Cooperation in a Complex World: The Role of Proximate Factors in Ultimate Explanations

Kim Sterelny

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Abstract Mayr’s distinction between proximate and ultimate explanation is justly famous, marking out a division of explanatory labor in biology. But while it is a useful heuristic in many cases, there are others in which proximate factors play an important role in shaping evolutionary trajectories, and in such cases, each project is sensitive to, and relevant to, the other. This general methodological claim is developed in the context of a discussion of human cooperation, and in particular, in a discussion on the puzzling stability of the social contract over the Pleistocene–Holocene transition. For I argue that while we have a plausible account of the stability of Pleistocene cooperation, the stabilizing factors of the Pleistocene disappear in the Holocene, but cooperation does not. Holocene humans solved many collective action problems; cooperation did not collapse despite the apparent growth of free-riding elites. So the article combines a methodological claim about the interaction of proximate and evolutionary biology with a substantive one about the ecology of human cooperation.

Keywords Collective action · Human cooperation · Proximate explanation · Social hierarchy · Strong reciprocity · Ultimate explanation

Theories and Frameworks

“Theory” is a multiply ambiguous term in biology, as elsewhere. In biology, its most obvious meaning is to pick out mathematical and computational representations of biological systems. However, there is an alternative use of “theory,” as exemplified in “neo-Darwinian theory,” “developmental systems theory,” or “the theory of niche construction.” In this sense, a theory is something like a research framework: a cohesive set of ideas that identify problematic, important phenomena; explanatory mechanisms; research strategies (Godfrey-Smith 2000). Thus niche construction theory, like all versions of Darwinism, takes the apparently design-like fit between organisms and their environment to be a key explanatory target. But it adds an explanatory mechanism to the standard toolkit: the effects of organisms on their own environment. There is an adaptation of environments to phenotypes, not just of phenotypes to environments (Odling-Smee et al. 2003). This article will be about this “framework” sense of theory: in particular, on Mayr’s (1961) famous division of labor within the life sciences. In that landmark paper, Mayr distinguished proximate questions of local causation from historical, selective questions, pointing out that historical explanations in biology complement, rather than compete with, those that specify physiological or molecular mechanisms. Everyone agrees that there is a core insight in Mayr’s work: we can usefully distinguish questions about, say, the physiology and local mechanism of bird migration from questions about its selective benefit or phylogenetic distribution.

However, Mayr’s division of labor was tied to the way he saw organisms as autonomous robots who self-assemble and operate on the world on the basis of their inherited design. On that way of seeing organisms, there are indeed

K. Sterelny (✉)
Philosophy and Tempo and Mode, Australian National
University, Canberra, ACT, Australia
e-mail: kim.sterelny@anu.edu.au

K. Sterelny
Victoria University of Wellington, Wellington, New Zealand

two complementary but relatively independent projects: How does the robot work? Why does the robot come to have its specific design? Moreover, Mayr's own example, bird migration, fits this model quite well. Migration is clearly an evolved behavior in birds: first, migrating can hardly be a primitive trait inherited from nonflying ancestors; second, it is found in many, often distantly related groups; third, in many species birds migrate independently of their parents, so it is not a learned behavior. We can be confident that it is the result of selection: migration is obviously expensive and risky, so it is clearly buying the birds something. Moreover, there is variation in the trait; for many species, not every bird migrates. In short, migration is an evolved, selected, canalized behavior. It is also a response to an autonomous, independent, and very stable feature of the environment (the effect of axial tilt on seasonality), a feature not changed by the fact of migration. There is no arms race, no coevolutionary interaction, between migrating bird and climate. We can see migration as an evolved, adapted, genetically canalized response to an autonomous environment. It is part of the design of the avian robot. The problem is that bird migration may be an unusually tractable case.

Kevin Laland and his colleagues have recently argued that many important cases are much less tractable; in particular, they are not profitably conceptualized using unidirectional causal chains. We need a framework that emphasizes the interactions between a population's response to selection and the selective environment, and we need a framework that emphasizes the interactions between organisms' proximate biology and the selectable variation available in the population built from those organisms (Laland et al. 2011, 2012).

I aim to develop this argument, using the evolution of human cooperation as my organizing example. That example is particularly important, because Stuart West and his colleagues have recently argued (West et al. 2011) that influential recent work on human cooperation is deeply flawed; flawed because of its insensitivity to the distinction between proximate and ultimate explanations. According to this new perspective, the evolution of human cooperation depends on the evolution of a distinctive motivational stance, "strong reciprocity," a stance combining a willingness to cooperate with a punitive attitude to free-riding (see, e.g., Fehr and Fischbacher 2003; Boyd et al. 2005; Gintis et al. 2008). I have two ambitions in focusing on cooperation. One is methodological. Fehr, Boyd, Gintis, and their allies are *not* confused. The niche construction framework, with its emphasis on the feedback between evolving lineage and environment, is more productive for understanding the evolution of cooperation than the approach encapsulated by Mayr's division of labor (Sterelny 2003, 2012a). The second is substantive: I aim to show that while

we have an appealing theory of the origins of human cooperation, we have a much less satisfactory account of its stability through the transition from foraging to farming and beyond.

Mayr's Framework and Human Cooperation

One of the most distinctive features of the human lineage is the emergence of rich, pervasive cooperation. Humans are obligate cooperators, and that cooperation often includes dependence for the necessities of life on other agents who are not close kin. Ernst Fehr, Sam Bowles, Herb Gintis, Rob Boyd, Pete Richerson, and their allies link the archaeology and anthropology of cooperation to developing experimental work on human choice in public goods games. They argue that this experimental work shows the importance of cultural context and cultural learning, but cultural learning interacting with a distinctive evolved psychology. Cooperation depends on interactions between prosocial emotions and social learning. Humans act prosocially, but the form and extent of prosocial behavior often depends on specific, local, but stable cultural traditions. For example, Henrich et al. (2005) in their cross-cultural survey of economic games noted that one group, the Orma, mapped the public goods game onto an important, cooperative local institution, and that probably helped explain their high rates of cooperation.¹ The general picture that emerges from this research tradition is that we have evolved (in part through cultural learning) a distinctive set of attitudes towards social interaction, that of "strong reciprocity." Strongly reciprocating agents enter social interactions intending to cooperate if others do, but they are also vengeful if others failure to cooperate (Henrich et al. 2005; Gintis et al. 2008; Bowles and Gintis 2011). We have evolved as a cooperative primate because we have evolved this distinctive psychology.

Stuart West and his allies regard this approach as confused, because it fails to distinguish questions about the acquisition and expression of cooperative dispositions from questions about the selective benefit of those dispositions² (see, e.g., West et al. 2007, 2011; Gardner 2009; Scott-Phillips et al. 2011). To the extent that the anthropological and experimental work on cooperation is sound, it should be seen as a contribution to proximate biology. Perhaps

¹ "The Orma, for example, immediately recognized that the PGG was similar to the harambee, a locally initiated contribution that Orma house-holds make when their community decides to pursue a public good, such as constructing a road or school. They dubbed the experiment 'the harambee game' and contributed generously (mean 58 % with 25 % full contributors)" (p. 811).

² They are also somewhat skeptical of the empirical foundations of work on strong reciprocity and cultural group selection.

prosocial emotions and social learning have an important role in explaining, say, cooperative responses in public goods games. Likewise, the psychological dispositions to acquire and act on norms may be part of the explanation of why the Orma cooperate in such games. But that tells us nothing about the *fitness consequences* of their cooperation (or of similar episodes of cooperation in human history), and hence tells us nothing about the evolution of the psychological dispositions that are triggered in the public goods experiments. Only explanations that identify the fitness consequences of such dispositions can explain their evolutionary origin and function.

West and his colleagues have a framework for specifying those fitness consequences. Instead of seeing human cooperation as distinctive, or needing special explanation, West and his colleagues attempt to incorporate it within their general framework: a heuristic of modeling agents as maximizers of inclusive fitness. They argue that cooperation evolves through a mix of direct and inclusive fitness effects. Indirect effects tend to be important in poster cases of cooperation; systems in which we see high levels of individually costly cooperative behavior (clonal groups and eusocial insect colonies). Such systems are skewed towards one end of a spectrum of cases, an end in which within-collective competition has largely disappeared, and the evolutionary dynamic depends on indirect effects. Cooperation between unrelated agents cannot evolve if direct costs exceed direct benefits: all parties must get direct benefits (as in cleaner fish-client interactions and the like). It is a mistake to see explanations that appeal to strong reciprocity as a potential replacement for kin-selective explanations of cooperation; if they add anything to a theory of human cooperation, it is by revealing the proximate mechanisms that generate cooperative acts.

This picture of the evolution of cooperation, and the division of labor between proximate and ultimate projects, is too simple. Proximate biology is crucial to an evolutionary explanation of human cooperation in three ways. First, in contributing to an explanation of the supply of variation to selection; second, in contributing to an explanation of trait heritability; third, in contributing to an explanation of the stability of cooperation through the Pleistocene–Holocene transition. While it is likely that the ecological, informational, and reproductive cooperation that characterized human life originated and spread because of the direct fitness benefits that accrued to cooperation (Sterelny 2007a, 2012a; Tomasello et al. 2012), its stability probably cannot be explained by those benefits after the Pleistocene–Holocene transition. Adaptation has limits, and those limits are relevant to the persistence of cooperation despite changes in the selective environment. We cannot usefully model Holocene humans as inclusive fitness maximizers. To put the point differently: the “phenotypic

gambit”—treating agents as fitness maximizers—has boundaries, and explaining those boundaries is part of the project of evolutionary biology, a project in which proximate considerations play a critical role. Let me briefly develop these ideas.

The Relevance of Proximate Biology to Evolutionary Explanation

Proximate Biology and the Supply of Variation

Evolutionary trajectories depend on fitness. But even setting aside the role of chance, that is not all they depend on. For evolutionary trajectories depend as well on the supply of variation at a time and over time. The cognitive and motivational factors that West and his colleagues exile to proximate biology are central to evolutionary explanations via their effects on the supply of variation. The limits of the proximate-ultimate conceptual framework are exposed when we consider cases where there is interaction between individual phenotypic plasticity, the supply of variation and evolutionary change. Such interactions are not rare. West-Eberhard (2003) argues that many evolutionary changes begin as manifestations of individual adaptive plasticity, as individuals adapt to a changed environment. Cane toads invade, and while some local predators die from their poison, others survive and acquire an aversion. If the environmental change is both important and long lasting, genetic accommodation takes place. Responses that were once the result of mechanisms of plasticity become modified or modulated by genetic change: there is selection on existing or newly arising genetic variations that accelerate aversion learning, or which reduce its costs.

Avital and Jablonka (2000) argue convincingly that this interaction between individual adaptive plasticity and genetic accommodation is especially important in the evolution of behavioral novelties, for initial innovations cause changes in foraging patterns and social interaction which in turn stabilize the innovation (Jablonka and Lamb 2005). Think, for example, of the establishment of stone tool making and use in early hominins, or the domestication of wild fire by Middle Pleistocene humans. Very likely, early innovations were improbable accidents, and the skills those accidents established were easily lost. But the use of stone tools could and did give early hominins access to new and important resources such as the marrow in large carcasses, often inaccessible to other scavengers. Once that opportunity was taken, stone tool use became a regular rather than an occasional activity, and once it was regular, in their ordinary trial-and-error exploration, juveniles would have had many opportunities to experiment

with stones and what they could do.³ A low-probability innovation becomes a routine, high-probability result of trial and error in a biased environment, one with many opportunities for rewarding trials. Once toolmaking and use became a central and enduring feature of the hominin way of life, selection pressures changed, with selection for genetic variation that enhanced tool-using skills and that accelerated our capacity to acquire them. Our minds and bodies are now adapted to use tools, and to learn to use tools (Ambrose 2001, 2010; Stout and Chaminade 2009; Stout 2011).

A similar scenario may well explain the expansion of cooperation early in the hominin lineage, as climate change exposed hominins to more seasonal and more vulnerable habitats. Groups who had individuals within them who could react by learning to cooperate better would have better prospects as individuals and as groups. Successful cooperation makes future cooperation more likely, just through associative learning. Critically (if baboons are any guide) the young of groups born into a more tolerant, less conflicted social environment themselves develop with more tolerant phenotypes (Sapolsky and Share 2004; Sapolsky 2006). Cooperation can be partially stabilized through mechanisms of learning and developmental plasticity (Sterelny 2012c) thus changing the environment in ways that would then select for genetic predispositions for tolerance and cooperation (Hare et al. 2007). Interim conclusion: to the extent that the evolution of behavioral capacities depends on initial individual plasticity and on mechanisms of social learning and cultural transmission, there is no clear separation of ultimate and proximate factors.

Proximate Biology and Trait Heritability

Scott-Phillips et al. (2011) argue that culture and cultural learning are important features of human proximate biology, for it is indeed true and important that many human traits develop as they do in part through social learning, especially socially learning from the previous generation. But these developmental facts are no part of an explanation of the evolved function of a trait. The fact that humans learn and act on norms tells us nothing about *why* we act on those norms. To answer the *why* question we need an

account of norms' effects on agent fitness. So while cultural learning is important, it is important only as part of proximate biology.

It is true that the effects of norm learning on fitness must be part of an evolutionary explanation of norm-guided action. But the fact that norms are learned culturally is *also* a key part of such an explanation. For selection drives evolutionary change by acting on *heritable differences* that cause fitness differences. Suppose it is true that a hunter's sharing large kills increases his fitness both directly through reciprocation and indirectly through kin-selected effects. These fitness effects would not by themselves explain why such sharing was common. For a trait to spread and stabilize through selection, it must both have positive effects on fitness *and* be heritable. Cultural learning helps explain why a whole raft of developmentally plastic traits are nonetheless selectable, and hence are candidates for selective amplification, modification, or suppression. Moreover, once high fidelity cultural learning together with selection makes a trait—a skill, for example—common in the population, near-neighbors of that skill become more likely to appear through a fortunate innovation. For example, Lombard and Phillipson (2010) show how the invention of bow and arrow technology was probably scaffolded by the prior invention of snares and bow drills. The invention, transmission, and amplification of these technologies thus seeded a late Middle Stone Age African culture with the crucial components from which bows could be built.

More controversially, cultural transmission can change the level at which selection acts from individuals to groups. When cultural transmission is vertical, it can support and sustain fitness differences within a local group. But with other transmission patterns, cultural learning acts as a homogenizing force. If social learning is strongly conformist, agents have a strong tendency to adopt the majority practices of their local community. Under those circumstances, social learning generates within-group homogeneity and between-group heterogeneity (Henrich and Boyd 1998). Other patterns of social learning can have the same effect. In particular, if intergeneration transmission is one-to-many, oblique transmission, with only a few high-profile individuals of generation N serving as models for most of generation N + 1, social learning will also homogenize learned behaviors within the group (Shennan 2002, 2008). These are the conditions under which group selection is powerful.

So when social learning is homogenizing, and when socially learned traits are differentially relevant to the survival or prosperity of the groups that manifest them, social learning makes possible a form of group selection that does not reduce to a special case of kin selection. West et al. (2011) are skeptical of this claim, noting that the mere

³ Restructuring juvenile learning environments as a by-product of a change in adult life ways might well be sufficient to stabilize a new skill. But young hominins certainly had some capacity to supplement trial-and-error learning with social learning as well: great ape capacity to learn by accurate imitation is at best limited, but they certainly can and do learn something by observing others; they can learn that stone is a resource that can be used to break into (say) a large bone, even if they cannot learn by observation just how the trick is done. Sterelny (2012) shows how this model of social learning is supported by the human archaeological record.

existence of competition between groups does not imply that group level adaptations evolve. They then claim that “while it is often argued that the group is a fundamental unit of cultural evolution, or that group selection is a group-level process ... there is no formal basis for this” (p. 248). But this line of thought depends on their very specific conception of a formal basis of a Darwinian theory. As West and his colleagues see it, a formalized evolutionary theory is the mathematical representation of agents as maximizers or optimizers. In their preferred framework, adaptive design is inclusive fitness maximization (Grafen 2007; Gardner 2009).

However, there is an alternative general formulation of Darwinism (dating most famously from Lewontin 1970) that explicitly distinguishes between the project of characterizing the minimal conditions for a selective regime, and the conditions under which selection acts as a powerful maximizing engine. Godfrey-Smith (2009) has recently extended and developed this framework (see also Okasha 2006). Godfrey-Smith distinguishes between minimal and paradigm Darwinian populations. A paradigm Darwinian population is one meeting the conditions that make it possible for natural selection to act as a powerful transforming force. In such populations, we may well be able to usefully model agents as inclusive fitness maximizers. But satisfying these conditions is a matter of degree. It is unlikely that locally homogenizing cultural learning produces a metapopulation of groups that constitutes a paradigm Darwinian population. So these groups are not plausibly seen as optimized for group competition. But it is likely that they meet the minimal conditions: there will be some sorting and change as a result of group-level processes (Richerson and Boyd 1999). So a second interim conclusion: the capacity to learn culturally is indeed a feature of the proximate psychology of agents. But it is still relevant to evolutionary, adaptive explanations, because cultural learning can make traits heritable, hence selectable, at the level of both individuals and groups.

Cultural Learning, Population Structure, and the Limits of Adaptive Design

A bird deciding how many eggs to lay in her nest, or whether she should attempt a second clutch in a good season, faces a difficult trade-off choice. She must strike a suitable balance between egg number and her own condition (hence her capacity to brood and provision) and between current and future reproduction. But while in most cases, breeding birds manage these trade-offs rather well, no one supposes that individual birds do much calculating. Rather, evolution has wired into them a sensitivity to a variety of internal and external cues, and as a result of this sensitivity, they approximate a wise trade-off between

competing demands. Intelligent fine-tuning is the result of many generations of sorting in (say) robin populations, not individual robin calculation. As a consequence, we expect robins and other birds to manage these trade-offs well only in environments that resemble those of their selective history.

Humans face trade-offs that are at least as informationally challenging as those of the robin, and yet human behavioral ecologists suppose that humans manage these trade-offs in novel environments; for example, while engaged in turtle hunting with the aid of motorized boats (Bird and Smith 2005). Human behavioral ecologists (like ornithologists) explicitly model the objective costs and payoffs imposed by the environment. But they implicitly suppose that agents have access to information about those costs and benefits, that they can use that information competently, and that they have mechanisms of proximate motivations that track their fitness interests. When these tacit assumptions are approximately satisfied, they are satisfied because mechanisms of cultural learning filter out maladaptive norms, and because they enable groups to accumulate enough information to leverage adaptive behavior (Sterelny 2012b). When all goes well, cultural learning allows humans to make adaptive choices even in response to changing environmental conditions. Thus, as Stephen Shennan points out, forager behavior often approximates that predicted by optimal foraging theory (and when it does not, that is probably because of the limits of those foraging models; Shennan 2002).

However, evolutionary biology aims to provide explanations of maladaptation and imperfect adaptation, not just good design. So, for example, explaining the causes and extent of Polynesian maladaptation to their current environment⁴ is a project in evolutionary biology. The phenotypic gambit has limits, and it is important to explain those limits. In our species, culture is especially central to explaining adaptive limits, for cultural learning also makes maladaptation possible: first, by increasing the heterogeneity of the environment and the rate at which it changes, thus exacerbating the problems of adaptive lag; and second, increasing humans' sensitivity to how others think and act; a sensitivity that increases their vulnerability (Sperber et al. 2010). It is instructive to compare the efficiency of traditional foraging with traditional medicine. When we look at medical practices in traditional societies, the folk do not approximate well-designed inclusive fitness maximizers. Despite a few poster triumphs, most traditional medicine is at best harmless; much of it is much worse than harmless (Edgerton 1992; Sterelny 2007b). Even in contemporary western societies many people waste significant resources on utterly worthless “complementary” medicine. Cultural

⁴ These peoples have often serious obesity-related health problems.

selection is very poor at accumulating medical expertise; because causality is very difficult to recognize; because humans change their environment so much, resulting in hyper-variability in the medically relevant aspects of human environments; and because prestige-biased social transmission heuristics can be exploited by charlatans. Since maladaptation is just as much a target of evolutionary explanation as adaptation, the phenotypic gambit is an important but limited heuristic. Folk medicine is one example, then, of design failure that has an evolutionary explanation: the environment is too noisy and too labile for trial-and-error learning, even supported by cultural amplification, to converge on adaptive response. In the next section, I show that while Pleistocene cooperation was a triumph of adaptive response (and one very likely mediated by learning), early Holocene cooperation was (probably) another example of design failure; the failure being the collapse of the mechanisms that controlled Pleistocene free riding. In the final section, I argue that only an interactive model recognizing the reciprocal causal interactions between proximate and selective factors can explain the limits on adaptive response to the incipient elites of the early Holocene.

Human Cooperation: The Early Holocene Puzzle

There are significant uncertainties about Pleistocene social life, but by the later Pleistocene, humans had become cooperative foragers, extracting with great efficiency a wide array of high-value plant and animal resources from their local environment. By this time, they were masters of a regionally varied and elaborate technology, which they used in combination with a detailed knowledge of their local environment (Foley and Gamble 2009). Local communities cooperated ecologically, reproductively, and informationally (Sterelny 2007a). Simple foraging cultures known from the historical and ethnographic record are remarkably egalitarian, without institutions of political leadership, and without marked, heritable differences in wealth (Boehm 1999; Smith et al. 2010). Very likely, ancient foragers, likewise, were egalitarian (Shultziner et al. 2010).

There is no consensus on the triggers that caused early hominins to evolve a more cooperative form of life than those of the great apes, but once cooperation established, the stability of Pleistocene cooperation is no mystery. There are a cluster of game-theoretical results collectively known as “the folk theorem” (Binmore 1994). These identify the environments that select for cooperation based on reciprocity. Cooperation evolves when there are profits to be had from cooperation, and when the cooperating parties share in those profits. Sharing pays if interactions

are frequent, and when the results can be identified and remembered, so cheats can be exposed; and when cheats can be sanctioned or excluded at costs that are low compared to the profit of cooperation. Pleistocene foragers satisfied these conditions. First: they lived in environments in which cooperation was profitable. Given the limits on their technology, a crucial resource, large game, could be secured only through collective action. The breadth of resources—large game, small game, birds, fish, a great variety of plant food—rewarded specialization and a division of labor: these resources are concentrated in different places; they are best harvested with specialized equipment (some, like fish, absolutely require specialized equipment); they are best harvested with specialized expertise. Think, for example, of the diversity of plants, and the difficulty of identifying many of them (Stiner 2001, 2002). Likewise, Hrdy, Hawkes, and their collaborators have shown that the size, the long immaturity; the metabolic demands; and the physiological stress of childbirth all select for reproductive cooperation (O’Connell et al. 1999; Hawkes 2003; Hrdy 2009).

So there were important gains to be had from cooperation. Moreover, social organization made it easier to realize those gains. Sometimes the benefits of cooperation are delivered immediately, and to all: for example, when the size and cohesion of a group enables it to detect, avoid, or repel a serious predator. But when cooperation is beneficial through reciprocal altruism, as an agent returns a favor with a favor, so that cooperating agents are advantaged by delayed but increased returns, it is of critical importance that groups are small, with repeated interaction, and these were just the groups Pleistocene foragers lived in. Since they lived in such intimate social worlds, detecting free-riding was fairly simple. Of course, deterring free-riding was another matter, especially if it consisted not just of idle free-riding but of active expropriation by dangerous bullies. Conflict always has costs, even if only risk costs, and bullies would often have been the most dangerous individuals in the community. Nonetheless, the intimacy and long mutual history of forager communities would make it possible to coordinate joint action, and reputation in such communities is an important asset. Life prospects often depended on social capital: on an agent’s network of allies and friends (Smith et al. 2010). Thus the costs of control would often have been worth paying, both to protect material and social resources, and as an investment in reputation.

Pleistocene foragers were no communist saints. Their social worlds were probably very violent, with high rates of murder (Seabright 2010). Moreover, if ethnography is any guide, their egalitarianism was policed. Norms against self-aggrandizement were backed by the credible threat of social and physical sanction (Boehm 1999). Nonetheless, the economic, social, and normative traits of the Pleistocene forager

world combined to support a foraging cooperative equilibrium. Foragers cooperated because most of the time, cooperating served their interests well, and evidently so, and this material fact supported, and was supported by, the norms and customs of their lives. Pleistocene cooperation is readily explained as maximizing individual fitness.

Cooperation and respect for the social contract continued through the Holocene. We see this in, for example, Peter Bogucki's survey of the origins of human society. He documents impressive public works (for defense, irrigation, ceremony) through a range of early farming societies. The Holocene brought with it a revolution in human ways of life. In particular, for an increasing fragment of the human population, the transition from the Pleistocene to the Holocene involved an economic revolution: the shift from a life as a mobile forager to life as a sedentary farmer (Bogucki 1999; Bellwood 2004; Cohen 2009). It is not easy to explain the initial attraction of farming to foragers. But once it does establish, it has huge consequences on both the developmental and the selective environment. Farming supports both denser and larger populations.⁵ In turn, size and density allow increased artisan specialization as market size expands. So Holocene worlds were more differentiated. They are less intimate, less informationally transparent, and the expectation of repeated interaction is less secure.

They were also more hierarchical. Success depends most on material resources, most especially fertile land, and such resources can be accumulated and inherited, often resulting in increasing differentiation in wealth as generations turn over (Shenk et al. 2010). Moreover, successful foraging requires foragers to be highly skilled, mobile, opportunistic in decision making, typically dispersed in low densities through considerable space, and often armed. So forager societies are not based on slavery. In contrast, farming societies are often slave-owning societies, because much farming work requires little skill, and the costs of supervision and control are low compared to the profits generated by forced labor (Kaplan et al. 2009). Political inequality grew too. Most forager societies lack political hierarchy: no adult has the acknowledged right to tell other adults what to do, or to make decisions for the group as a whole. Before the establishment of the early states, the archaeological signatures of formal political leadership are more ambiguous (Bogucki 1999). But the first half of the Holocene saw the widespread emergence of chiefdoms and other pre-state political formations.

Farming and its consequences transform the selective environment. In particular, changes in the Holocene

undermine both the objective cost-benefit profile, and the conditions of mutual information that stabilized and rewarded Pleistocene cooperation. The factors that made cooperation typically profitable were undermined through the Holocene. These changes did not take place everywhere, nor all at once. But the Pleistocene stability conditions eroded increasingly, as farming became established in the Middle East, Egypt, East and South East Asia, India, and (later) Central and North America. As social and political hierarchy develops, dealing is less fair: an ever-smaller share of the profits of cooperation flow to those lower in the hierarchy. Farming societies ultimately became extraordinarily unequal (Kaplan et al. 2009).

We are faced with an early to middle Holocene paradox. There are two cooperative equilibria in human social life: the Pleistocene exemplifies one, the egalitarian equilibrium of fair dealing in intimate, transparent, stable worlds. The later Holocene exemplifies the other (Seabright forthcoming). Once states have appeared, with efficient mechanisms of policing and coercion, cooperation by the humble is no mystery. They are making the best of a bad deal. Both equilibria are buffered: the state-based equilibrium by mechanisms of coercion and control; the egalitarian equilibrium by anti-dominance mechanisms of the kind Boehm documents. Yet cooperation persisted, despite elites, in effect, becoming voracious free-riders, enjoying a large part of the benefits of cooperation, while paying few of its costs. The Holocene story is the story of free-rider escape, as the Pleistocene mechanisms of control failed. Perhaps there would be no mystery if the historical record showed rapid, phase-transition flips from one equilibrium to the other (perhaps through external disturbance). But it does not: in many cases, it seems to show an incremental, hill-climbing transition from the egalitarian to the coercive equilibrium,⁶ taking hundreds or thousands of years. That is the puzzle to be explained, and the explanation needs to be robust, not depending on special conditions. For this incremental walk to complexity and hierarchy seems to have occurred independently several times (Bogucki 1999; Cohen 2009).

From Foraging to Farming

I do not think this transition can be explained by modeling early Holocene humans as well-designed fitness maximizers. Instead, we need a framework that recognizes and explains the constraints on optimal response. These constraints flow from the intrinsic features of agents' psychology,

⁵ Most obviously, because resources are tapped into lower in the food web, but also because farmers suppress grain-bearing plants' competitors, so a larger fraction of the total productivity of that trophic level is made available to human consumption.

⁶ And perhaps transitions in the opposite direction too: there is a preliminary analysis of Pacific and South East Asian cultures that suggests that the increase in social complexity is incremental, but complexity can be lost too, and when it is, the decline need not be incremental (Currie et al. 2010).

from increasingly challenging coordination problems, and from an increasingly opaque informational environment. Individual psychology, social life, information flow, metapopulation structure, and the selective environment all interacted. We can explain the stability of cooperation through that transition only by identifying those interactions.

Farming as a Fitness Trap

Once farming is established, farming changes the social environment, and those changes erode the power of anti-dominance coalitions. The trust needed to act in concert against dangerous and powerful individuals depends, to a considerable degree, on face-to-face interactions, and on a history of successful collective action. Community expansion, and the more family-based economy of farming, undermines those factors. So too does the fact that life success in farming cultures depends less on social capital and more on material wealth (Shenk et al. 2010). The esteem of your peers matters less; the extent of your land matters more, and so there is less need to accept the risks of enforcement to secure a good reputation. The price of social disruption may well have increased at around the same time. The archaeology of early farming cultures suggests that intergroup relations were more threatening (Choi and Bowles 2007). If intergroup interactions were truly predatory, there would be strong group-level selection for cohesive groups, even if individual selection favored refuseniks. But the climate of intergroup hostility helps explain why continued cooperation by the poor would often be the least bad choice; they might rationally fear that internal conflict would make them vulnerable to outsiders. Being poor amongst your own is typically better than being a slave (or worse) of the neighboring tribe. If the cost of social disruption was military vulnerability, potential malcontents faced a less favorable risk/benefit tradeoff. In summary, once farming is established, with its economic and demographic consequences, the option of moving away is lost, and elites become more difficult to control. There are objective changes in the costs and benefits of being part of anti-dominance coalitions; changes that make joining those coalitions less attractive to the ideally rational peasant. As we shall see, these changes interacted with changes in the decision-making environment, and with features of agent psychology to further limit the power of anti-dominance strategies.

Boiling the Peasant

I noted above an environment of group-group conflict increases the objective risks of social disruption. But it also militates against social collective decision by consensus. Forager collective decision making is rarely urgent: if the

choice is when and where to move, for example, the time frame of discussion and consensus formation suffices. An environment of intergroup tension and raiding selects for command-and-control coordination. Decisions are urgent and the stakes are high. So group decision making from below becomes more difficult as it becomes more urgent and critical, for farming communities are larger and more dispersed than simple forager bands. Larger, more dispersed communities find bottom-up coordination more difficult. Presumably, consensus-based decision making is still more difficult if the group has lost the cohesion of common interest as incipient elites, their clients, those in the middle, those sinking socially, all interact. But once command-and-control decision-making institutions have established in a group, political elites will be tempted to self-aggrandizing strategies, and the difficulties and costs of control will rise.

In short, once farming establishes, and especially if it establishes in a world of predatory intergroup relations, those outside the elites thus face a difficult decision-making environment. Even if their strategic interests would be served by forming anti-dominance coalitions that expropriate land from incipient elites, recognition of that option, securing trust, and coordinating might well pose intractable problems, problems exacerbated by subjective factors. Prestige-biased (and conformist) cultural learning will make it harder to recognize those interests, as prestige-biased learning will tend to inculcate norms that favor the status quo. The psychology of group identification is likely to make the risks posed by outsiders more salient, those posed by internal elites less salient. Incremental change also makes risks and interests harder to recognize. There is an apocryphal story about frogs: you can boil one without its trying to escape, if the frog is first placed in cold water that is gradually heated. There is no sudden change in temperature to trigger alarm. Likewise, perhaps, the less wealthy were apt to see continued respect for the social contract as their least bad option in part because their relative position declines gradually. Rupturing the social fabric is inevitably costly, risky. If those costs meant that last year accepting an inequitable bargain was the least bad choice, it will seem to be so again this year, for this year the bargain is only a little worse. Very often, there will be no obvious threshold that marks the transition from the tolerable to the rejection point.

Moreover, the transitions to poverty and landlessness will not be synchronized: natural allies will not experience their tipping point, even if it were evident, simultaneously. Trust with those natural allies might be impossible to establish if, as Paul Seabright suggests, the land-poor included slaves secured by collective predation on neighbors (Seabright forthcoming). If so, the choice of the middle to ally up rather than down is still more understandable. There

would then be objective and subjective barriers to trust and coordination between those with only just enough land of their own, and those without enough. In sum, then, the stability of cooperation over the Pleistocene–Holocene transition, prior to the establishment of efficient mechanisms of state coercion, depended on the interaction of changes to individual payoff, increased coordination challenges, and an increasingly opaque decision-making environment.

It is time to summarize the state of play. Mayr's division of labor is sometimes useful. But it is no help when we are interested in explaining the evolution of the social behavior of agents whose developmental trajectory is sensitive to their social environment; who learn from each other; and whose acts, individual and collective, influence both their selective and the developmental environment. Niche construction theory treats these phenomena as critical drivers of evolutionary change, and so offers the right framework for investigating the behavioral evolution of a labile and social species, and one with a heavy environmental footprint. That is especially so when part of the project is to explain the limits of individual adaptation. Human cooperation illustrates both the extraordinary power of selection when culture amplifies the range of traits that become heritable enough for selection to act, but it also illustrates one of the constraints on selection: agents cannot at the same time be optimized for learning from others, and safe from exploitation by others.

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