensures that all individuals have adequate resources to contribute to the total output of eggs. These indirect effects also contribute to the response to community selection. For example, Goodnight (1990b) showed that the response to community selection in two species communities of *Tribolium castaneum* and *T. confusum* depended on maintaining the genetic structure of the community.

Ultrasociality concerns the evolution of complex societies with a high degree of specialization of society members. Individual selection cannot by itself lead to the evolution of such complex sociality. Group and community selection can act on indirect genetic effects, and the specialization of the members of a society can be considered an example of IGEs, or in the case of humans, indirect cultural effects. Thus, we can argue that group selection may be essential for the evolution of ultrasociality.

Particularly intriguing is the possibility of community selection being important in the evolution of ultrasociality. As G&K point out, Atta (leafcutter ants) and their fungi are closely coevolved, with the ants being dependent on the fungi as a source of food, and the fungi dependent on the ants for food and protection

from pathogenic bacteria. Similarly, Meso-American agriculture was dependent on maize as the basis of the inhabitants' diet, and maize is a derived crop that cannot survive without human intervention (Landon 2008). Such coevolution may well be the result of selection acting directly on the community (Goodnight 1990a). For example, in an *Atta* colony, an infected fungus may lead to death of not only the fungus, but also the ants that depend on it. Those colonies in which the fungus is resistant to bacterial infection, whether due to intrinsic resistance of fungus or the behavior of the ants, will have a higher overall fitness. Similar scenarios can be imagined for humans and their crops.

Thus, G&K are correct to suggest the role of multilevel selection in the evolution of ultrasociality; however, we should also consider the possible role of community selection.

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## Rome was not built in one day: Underlying biological and cognitive factors responsible for the emergence of agriculture and ultrasociality

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**Abstract:** Agriculture represented a major transition in human evolution, but the appearance of ultrasociality must have included previous steps. We argue that ultrasociality would not have suddenly emerged with agriculture, but rather developed from pre-existing cognitive and social mechanisms. Discussions must include necessary depth about the historical origins of human ultrasociality, and agriculture's aftereffects on large-scale social organization.

Gowdy & Krall (G&K) make a strong argument that agriculture was a major evolutionary step toward ultrasociality in human social organization. We agree that, with the introduction of collective management of food production, new emergent properties appeared that are similar in overall function to those seen in eusocial species of ants and termites. We disagree, however, with the authors' view that ultrasociality would have abruptly appeared with the advent of farming. Sophisticated civilizations and technology, which emerged over a relatively short period of human evolutionary history, would have required a foundation of highly cooperative pre-existing social structures to develop. We argue that the target article lacks depth about the phylogenetic origins of human sociality and culture, including the cognitive mechanisms required to learn agricultural processes, neural plasticity during development that allows for the learning process to occur, and the existence of organized warfare and social hierarchies prior to the advent of agriculture.

Even though they share many of the defining features, humans employ a different set of social and cognitive mechanisms than insects do to generate and maintain agriculture. Habitual planting, cultivation, and harvesting in human farming systems are dependent on tool use, which necessitates abilities such as the cognitive manipulation of objects and symbols, observational trial and error learning, linguistic instruction, semantic knowledge, intentional modelling and imitation, and procedural memory (Guilmet 1977; Mahaney 2014). The evolution of tool use itself is the product of millions of years of evolution, and requires

sophisticated problem solving skills as well as the ability to flexibly read social cues in cooperative-communicative contexts to successfully pass down technological knowledge to future generations (Hare 2007). For agricultural practices to spread horizontally across populations and vertically down generations, humans had to teach each other how to implement new technologies, which would have involved pre-existing neural mechanisms, such as a mirror neuron system and the capacity for true language. While the emergence of language remains debated, with some theorists promoting a gradualist view and others an integration view, its origins still dramatically predate the appearance of agriculture, with language appearance estimates between 750,000 years ago to 100,000 years ago (Berwick et al. 2013; Boeckx & Benítez-Burraco 2014; Corballis 2014; Nóbrega & Miyagawa 2015). Without these neural systems and cognitive capacities, agriculture could not have appeared so suddenly.

Possibly the strongest evidence that humans transitioned to a unique stage of social evolution during phylogenetic development, prior to the existence of agriculture, is the biological mark that the stage has left on ontogeny. Humans have an extended period of altricial development and dependency on others, compared to other animals and primates, which requires sustained nurturing, time, and resources from parents, grandparents, and non-related adults (Hrdy 2005). As well, infants display altruistic behaviors and will expend energy to assist non-kin strangers with no reward (Warneken & Tomasello 2006). Even though one-year-olds can make distinctions between the recipients of their prosocial actions (Hay & Cook 2007), young children will display indiscriminate sharing with non-related others and will do so prior to the emergence of contingent and indirect reciprocity, indicating strong intrinsic influences on prosocial behavior (Dahlman et al. 2007; House et al. 2013; Kenward & Dahl 2011; Sebastián-Enesco et al. 2013; Warneken & Tomasello 2013).

Additionally, G&K's claim that social hierarchies and warfare were products of agriculture may not be completely accurate. Dominance hierarchies, created by alpha status individuals through unequal fighting ability and/or inheritance, have deep evolutionary roots in many group-living animal species, including chimps, who display strong social inequality. Similar structures are also seen in modern hunter-gatherer societies (Drummond 2006; Holekamp & Smale 1991; Smith et al. 2010). Regarding organized warfare, Fry and Soderberg (2013) found that deaths occurring by warfare did occur in modern-day hunter-gatherer societies, and that disputes over resources were uncommon. Moreover, evidence exists that warfare predates the Neolithic period and very likely emerged during the Paleolithic (Choi & Bowles 2007; Thorpe 2003).

Human agricultural systems must have been based on at least one previous evolutionary step to ultrasociality, from aggregate loosely tied groups based primarily on kinship to cooperative social networks based on culture and symbolism. Humans' exponential population growth, and successful migration and survival across different ecosystems, in addition to the advent of culture, also occurred prior to the advent of agriculture and would have represented a major evolutionary transition in social organization beyond kin-selection and what is seen in other primates (Nowak & Highfield 2011; Warneken & Tomasello 2009; Wilson et al. 2008). The requirements for social and cultural learning, such as shared intentionality, symbolic representation, empathy, imitation, and theory of mind, would have required a substantial phylogenetic period of prosocial interaction for the genetic and neurophysiological changes to become established within the human species (Henrich 2004; Tomasello et al. 2005). The advent of agriculture would have facilitated a new evolutionary transition in human social organization, and would be responsible for new social behaviors and structures such as written language (Basu & Waymire 2006); however, these innovations would have to be predicated on pre-existing social behaviors and structures such as spoken language.

G&K provide a strong case for agriculture catalyzing ultrasociality in humans, but we cannot restrict the causes to agriculture alone without considering the preceding socio-cognitive

machinery in early humans. Overall, discussions of a major evolutionary transition into ultrasociality and agriculture must address the adaptive mechanisms and transitions that allowed such adaptability to occur in humans.

## The similarity and difference between ant and human ultrasocieties: From the viewpoint of scaling laws

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**Abstract:** Complementary to Gowdy & Krall's comparison between ants and humans, I use economy scaling laws to discuss the similarity and difference between them quantitatively. I hypothesize that individual variations in society result in higher energetic efficiency in larger groups, and that the difference in the sustainability between these species originates from the driving forces of growth with different scaling powers.

Comparing the ultrasociality of humans and ants, Gowdy & Krall (G&K) argue that ants and humans “face similar problems,” and “similar patterns of economic organization emerge through similar selection pressures” (sect. 1, para. 1). As the results of the “convergent selection” (sect. 1, para. 1), both ultrasocieties capture an advantage of the division of labor and increasing returns to larger scale and larger group size. Complementary to G&K's qualitative arguments, here I give a few quantitative considerations and discuss the similarity and difference between ant and human ultrasocieties from the viewpoint of scaling laws.

It has been found recently that the metabolic rate (energy usage rate) of an ant colony is significantly lower than the sum of individual energy usages, and scales sublinearly with colony size (Cao & Dornhaus 2013; Hou et al. 2010; Shik et al. 2012; Waters et al. 2010), indicating that per capita, a worker requires less energy to function in a larger colony. Similarly, properties of a human society that account for infrastructure, such as total road surface and the length of electrical cables, also scale sublinearly with population size (Bettencourt & West 2010; Bettencourt et al. 2007). The similar economies of scaling in both ant and human societies reflect, as G&K point out for ants, that a larger group size is more energetically efficient.

The origin of the sublinear scaling is unclear. Here I hypothesize that individual variation gives rise to the nonlinearity of group energetics. Social inequality is believed to be closely associated with the transition to agriculture (Price 1995). Let us consider a group with  $p$  classes, each class with  $n_i$  members, where subscript  $i$  denotes the class. The total population of the group is:  $N = \sum_{i=1}^p n_i$ . Assuming that each member in class  $i$  acquires (or consumes) an amount of energy,  $E_i$ , then the total energy usage of the group is:  $E = \sum_{i=1}^p n_i \times E_i$ . It is straightforward to see that if energy is evenly distributed across the classes, that is,  $E_i$  is a constant for all of the classes, then the group energy usage will be linearly proportional to the group size, that is,  $E = E_i \times \sum_{i=1}^p n_i = E_i \times N$ . The sublinear scale will emerge only if the fraction of the class that acquires more energy decreases when the whole group size increases. In other words, when the group size increases, relatively fewer individuals consume a lot, and more consume a little.

I need to clarify that the division of labor may not be the only cause of inequality. In fact, as mentioned by G&K and observed by Waters et al. (2010), the number of ant caste members may stay as a constant fraction, when colony size gets larger. However, ultrasocial living, such as managing crop production, requires a network of social interaction, and the inequality may originate from the heterogeneity in the activity level of individuals in

the network; for example, few members are highly active and have more interactions with others, and most are inactive, as seen in ants (Pinter-Wollman et al. 2011). Needless to say, the active individuals consume more energy. I hypothesize that this activity heterogeneity is the consequence of the trade-off between two evolutionary optimization rules. First, the speed of information flow is maximized in the network, which would require most individuals to be highly interactive, but this would also result in high group energy expenditure. Second, the group energy expenditure is minimized, which would require most individuals to be inactive, but this would also result in a slow information speed. If only one of these rules were applied, linearity between energy expenditure and group size would be observed, because the variation among individuals would be the minimal (individuals are either all active or all inactive). It remains to be revealed how exactly the transition to agriculture plays a role in these optimization rules.

In the last two sections of the target article, G&K discuss the expansionary nature of the ultrasocial society and compare the sustainability of ant and human societies as the consequence of the expansion. They argue that as it expands, human ultrasociality faces collapse due to the exhaustion of resources (among other negative factors), whereas ant ultrasocieties have achieved sustainability. G&K believe that the reason for the difference is that social insects have gone through a much longer “evolutionary trial and error to hone sustainable cultures” than humans. They ask: “Can human[s] learn something about sustainability from insect farmers?” (sect. 5.1, para. 3).

Here, in the light of the work by Bettencourt, West, and their colleagues (Bettencourt & West 2010; Bettencourt et al. 2007), I discuss the difference in the economies scaling laws between humans and ants, which may be the fundamental reason for the different sustainable cultures in these species, in addition to what G&K suggest. Bettencourt et al. (2007) show that, besides the infrastructure properties that scale with the population size in the same way as in ant colonies, human society also has a suite of unique properties “reflecting wealth creation and innovation” (p. 7301), which have no counterpart in ant society. These properties, such as wages, rate of new patents, and bank deposits, scale superlinearly with the population size; that is, in contrast to the infrastructure properties, the unique human properties are associated with higher per capita values in larger populations (increasing return).

The growth (expansion) of an ant colony is driven by the colonial energy usage rate (efficiency driven) with sublinear scaling, whereas the expansion of a human society is probably, as suggested by Bettencourt et al., driven by innovation and wealth creation, which scale superlinearly. Theoretical models predict that driving forces with different scaling powers will generate sharply different growth patterns. Supporting the theory, the data of ant colonies show sigmoidal growth curves; that is, the growth eventually levels off (Hou et al. 2010). In contrast, the superlinear scaling in a human society inevitably results in unbounded growth (Bettencourt et al. 2007), which is obviously unsustainable.

How to solve the dilemma imposed by a desirable increasing of wealth and the unsustainable consequences of unbounded growth? Perhaps G&K are right: “Solving the daunting problems we face requires structural changes in the human economy, not merely changing individual values” (sect. 6, para. 7).

## Ultrasociality: When institutions make a difference

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**Abstract:** We present arguments that the analogy between humans and social insects is coincidental, rather than based upon real similarities. In their claims, Gowdy & Krall largely omit the role of institutions in the formation of complex societies, warfare, and regulation. They also offer no strong explanation for the expansion of agriculture despite its early detrimental effects except the “mistake hypothesis” (cf. Diamond 1987).

In their interesting attempt at analogies, Gowdy & Krall (G&K) make, we think, some critical omissions that deserve to be commented upon. First, it is somewhat commonplace in economics (at least from Adam Smith on) to recognize the fact that *biologically identical* groups of people (societies) may come out very *different* depending on the rules and cultural norms governing their behavior – a set of factors modern economists like to bundle as *institutions*. Unsurprisingly, these institutions play a significant role in the origins of human ultrasociality (Acemoglu et al. 2005; North & Thomas 1976; Richerson et al. 2016), a fact that G&K “fully recognize” in the introduction (sect. 1) but choose to blot out almost entirely in the rest of the article. This is understandable, as it would undermine the purport of their article – the analogy between humans and social insects. Instead, they prefer to focus on one single aspect of ultrasociality – the transition to agriculture – buying uncritically into Jared Diamond’s famous thesis (about this being the “worst mistake” in human history; Diamond 1987).

We argue, however, that agriculture is not the necessary and the only possible prerequisite of ultrasociality, but is rather incidental to it. Agriculture happens to be a natural candidate for triggering ultrasociality as food is typically the first scarce thing an individual (human or termite) seeks to secure. However, had food been plentiful, other scarce resources would have led to ultrasociality in species that already had a complex social organization capable of division of labor. In other words, once institutions are included in the analysis, G&K’s analogy starts crumbling: There is nothing about human agriculture (or more broadly, development and economic growth) and resulting ultrasociality

that makes it inherently and inescapably unsustainable in terms of inequality, environmental degradation, or violence. In all of these aspects, the effect of development is not necessarily negative (see the research program initiated by Kuznets [1955] for inequality and Grossman & Krueger [1995] for environment, or see e.g., Pinker [2011], which we refer to below, for violence) and is critically dependent on institutions.

Second, among human hunters and gatherers, division of labor – as a lower degree of ultrasociality – is also present. Some societies practicing agriculture have not reached much greater complexity than hunter-gatherer societies (Easterly & Levine 2003; Hibbs & Olsson 2005). However, social groups with strong institutions promoting trade, growth, and expansion have flourished through cultural group selection (Houdek & Novakova 2016; Richerson et al. 2016). The notion that institutions rather than agriculture per se fostered the emergence of ultrasociality is also supported by the fact that the regions within the Western world which had made a transition to Neolithic agriculture earlier are now generally poorer than the regions that had made it much later (Olsson & Paik 2013). Such economic disparity does not seem to stem from the later arrival of industrial revolution. While its cause remains unresolved, Olsson and Paik suggest that the development of early autocratic states created extractive institutions and that increased rent seeking, looting, and technological inertia could have led to the deterioration of these regions (i.e., low GDP per capita today), whereas the later adopters’ institutions (e.g., with stronger emphasis on property rights) prevented such an outcome; see our Figure 1. (See also Buonanno et al. 2015), who offer a twentieth century example of weak formal institutions resulting in the emergence of mafia-type organizations).

Third, the claim about increased mortality due to violent deaths in agricultural societies in section 3.3 of the target article does not stand in light of evidence of violence-induced mortality across prehistoric societies (Bowles 2009; Thorpe 2003; Walker 2001). While G&K suggest a probable increase of violence in early, small agricultural communities, it seems that in larger and more organized societies, the per capita level of violence actually dropped. We should make a distinction between violence and war: though the latter appeared more in the complex agricultural societies, the former (including deaths in personal disputes as well as larger-scale conflicts) decreased. The cause may have been the formation of states and larger units, as Pinker (2011) argues. We

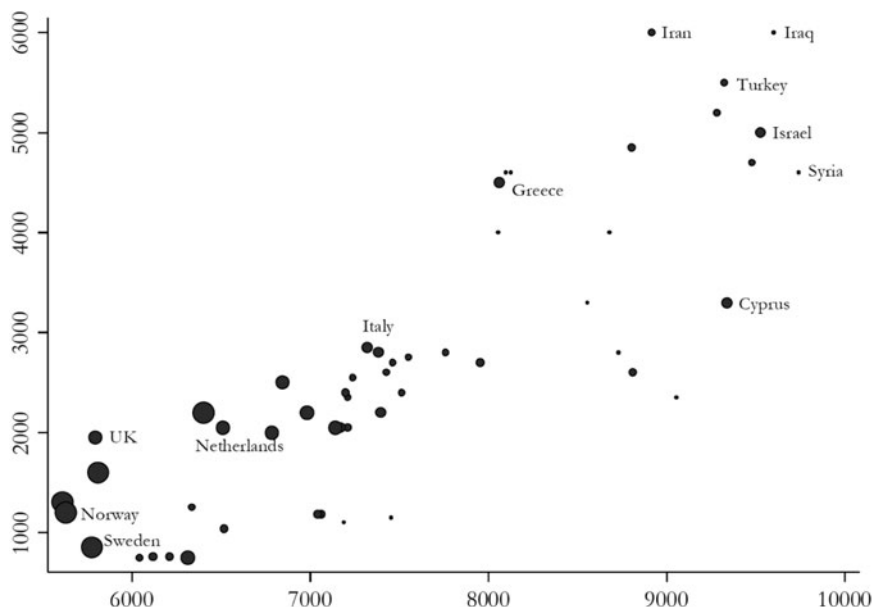


Figure 1 (Houdek et al.). Time (years) since first state formation (*y*-axis) and average time since agricultural transition (*x*-axis) for 52 Western countries with markers weighted by GDP per capita in 2005. Reprinted by permission from Olsson and Paik (2013, Fig. 4).

would like to stress that warfare itself is unlikely to contribute to the formation of complex ultrasocial societies without proper institutions.

Finally, on more abstract, purely economic (choice-theoretic) grounds, the very notion that humans gave up hunting-gathering and replaced it with agriculture only to find themselves worse off, begs the question of why they chose it in the first place and why they did not opt out to revert back to hunting-gathering. Mistakes and lock-ups are certainly possible: People can never foresee all consequences of their decisions and some may *ex post* turn out detrimental. Sooner or later, and certainly within the hundreds and thousands of years that G&K consider, one would expect people to have learned from and corrected their mistakes, or, eventually, be outcompeted by those who had not committed such mistakes in the first place (hunters-gatherers) or who had indeed corrected them. Either way, it is customary in economics that the burden of proof be placed on those who claim that people seem to act irrationally. G&K should have offered a theory that explains why that kind of bounded rationality behavior prevails or how group-level forces create and preserve such behavior (e.g., Ostrom 1990; Simon 1990). In contrast, G&K have chosen not to carry that burden of proof very far. Admittedly, they still may be correct. But in their article they provide no theory (much less an economic one) of why people engage in farming despite its early detrimental effects. And this is rather regrettable in a piece claiming to unveil the “economic origins” of ultrasociality (i.e., agriculture) in its title.

## Agriculture increases individual fitness

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**Abstract:** We question the need to explain the onset of agriculture by appealing to the second type of multilevel selection (MLS2). Unlike eusocial insect colonies, human societies do not exhibit key features of evolutionary individuals. If we avoid the mistake of equating Darwinian fitness with health and quality of life, the adoption of agriculture is almost certainly explicable in terms of individual-level selection and individual rationality.

Gowdy & Krall (G&K) propose treating social insect colonies and groups of humans as evolutionary individuals (i.e., units of selection) in virtue of their ultrasociality. They argue that economic factors connected to the development of agriculture explain ultrasociality's emergence. While it is indisputable that there is an important link between agriculture and the social organization of humans and some insects, we think viewing human societies as evolutionary individuals obscures more than it explains. In neither ants nor humans is the connection between agriculture and individuality as tight as G&K suggest, and individualist models are better suited than the second type of multilevel selection (MLS2) to shed light on the puzzles associated with the human transition from foraging to farming.

Ultrasociality among insects does not depend on agriculture. Many non-agricultural social insect species are ultrasocial, and colonies of these insects are also reasonably treated as evolutionary

individuals because they exhibit reproductive specialization, a criterion biologists often use to identify units of selection (Maynard Smith & Szathmari 1995). The division of labor may well reach its zenith in the agricultural ants, but G&K ignore the fact that agriculture followed, rather than led to, individuality. While agriculture in ants is about 50 million years old (Schultz & Brady 2008), reproductive division of labor probably originated in the mid-Cretaceous, over 100 million years ago (Grimaldi & Engel 2005). Thus, even if it were true that agriculture facilitated the emergence of individuality at the level of human societies, this would be a disanalogy rather than a similarity between the evolutionary histories of humans and social insects.

Human societies, however, cannot be treated as evolutionary individuals. Modern thinking about the evolution of individuality emphasizes the need for bottlenecks separating generations, reproductive specialization, and demarcation mechanisms (Clarke 2013; Godfrey-Smith 2009). These features are absent or only weakly present in human groups and almost never obligate. For example, reproductive skew in human societies never rose to the levels seen in social insects (Summers 2005), and in many agricultural societies it stayed very low through institutions of monogamous marriage. The rate of migration between human groups is high enough to prevent sharp genetic or cultural demarcation of one group from another, which reduces the potential for them to act as distinct evolutionary units.

In making their case for the insufficiency of multilevel selection 1 (MLS1), G&K conflate individual well-being and fitness. The MLS1 framework explains how apparently costly traits can evolve by providing an indirect fitness benefit to the individual possessing them. G&K argue that the human transition to agriculture does not provide such a benefit because the emergence of agriculture meant poorer nutrition, a shorter lifespan, and a loss of individual autonomy for the average person. But unless these decreases in quality of life led to a net loss of reproductive success, they did not constitute a loss of Darwinian fitness. On the contrary, as reviewed by Lambert (2009), the transition to agriculture was associated with increased fertility. This finding is perfectly consistent with basic life-history theory, which shows that reduced longevity and body condition can be selected to increase or decrease, depending on their trade-offs with reproduction (Stearns 1992). In other words, a less healthy life is consistent with increased individual fitness if it leads to higher reproduction.

One model that successfully disentangles quality of life and fitness comes from the tradition of human behavioral ecology. Testart et al. (1982), Watkins (2005; 2010), and Sterelny (2015) respectively provide an incremental account of the transition from a hunter-gatherer lifestyle to an agricultural one, despite the physical and cultural costs this transition exacted. On their model, hunter-gatherers have incentive to develop agriculture under two conditions: (1) if their foraging activities lead to resource scarcity; and (2) if efficient harvesting and storage options allow them to take advantage of predictable seasonal variation in resource availability. When these conditions hold, it is individually rational to adopt storage-dependent foraging and establish permanent bases around which groups can conduct foraging trips. Permanent storage and a reliable resource flow leads, in turn, to a larger and more sedentary population. As the larger population places additional stress on the available supply of resources, it prompts people to experiment with organized planting and cultivation of the resources they had previously gathered but not actively managed.

After the establishment of permanent communities, subsequent generations face food shortages due to overuse of foraging and hunting grounds. The costs of migration are high, so people come to rely more heavily on cultivated crops, even if the yield is lower or less diverse than that produced by migrant hunting and gathering. Groups engineer more complex divisions of labor to better exploit their agricultural resources, and these, in conjunction with a less diverse diet, may lead to the decreases in quality of life that G&K allude to.

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 group-level 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 been 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 evolved 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,

which are dramatically different in insects and humans. The authors' focus on managed agriculture obscures the role that divisions of sex and reproductive labor may have played in the development of eusociality and collective economic activity, including relative to hunting and gathering.

Because food cultivation has emerged in only four types of animals – ants, termites, humans, and ambrosia beetles – similar evolutionary mechanisms are suspected to have driven its development (Schultz & Brady 2008). However, proving the hypothesis and identifying the common mechanisms “requires an understanding of the historical sequence of events that generated each system” (Schultz & Brady 2008, p. 5438), which is hard to come by. Large-scale phylogenetic analyses of termite species have failed to identify even the origin of “true workers” (Inward et al. 2007).

Researchers studying these four types of animals, and the only eusocial mammal, independently conclude that the shift from the care of young by parents to care by others (alloparenting) played a critical role in the development of eusociality – if not in food cultivation, which in some orders (notably, beetles) can occur in the absence of eusociality (Biedermann & Taborsky 2011).

In terms of phylogeny, reproduction and development, and agricultural subsistence, ants and termites highlight how variation in critical parameters can make it very difficult to determine the ecological constraints or evolutionary mechanisms involved.

Termites developed from a “social cockroach” about 130 million years ago, and evolved eusociality just once. They are diploid with a somewhat equal, albeit complex sex ratio, and with altricial offspring that are frail, dependent, and lack the intestinal symbionts necessary for the complex metabolic processes that sustain both organisms (Nalepa 2015). Cladistics and life history analysis suggest that the shift to alloparental care of altricial offspring was the “tipping point” in the evolution of termite eusociality (Nalepa 2015). Phylogenetic analyses of 250 termite species suggest that fungus-growing evolved from wood-feeding and may have been the ancestral condition, with soil-feeding lineages developing from the ancient fungus growers, and wood-feeding re-evolving (Inward et al. 2007). Insect agriculture thus is not evolutionarily recent.

Hymenoptera evolved eusociality independently in 11 different lineages (Korb 2007), and fungus-growing once (Mueller et al. 2005). Cutting leaves to feed fungi is a recent development (about 8–10 million years ago), as is the complex social organization featuring striking morphological differences among different workers that evolved with it (Schultz & Brady 2008). Eusocial hymenoptera are haplodiploid: Unfertilized eggs become male. Workers in all castes are overwhelmingly female; males serve principally reproductive roles (Wilson & Hölldobler 2005). The single-stage larvae are helpless, requiring extensive care.

The fungus-growing haplodiploid ambrosia beetle *Xyleborinus saxesenii* is primitively eusocial (Biedermann & Taborsky 2011). Although each female is capable of breeding and establishing her own “gallery,” group members engage in the diverse cooperative tasks involved in brood care, gallery maintenance (fungiculture, digging, defense, waste disposal), and grooming of adults and larvae. Although free to mate themselves, females tend to remain in the natal gallery if brood size is large, requiring greater care, but will disperse when numbers of mature females relative to brood is high (Biedermann & Taborsky 2011). Alloparenting thus appears to be privileged over personal reproduction.

Cooperative brood care is also thought to ground the evolution of eusociality in two genera of African mole rat, which dwell in subterranean colonies, harvest tubers, and are thought to be the only mammals to have evolved eusociality (Burda et al. 2000). Reproduction in eusocial mole rats is limited to queens that mate with one to three males, while workers engage in brood care, food gathering, digging, cleaning, and collective defense. Alloparenting is critical because mole-rat queens don't store fat and require regular provisioning during gestation and lactation, which are longer in these genera. Reproductive strategies

diverge greatly. In naked mole-rat colonies, reproductive capacity in both sexes is equally suppressed, and more than 99% of offspring never reproduce (Faulkes & Bennett 2001). Colonies are highly inbred, and are reported to have a higher degree of relatedness (0.8%) than hymenoptera colonies (Faulkes & Bennett 2001). By contrast, Damaraland mole rats cannot breed with nest-mates, and only female reproductive capacity is dramatically suppressed. Nevertheless, up to 90% of colony members never breed (Faulkes & Bennett 2001).

The human case is more complex due largely to culture, as G&K note. However, allomaternal care is increasingly recognized as a critical precursor to the evolution of complex human social organization and advanced labor specialization (Smaldino et al. 2013). Allomaternal care is the best predictor of prosociality among primates (Burkart et al. 2014), and helps to explain significant differences in the life histories of human females compared to other apes, such as long childhoods, menopause, and long post-reproductive life (Mace 2013).

Among contemporary hunter-gatherers, alloparenting is commonplace, as is food sharing and cooperative foraging with unrelated individuals (Dyble et al. 2015). These groups are widely known to be egalitarian and to pair-bond. Gender equality probably coevolved with higher offspring costs, the need for biparental investment, and the advantages of circulating through networks of kin (Dyble et al. 2015). Paradoxically, although foragers of both sexes prefer living with close relatives, they invariably live with high proportions of unrelated individuals. Recent modeling experiments and field observations suggest that shared influence in decisions about group composition is the most probable cause (Dyble et al. 2015). Greater influence by one sex results in higher relatedness within the group, and a bias in fitness benefits advantageous to the sex with the most influence (usually male).

The consistency of the association between eusociality and alloparenting of altricial young, with a somewhat lesser correspondence with female-biased sex ratios, suggests that significant fitness benefits accrue to a division of labor in breeding and alloparenting. These reproductive economics provide a platform for enhanced subsistence strategies, with symbiotic food cultivation and agriculture being two possibilities.

Understanding the differences in reproductive organization and their implications for structuring sociality more generally is essential for determining whether the same evolutionary forces are at work in the evolution of eusociality in agricultural insects and ultrasociality in agricultural humans – as G&K suggest – or whether a resemblance of outcomes has arisen from different forces.

## Ultrasociality, class, threat, and intentionality in human society

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**Abstract:** Gowdy & Krall neglect an important aspect of human societies, which is that class systems are not genetically based but rather based on threat. In turn, threat presupposes intentionality, so seems to distinguish human from arthropod ultrasociality. Class systems, in turn, seem to explain the distinctive mixture of persistence and instability characteristic of human, but not arthropod, ultrasocial populations.

Gowdy & Krall (G&K) discuss common features of certain human and arthropod societies, which are characterized as ultrasocial societies. In this, they draw selectively on “the economics of

production.” Their theory of production seems to parallel mine in McCain (2014), which I denote as a “complex combination of labor” theory. Georgescu-Roegen’s theory is narrower (Georgescu-Roegen 1970; 1977b; 1977c; cf. Daly 1977). However, G&K neglect the role of class systems, and their basis in threat, which may distinguish human from arthropod ultrasociality.

The early agricultural societies on which G&K focus much of their attention (see sect. 1) are what Samir Amin (1989) calls tributary societies. A tributary society is one in which the productive surplus of a group is seized by an armed minority by means of the threat of violence. This is an instance of a class society, in the Marxist sense, and seems to be the common form of the earliest class societies. The armed minority that G&K describe as specializing in defense (sect. 3), are also the dominant tribe who enforce both the loss of autonomy and the transfer of the surplus to themselves. The importance of class structures in human societies both provides an alternative to evolution to explain the persistence and growth of human societies and resolves some of the difficulties G&K acknowledge in their view. Among these are the combination of persistence and instability that human, but not arthropod, societies display.

A class society may be defined by the process by which it reproduces itself; this principle may differ from one class society to another. This is a mechanism by which the dominant class extracts the surplus from the group of which it is part and uses that surplus to recreate its ability to extract the surplus. In the case of a tributary society, a dominant tribe, cult, town, or city requires tribute from the producers in the society as a condition of being left in peace, and this surplus is redistributed among the armed force and its commanders, in such a way that their dominance is recreated.

In case this circular causation seems too facile to constitute a theory, the point can be illustrated by game theory. In non-cooperative game theory, a threat is considered credible if it corresponds to a subgame perfect Nash equilibrium. (e.g., McCain 2009, Ch. 6) While a three-person game will be a radical simplification of what in fact will be a large-N game, it will provide a useful illustration. Accordingly, consider Figure 1. There are three agents, an armed agent (A), and two unarmed agents (U1 and U2). The armed agent can choose between two strategies: a strategy of punishing either of the unarmed agents if one disobeys, or not doing so. These correspond to the first two arrows in the game tree in the figure, and those lead to subgames in which

the two unarmed agents simultaneously choose to obey or not to obey. The numbers at the right are assumed proportionate to the payoffs to the armed agent (A) and the two unarmed agents (U1 and U2), respectively. Thus, for example, if A adopts the strategy of punishing disobedience, he must divert one-third of his tribute to maintenance of the capability of punishment, and actually imposing punishment costs the balance of it, also reducing the payoff of an obedient unarmed agent by one-third.

In case of universal disobedience, the payoff to the armed agent is zero, but the payoffs to the unarmed agents are given as unknowns, because there is some difference of opinion about well-being in the “state of nature.” (Compare McCain 2014, pp. 208–212.) For now, assume that  $X = Y = 0$ , that is, where individuals act on individual autonomy productivity is reduced very drastically. This seems consistent with the schema of G&K, if not of Rousseau (1762). Then the only Nash equilibrium in the upper game is one at which both unarmed agents obey, and the payoff to the armed agent is 2. This is the subgame perfect equilibrium of the game. Scaled up to an appropriate number of agents, this seems a reliable sketch of a tributary society.

Threat presupposes intentionality, in that the person who submits the threat does so for the purpose of avoiding punishment, and the person who poses the threat does so for the purpose of obtaining this submission. That there is resistance to class dominance indicates that there is a decision; that a great majority make the decision along the lines suggested by the game model indicates that purpose plays a role in the decision. The resistance of the minority may reflect irrationality, but the payoffs in Figure 1 refer to an average unarmed agent, and might in an exceptional case differ sufficiently that the equilibrium would shift to disobedience. This could also be a factor in intergroup conflict. This is not to adopt the Marxist view that all conflict is at base class conflict. In tributary societies, dominant tribes and groups may lead their communities into aggressive conflict with one another, as G&K suggest. However, intragroup conflict and revolution become possibilities (see McCain 2014, p. 212), as they do not seem to be in the arthropod societies.

One of the consequences of a class society is that a portion of the surplus may be diverted into the accumulation of what Austrian economics calls higher-order goods (McCain 2014, pp. 18–25) in ways that increase the *rate of surplus*, that is, the surplus per producer. Of course, this is most directly associated with capitalist societies, but in the context of tributary societies we may note, as G&K do (sect. 1), the importance in early agricultural societies of canals and aqueducts and other structures. Dynamic growth might be a result of this accumulation.

In short, G&K seem to have neglected one of the most important determinants of the dynamics of human societies, the role of class systems based on threat. Because threat presupposes intentionality, and intentionality is not attributed to arthropods, this seems an important distinction.

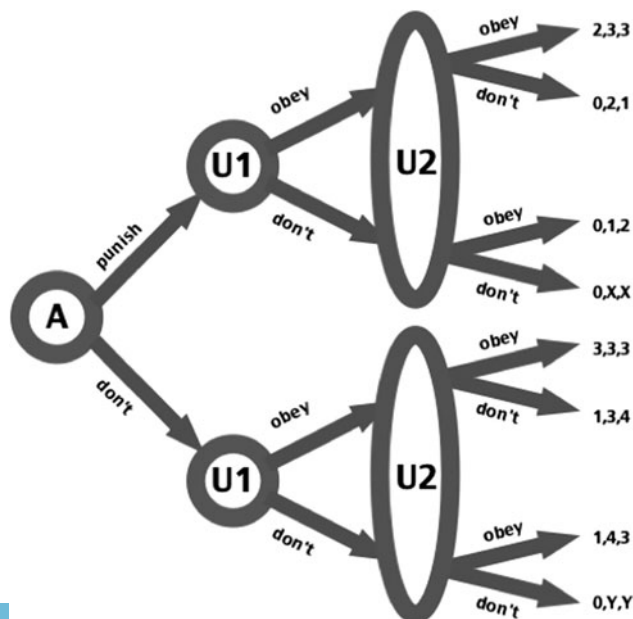


Figure 1 (McCain). A Game of Threat.

## Contributions of family social structure to the development of ultrasociality in humans

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**Abstract:** The evolution of ultrasociality in humans may have involved the evolutionarily significant mechanisms that govern family social structure in many animal species. Adverse effects of ultrasociality in humans may be

mediated by maladaptive effects of modern civilization on family groups, as many of the effects on both families and societies are especially severe in dense populations made possible by agriculture.

An additional topic that is relevant to this discussion of the evolution of ultrasociality in insects and humans is *human family groups* and the evolutionarily significant mechanisms that mediate family social structure in many animal species, especially mammals. There is clearly a robust genetic component to ultrasociality in insects that is more similar to family groups in humans than entire civilizations, but it is likely that the mechanisms that mediate family social behavior also mediate ultrasociality at the civilization level. Human culture (mediated by conserved affiliation-based social mechanisms) is a strength that has maintained the important independence between genes and phenotypes. This independence allows for flexibility in life trajectories and the appearance of individuals with no roles in the production, defense, or stock of agricultural products.

Gowdy & Krall (G&K) compare insect colonies with human societies, but many characteristics of insect colonies could be compared with vertebrate family groups: related individuals (Nehring et al. 2011), alloparental care (Lopes et al. 2005), or adoptions (Fouks et al. 2011). Interestingly, the social behavior of ultrasocial insects is almost entirely driven by chemical communication, which is also involved in kin recognition in vertebrates, including humans (Schaal & Porter 2003). The adverse effects of ultrasociality in humans may be mediated by maladaptive effects of modern agricultural civilization on family groups, as many of the effects on both families and society are especially severe in regions with high population densities made possible by modern agriculture.

**Family based drivers of ultrasociality.** Compared with other ultrasocial species, humans present a unique case of extensive cooperation with unrelated individuals (Bowles & Gintis 2004; Rand & Nowak 2013), and it is suggested that agriculture and extensive food provisioning played a role in the evolution of this unique social complexity. While initially considered to be composed of close kin, highly cooperative hunter-gatherer bands exhibit low relatedness (data obtained from present-day foraging societies), suggesting that this cooperation with non-related individuals could be older than the development of agriculture (Hill et al. 2011). Complex social interactions between humans depend not only on kinship and multilevel and spatial selection, but also on social experience, including direct and indirect reciprocity (Rand & Nowak 2013). The social behavior of humans at the societal level is mediated by the same neurochemical mechanisms as affiliative family interactions, often involving the neuropeptides oxytocin and arginine vasopressin (De Dreu et al. 2010), which have been implicated in the evolution of social behavior (Insel & Young 2000). These genetic and experiential mechanisms give much more phenotypic flexibility than the rapid and almost absolute responses of ultrasocial insects towards unrelated individuals (i.e., individuals that do not wear the chemical signature of the colony).

The unit determining the social group of ultrasocial insects is clearly delineated as the colony, but humans belong to several clustered social groups including family and society. Agriculture gave greater significance to both family and society and to their mutual influence on phenotypic development. In terms of the transition from hunter-gatherers to agriculture and the role of the family, the hunter-gatherer lifestyle involves greater challenges to survival and reproduction compared to a more stable agricultural existence. There are risks to survival involved with hunting and a nomadic lifestyle, as well as exposure to related stresses that decrease reproductive success (e.g., unpredictable food supply, decreased social support for offspring care) and pose challenges to maternal care. Agriculture fosters the development of larger families with more extensive maternal care. Improved survival of individuals with longer periods of maternal care may have facilitated the growth of agricultural communities through larger families. Agriculture also affected social group sizes, which,

given the extensive ability of human for innovation and social learning, accelerated the development of global culture.

This effect of maternal care on the development of ultrasociality in humans involves both increased offspring survival as well as the enhanced development of social behavior during the extended nurturing. Early life care in altricial species is selected for not only through increases in survival, but also through the development of improved environment-specific physiological responses to stressors and improved reproductive success of offspring. Social behaviors, including same sex affiliation, reproductive affiliation, parental care, and alloparental care involve transgenerational mechanisms that could lead to the establishment and growth of societies over time (Champagne 2008).

**Adverse consequences of ultrasociality in humans.** The adverse effects of ultrasociality in humans can be most easily seen in large urban areas where there are high crime and disease rates as well as excessive pollution (Phillips 1993). Just as family structure mediates the development of large interdependent communities, the adverse effects of ultrasociality on humans may be mediated through transgenerational maladaptive changes in family dynamics. Intense competition for space and resources results in exposure to elevated levels of social stress, associated neural changes (Lederbogen et al. 2011), and increases in mood and anxiety disorders (Peen et al. 2010), which can lead to the fracturing of families. These developments decrease social support for mothers, increase rates of maternal depression and anxiety (Robertson et al. 2004), and impair the social development of offspring and future generations through impaired parental care (Goodman et al. 2011). As explained by E. O. Wilson and mentioned in the G&K article, humans do not benefit from imitating ants, yet what is often found in cities is a perceived and/or real lack of flexibility in life trajectories that is similar to that observed in ant societies. It is suggested that the key to healthy social development at any level is the preservation of a strong family structure, the foundation of a sustainable society.

## Ultrasociality and the division of cognitive labor

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**Abstract:** Gowdy & Krall describe the development of ultrasociality in terms of economics and the division of labor. We propose that the division of *cognitive* labor allows humans to behave in an ultrasocial manner without the radical evolutionary changes that are experienced by other species, suggesting that species may traverse different paths to achieve ultrasociality.

Gowdy & Krall (G&K) propose that the interplay between managing food production, developing a complex division of labor, and increased production scale and group size in a species transitioning to an agricultural lifestyle creates selection pressures that favor ultrasociality. Ultrasociality, in turn, provides these species with benefits that allow them to dominate their ecosystems, but not without serious costs to individual group members. We find the general narrative – that shifts in lifestyle and exposure to economic pressures provoke ultrasociality – to be very compelling. However, it is unclear if the path charted by G&K represents a unique, and required, path for the development of ultrasocial species.

Did ants, humans, and termites develop ultrasociality because they serendipitously stumbled on exactly the right path to

ecological domination, or are there multiple paths that lead to the same destination for some species? We propose that G&K's path is sufficient to provoke ultrasociality, but that the positioning of the adaptations that support ultrasociality may not be necessarily tied to the agricultural transition. Indeed, G&K provide some tacit support for this position when they acknowledge that "the division of labor is both a characteristic of ultrasocial systems and a preadaptation that enabled ultrasociality" (sect. 3). Here, we discuss one such preadaptation: the division of *cognitive* labor.

One of the central claims presented by G&K is that sharp "evolutionary" departures were necessary for the emergence of ultrasociality in both humans and social insects. In ants and termites, this process resulted in selection pressures that dramatically transformed the biology and behaviors of individuals, but it is not clear that the agricultural transition influenced humans in the same way through the same mechanism. According to G&K, characteristics of agricultural transition modify selection pressures to favor individuals and groups that best adapt to the task of resource management, identifying the critical mechanism for successfully navigating this task as the "expansion and sharpening of the division of labor" (sect. 3.2, para. 1). In ants and termites, this process results in selection pressures that can dramatically transform the biology and behaviors of individuals. However, unlike ultrasocial insect species, humans exhibit relatively little polymorphism. Thus, the primary driver for the division of labor in humans may be cognitive, rather than physical.

Although a particularly strong body may grant one hunter or farmer or worker an advantage over another, we propose that human knowledge and expertise are more indicative of fitness than most physical attributes. Indeed, the term "hunter-gatherer" references a social organization and distribution of knowledge, skills, and expertise that may represent the seeds of human ultrasociality. Thus, although humans exhibit many of the same tendencies as social insects, and our ultrasociality may have similar characteristics and consequences for long-term survival, it is not clear that our path to ultrasociality is the same as that traversed by ants and termites. Whereas other species may require special circumstances to develop a division of labor, individual humans exhibit an early emerging division of *cognitive* labor, which we propose provides an explanation for human behavior in large, agrarian groups.

Both adults and children recognize that knowledge is not equally distributed among individuals, but rather it clusters according to distinct areas of expertise that can be organized in a number of ways (Keil et al. 2008). This understanding is early emerging. Children as young as age 4 demonstrate an understanding that knowledge pools unequally across individuals (Lutz & Keil 2002), and by age 5, they can conceptualize expertise in terms of disciplines, goals, and even narrow topics (Danovitch & Keil 2004). Through exposure, children can also sharpen or expand these representations, and there is evidence that children readily comprehend even very specific or unusual areas of expertise (Koenig & Jaswal 2011; Landrum & Mills 2015). Thus, in terms of the division of cognitive labor, even the youngest humans appear to be prepared for shifts in population density and lifestyle.

We propose that the division of cognitive labor is a preadaptation that provides an avenue for a species to arrive at ultrasociality. Pre-agricultural humans might reasonably possess this competency, and critically, it represents a mechanism for addressing the challenges species face when transitioning from foraging to agriculture lifestyles. If humans already possessed the ability to represent expanded divisions of labor, then those complexities may be addressed by shifts in their mental representations without requiring the kinds of dramatic evolutionary and morphological shifts experienced by social insects. Thus, ultrasociality in humans may represent a quantitative change—a preadaptation scaled up to address a shift in living conditions—as opposed to a qualitative, evolutionary change in the human species.

In conclusion, we believe that the proposal outlined by G&K is important. It integrates modern considerations of economics with

evolutionary theories about the development of complex social groups, highlighting how expertise from multiple disciplines may be employed to understand the development of complex behaviors in species. Although we find the narrative presented by G&K to be compelling and informative, we challenge G&K's suggestion that all species must traverse the same path to ultrasociality by proposing that humans may have possessed a preadaptation allowing them to navigate the challenges of agricultural transition in a manner that, while arriving at the same destination, diverges from the adaptation of social insects. Although the theory outlined by G&K might benefit from additional discussion and refinement, we believe that the species-general linkage between transitions in living and social structures proposed here is particularly critical, as it identifies several areas for future theoretical and empirical consideration.

## The day of reckoning: Does human ultrasociality continue?

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**Abstract:** To counter human ultrasociality, alternative communities can arise (ongoing), and, unlike insects, lower echelons can unite and rebel. Examples include movements such as: "Black Lives Matter," "Fight for \$15," "Occupy," and the "Village Movement." To strengthen ultrasociality, a surplus bottom echelon can be reduced: for example, by means such as imprisoning Blacks, deporting immigrants, wars, and the Holocaust. Alternatively, a new structure could be created, for example, ISIL (even more ultrasocial?).

Our "imperfect human ultrasocial system creates openings for change," write Gowdy & Krall (G&K) in the target article – something that's needed if "our day of reckoning" is to be avoided (sect. 6, para. 5). How to counter that reckoning, the increasing inequality and ecological degradation? Some needed societal structural changes *may* be promoted through *fear* experienced by both the 1% and some of the 99% – fear of the lower echelons and of unrest and rioting impacting the higher classes' lives. Some in higher echelons may recognize the injustices but also their relatively safe, isolated existence. Note recent events in Baltimore and other locations over police killings of Blacks (Blinder 2015).

Those widespread demonstrations are an example of resistance, unavailable to the ants, of the lower echelons cohering as a mass, incorporating some of the middle, even the upper class, in their struggles; as often happens in movements. One such movement, "Occupy Wall Street," can be viewed as largely responsible for creating the conceptualization and national dialogue about the 99% versus the wealthy, powerful 1% and 0.1%. It can be argued that the recent election of a progressive mayor in New York City is largely a consequence of that conceptualizing (Newman 2013).

Movements are arising: "Black Lives Matter" has recently garnered national attention, notwithstanding the fact that unarmed black men have been killed by urban police in the past. "Fight for 15" – to create a national minimum wage of \$15 per hour – continues, including legislation passed in 14 cities, counties, and states (and Chicago at \$13) (Medina & Scheiber 2015; National Employment Law Project 2015). More attempts to strengthen unions have arisen, as well as strong, successful attempts to limit their already limited power (Kaufman 2015; Simmons & Harding 2013). Social media play positive and negative roles in all of these movements.

Movements and communities are strengthening that counter national or global cultures and looming ecological disasters. Unlike bees, we cannot totally break out of our global community and start anew if conditions require, for example, a population too large for the hive or available resources. Locavores moderate



climate change by reducing energy for transportation while promoting local sustainability and avoiding the corporate food chain. Vegetarianism reduces both energy for meat production and cows' methane, a potent greenhouse gas.

Alternative communal groups create shared flower and vegetable gardens, even their own currency (Hallsmith & Lietaer 2006). The Dudley Street Neighborhood Initiative in Massachusetts (see: [www.dsni.org](http://www.dsni.org)) was ambitiously established to re-invigorate a Black/Hispanic/White community that was overrun with toxic waste, abandoned houses, and divestment by the Boston area banks. The grassroots movement obtained the power of "eminent domain" allowing community control of development and land use; it is a model for visiting national/international community organizers (Medoff & Sklar 1994).

"The Village Movement" (see: [www.beaconhillvillage.org](http://www.beaconhillvillage.org); [www.vtvnetwork.org](http://www.vtvnetwork.org)) is an effort by the increasing proportion of elderly to remain independent: living in their own homes; creating business, social, and entertainment opportunities; and offering mutual assistance and alternative, affordable support services. Over 140 villages operate globally, with more in progress.

Broad inclusiveness remains a difficulty in all of these endeavors, with our strong human propensities towards creating "in-groups" which exclude and often vilify others (Tajfel et al. 1971). However, those tendencies for group bonding can also serve our interests well. Encouraging multiculturalism promotes ethnic bonds within the context of the larger social/national group, aiming to promote respect for each other's group, while recognizing the importance of bonding and group identity (Moghaddam 2008).

Groups are distinguished in at least the social ants by distinctive body shapes, in humans through culture (Smaldino 2014, p. 248, as cited by G&K in sect. 2.3, para. 4, of the target article). Yet humans often perceive group differences as innate (Bastian & Haslam 2006) – n.b. Nazis – thereby yielding greater credence to those differences, with sometimes deadly effect. This was evident in my community work in Nigeria, where clan membership is a significant aspect of one's self-identity, deriving from the village founders' bloodlines according to each village's patrilineal or matrilineal rules. The strong association of the village land with clan identity and blood line (an innate heritage) can thereby become a lethal combination as competition for land use emerges between different clans (Ristau & Knight 2008).

It should be recognized that these various movements and communities entail a strong emotional component. Again, human ultrasociality differs from that of insects, although both plants and animals, including insects, do emit hormones to arouse and coordinate certain activities, usually defensive or aggressive (Heil & Ton 2008; Wyatt 2014).

Now, suppose that instead of the suggested positive developments, the negative predominate. How to deal with too many members at the top of the hierarchy? One could create a new top, with more wealth and power, as is happening now, the 0.1%.

Suppose there was too large a bottom, those economically or otherwise undesirable, lacking skills needed in contemporary society. Such is happening now, with the bottom 97% holding less than half the wealth (Piketty 2014; Stone et al. 2015). One could eliminate or reduce the impact of the lower echelons. For example, honey bees kill off any remaining drones once the Queen has been inseminated, thereby conserving the colony's winter honey supply. Are the following examples among humans comparable? The Holocaust, whereby the exterminated undesirable inferiors included not only Jews, but also political dissidents, the disabled, and others (*Holocaust Encyclopedia* 2014); wars, using an army of volunteers with few other viable economic alternatives; low wages, often part-time jobs, whereby workers have several jobs with little energy for anything else, including resistance; Black males imprisoned, with reduced job possibilities from that history (Alexander 2010); and deportation, with some temporary work permits so immigrants can harvest crops, but are not permanent society members. However, these eliminations create societal problems: With insufficient harvesters, food rots in

the fields (Asbed & Sellers 2013). Imprisonment is expensive, prompting attempts at reducing prison terms (Aos et al. 2007).

Perhaps a totally different political, social, and economic structure could be created, a goal of Occupy (The People 2010) and other previous movements. ISIL (Islamic State for Iraq and the Levant) can be promulgated as an attempt to give power to the people and to create a "pure" Islamic state, devoid of impure Muslims and despoiled non-Muslims and Westerners. Suicide bombers help the whole to survive. The "selective 'pull' of the group," as G&K put it (sect. 5.3, para. 3) is strong, especially for the poor, strengthened further by emotions and religion. Some high in the hierarchy manipulate. Many, many are killed.

Thus, it seems pertinent to pose the question: Will human ultrasociality survive?

## Malthus redux, and still blind in the same eye

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**Abstract:** Gowdy & Krall (G&K) essentially recapitulate Malthus's classic argument for ecological pessimism in modern biological dress. Their reasoning also reproduces Malthus's blindness to the implications of technological innovation. Agriculture might have suppressed human individualism as G&K insist, but technology has tended to foster it. This complicates human ecological prospects in a non-Malthusian way, and it might additionally provide the resources for deliverance from disaster.

Gowdy & Krall (G&K) aim to provide an "economic" logic to characterize the unusual ecology of *H. sapiens*, but at no point do they strip away the biological features of the story to expose the economic core. So let us do that. The convergently evolved ultrasociality of humans, ants, and termites is a pattern of organization on what economists call the production side, in which individuals develop extreme and varying comparative advantages that tightly link the overall productive capacity of groups to specialization of labour. Following the classic argument of Adam Smith, such specialization allows for exponential increases in output capacity, which explains why the ultrasocial species have come to dominate their competitive spaces. Proportionately large aggregate biomass of ultrasocial species is analogous to dominant market capitalization in a firm. Domination is also reflected in radical asymmetries in the extent to which the strategic alternatives available to competitors are restricted by the presence of the dominant firm (ultrasocial species). The dominant firm or ultrasocial form of organization crowds alternatives into ever more marginal niches, or else drives them to bankruptcy (extinction), in the same way that, to invoke a standard textbook example, mass production of standardized goods tends to crowd out artisanal manufacturing.

This is a useful theoretical perspective for a variety of purposes, though it has been developed in greater detail by others. Herrmann-Pillath (2013) has arguably explored it with the most rigour among treatments to date, though he obscures the clarity of the logic by not drawing attention, as G&K do, to the difference in economic kind between ants and their close genetic relatives, social bees and wasps, that live in large cooperative colonies but do not practice agriculture.

G&K rightly devote attention to differences among the ultrasocial species. Ants and termites specialize by evolving varying morphological forms, whereas humans do it by following, and guiding their offspring along, alternative learning paths that are culturally

constructed as responses to market opportunities. But any economist is likely to be struck by the familiarity of a specific limitation in the extent to which G&K work through the implications of this difference, a limitation that recapitulates the history of economic thought after Smith.

Smith's intellectual successor Thomas Malthus (1798/2008) noticed, like G&K, that agriculture led to exponential growth of human populations. Unfortunately for the sake of his own subsequent reputation, Malthus maintained this central emphasis on the causal weight of agriculture into his forecast for the future economic career of the species. Ultimately, he predicted, human populations would exceed the carrying capacity of agricultural resources that was optimal for per capita human welfare, even while maximizing productive output. Famously, Malthus neglected to consider that human technological innovation might promote increases in agricultural efficiency that would allow yields to expand faster than populations, and which would in turn liberate labour and capital for investment in expanding non-agricultural production. By almost all sensible methods of aggregate measurement, human material welfare has massively improved since Malthus's time, even as the global population has become eight times larger.

G&K's perspective is so similar to this as to deserve the label "neo-Malthusian." When they explain how the emergence of ultrasociality has been driven by radically multilevel selection, in which the fitness of the group can compete with the fitness of individuals, they echo in modern biological terms Malthus's point that aggregate increases in production can accompany per capita welfare decline. They then reiterate Malthus's central claim that the effects of human ultrasociality will catastrophically erode the conditions necessary for the flourishing of individuals unless humans can use their cultural flexibility to fundamentally modify their economic dynamics. G&K are not very hopeful about this prospect, so they echo Malthus's generally pessimistic forecast.

It is easier to excuse Malthus, who lived at the dawn of industrialization, for ignoring the impact of technological change than to overlook this gap in G&K's reasoning. Given the unimpeachable evidence of human-caused rapid climate change and the game-theoretic barriers to the forms of collective action that might reverse it, we have good grounds for resisting anti-Malthusian complacency. But the point remains that Malthus's argument was overturned by subsequent history, and G&K's argument is ultimately just Malthus's in modern biological dress.

G&K are rightly ambivalent about the extent of the analogy between human and insect ultrasociality. Ultrasocial insects, they say, do not tend to push their ecological circumstances beyond sustainable equilibria because they cannot use technology to transcend the mutualism of monocultural farming. This may well be a valid disanalogy, but it curiously acknowledges only one side of the coin, as it were, of the importance of technological innovation to human social evolution. G&K stress that ultrasocial evolution tends to undermine the capacities of individual ants and termites, and they imply that this is also analogous to the historical pattern in humans. They thereby bury another disanalogy, this one related to the amplification of enlightenment norms that was promoted by industrialization (Phelps 2013). As G&K note, the transition to agriculture fostered widespread adoption of slavery in many human populations. But, initially in European and subsequently in almost all other cultures, technological modernity encouraged the emergence and eventual dominance of normative individualism (Morris 1972; Ross 2013; 2014). Modern humans are likely more individualistic, not less so, than pre-ultrasocial hunter-gatherers.

Some critics contend that this individualism, which encourages tragedies of the commons, is among the forces currently obstructing collective action to resist climate change and environmental destruction (Hamilton 2010). But it is at least as plausible to predict that incentives operating at the scale of individuals will produce the technology that delivers planetary salvation (Keith 2013); and there is strong reason indeed to think that it is the individualism of women who seek education and careers instead of serial child production that is causing global human population

growth to level off. At the very least, to the extent that individualism is among the obstacles to collective environmental action, the dynamics that threaten the human future are importantly different from G&K's neo-Malthusian picture.

## Human agricultural economy is, and likely always was, largely based on kinship – Why?

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**Abstract:** We question the sequence of evolutionary transitions leading to ultrasociality in humans proposed by Gowdy & Krall. Evidence indicates that families are, and likely always have been, the primary productive units in human agricultural economies, suggesting that genetic relatedness is key to understanding when the suppression of individual autonomy to the benefit of subsistence groups, that is, extended families, evolved.

While ultrasocial insects are genetically closely related, contemporary human societies are not. Gowdy & Krall (G&K) suggest that it was the economic requirements of their agricultural subsistence regimes which led to a convergent evolution towards ultrasociality in all of these species. In humans, they propose, the irreversible transition from independently foraging groups of closely related, mobile hunter-gatherers to large, sedentary pre-state and state societies characterized by low relatedness and high levels of division of labor, enabled the evolutionary subjugation of individual (fitness) interests to the benefit of the respective subsistence groups through multilevel selection.

If this were the case, we wonder, why do we then find that human agricultural production is, and has likely always been, largely based on kinship? The European Union (EU) farm structure survey from 2010, for example, reports that 94.8% of all farms in the EU operate exclusively through the work of a single family (Eurostat 2015). In the United States, farms with 50% or more ownership interest held by the operator and/or his or her relatives accounted for 96.7% of all farms in 2012 (National Agricultural Statistics Service 2014). Furthermore, the Food and Agriculture Organization of the United Nations (FAO) estimated that in 2014 more than 90% of all farms worldwide were family farms (FAO 2014). While these estimates vary to some extent with the respective definitions of "family farm" employed (Garner & de la O Campos 2014), they still show that family labor is central to agricultural production even in contemporary industrialized countries. In addition, historical research clearly indicates that this is not a new phenomenon (Gasson et al. 1988; Hanson 1999; White 1970). Recent anthropological research even suggests that the transition from hunter-gatherer subsistence to horticulturalism, that is, the earliest form of agriculture, was accompanied by an increase, and not a decrease, in genetic relatedness (Walker 2014; also see: Dyble et al. 2015).

In G&K's deliberations, we urgently miss an explanation for this global prevalence of family farming and its vast temporal extent throughout human (pre)history. Although we do not think that their entire argument is rebutted by this observation, we do think that their claim that kin selection is "challenged to explain the extreme interdependence and coordination that occurs with agriculture" (target article, sect. 2, para. 1) has to be revisited in the light of this evidence.

In contrast to G&K, we suppose that the human capacities required for "extreme interdependence and coordination" did not

occur with agriculture but evolved (long) before it (also see Sterelny 2014; Tomasello et al. 2012). Following Hrdy (2009), we think, instead, that the transition to a cooperative breeding system and the cognitive adaptations that came along with it (Burkart et al. 2009) are key to understanding the evolution of human pro- and ultrasociality. Recent comparative studies have established, for example, that, compared to non-cooperatively breeding species, cooperative breeders show higher levels of unsolicited prosociality (Burkart et al. 2014) and solve collective action problems better, including cooperative resource defense (Willems et al. 2013; Willems & van Schaik 2015), which is a necessary precondition for the advent of agriculture (see, e.g., Gat 2008, for a detailed account of the importance of working group defense for sedentariness in humans). Cooperative breeding is closely associated with living in family groups in many animals (Hatchwell 2010; Hughes et al. 2008; Sharp et al. 2011), and humans here are no exception (Hill et al. 2011; Walker 2014). We therefore hold that this earlier phylogenetic phase is a better candidate for the evolutionary stage during which the suppression of individual fitness interests for the benefit of the respective subsistence groups was promoted by natural selection. In the case of humans these subsistence groups consisted of cooperatively breeding families. Therefore, kin-selection (with due regard to parent–offspring conflict dynamics; see Trivers 1974), in our view, suffices to explain why we evolved a readiness to bend to the interests of our families (Voland 2014) and our extended in-groups, even if this entailed substantial individual fitness costs (Rusch 2015) potentially even as high as one's own life (Rusch 2014).

Taking these considerations into account, we suggest that only after cooperative family units had eventually become the fundamental building blocks of our species' social organization, larger societies became possible, that is, functional collaborations of multiple extended families. In line with G&K's deliberations again, we also think that the Neolithic transition marks an important later phase in which coalitions of families that were able to collaboratively cultivate and successfully defend their resources began to reap the benefits of agricultural economy allowing for surplus production, high levels of division of labor, and, eventually, large pre-state and even larger state societies. For this late phase of human prehistory, we agree with G&K that our evolved nepotistic preferences alone might not suffice to explain why these larger societies held together. It is indeed very puzzling, for example, why almost every historical agricultural population readily fought their societies' wars, which were often started by remote chiefs, kings, or governments. The economic constraints highlighted by G&K, we think, will certainly prove to be important parts of a successful explanation of this phenomenon (see, e.g., Turchin et al. 2013).

In summary: We think that G&K correctly identify the requirements of agricultural production as an important component of the last part of the human evolutionary trajectory towards ultrasociality. We would like to add, however, that not only in eusocial insects, but also in humans, genetic relatedness likely has played a decisive role in the evolution of the social structure allowing for this new form of economy. There is an important intermediate level between the individual and "society" in humans: the (extended) family. Thus, we suggest that G&K's outline of the evolution of human ultrasociality would benefit from incorporating the family-level of human social organization – particularly because the importance of kinship is so obvious in the organization of agricultural production even today.

## 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.

## Does ultrasociality really exist – and is it the best predictor of human economic behaviors?

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**Abstract:** We agree that human economic structures can be informed by comparative analyses; however, we do not agree with several of Gowdy & Krall’s specific assertions, which may hinder the generative potential of

their model. We discuss these limitations from both biological and economic perspectives, and offer an alternative explanation for the expression of human economic behaviors based on individual optimization strategies.

We agree with Gowdy & Krall (G&K) that human economic behaviors and group structures can be informed by comparative analyses; however, we also believe that several of their specific assertions do not converge with conventional biological and economic perspectives, limitations that may be better explained by individual optimization models. From a biological perspective, it is unclear which convergent evolutionary selection forces would have resulted in both complex human behaviors and behaviors found in a select handful of insect species. For one, insects evolved in the context of competition with external forces in nature (e.g., climatic changes, predator–prey interactions, geography), potentially supporting G&K’s proposition that ultrasocial insects are inherently motivated to increase the size of their population. By comparison, the types of adaptations (e.g., abstract cognitive representations, theory of mind, mental time travel, psychosomatic illness, emotional expression) that characterize humans are instead believed to have arisen from intra-species selection pressures and hence competition *among* humans (Alexander 1989; Vigil 2009). Under these circumstances, where unrelated conspecifics pose the greatest selection forces to the individual, increasing one’s number of competitors does not appear to offer a discernible fitness advantage. Likewise, because population size is related to the extent of societal stratification (class hierarchies, disparate access to resources) within the population, it is difficult to imagine how individuals who may reap very little from the broader economic system (and may even be compromised by the efficiency of its structure) would be incentivized to contribute to such a system – for example, via labor specialization – at the cost of individual fitness losses.

Further, the insects that G&K discuss (e.g., ants, bees) tend to share high degrees of genetic relatedness and engage in reproductive patterns (e.g., monogamous mating) that limit genetic variability (Andersson 1984; Hughes et al. 2008). Therefore, the expression of eusociality in these species can best be explained by the concept of *inclusive fitness*, or the maximization of collective (genetic) fitness via the propagation of shared genes (Hamilton 1964). Unlike any known insect species, humans also engage in selective acts of *reciprocal altruism* with non-kin in order to maximize the individual’s personal competitiveness and genetic fitness (Trivers 1971; Vigil 2007; 2009). Lastly, it is unclear why economic behaviors may be best informed by observations of non-human species viewed as “ultrasocial,” rather than, for example, (a) *less* social species (e.g., crickets) or (b) *more* social species (e.g., primates), which could, respectively, offer either a broader behavioral framework or more precision in predicting specific economic structuring.

From an economic perspective, the transition from fragmented groups of hunters and gatherers to large agricultural societies is also not explained well by ultrasociality, and the characteristics of ultrasociality do not manifest consistently across humans and ants. The authors state that ultrasociality (which leads to labor specialization, economies of scale, and ecological dominance) arises from the competitive advantage associated with producing one’s own food and leads to greater economic surplus. However, *comparative* advantage suggests that specialization by groups leads to greater economic surplus than one group managing the entire process of food production. The benefits of labor specialization also arise from comparative advantage. In the case of ants, phenotypes determine which types of ants have the lowest opportunity costs for different roles in the colony, and, with only one food source, there is little benefit in trading across colonies. In humans, culture and social prejudice continue to prohibit optimal division of labor, especially across genders and racial/ethnic groups, with women and minority races assigned to lesser positions regardless of the actual opportunity cost associated

with their labor in a particular role. In addition, the wide range of food sources consumed by humans supports increasing specialization at the group level with trade among groups, rather than high levels of specialization within the group. Finally, diseconomies of scale exist as much as do economies of scale, and particular complications associated with larger-scale economies would appear to disincentivize individual investment in communal goals, including free-riding and instability, especially as goals become more diverse and numerous.

A fundamental question also remains as to what are human and ant societies maximizing that cannot be better explained by individual (level 1) utility maximization theories? The target article assumes a variety of success measures – population size, ecosystem dominance, and economic surplus – without clear definitions or consideration of their construct validity. Although perhaps correlated with “success,” all three measures are problematic as direct measures of success. Human societies do not maximize population size, as evidenced by public policies (e.g., China’s one-child policy) or the decrease in birth rates associated with development. Measuring ecosystem dominance with population weight or dry biomass suggests that maximizing obesity would result in more successful societies. As for economic surplus, ants likely do maximize productive output (e.g., “economic surplus”). In human societies, however, religion, social mores, and political systems ensure that productive output maximization is constrained by factors not exhibited in ant societies, such as the desire to limit inequity or avoid taboo activities, for example, usury or organ sales. In other words, human social welfare maximization includes factors not adjusted for in total productive output and may take on ordinal rather than cardinal properties, as do underlying individual utility functions.

In conclusion, we are not convinced that the concept of ultrasociality adds to our understanding of the similarities between human and ant societies, nor that ultrasociality characterized the transition from hunting and gathering to agricultural societies. We believe that biological differences and the distinct goals pursued by humans and ants could not have plausibly allowed convergent evolutionary process to occur beyond basic (e.g., approach/withdrawal) motivational systems and expressive gesturing (Vigil 2009). As for the transition from hunting and gathering to agriculture, we assert that the benefits of agriculture were not so much in the economic benefits to the group as in the opportunity for consolidation of power by powerful utility-maximizing individuals. This thesis also offers corresponding explanations for various characteristics of group-level economic structures, including large size, division of labor, dominance hierarchies, and loss of autonomy among the lower ranked individuals.

## Agriculture and the energy-complexity spiral

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**Abstract:** The study of cultural complexity is entwined with ancestors myths from contemporary cosmology. Gowdy & Krall expose this mythology by arguing that complexity emerged from economic changes following cultivation. There is more, however, to the development of cultural complexity. Complexity can emerge from abundant energy or from addressing societal problems, which compels still further energy production.

If fish were scientists, suggests my colleague Timothy Allen, the last thing they would discover would be water. Fish cannot

discover water because it is the context in which they are immersed. Humans have a context that is similarly intangible and obscure: culture. During socialization, a child is taught to regard a cultural order as a natural order. The context in which the child is raised thus appears normal and natural. The processes that produced the current order seem to have been inevitable. Asking a person to discern the cultural forces that produced his or her life is like asking a fish if its nose is wet. Culture influences even academics in what they choose to study, what questions they ask, and what frameworks of interpretation they use.

The target article by Gowdy & Krall (G&K) continues a long tradition in history and social science: understanding how and why societies went from undifferentiated and simple to differentiated and complex. (Complexity, in this sense, refers to differentiation and organization [Tainter 1988].) The study of cultural evolution has often succumbed to what I call the bias of valuing complexity. Scholars themselves were raised and socialized in a complex society, leading us to think of complexity as the inevitable outcome of cultural evolution. Cultural complexity is known in popular discourse by the more common term “civilization,” which we believe our ancestors achieved through the phenomenon called “progress.” In progressivist thought, complexity is considered intentional, something our ancestors strove to achieve (e.g., Diamond 1997). The concepts of civilization and progress have a status in contemporary cosmology that amounts to what anthropologists call “ancestor myths.” Ancestor myths validate a contemporary order by presenting it as a natural and sometimes heroic progression from earlier times. Thus, we tell stories of how our ancestors discovered fire, developed agriculture, invented the wheel, and subdued untamed continents.

V. Gordon Childe may be the prehistorian who has contributed the most to this mythic narrative. He wrote:

On the basis of the neolithic economy further advances could be made ... in that farmers produced more than was needed for domestic consumption to support new classes ... in secondary industry, trade, administration or the worship of gods. (Childe 1944, p. 12)

Eventually, in this line of reasoning, agricultural surpluses led to the emergence of cities, artisans, priesthoods, kings, aristocracies, and all of the other features of archaic states (Childe 1944, p. 22). G&K have performed a valuable service in helping to undermine historical narratives that underpin this ancestor myth. They argue that complexity emerged not from human intentions, but from economic changes and enhanced energy capture in the practice of agriculture.

It takes energy to maintain a system in a state of complexity. The most important point to understand about cultural evolution is that complex societies are costlier to maintain than simpler ones (Tainter 1988). In organisms, complexity has a metabolic cost, measurable in calories. Among humans, the cost of complexity is measured in such currencies as work, time, and money, which are transformations of energy. We are largely unaware of this today because, to us, complexity appears to be free. We pay for it through fossil fuels. In the past, though, the cost of supporting more complex societies meant that people worked harder. The monuments of ancient societies, their wars, and their intellectual achievements were paid for by peasant agriculture. This point undermines the conventional myth that complexity (civilization) is an achievement won by hard work and ingenuity. Before fossil fuels, the cost of complexity would have inhibited its development.

How, then, did human societies become more complex? There have been two conditions for complexification. The first occurs in those rare instances when humans have abundant, inexpensive energy. Given human ingenuity, abundant energy allows complexity to grow. This is the condition described by Childe, and by G&K. Consider, though, Boulding’s comment on Malthus’s (1798) essay on population:

Any technical *improvement* can only relieve misery for a while, for as long as misery is the only check on population, the improvement will enable population to grow, and will soon enable *more* people to live

in misery than before. The final result of improvements, therefore, is to increase the equilibrium population, which is to increase the sum total of human misery. (Boulding 1959, p. vii; emphases in original)

The implication is that humans have rarely had surplus energy. Surpluses are quickly dissipated by growth in consumption. So rare and transient are the occasions when humans have had abundant energy that we indicate them by terms signaling a new era: the Agricultural Revolution and the Industrial Revolution. G&K's target article addresses the complexification attendant upon food production.

Most of the time, complexity increases from efforts to solve problems. Confronted with challenges, we invent more complex technologies, differentiate economically, establish new roles and specializations, create more levels of organization, or gather and process more information. Consider the new government agencies, and the new controls on behavior, that emerged after the attacks of September 11, 2001. Or consider how pollution and oil prices spurred the development of automobiles that have two means of propulsion, where previously one was sufficient. Complexity increases to solve problems that range from mundane to existential. Complexity that emerges in this way will usually require additional energy. Complexity in problem solving compels increased resource production, including in agriculture.

This process is the energy-complexity spiral (Fig. 1). Abundant energy allows complexity to grow, but higher complexity requires still more energy. Problem solving also generates complexity, necessitating still more energy. This relationship drove ancient societies to collapse (Tainter 1988).

G&K are correct that ultrasociality suppresses autonomy. Complexity simplifies behavior. Ultrasociality and ecosystem domination, however, appeared before agriculture. Hunters often undertook ultrasocial cooperation, over large land areas, to drive game into traps (e.g., Steward 1938). Native Californians, and other people, used fire systematically to maintain vegetation at early seral stages (Lewis 1973). Rather than emerging with

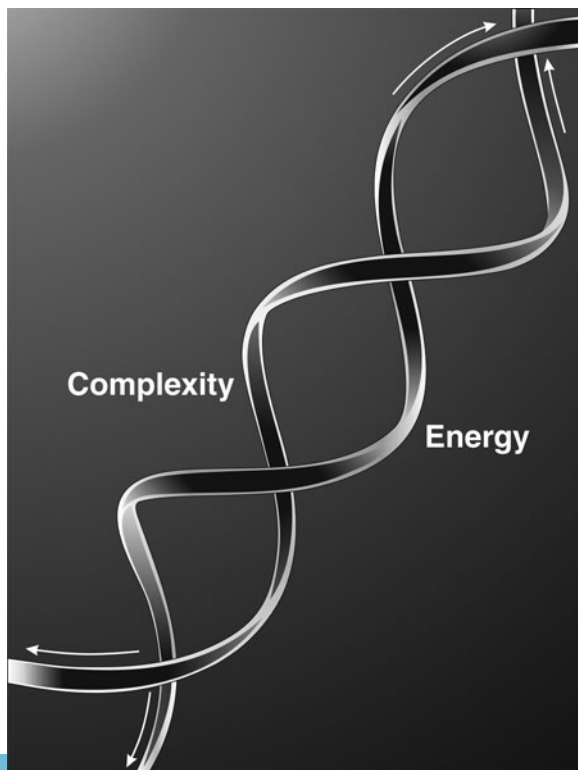


Figure 1 (Tainter). The Energy-Complexity Spiral.

agriculture, Occam's Razor suggests that ultrasociality has long been a human capacity.

## Differences in autonomy of humans and ultrasocial insects

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**Abstract:** The target article is built on an analogy between humans and ultrasocial insects. We argue that there are many important limitations to the analogy that make any possible inferences from the analogy questionable. We demonstrate the issue using an example of the difference between a loss of autonomy in humans and in social insects.

Gowdy & Krall (G&K) build their article on an analogy between humans and ultrasocial insects. While we agree that humans and ultrasocial insects share some common features and that the analogy can be sometimes illuminating, it more often breaks down than not. Although G&K passingly acknowledge differences between humans and other ultrasocial species and note exceptions and limitations to the analogy, the exact pattern of these limitations is unclear. Therefore, any knowledge of ultrasocial insects cannot be reliably applied to humans and vice versa – the analogy lacks predictive power, which turns any possible inferences based on it into mere speculations. The lack of predictive power also poses a problem for any critical commentary because it is often hard to pinpoint the implications of authors' arguments. Even though the shortcomings of the analogy are present throughout the target article we illustrate them here focusing only on the difference in autonomy between humans and ultrasocial insects.

G&K believe that ultrasociality led to “the suppression of individual autonomy” (sect. 1, para. 1). They don't define the concept of autonomy, although they often discuss it in relation to sacrifice of individual interests for the good of a group. While there may be some superficial similarities in the suppression of autonomy in humans and social insects, we believe that the differences are more fundamental.

We agree that individual interest is secondary to interests of a group in social insects, but this is true even for species that have not reached ultrasociality, as defined by the authors. This shows that the loss of autonomy precedes ultrasociality in insects instead of being brought by it. In humans, ultrasociality is reached by groups of autonomous individuals who are able and motivated to seek their own self-interest. Stability of these groups is achieved by moral norms that limit self-interest and enable cooperation and coexistence among non-kin members (Haidt 2008).

One could argue that moral norms cause a loss of autonomy similar to the loss of autonomy in social insects. However, only some moral norms present in humans are focused specifically on promotion of group interests. In terms of the Moral foundations theory (Graham et al. 2013), those are the so-called binding foundations: loyalty, authority, and sanctity. Despite the fact that these moral foundations focus on subjugation of an individual to a group, people can usually choose the group to which they want to subjugate themselves. More importantly, other essential aspects of human morality cannot be subsumed under the three binding foundations. Concerns about individual well-being and rights of others are captured by the moral foundations of harm and fairness. Although these foundations also help coexistence in groups, they can easily form a basis for behavior that goes against group interest: for example, when the rights of

individuals outside of one's group are respected and help is provided regardless of group membership. This behavior can be seen especially in developed societies where division of labour (one of ultrasociality characteristics) is more prominent.

Moreover, moral norms do not eliminate self-interest completely; people are still aware of the possibilities of their own gains at the expense of others, but they usually decide to forgo such opportunities. And various findings in social and moral psychology suggest that the salience of self and personal identity is important for acting morally—people sacrifice themselves for a group (Swann et al. 2010) and cheat less (Mazar & Ariely 2006) when their self is made salient, and they act more selfishly when they are a part of a large anonymous group (Brewer & Kramer 1986; Milinski et al. 2002).

Furthermore, sacrifice of a personal benefit is seen as exhibition of extraordinary personal qualities, not as a strict obligation (Janoff-Bulman et al. 2009). This is supported by our recent study (Bahník & Vranka, in preparation), which suggests that self-sacrifice for a group is considered virtuous and praiseworthy, but not normative or obligatory. An inherent respect for the autonomy of others when making self-sacrificial decisions is further demonstrated by the finding that people judge sacrifice of another person as morally worse than self-sacrifice (Bahník & Vranka, in preparation), and that people are less willing to sacrifice strangers than their close relatives and friends (Kurzban et al. 2012).

G&K acknowledge some limitations of the analogy between ultrasocial insects and humans. For example, they write that the loss of autonomy in humans was less extreme and mediated by culture, and that humans often resist subjugation to a group. While G&K seem to discount these differences between humans and ultrasocial insects, we believe that they are of utmost importance. It is unclear what knowledge of the loss of autonomy in insects is still applicable to humans if culture, customs, and social institutions are taken into account. While we have focused only on the differences concerning the loss of autonomy, a similar analysis of the effect of norms, culture, and human reasoning could be applied to other aspects of the analogy with a similar result.

## Humans are ultrasocial and emotional

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**Abstract:** Given the highly social nature of the human emotion system, it is likely that it subserved the evolution of ultrasociality. We review how the experience and functions of human emotions enable social processes that promote ultrasociality (e.g., cooperation). We also point out that emotion may represent one route to redress one of the negative consequences of ultrasociality: ecosystem domination.

Human emotions are not only often experienced in social contexts, but also shape social behavior. These social features point to a potential role for emotion in the evolution of ultrasociality. We propose that human emotion played and continues to play a core role in the evolution of sociality and therefore of ultrasociality.

Successful survival for all animal species, human and nonhuman alike, requires engaging in behavior on the basis of differentiating what is good from what is bad. That is, successful navigation of one's environment involves computing the affective value of

features in the environment and then using that affective information to avoid that which can cause harm and approach that which might serve a benefit (for a review on affect, see Barrett & Bliss-Moreau 2009).

Like other animals, humans possess an affective system that enables distinguishing good from bad—food from poison, threat from opportunity, and friend from foe. But the human affective system also has unique characteristics, including highly developed conceptual information about what emotions are and the ability to represent internal states using language (for reviews, see Barrett 2011; Barrett et al. 2015; Lindquist et al. 2015). These features of the human affective system enable experiences that are more complex and nuanced than broad positive or negative affective states. For example, humans do not simply experience a threat as bad—threat is met with fear or dread, anger or rage. In this view, humans are most certainly *emotional*.

Human emotions are theorized to have adaptive functions: they shape behaviors in ways that are responsive to context and that promote outcomes beneficial to the individual (e.g., Barrett & Campos 1987; Keltner & Gross 1999; Tooby & Cosmides 2008). For example, disgust felt at the sight of rotting food guides avoidance of consuming it in order to prevent disease (Oaten et al. 2009). Many emotions have social functions that may have subserved the development of human ultrasociality. Gratitude prompts prosociality (e.g., DeSteno et al. 2010) and contempt drives social exclusion of errant peers (Fischer & Roseman 2007). Given that so much of human experience is in the real, imagined, or implied presence of others (Baumeister & Leary 1995), this social orientation of human emotion functionality is sensible.

In fact, some theorists have suggested that there is a special class of emotions that are uniquely social (e.g., compassion, embarrassment, jealousy, and pride; see Hareli & Parkinson [2008] for a review). But a closer look at the literature suggests that many emotions, even those not typically considered to be “social” in nature are, in fact, social in many respects. For example, humor-evoked positivity is enhanced in the presence of other humans (Jakobs et al. 1999), and disgust can take human targets (Chapman & Anderson 2013). As such, a case can be made that many if not all human emotions are social in nature.

Humans also possess sophisticated emotional language that can be used to communicate about internal states. One possibility is that language-enhanced emotion communication provides an adaptive advantage because individuals can use that information to predict the intentionality of others, to coordinate shared experience, and to enhance group performance. Extant evidence suggests this may be the case: Groups that share emotions are more cohesive (Páez et al. 2015), and cohesive groups are more productive (Beal et al. 2003).

How did the human emotion system promote the evolution of ultrasociality? While there are many possible routes, one possibility is that emotions supported the cooperation required to maintain effective division of labor. With increasing reliance on others, ultrasocial humans would have needed mechanisms to encourage and maintain cooperation. Robert Frank's (1988) proposal that emotions serve this role has received abundant empirical evidence. For example, feeling gratitude promotes reciprocation of a received favor or resource (Bartlett & DeSteno 2006). Furthermore, individuals who say thank you, indicating that they are the type of person who feels grateful, leads to them being the target of social affiliation (Williams & Bartlett 2015). Thus, human emotions such as gratitude may subservise cooperation via the behaviors they shape and reputations they build.

Given our brief review above, it might appear that emotions serve strictly positive social functions. Yet, as Gowdy & Krall (G&K) point out, human ultrasociality can have negative consequences, such as ecosystem dominance. Modern humans have had and will continue to have a radical impact on the natural world that often has severe negative consequences (Goudie

2013). While emotions may have contributed to human's "way in" to the current perilous state of ecosystem dominance by promoting ultrasociality, we suggest that emotions may also represent a "way out." Indeed, scholars recognize that emotion is an important piece of the sustainability-mindset puzzle (e.g., Kals et al. 1999; Searles 2010; Vining & Ebreo 2002). Empirical evidence highlights how many socially oriented emotions (e.g., guilt, pride) are important determinants of environmentally sustainable actions (e.g., Antonetti & Maklan 2014; Onwezen et al. 2013). It should therefore be possible to capitalize on the social-behavior-shaping design of the human emotion system in order to promote conservation efforts.

One particular socially oriented emotion appears to be a viable candidate for promoting sustainability and conservation: compassion. When directed towards other humans, compassion promotes efforts to alleviate suffering and protection (Goetz et al. 2010). G&K rightly question whether compassion is sufficient for promoting conservation. The key may rely on the recognition that the targets of compassion need not be human. Just as compassion felt towards another human promotes aid, compassion towards one's ecosystem might impel protective action. As yet, little is known about which other emotions might be harnessed to effectively address the negative effects of ecosystem dominance, and, further, when and how those emotions might be harnessed. Hence, multidisciplinary work informed by emotion theory is needed.

In conclusion, while human emotion may have been one mechanism by which ultrasociality—with all of its benefits and drawbacks—arose, it may be a route via which humans are able to correct its effects.

## Laying the foundation for economics

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**Abstract:** The target article is a major step toward integrating the biological and human-related sciences. It is highly relevant to economics and public policy formulation in the real world, in addition to its basic scientific import. My commentary covers a number of points, including avoiding an excessively narrow focus on agriculture, the importance of multilevel selection and complex systems theory, and utopic versus dystopic scenarios for the future.

Evolutionary theory since Darwin has developed more or less continuously in the biological sciences, but has experienced a case of arrested development in relation to human affairs. The reasons are complex, but the bottom line is that terms such as "evolutionary psychology," "evolutionary anthropology," and "evolutionary economics" only started appearing in the 1980s, signifying a renewed attempt to rethink these disciplines from a modern evolutionary perspective. A lot of progress has been made in the last three decades or so. An expansion of Dobzhansky's (1973) dictum, to read "Nothing in biology or humanity makes sense except in the light of evolution," is increasingly within reach.

The target article by Gowdy & Krall (G&K) is a major step in this direction, especially because it goes beyond human genetic evolution to include human cultural evolution, while remaining fully biological in its comparison with insect societies and recognition that all evolutionary processes can be studied from a single theoretical perspective, regardless of the inheritance mechanism. Another notable feature of the target article is its relevance to human affairs in a practical sense. This topic should not remain inside of the ivory tower. It needs to become part of a new

foundation for economics and public policy (Wilson & Gowdy 2013; 2015), which some of us are calling *economics* (see <http://evonomics.com>). My commentary focuses on both the basic scientific aspects and the practical implications of the target article.

**Avoiding an excessively narrow focus on agriculture.** One flaw in G&K's analysis is an excessively narrow focus on agriculture in their definition of ultrasociality. The key condition for ultrasociality is a surplus of resources, making division of labor possible. Many species of eusocial insects meet this condition without practicing agriculture (e.g., army ants; Hölldobler & Wilson 2008). Likewise, eukaryotic cells and multicellular organisms represent major evolutionary transitions, from groups of organisms to groups as organisms, without practicing agriculture. The fact that the cells of a multicellular organism are totipotent at the genetic level, but also capable of extreme specialization through the differential expression of genes, provides a useful frame of reference for thinking about human division of labor. Expanding the comparative view beyond social insects that practice agriculture does not detract from G&K's main thesis.

**The importance of multilevel selection and complex systems theory.** The majority of authors writing peer-reviewed articles on social evolution agree that the major theoretical frameworks (e.g., multilevel selection theory, inclusive fitness theory, evolutionary game theory, and selfish gene theory) are equivalent ways of accounting for evolutionary change. They offer different perspectives on a single causal process, rather than invoking difference causal processes, and therefore deserve to coexist to the extent that their perspectives offer useful insights. In this sense, the controversy over group selection (e.g., the question of whether traits evolve by between-group selection, despite being neutral or selectively disadvantageous within groups, as these terms are defined within multilevel selection theory) is over (Wilson 2015b).

It is possible for two theoretical frameworks to be equivalent in some but not all respects (Wilson 2015a). As an example, inclusive fitness theory attempts to describe the evolution of a trait in the form  $rb - c > 0$  (Hamilton's rule), where  $c$  is the absolute fitness effect on the actor,  $b$  is the absolute fitness effect on the recipient, and  $r$  is a coefficient of relatedness (which need not be genealogical relatedness). This framework is well suited for the study of traits that can be clearly measured in individuals and have a simple genetic basis (e.g., what Okasha [2006] calls multilevel selection 1 [MLS1] traits) but can become unworkable for traits that can be measured only in groups and/or have a complex genetic basis (e.g., what Okasha [2006] calls multilevel selection 2 [MLS2] traits).

Against this background, it is unsurprising that multilevel selection has become the theoretical framework of choice for the study of human cultural systems as units of selection (Yaworsky et al. 2014). The group-level properties that are being selected are too systemic to be rendered in the form of Hamilton's rule. This doesn't mean that reductionistic analysis is impossible, only that it reveals so many lower-level traits interacting in such a complex fashion that if the three terms of Hamilton's rule can be calculated for a lower-level trait at all, they take the form of complex multi-term equations that are difficult to measure or interpret and are often frequency-dependent, so their value changes with every generation (e.g., van Veelen et al. 2012). Multilevel selection theory avoids these problems by measuring phenotypic variation, selection, and heritability at the level of groups, which does not require detailed reductionistic understanding of the traits and their heritable basis. Against this background, G&K's reliance on multilevel selection theory is thoroughly warranted and should be uncontroversial.

**Utopic and dystopic scenarios for the future.** In my own recent (coauthored) BBS target article titled "Evolving the future: Toward a science of intentional change" (Wilson et al. 2014), we stress that left unmanaged, evolution often takes us where we don't want to go. Enlightened public policy requires becoming wise managers of evolutionary processes. One dystopic scenario



is that lower-level selection prevails over higher-level selection, resulting in various “tragedies of the commons” such as global warming, extreme inequality, and societal collapses that are already taking place in some parts of the world. G&K outline another dystopic scenario that is equally disturbing: Even if higher-level selection prevails over lower-level selection, the cost of a well-run society might be a loss of individual autonomy and intelligence. The decline in human brain size during the last 10,000 thousand years suggests that this trend is already underway.

Without being naively optimistic, I think that utopic scenarios for the future are still possible. It is encouraging that inclusive nations function better as large-scale societies than nations governed by a small group of elites (Acemoglu & Robinson 2012; Pickett & Wilkinson 2009). Evidently, egalitarianism is needed at all scales. All societies must become socially differentiated as they increase in size, but “structure” can embody an egalitarian ethos of “communitas,” as the anthropologist Victor Turner (1969) put it. The moral philosopher John Rawls’ (1971) concept of the “Veil of Ignorance” – which asks us to design a society subject to the constraint that we will be randomly placed within it – makes the same point. The fact that cultural evolution must increasingly be guided by policies informed by science and formulated with the global good in mind means that we must become more mindful, rather than more mindless, if we are to succeed at all.

## Authors’ Response

### Disengaging from the ultrasocial economy: The challenge of directing evolutionary change

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**Abstract:** We appreciate the depth and breadth of comments we received. They reflect the interdisciplinary challenge of our inquiry and reassured us of its broad interest. We believe that our target article and the criticisms, elaborations, and extensions of the commentators can be an important contribution to establishing human ultrasociality as a new field of social science inquiry. A few of the commentators questioned our definition of ultrasociality, and we begin our response with an elaboration of that definition and a defense of our argument that human ultrasociality began with agriculture. We then respond to the second major area of controversy, namely, our use of group selection to explain the economic drivers behind the agricultural transition. We then focus on the issue of human intentionality raised by the phenomenon of collective intelligence. The intriguing question is to what extent can an entire culture change its own destiny? We then address the issue of the division of labor raised by a number of commentators. The complex division of labor was both a driver and a defining characteristic of ultrasociality, even though it was present in simpler forms in earlier societies. The remaining issues addressed include energy and complexity, expansion and sustainability, and the accelerating evolution of human ultrasociality. These were raised by only a few commentators, but their importance warrants further elaboration.

### R1. Introduction

We greatly benefitted from the number and breadth of the responses we received on our target article. These comments helped us to further hone and refine our thesis, and we are grateful to the commentators for offering us this opportunity. It is understandable that several of the commentators disagreed, in varying degrees, with our thesis. It is difficult to believe that what we generally mark as the beginning of “civilization” (agriculture) was not caused by human uniqueness and ingenuity but instead resulted from natural selection and economic processes that reconfigured very different species similarly. This was a major evolutionary transition for unrelated species where all evolved to become ultrasocial. Our observation helps to extend and refine an understanding of group selection and the importance of economic drivers and economic configuration in the matrix of social evolution. We have structured our responses to the comments according to categories. The categories highlight and clarify points of agreement and disagreement and further elaborate various points essential to our arguments.

### R2. What is ultrasociality?

There is no generally accepted definition of ultrasociality. We chose a modified version of one proposed by Donald Campbell because we wish to focus on the fact that the agricultural transition marked a sharp, clear, and radical break with the past – so much so that agricultural groups themselves, as well as group-level traits related to food production, comprise the units of selection. It is important to make a clear distinction between ultrasociality and sociality. We realize the difficulty in defining ultrasociality and clearly demarcating it from prosocial behavior. We also consider the objections to our claim that ants, humans, and termites that practice agriculture evolved productive configurations that made all three similarly ultrasocial. We define ultrasociality so as to place it in the context of economic life. We emphasize that ultrasociality has led to the social conquest of Earth, and an interdependence forged through the complex division of labor necessary for agriculture, and thus also led to the expansionary economic dynamic that remains with us today.

Our discussion of ultrasociality is grounded in theories of multilevel selection (MLS; see sect. R3), theories rejected by several commentators. We carefully discussed our definition of ultrasociality, recognizing the lack of consensus over the term. Yet **Vranka & Bahník** declare that “ultrasociality is reached by groups of autonomous individuals who are able and motivated to seek their own self-interest.” Likewise, **Kovaka, Santana, Patel, Akçay, & Weisberg (Kovaka et al.)** assert that “individualist models are better suited than the second type of multilevel selection [MLS2] to shed light on the puzzles associated with the human transition from foraging to farming.” These views reflect a reductionist philosophy, reflected in neoclassical economic theory, and apparently in contemporary psychology (Kesebir 2012) that the group is never more than the sum of its individual parts. This is exactly what we are arguing against in our presentation of ultrasociality.

Several commentators (**Carpendale & Frayn; Grotuss & Beard; Houdek, Petr, Novakova, & Stastny [Houdek**

et al.]; **Krasnow**; **Levine**; and **Rusch & Volland**) assert that we fail to acknowledge the sociality of pre-agricultural humans. In fact, in our target article, we fully appreciate the antecedents to ultrasociality in hunter-gatherer societies, such as the division of labor (sect. 3.2), cooperation with non-kin, and caring for others (sect. 5.2) present in the Pleistocene if not earlier. We more extensively discuss the pre-adaptations that facilitated ultrasociality in two earlier papers (Gowdy & Krall 2013; 2014). In particular, see Gowdy and Krall (2014), section 4, “The co-opting of cooperation.” Were hunter-gatherers exceptional in their degree of sociality? Of course, as we state repeatedly in our work. Humans became compassionate and empathetic, employed a division of labor, lived with non-kin, and so forth, before agriculture. But we argue that the ability to cooperate and share with unrelated individuals was co-opted with agriculture and became a matter of almost mechanistic coordination and subjugation to authority, with limited room for individual agency compared to hunter-gatherer social organization.

We are puzzled by the failure of several commentators to appreciate the difference between hunting and gathering and agricultural state societies. Individual humans were “social” as members of hunter-gatherer bands and “social” in large-scale state empires. Why does this imply that the economic and social characteristics of these two radically different forms of social organization, and the place of individuals within them, were the same? **Krasnow** errs when he simplistically asserts that because “the social world of ... our hunting and gathering ancestors was complex” our argument is refuted. Again, our point is not to deny the sociality of pre-agricultural peoples but rather to point out that the nature of sociality changed profoundly with the onset of agriculture. With agriculture, human economic structure took a form strikingly similar to that of agricultural insects. Humans became more materially interdependent, and it became necessary to support a greater non-food-producing population. Production of surplus was an inherent aspect of the altered configuration of society.

A basic confusion on the part of several commentators is a failure to recognize the difference between individual behavioral characteristics (e.g., altruism, cooperation) and group behavioral characteristics, which we deem ultrasocial (e.g., extremely complex division of labor and extensive interdependency around an “internalized” system of food production, ecosystem domination). The extent of differentiation and cohesion around food production created a qualitatively unique “group” having an evolutionary force of its own. The productive reconfiguration of society that came with agriculture is an important matter, and little attention has been paid to this radical change in the evolution of human society.

**Levine** maintains that our definition of ultrasociality “obviates the possibility of comparing human sociality with that of chimps, and draws an excessive dichotomy between human foragers and agriculturalists.” We obviously do not agree with Levine that “comparisons of shared (homologous) and derived characteristics among closely related species would be far more relevant and instructive for understanding the issues at hand.” Having said that, our discussion of ultrasociality in no way prevents comparisons of sociality in humans and other primates.

Studies of primate behavior have greatly enriched our understanding of human behavior. But consider this thought experiment: Suppose we discovered, deep in the Congo, a chimpanzee society with complex agriculture, including the sophisticated use of antibiotics and monoculture, social classes, highly organized warfare with other agricultural chimp groups, cities, a sophisticated communications network, and so on. Such a discovery would shake the foundations of the human sciences. Why are ants and termite societies with these similar characteristics relegated to the category of mildly interesting analogies with little relevance to human society?

We fail to understand the logic beyond **Vranka & Bahník**’s blanket assertion that, because we acknowledge the difference between humans and social insects, “any knowledge of ultrasocial insects cannot be reliably applied to humans.”

A final point in this regard: Several of the commentators assert that the similarities between ants and humans are merely coincidental and not much more. **Levine** comments: “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.” His comment is also repeated in one way or another by **Houdek et al.** who claim our analogy is merely “coincidental.” The most concrete manifestation of our sociality is found in the way we configure ourselves to alter the external world in order to meet our material needs. It is not clear to us why there is a tendency to discount the importance of this matter in the evolutionary matrix. Radically different species developing similar solutions to the contingencies of productive life means that they all have a capacity to do so. This is not to deny that the mechanisms for reconfiguring productive life might be unique for different species. Nonetheless, the configuration of productive life is an intimate and significant expression of the social life of a species, and the fact that diverse species come to configure themselves so similarly with agriculture cannot be a mere coincidence. In fact, it illustrates the importance of the productive configuration of a species in the determination of species life.

### R3. Group selection is essential to explain the origin of ultrasociality

Several commentators focused on why they think group selection does not exist or is of no use in explaining human ultrasociality (**Kovaka et al.**; **Krasnow**; **Stith & Vigil**; and **Sheskin, Lambert, & Baumard** [**Sheskin et al.**]). Models of individual selection are thought by these critics to be more incisive in explaining it. We are convinced that social evolution cannot be understood without considering groups and group traits as units of selection (see commentaries by **Ainsworth, Baumeister, & Vohs** [**Ainsworth et al.**]; **Farley**; **Goodnight**; and **Wilson**; also see studies by **Baumeister et al.** [2016]; **Richerson et al.** [2016]; **Smaldino** [2014]; **Wilson et al.** [2014]).

We agree with **Goodnight** that the arguments for evolutionary mechanisms beyond the level of the gene are convincing. We are convinced that the rapid growth of state societies after the onset of agriculture was the result of competition between groups.

Group selection (and MLS) has been extensively debated in the pages of this journal at least since the seminal article by Wilson and Sober (1994), a paper instrumental in resurrecting the group selection debate (see, e.g., Baumeister et al. 2016; Richerson et al. 2016; Smaldino 2014; Wilson et al. 2014). We see no need to repeat the extensive discussion from the previous BBS articles and commentaries. Our work demonstrates that the argument that *individual fitness* is the sole currency of natural selection is a misleading simplification. For a detailed discussion of the current state of the multilevel selection debate, see Jablonka and Lamb (2014) and D. S. Wilson (2010).

It is important to be wary of frameworks that eliminate any possibility of considering a level of selection apart from the individual. For example, **Stith & Vigil** want to focus on “individual optimization models.” They say the focus should be competition *among* humans, whereas we stress the evolution of the whole system, not just isolated parts. They assert that it is “unclear which convergent evolutionary selection forces would have resulted in both complex human behaviors and behaviors found in a select handful of insect species.” By contrast, our target article is clear that the convergence in these species resulted from the similar economic forces driving the expansion of surplus production.

Likewise, **Kovaka et al.** accuse us of misusing MLS2 and claim that individualistic models are more appropriate. Their assertion is that units of selection must exhibit reproductive specialization in members of those units. Clearly, we do not agree with this requirement.

**Sheskin et al.** argue that “biological markets” explain the formation of large-scale societies. According to these authors, “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” (emphasis Sheskin et al.’s). For this reason they claim that “individuals in large-scale societies have higher average fitness.” This is a variation of inclusive fitness: the idea is that individuals selfishly maximize their own well-being by being prosocial because prosocial behavior increases their chance of survival. The problem with this explanation is that it begins with the assumption that the individual is the only proper unit of analysis and that humans voluntarily engage in productive activity together—it is a matter of rational individual choice. Our analysis takes a more critical look into the black box of agricultural production.

We are baffled by **Kovaka et al.**’s assertion that “The rate of migration between human groups is high enough to prevent sharp genetic or cultural demarcation of one group from another, which reduces the potential for them to act as distinct evolutionary units.” There are obviously sharp cultural distinctions between human groups, and there exists a vast literature on group trait differences and their evolutionary impacts. (The work of Peter Turchin is one example: see Turchin 2006a; 2013; and his project on “cliodynamics” available at: <http://peterturchin.com/cliodynamics/>.)

The commentaries on “fitness” and “well-being” clearly illustrate the importance of D. S. Wilson’s (2014) admonishment to be clear about the hierarchical level of the functional analysis. Darwinian fitness applies to a population,

while “well-being” is a human construct applying to individuals.

**Kovaka et al.** erroneously claim that we conflate the distinction between fitness and well-being. Contrary to their misreading of our target article, we clearly distinguish between Darwinian fitness and individual well-being. Agriculture gave ants, humans, and termites a tremendous advantage in Darwinian fitness because it gave them the ability to produce their own food. Once agriculture was established, other derivative forms of complex social organization, like raiding agricultural societies for food and slaves, became possible (see **Lyon & Caporael**’s commentary). We focus our discussion on changes in human individual well-being and not Darwinian fitness. A group can become more “fit” and still leave the average individual in the group worse-off. Of course, we recognize that “well-off” and “worse-off” are human judgment calls. But most people would agree that a decline in individual health and physical fitness makes a person worse-off. Individuals in agricultural groups have less productive autonomy with regard to food provisioning than individuals living as hunters and gatherers. Whether this bothers ants or not, we cannot say. But for humans, it is problematic because the engagement with the external world to reproduce material life is a creative activity demanding skills and executive functions that became more limited for most people. In this sense, the autonomy and integrity of the individual human is greatly compromised with agriculture; humans became creatures fighting thistles and weeds and working like draft animals for many hours a day. With agriculture, we became inured to a diminished life. None of this was likely apparent at the time-scale of the individual as things were unfolding. The transition was not a matter of rational choice, and neither did it diminish fitness in a biological sense.

Historically, social scientists have been shut off from the benefit of evolutionary thinking because of the justifiably bad reputation of crude socio-biology (**Wilson**). We intend to reclaim the domain of evolution in social science, and our thesis is that economic configuration can be a target of selection. We do not claim that there is a loss of Darwinian fitness in the transition to agriculture. On the contrary, we point out that the active management of food supply gives a species a tremendous evolutionary advantage that leads to ultrasociality. It might still be the case that the percentage of males who reproduce could decline with the onset of agriculture as more men are relegated to defense and subordination to those in authority (Betzig 2014).

Contrary to **Sheskin et al.**, we do not argue that agriculture resulted in “evolutionary costliness to an individual.” Individuals do not evolve; populations evolve. Sheskin et al. claim that separating quality-of-life costs from fitness cost is important and that we have conflated them. They maintain that only fitness costs matter for natural selection. The former is an inaccurate reading of our target article, and the latter is confused. They claim that our over-reading of the cost to the individual (by conflating fitness and quality of life) leads us to invoke group selection. This too is not a correct reading of our nuanced argument. We are well aware that fitness, as it is defined by biologists, refers to reproduction of genes, and that in humans, with agriculture, we get the successful reproduction of genes, but the quality of life goes down on average. Superficially,

it seems odd that cultural practices are adopted make life more difficult for most individuals, but our point is that individual decision making is not the driving force in the evolution of the ultrasocial group. Again, with multilevel selection the analysis should focus on the level of the phenomenon being examined. The structure of economic life (that changed dramatically with agriculture) is not properly understood as a matter of individual decision, but it does provide an altered context in which decisions are made. Once again, our purpose in invoking group selection is to demonstrate that an altered group formation took hold with agriculture. Of course, it is based on the potential of the species to be altered (e.g., the preexistence of prosocial behavior). But the alteration that took hold with agriculture is a case of emergent characteristics that coalesced to make a new system. The extensive division of labor, economies of scale, coevolutionary success with annual grains, and a huge stock of soil carbon, in addition to the Holocene warming and all of the prosocial traits that had already evolved in humans, are all ingredients that mix together to emerge with an altered configuration of food production that makes the species expansionary and interdependent in a way that it had not been before.

#### R4. The false allure of human exceptionalism

Perhaps the most contentious part of our target article for the commentators is our claim that the evolution of human ultrasociality is a consequence of the same mechanistic (i.e., not consciously directed) evolutionary forces that govern other species. It is disturbing to consider that “mindless” creatures like ants can duplicate complex aspects of human social structure. We began with the observation that the configuration of ant and human agricultural societies are very similar and then focused on outcomes (ecosystem domination, complex division of labor, the subjugation of individuals for the group goal of surplus production), rather than individual intentionality. Similar outcomes in insect and human ultrasocial systems suggest common drivers of social evolution independent of intentional behavior and planning. Ultrasociality challenges the notions of human exceptionalism and intentional behavior at the individual level, and at the level of society.

Darwin’s heretical idea was that humans are subject to the same evolutionary forces and natural laws that govern the evolution of other species. As economists, we have throughout our careers challenged the notion of many of our fellow economists that human ingenuity and the human institution of markets will solve any environmental or social problem. The notion that humans are unique should not overshadow the simultaneous reality that the similarities between humans and other unrelated species have amounted to something significant in the course of evolution. **Sheskin et al.** assert that humans have a “moral psychology . . . not present in even our closest evolutionary relatives.” **Williams & Bliss-Moreau** make a case that human emotions are unique in the animal kingdom. **Carpendale & Frayn** argue that humans are unique in their ability to *consider* their patterns of interactions with others. It is easy to see human history as a story of progress and perfectibility based on individual initiative and the ability to plan for the future (**Kovaka et al.**; **Ross**; **Sheskin et al.**). But others argue that our moral capacity

often makes the world worse, through, for example, “righteous violence” (**Fiske & Rai 2015**).

The strong cultural belief in western societies in the primacy of individual choice leads to an exaggeration of the ability of individual humans to control their own destiny and the destiny of human society. This is expressed in technological utopianism (**Ross**) and in an exaggerated belief in social mobility (**Sheskin et al.**; **Vranka & Bahník**). **Sheskin et al.** fail to grasp the meaning of “totipotency” as discussed in our target article. There are more ways in which a person can make a living in large-scale societies but the opportunity for a particular individual to choose an occupation is severely constrained, particularly in the highly stratified early state societies (**Betzig 2014**). The ability of individuals to choose occupations, even in modern western democracies, is greatly exaggerated in the popular imagination. In a study of social mobility, the economist Gregory Clark found that societies as different as communist China, the United States, and Japan, are characterized by low social mobility rates and these rates are resistant to social policies. **Clark (2014, p. x)** writes: “Having for years poured scorn over my colleagues in sociology for their obsessions with such illusory categories as class, I now had evidence that individuals’ life chances were predictable not just from the status of their parents but from that of their great-great-grandparents.” Contrary to **Vranka & Bahník’s** confusing assertion that people are able to “choose the group to which they want to subjugate themselves,” social mobility is limited even in progressive Western societies, and much more so in the rigid caste systems that prevailed for most of the past 10,000 years.

The uniqueness of human intentionality is also being challenged by another line of research stretching the notion of “intentionally” to include not only non-human sentient species, such as the other primates, whales, dolphins, and elephants, but also plants. **Schull (1990, p. 63)**, quoted in **Trewavas (2008)**, writes: “Plant and animal species are information processing entities of such complexity, integration and adaptive competence that it may be scientifically fruitful to regard them as intelligent.” **Trewavas (2008)** makes a strong case that plants exhibit intelligence in the sense of adaptive behavior in response to signals. To focus only on aspects of intelligence peculiar to humans is biased and subjective because it is based on the prejudices of the observer (**Warwick 2001**).

Above the level of the individual, the notion of intelligent action has been extended to include group behavior (**Baumeister et al. 2016**). Evidence for some sort of collective consciousness exists in humans as well as in non-human species. This again points to the need for a multilevel perspective and an awareness of the need to focus sharply on the particular level (gene, individual, group) being examined (see **Wilson**).

The prevailing mythology is that humans before agriculture were savage brutes, and life was nasty, brutish, and short (**Hobbes**). Humans then became clever enough to invent agriculture (**V. G. Childe**; see, e.g., **Childe 1936**). Civilization made us more human, less violent, cooperative, and democratic (**Pinker 2011**). Evidence based on contemporary or historical hunter-gatherers suggests that people living in mobile, small-scale foraging societies rarely or never engage in “warfare” (**Culotta 2013**; **Fry & Söderberg 2013**). Lethal conflicts are rare and are usually the result of

personal disputes, not “tribal warfare.” Pinker’s “decline in violence” story has been widely accepted because it plays into the myth of linear progress in the human condition and overcoming our animal nature to become civilized (Ryan & Jethá 2010).

The question raised by ultrasociality, as commentators **Crespi**, **Hou**, and **Wilson** variously discuss, is: Can we intentionally take control of our destiny as an ultrasocial species? How do we get away from the dystopic implications of our target article? We believe that intentional change is possible, even a radical redirection of society. An example of an intentional radical change in an entire culture is the case of Tikopia, a small island in the South Pacific with a culture headed down the same path as Easter Island and many other Polynesian cultures—massive deforestation, extinction of native species, soil erosion, and rapid population growth. But Tikopia managed to change course and achieve a stable existence. Archaeological evidence indicates that, sometime around 1700 C.E., all pigs and dogs were eliminated from the island, and slash and burn agriculture was replaced with a “complex system of fruit and nut trees forming an upper canopy, with aroids, yams, and other shade tolerant crops under these” (Kirch & Yen 1982, p. 353). Tikopians adopted a variety of customs to ensure zero population growth, and the island’s culture was apparently sustainable until missionaries arrived in the 1900s (McDaniel & Gowdy 2000).

## R5. The division of labor, interdependence, and class

The division of labor is the most important economic driver in the march to ultrasociality. We are well aware that the division of labor predates agriculture (Gowdy & Krall 2014). We do not doubt that the reproductive division of labor in ants originated in the Cretaceous, and that this may have given ant society cohesion before the advent of agriculture (**Godzińska**; **Kovaka et al.**). We argue that the division of labor innately increases efficiency, and that it was necessary for agriculture to become a viable strategy because it requires a large number of interconnected tasks. Humans and certain species of ants and termites were capable of employing an elaborate division of labor and were therefore positioned to make the transition to agriculture. Humans, ants, and termites thereby became much more highly interdependent and almost mechanistically structured in food production. And each individual role in the execution of agricultural tasks was more circumscribed, thereby rendering individuals less capable of independent survival. Thus, the division of labor specific to agriculture is central to ultrasociality because it sets up a profound interdependence where individuals essentially become part of a “superorganism.” This becomes obvious with large-scale “institutional agriculture,” which evolved very rapidly after the onset of agriculture (Shepard 1973).

Hunters and gatherers had a simple division of labor but it did not come close to the complexity of labor differentiation in ultrasocial societies. We agree with **Noles & Danovitch** that a “division of cognitive labor” may be a preadaptation to ultrasociality. We do not claim that societies that adopt agriculture always reach a high level of complexity, nor do we deny that pre-agricultural societies can

have some complexity as indicated by hierarchy. As we mentioned in our target article, the northwest coast Indians had settled communities and the beginnings of a hierarchical society without agriculture due to the unique natural bounty in the northwest coast. Salmon could be stored (surplus production), and the best salmon areas could be monopolized. This strengthens our case of the importance of surplus production leading to hierarchies. Control of surplus cannot be separated from the control of capital (Woodburn 1982).

We fully recognize the problem of class conflict and power in human societies. The combination of the division of labor and the existence of surplus created an opening for institutional mediation in the specific allocation of jobs and command of surplus. But we want to stress interdependence. Hierarchy in itself is not a defining attribute of ultrasociality. The most advanced social insect societies are not hierarchical (Gordon 2007). It is the rigid interdependence in food production that initially defines ultrasociality. No matter what role or which class one occupies, all have a vested interest in the stability and smooth functioning of a system in which they all participate and indeed must participate if they are to survive.

**McCain** points to the importance of class and power, characteristics that distinguish arthropod and human societies. But the issue of hierarchy and class involves more than power. It is also the acquiescence to power that comes from the interlocking coordination of classes in complex production. We fully recognize that this acquiescence is incomplete in humans. This difference was discussed at length by Georgescu-Roegen (1977a), who pointed out that insect societies are organized into castes according to the endosomatic (within the body) attributes. Doorkeeper ants have large heads to block entrances, and soldiers have large mandibles for fighting. Humans, on the other hand, have become dependent on the exosomatic (outside of the body) instruments of our material culture. Because there are no genetic reasons why a particular person or group of persons should have control of these instruments, they become a source of social conflict.

**McCain** accuses us of neglecting the role of class systems based on threat. We recognize the role of coercion and threat. But we focus on something more basic to ultrasociality—with ultrasociality, even the most oppressed classes have a vital stake in preserving the system. We chose to conceptualize our current ecosphere/economy challenges in an evolutionary framework rather than to use an evolutionary game theory model as McCain suggests. Our research has led us to conclude that there is an evolutionary story to the transition to ultrasociality and to our present set of circumstances. The prisoner’s dilemma highlights the relationship between individuals and cooperative behavior, including the division of labor, but leaves us with limited insight about the social context of these behaviors.

**Crespi** claims that in humans, divisions of labor are not primarily cooperative but competitive. He argues that the presence of surplus and the division of labor gives way to hierarchy in humans and interprets this as “competitive” when it leads to enhanced reproduction and consumption rates for city-state rulers. The more important issue with regard to cooperation is the unbridled interdependence of agricultural society, which rigidly structures productive life and turns cooperation into coercion. As for the

reproductive division of labor, while it is true humans do not have the same division of labor in reproduction as social insects, for most of human history it was clearly not true that “human groups almost certainly benefit at the cultural group level from high fecundity of their female members” (Crespi). But in agriculture, high fecundity of female members meant that the division of labor by gender became more pronounced, and this was not a positive change for women. By contrast, the imperative for hunter-gatherers was to keep population rates low. Agriculture and the ensuing 10,000 years has been the exception.

**Crespi** states that the “human reproductive division of labor” is precluded. This is too strong a statement. A large literature exists about the long period of post-menstrual life in human females. Another interesting phenomenon here is the replacement of human workers by robots, a non-reproducing class of workers. Is this another example of the human transition to an ant-like production system?

## R6. Energy and complexity

Our analysis of the evolution of ultrasociality with agriculture cannot be reduced to a matter of energy, although there are clearly energy implications to this change in social organization. Given that the species that practice agriculture are expansionary and come to dominate ecosystems, the relationship of these species to energy is obviously important. The relationship between energy and expansion is approached in a nuanced and systemic way in our analysis. Expansion is seen through the lens of the complex evolutionary process of group formation specific to agriculture, and energy is obviously part of that process.

One of our claims is that the formation of ultrasociality was boosted with agriculture as humans were able to tap into the stocks of carbon. We make a similar claim for ants that practice agriculture. But the energy story is further complicated for these species because tapping into stocks was only one aspect of their relationship with energy. Agriculture allowed for a redirection of solar energy to the species that were able to redirect it through cultivation, thus providing more food. Humans and species of ants and termites were able to manage agriculture by virtue of a social reconfiguration of their relations of production. In other words, it was necessary to implement a more elaborate division of labor to engage agriculture, and these species were able to do so. The altered division of labor with agriculture enabled the species that practiced it to tap into certain economies of scale in energy use, which in turn reinforced the expansionary dynamic.

**Hou**'s remarks help disentangle the complex story of energy. Hou talks about this in the language of *sublinear scaling* (Bettencourt et al. 2007; Hou et al. 2010) and points out that: “The similar economies of scaling in both ant and human societies reflect, as G&K point out for ants, that a larger group size is more energetically efficient.” Thus, the tendency (based on sublinear scaling) would be toward a larger colony size because larger size is able to capture scaling benefits. If this were all that was at work, the ultimate restriction on expansion would emerge when the species reached carrying capacity. Hou suggests that sublinear scaling is a matter of inequality in energy use

owing to the “heterogeneity in the activity level of individuals in the network”; when “group size increases, relatively fewer individuals consume a lot, and more consume a little.” This interfaces nicely with our observation that agriculture demands and lends itself to a more elaborate division of labor, making it quite likely that there are differing energy demands between individuals involved in different roles.

Referring to the work of Bettencourt et al. (2007), **Hou** further claims that, “Theoretical models predict that driving forces with different scaling powers will generate sharply different growth patterns.” In particular, “Bettencourt et al. (2007) show that, besides the infrastructure properties that scale with the population size in the same way as in ant colonies [i.e., sublinearly], human society also has a suite of unique properties ‘reflecting wealth creation and innovation’ (p. 7301), which have no counterpart in ant society.” These properties scale superlinearly rather than sublinearly, making the relationship to energy and the growth cycle and its end different for humans. Specifically, humans are more inclined to collapse as sublinear energy scaling is not sufficient to counteract superlinear scaling, exacerbating the ever greater demand for energy as group size increases (Brown et al. 2011). Because humans exhibit both sublinear and superlinear scaling, Hou tells us that “superlinear scaling in a human society inevitably results in unbounded growth.” That is, of course, until the systems crash.

**Hou** does not analyze the superlinear scaling apparent in human societies, but if one interjects the overlay of economic structure, it is fairly easy to see what is happening. Surplus production and expansion in humans that begins in agriculture leads to markets (an institutional arrangement to redistribute surplus), and markets eventually evolve into market society. Market society (capitalism) is driven by the production of exchange value (and not the production of use value), but the production of exchange value is not directly linked to biophysical foundations. Exchange value is simply a term used to convey the idea that the purpose of production (or any economic activity) is not primarily to produce useful things, but to make money. With the advent of the use of fossil fuel, this non-organic aspect of economic evolution was supercharged, and the economic system became supra-organic. As well, in market capitalism fueled by fossil fuel, the cost of sublinear scaling was a tremendous increase in productivity, creating internal contradictions in the system. In the end, we are left with an ironic outcome—we have an economic system that has profound biophysical implications (take climate change as an example) but one that is nonetheless framed by an imperative that is not directly tied to biophysical limits. The probability of collapse is enhanced. But all of this begins with agriculture. We discuss this extensively in another paper (Gowdy & Krall 2013).

**Tainter** maintains that we have done a “valuable service in helping to undermine historical narratives that underpin this ancestor myth” (the notion of the “heroic progress” of human society). Tainter has understood that our analysis gets into the “black box” of progress to examine the altered way society was differentiated and reconfigured with agriculture. Our analysis does not offer an ancestor myth (appealing to the special status of humans and their propensity for ingenuity), nor a simplistic energy interpretation of the transition to agriculture and human expansion.

Tainter points out that before fossil fuel use the “cost of complexity would have inhibited its development.” This can be seen in the collapse of many large-scale state societies where the energy accommodation to complexity would have been limited primarily to agriculture. Were it not for the advent of the use of fossil fuel, it is likely that the evolution of market society (capitalism) would have been hampered. But with the advent of fossil fuel, the energy/complexity spiral continues to grow, or as **Hou** and Bettencourt et al. (2007) claim, energy scales superlinearly. In some sense those limits will be determined by the interplay of the energy demands of complexity and the dual dynamic of sublinear and superlinear scaling.

**Farley** rightly points out that “fossil fuel use and monetary exchange have taken human ultrasociality and economic organization in new directions.” This claim is substantiated by **Hou** as well as the work of Bettencourt et al. (2007) and **Tainter**. We would argue that Farley is not altogether correct in his claim that, “The modern capitalist economy emerged not with the transition to agriculture, but rather, simultaneously with our ability to tap fossil fuel stocks.” We talk more extensively about this in section R8.

Certainly, the energetics of society changed dramatically with agriculture. The framework of sublinear and superlinear scaling of human society in terms of energy and size seem potentially fruitful ways to understand the complex energy dynamic that clearly begins with agriculture. Superlinear scaling would have been greatly expanded with the advent of capitalism and the use of fossil fuel, or in **Hou**'s words, “the expansion of a human society is probably ... driven by innovation and wealth creation which scale superlinearly.” Infrastructure is a matter of sublinear scaling, but “‘wealth creation and innovation’ (Bettencourt et al. 2007, p. 7301), which have no counterpart in ant society” scale superlinearly.

The question that remains temporarily unanswered here is whether the energy used by hunter-gatherers scaled sublinearly and/or what the size constraints on the process of scaling might have been. Were they different than for humans who employed agriculture? Because these societies remained low in population, it is likely that there were no scaling dynamics pushing them in the direction of expansion. If this is true, then the case can be made that scaling in terms of size of group and energy might be considered one indicator of ultrasociality.

## R7. Expansion and sustainability

We make the claim that the evolution of ultrasociality in humans, ants, and termites is a case of convergent evolution. More specifically, we claim that “in all three lineages similar patterns of economic organization emerge through similar selection pressures” (target article, sect. 1, para. 1). We do not deny the role of culture or institutions in reinforcing and interpreting the pattern of economic organization established with agriculture. We recognize that the “details of ultrasociality in humans play out in ways that are mediated by human intentionality and cultural norms” (sect. 1, para. 1). While the role of gene-culture co-evolution has long been recognized (Richerson & Boyd 2005; Wilson 1997), as has the validity of MLS and group selection, little work has been done on the organization

of economic life as a particularly significant component of social evolution. **Wilson** recognizes that we move “beyond human genetic evolution to include human cultural evolution, while remaining fully biological in [our] comparison with insect societies.” We use MLS and group selection fully recognizing that insects and humans may have different mechanisms of inheritance. We identify economic structure and economic drivers that are unique and significant in determining the commonalities of ants, termites, and humans. Economic structure and its drivers are intentionally highlighted in the matrix of the social evolution of the species we explore.

Some commentators object that we did not emphasize the roles of hierarchy (class), warfare, and institutions in the formation of complex societies (**Houdek et al.; Levine; McCain**). Houdek et al. assert that institutions, not agriculture, are responsible for ultrasociality. They confuse proximate and ultimate causation. What we say is that agriculture resulted in institutional arrangements reinforcing surplus production and expansion. For example, there is no question that the institution of property rights was important in the cultural configuration of agriculture. We fully recognize that defense is necessary to protect the sites of agricultural production and storage, and that warfare can take on a life of its own, particularly when wedded to hierarchy. These are particular human institutional interpretations of the demands of agriculture, and there is no question that the presence of augmenting institutions reinforced the system. In fact, we argue that those early post-hunter-gatherer societies that had institutions favorable to surplus production were able to out-compete others. The transition to agriculture, like other major transitions, is a complex evolving process depending on myriad interacting phenomena. But our perspective is that economic structure provides foundational material conditions that frame and direct institutional possibilities. We fully acknowledge that in humans, cultural mediation of economic structure is possible and can influence the direction of economic evolution. But cultural mediation is unlikely to fundamentally alter the dynamic and structure of the economic system unless the contradictions of the system become so great that they simply are no longer workable. Interdependence is profound in agricultural societies whether they are ruled by kings or not. And the presence – indeed, the imperative – of surplus in agricultural societies gives rise to institutional accommodations, like markets, which, as we have argued, may take on a life of their own without fundamentally changing the essential aspects of ultrasocial economic society: division of labor, interdependence, expansion, domination of ecosystems, and loss of autonomy (Gowdy & Krall 2013).

**Houdek et al.** state that, “There is nothing about human agriculture ... that makes it inherently and inescapably unsustainable in terms of inequality, environmental degradation, or violence. In all of these aspects, the effect of development is not necessarily negative.” First of all, we do not argue that agriculture is “inescapably unsustainable,” but we do assert that: “The basic problem is that ultrasocial societies are expansionary ...; and because of their tremendous interdependence, they are particularly difficult to disengage before they reach the point of collapse” (target article, sect. 5.1, para. 1). Houdek et al. refer to the Kuznets curve and the environmental Kuznets curve as evidence for their assertion that we are not correct. These

curves refer to evidence for an inverted U relationship between inequality and economic growth, and between pollution and economic growth. Both have been thoroughly discredited as general relationships. As Piketty (2014, pp. 13–160) points out, the Kuznets curve for inequality, the idea that as an economy develops inequality first increases then decreases, was a product of the Cold War and the desire to keep underdeveloped countries within the sphere of influence of the free world. The empirical evidence behind the inequality bell curve was shaky, according to Kuznets himself (Kuznets 1953, pp. 24–26, quoted in Piketty, p. 581): “This is perhaps 5 percent empirical information and 95 percent speculation, some of it possibly tainted by wishful thinking.” The sharp reduction in income inequality after WWI until the end of WWII, the period of Kuznets’s evidence, was an aberration, not a general law of development. Piketty (2014, p. 15) summarizes: “The sharp reduction in income inequality that we observe in almost all of the rich countries between 1914 and 1945 was due above all to the world wars and the violent economic and political shocks they entailed (especially for people with large fortunes). It had little to do with the tranquil process of intersectoral mobility described by Kuznets.” An alternative is that inequality increases over time, and this eventually leads to a point where it is not sustainable in a capitalist economy.

Evidence for the environmental Kuznets curve, that with development and economic growth, pollution increases then decreases, is at least as discredited (Stern 2004). The history of development in advanced Western countries shows a negative relationship between some kinds of pollution and economic growth (urban air quality for example), but a positive relationship between other kinds of pollution and economic growth (climate change for example). And given the mounting evidence on climate change, rates of extinction, deforestation, decline in fisheries, and so on, we think it is safe to say the current rendition of ultrasociality (globalized monopoly finance capital), or rather the current assault on the rest of the natural world, is not sustainable.

We hope that Ristau is correct in her optimism about the possibility of radical intentional change. We acknowledge the exciting new field of study of “directed evolution” and intentional change (Wilson et al. 2014).

Ross accuses us of being neo-Malthusians and asserts that individual initiative and technology will solve our environmental and social problems. Malthus wrote his “Principles of Population” essay in 1798. It was immediately criticized by William Godwin, who argued that the “perfectibility of mankind” would overcome any scarcity. Ross echoes this 200-year-old argument: “But it is at least as plausible to predict that incentives operating at the scale of individuals will produce the technology that delivers planetary salvation.” Fortunately, the Malthusian debate about technology versus exponential growth has matured considerably during the last 200 years (see, e.g., Nekola et al. 2013).

We do not mention Malthus in our target article, nor do we defend doomsday population scenarios. Whether or not Malthus will be proven correct in the coming decades, remains to be seen. Economists are notoriously optimistic about the ability of technology to overcome any resource scarcity or pollution problem. The widely quoted economist Julian Simon wrote: “We now have in our hands – really in

our libraries – the technology to feed, clothe, and supply energy to an ever-growing population for the next seven billion years” (<http://www.azquotes.com/quote/808123>). It may be possible to feed the projected human population of 9.6 billion in the year 2050 (see United Nations, Department of Economic and Social Affairs, Population Division 2013). But unlike Ross, we do not assume that technology will automatically solve the food production problem, or the problems of destabilizing climate change, ocean acidification, and biodiversity loss. Will population growth continue unabated or will the human global society collapse? Will the benefits of technology outpace the destabilizing effects of increased complexity (Tainter), social instability (Nephew & Pittet; Ristau), and environmental degradation (Farley)? The human population is expected to peak at about 10 billion around the year 2100 and decline after that. If we are to survive the bottleneck of the 21st century, we need more than a blind faith in technology and individual initiative.

According to Ross, individual initiative is the key to innovation, and the more individualistic humans are, the better: “Modern humans are likely more individualistic, not less so, than pre-ultrasocial hunter-gatherers.” As Farley points out, markets and money make people more selfish and less sociable. But is this good? Surely, getting control of common destiny depends on more cooperation, not more selfish behavior (Wilson & Gowdy 2015).

Perhaps the more critical consideration is not how many people can be technologically supported on this planet. One thing we know is that the more humans there are, the less diverse the ecosphere will be. We have a complex and essentially contradictory evolutionary history. The human ecologist Paul Shepard (1982, p. 6) conjectured more than three decades ago that the ontogeny of tribal peoples (hunters and gatherers) is “more normal than ours and that it may be considered to be a standard from which we deviated.... Theirs is the way of life to which our ontogeny was fitted by natural selection.” Shepard does not discuss ultrasociality, but he extensively explores the abrupt change in the history of humankind marked by the transition to agriculture. We offer that this too was the result of natural selection but it was in conflict with the healthy ontogeny that had evolved in the Pleistocene. Our present circumstances should nudge us to critically consider this complex social evolution and its conflict with our Pleistocene genome. Psychologists might ask the question of whether we are better adapted to mature in a healthy manner in this world of profound interdependence and expansion with little of the natural impulse of the planet around us or whether our individual ontogeny is best adapted to a different world that was undermined when we turned to agriculture.

## R8. The accelerating evolution of human ultrasociality

The analysis of the evolution of ultrasociality from agriculture to global capitalism is a natural extension of our work. We have previously begun that exploration in our paper “The Ultrasocial Origin of the Anthropocene” (Gowdy & Krall 2013). We appreciate Farley’s comments because he rightly acknowledges that the direction ultrasociality has now taken is distinct. But we raise a cautionary



note – while global capitalism has its own distinct character it is nonetheless the direct descendant of agriculture so it is important to understand both its connection and its difference.

As we mention in section R6 (para. 7), **Farley** states: “The modern capitalist economy emerged not with the transition to agriculture, but rather, simultaneously with our ability to tap fossil fuel stocks.” At the start of his commentary he writes: “I would suggest, however, that fossil fuel use and monetary exchange have taken human ultrasociality and economic organization in new directions.” Later, Farley tells us, “A monetary fossil fuel economy is very different from a pre-monetary agricultural one.” No one would argue with the claim that the use of fossil fuels fundamentally altered market society, or what Farley refers to as “monetary exchange” (cf. Gowdy & Krall 2014; Klitgaard & Krall 2012; Krall & Klitgaard 2011). It is important to understand that evolution is a continuous process yet there are major evolutionary transitions. We argue that the leap from hunting and gathering to agriculture was a major evolutionary transition. Global capitalism is the descendant of this transition.

A few points of clarification are in order. The term “monetary exchange” is vague. Monetary exchange took place in many state societies which also had markets, but no one would argue that these were equivalent to market society (capitalism). Thus, “monetary exchange” does little to help us distinguish capitalism from other societies that had markets and produced surplus. A more exact vocabulary must be used to distinguish between previous ultrasocial societies and global capitalism as an ultrasocial society. We have argued that capitalism is economically distinct, but in an evolutionary sense it is the continuation of the revolution in the biophysical dynamic of human society that took hold with the transition to settled agriculture. The parsing of capitalism requires accounting for its connection to previous ultrasocial system(s) and also identifying its unique rendering of ultrasociality. The extreme division of labor in productive life, interdependence, the production of surplus, and the dynamic of expansion distinguish ultrasocial economic systems from those of the hunter-gatherer past, which had only a rudimentary division of labor, limited interdependence in productive life, little or no surplus, and no expansionary dynamic. It is also the case that hierarchy did not dominate pre-agricultural societies but came to dominate the structure of society beginning with agriculture.

We posit that the uniqueness of capitalism can be understood by making the distinction between the evolution of “societies with markets” and the later development to “market society.” These are two different things. Although **Farley**’s instinct that there is something unique about the era of fossil fuel and capitalism is appropriate, his terminology (referring to capitalism as “monetary exchange”) is vague and does not lead to a clear understanding of what makes capitalism stand apart. In market society the division of labor is further expanded, and the production of surplus takes on a distinct institutional structure. A market economy, as opposed to an economy with markets, “is an economic system controlled, regulated, and directed by markets alone; order in production and distribution of goods is entrusted to this self-regulating mechanism” (Polanyi 1944, p. 68). And as we have argued in other papers, market society was a distinctive rendering of the

dynamic of surplus production (Gowdy & Krall 2013). In market society the purpose of production is not primarily to produce useful items, it is to produce profit – or put another way, the purpose of the economy is not the creation of use value, but the creation of exchange value. Surplus is obtained at the point of production and realized when goods are sold. Surplus ultimately takes the form of profit, which has the imperative of then finding further outlets for making even more profit. The advent of fossil fuels gave this altered structure of surplus production and expansion an added impulse. The production of exchange value, already institutionally disconnected from a biophysical basis, was given a seemingly unending supply of energy, giving capitalism an almost supra-organic dimension. Landes gives us some idea of the expansionary force when he tells us that coal use in the United Kingdom had increased to 100 million tons by 1870, which was “equivalent to 850 million calories of energy, enough to feed a population of 850 million adult males for a year (actual population was then about 31 million)” (Landes 1969, p. 97). One can justifiably ask the question: What would capitalism have looked like without the use of fossil fuel? There is no question that it would have looked much different, as Farley clearly understands. But the roots of a new system had already been laid previously in the revolution that took place with agriculture. And, in fact, the evolution of markets to market society had already taken form before the advent of wide-spread use of fossil fuel technology.

**Farley** maintains that “current environmental challenges can all be characterized as prisoner’s dilemmas: The best outcome for the individual is selfish behavior, regardless of what others do, but the best outcome for society is cooperation.” There is no question that what might be good for a person at one level is not good at another level (**Wilson**). But this approach leads us to believe that if we can only overcome individual selfish behavior (greed) through cooperation then we can see our way out of this mess. It may well be the case that it is important in the modern era to cooperate at a global level to solve some of our worst problems (like climate change), but we must acknowledge that our propensity for cooperation has been structured – it is embedded in the fabric of our economic system and is apparent in the division of labor, class formation, and the profound productive interdependence. An evolutionary approach to group formation and selection helps to highlight the significance of this fact. As **Wilson** points out, when “many lower-level traits” interact in a “complex fashion” multilevel selection theory steps in avoiding a “detailed reductionistic understanding of the traits.” The reason we concentrate on ultrasociality with agriculture is because it was evident that an altered system had taken hold that structured cooperation in a different way. We surely have the capacity for cooperation, but our more important challenge is to understand how our capacity for cooperation manifests itself in our present system. Cooperation (or greed for that matter) is socially and economically complex and embedded as part of the structure of productive life. Cooperation is but one of the traits that form a “group” with evolutionary significance. It cannot be reduced to an individual trait. In the same way, selfish behavior does not provide the cornerstone for understanding our present economic system. Corporations and individuals may be greedy, but they are supported in their greediness by institutions of property, rights of

corporations, and the dynamic life of market society where the rewards of greediness serve the process of accumulation and expansion.

## R9. Human biological evolution since agriculture

There have been significant physical and behavioral changes in individual humans with ultrasociality. Michod and Nedelcu (2003, p. 64) pinpoint the basic problem in understanding major evolutionary transitions—how does a group of individuals become a new kind of individual having heritable variation in fitness? As we discuss in our target article and as mentioned by several commentators, a necessary precursor to a major transition is cooperative interactions among lower-level units. We argue that in the human transition to agriculture, the striking ability to cooperate that arose before agriculture paved the way for a radically different kind of cooperation, more properly called coordination, that was harnessed to facilitate the complex organization of food production. This involves the “co-option of lower-level processes for new functions at the higher level” (Michod & Nedelcu 2003, p. 64). With ants and termites, the transition to ultrasociality was accompanied by dramatic changes in the genotypes and phenotypes of individuals. Can we see biological changes in humans after the transition to agriculture?

Considerable evidence exists for the shrinking human brain after agriculture. The reasons for this are complex, but we know that the human brain is an expensive organ to maintain in terms of energy use. If a larger brain is no longer necessary for survival because survival is supported by high-density protective societies, then brains should become smaller. Moreover, our intellectual and emotional abilities are genetically fragile—between 2,000 and 5,000 genes are needed for intellectual and emotional function (Crabtree 2013a)—implying that changes in these abilities can be quite rapid. The agricultural transition brought a new set of selection pressures unrelated to intelligence. Crabtree (2013b, p. 4) writes: “When might we have begun to lose these abilities? Most likely we started our slide with high-density living, which was enabled by the transformative invention of agriculture. Selection may have begun operating on resistance to diseases that naturally grow out of high-density living, switching the pressure from intelligence to immunity.”

Does the shrinking brain imply a loss of intellectual and emotional intelligence? Crabtree (2013a) is unequivocal on this question:

I would wager that if an average citizen from Athens of 1000 BC were to appear suddenly among us, he or she would be among the brightest and most intellectually alive of our colleagues and companions, with a good memory, a broad range of ideas, and a clear-sighted view of important issues. Furthermore, I would guess that he or she would be among the most emotionally stable of our friends and colleagues. I would also make this wager for the ancient inhabitants of Africa, Asia, India, or the Americas, of perhaps 2000–6000 years ago. The basis for my wager comes from new developments in genetics, anthropology, and neurobiology that make a clear prediction that our intellectual life and emotional abilities are genetically surprisingly fragile. (Crabtree 2013a, p. 1)

There exists a large and interesting literature about human domestication (see Leach 2003). Characteristics of the domestication of wild animals include reduction in size and skeletal robustness, cranio-facial shortening, and reduction in cranial capacity. All of these changes have occurred in humans since the adoption of agriculture. Leach (2003, p. 349) makes a case for human domestication based on “the effects of the built environment, decreased mobility, and changes in diet consistency associated with increasing sedentism.” Behavioral changes highly relevant for the human transition to agriculture include submission to hierarchy, and “a reduction in environmental awareness” (translated from the German phrase *Verarmung der Merkwelt*). The impoverishment of the observed world that came with agriculture has been described by the human ecologist Paul Shepard (Shepard 1998, p. 57): “Stated simply the ‘civilized mind’ attempts to simplify and level the world whereas the ‘savage mind’ is not afraid to become enmeshed in its complexity.” A major reason for the environmental crises that threaten to eliminate the human species is the loss of “oneness” with the natural world.

Domestication and submission to hierarchy can be clearly seen in a comparison of dogs and wolves. Range and Virányi (2014) performed a controlled experiment testing the sociality of dog and wolf packs: They tested the tolerance of each species by pairing a high-ranking dog with a low-ranking one and gave them one bowl of food. They gave the same test to a pair of wolves. In every dog matchup, the higher-ranking dog monopolized the food, but with the wolves, both high-ranking and low-ranking animals had equal access. A report on the study summarized, “Wolves cooperate but dogs submit” (Morell 2014). Human domestication should raise a red flag over “just-so” stories about the progressive evolution of cooperation and peacefulness. Rather than better angels, have we become better servants to those at the top of the hierarchy?

There have been changes in human reproduction patterns since agriculture. Hunter-gatherer societies had low reproductive variance, and dispersal possibilities were high. In state societies reproductive variance was high, and dispersal options were usually low. Betzig (2014, p. 81) uses examples from early state societies and from ultrasocial and eusocial insect societies to argue that reproductive inequality goes up with settled life. In civilizations from the Near East, India, China, Greece, and Rome, kings collected thousands of females and guarded them with thousands of eunuchs. Genghis Khan fathered hundreds of children, and as a result, millions of Asian men have a similar Y chromosome lineage. These cultural patterns have left a mark on the human genome (Aitken). According to Karmin et al. (2015), the hoarding of females by high-ranking males led to a dramatic decline in male genetic lineages 4,000 to 8,000 years ago. The research suggests that the accumulation of wealth and power caused a genetic bottleneck in Y chromosomes lineages. The accumulation of wealth and power that came with agriculture produced a detectable reproductive skew in current human populations.

Hou discusses scaling laws with respect to ant and human “ultrasocieties.” His research has uncovered similar economies of scaling and found that in both societies a larger group size is more energetically efficient. The evidence is only suggestive, but it seems that the

basic metabolism of human society changed dramatically with the transition to agriculture. Hamilton et al. (2014) found that residential mobility in hunter-gatherer societies is predicted by average human body size and by limits to the ability of mobile hunter-gatherers to store energy internally, that is, by the characteristics of individuals within a society. Hamilton (p. 2) writes: “Our results demonstrate that large-scale evolutionary and ecological processes, common to all plants and animals, constrain hunter-gatherers in predictable ways as they move through territories to effectively exploit resources over the course of a year.” The energetics of hunter-gatherer bands are no different from those of, say, a wolf pack or a chimpanzee group. The energetics of ultrasocial societies, however, point to a major evolutionary transition such that the metabolic characteristics of the society resemble those of an individual organism (Bettencourt et al. 2007; Hou et al. 2010; Shik et al. 2012).

## R10. Conclusion

We come from the discipline of economics, a discipline especially prone to insularity and inbreeding (Fourcade et al. 2015; E. O. Wilson 1998). It is dominated by a narrow discourse which emphasizes an isolated individual making rational decisions in the immediate present. And yet, as we observe the economic world, we see a vast, globally interconnected, and expansionary economic system of people and institutions, unfolding in historical time. In fact, it seems rather miraculous that humans went from a nearly 200,000-years history of hunting and gathering to the present economic world in a mere 10,000 years – a drop in the bucket of evolutionary time.

It is easy to attribute this radical change to the inevitable progress of humans, given their intelligence and ingenuity. But we reject this pre-analytical vision of human uniqueness because we are struck by the similarities in the economic configuration of ultrasocial human, ant, and termite societies. We came to the conclusion that the similarity in economic life of these dissimilar species could not be answered through the lens of economic analysis alone. Explaining this convergent evolution calls for an interdisciplinary approach.

As we entered the largely unfamiliar world of contemporary evolutionary biology, we were astounded by the similar approaches of many biologists who believe that evolution works only at the level of the gene and those economists that hold that economics can be reduced to the behavior of isolated individuals in an ahistorical and institutional vacuum. But alternative frameworks exist in biology and to a lesser degree in economics. Tapping into the alternative frameworks of multilevel selection (MLS), evolutionary economics, and cultural evolution provided fertile ground for exploring convergent evolution.

Our target article focuses largely on the transition from hunting and gathering to early agricultural state societies and the role of economic organization in this transition. But our motivation for this study was our life-long concern with the seemingly intractable problems of environmental degradation and social injustice. The immediate problems faced by our species have obviously reached a crisis point. Why does human society seem incapable of addressing them? We believe that our answer to this question is revolutionary. Humans have evolved similarly to other

species into an expansionary superorganism configured to produce economic surplus. It is very difficult to disengage from this evolutionary dynamic.

Wilson objects to our “excessively narrow focus on agriculture.” He writes: “The key condition for ultrasociality is a surplus of resources, making division of labor possible.” But this implies that there was an exogenous increase in resources that made a greater division of labor possible. We argue that a reconfiguration of food production entailed a more elaborate division of labor that made it possible to tap into existing resources by actively managing them. This altered economic configuration and dynamic was reinforced by new institutions and belief systems, and it evolved over time. These belief systems have taken various forms, from divine right, to contemporary welfare economics, to the pre-analytical belief in human uniqueness and the course of human progress.

Where does this leave us? One implication is that we cannot rely on “the market” to save us. In fact, our salvation lies in a more radical and evolutionary understanding of market society that can lead to a transformational change. In order to avoid ecological and social disaster, we must get control of the superorganism that is the global market economy. First steps include global controls on carbon emissions, protection of the earth’s remaining biodiversity, and insuring an equitable distribution of material output. But these are not enough. A more incisive understanding of economic structure and an appreciation for the dynamic of expansion and resource exploitation are requisite to alter the economic trajectory.

As Wilson discusses in his commentary and in Wilson et al. (2014), a science of intentional change based on notions of complexity and evolution is beginning to take shape. Evolutionary theory has been used successfully to modify individual behavior (as in anti-smoking campaigns), and to shape decision-making in small groups (as in Elinor Ostrom’s core design principles; Ostrom 1990). But what is urgently needed now is more expansive institutional change. The question implicitly raised by ultrasociality is whether we leave our fate as a species to the whims of the blind evolutionary processes that have brought us to our current state of ecological collapse, profound inequality, and intractable problems like climate change, or whether appropriately informed intentional change can alter our future.

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[The letters “a” and “r” before author’s initials stand for target article and response references, respectively]

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