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SHORT ARTICLE

2 Colloquium on Paul Seabright's The Company of Strangers

- 3 The Three Musketeers: What do We Still Need to Know About Our Passage Through
- 4 Prehistory?
- 5 Paul Seabright
- 6 Received: 12 November 2011 / Accepted: 20 November 2011
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Abstract In this article I pose six questions about the transition from foraging to agriculture. (1) Was Pleistocene life transparent enough for prudent calculation based on self-regarding preferences to support cooperation? (2) How violent was the Pleistocene? (3) Was interaction with strangers frequent or rare? (4) What would have been necessary for a psychology adapted to the Pleistocene to make sense of a much more frequent exposure to strangers in the Holocene? (5) What ensured that when agriculture arrived the social contract did not either (a) collapse or (b) remain sufficiently robust to resist substantial increases in inequality? (6) How does the psychology we inherited from the Pleistocene continue to shape the way we interact with strangers in modern societies?

23 **Keywords** Agricultural transition · Cooperation ·

24 Foraging · Social contract · Violence

Any author is lucky to have readers, but to have three readers as subtle, attentive, and generous as Geoff Brennan (GB), Ben Fraser (BF), and Kim Sterelny (KS) is a privilege indeed. I have learned much from all three of them, both from these pieces and more generally from their other writings and the discussions we have had. I am grateful to

- them for the many generous things they say about *The*
- 32 Company of Strangers (hereafter TCOS), and in particular
- for agreeing that the ease with which we citizens of pros-
- 34 perous modern societies interact with strangers is a puzzle
- 35 given our prehistoric origins. But all three chide me, dip-
- 36 lomatically though firmly, for imprecision about some
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crucial aspects of the transition of humankind from hunting and gathering to modern society, for appealing to metaphors (such as "tunnel vision" and "honorary friends") instead of mechanisms. I think there is much truth in this criticism, and I would like to take this opportunity to say more about what we know—and, crucially, about what we still don't know—about how this transition happened.

To do this I propose not to answer the questions and criticisms of the three commentators point by point. Instead I shall set out six broad questions about the transition, each of which is posed explicitly or implicitly by one or more of these commentators and about which they are right to point out that TCOS does not have enough to say. In some cases this is because the state of our collective knowledge is inadequate, in others because TCOS does not clearly enough reflect that collective knowledge.

These are the questions:

- (1) Was Pleistocene life transparent enough for prudent calculation based on self-regarding preferences to support cooperation via mutual monitoring, punishment of defectors, and incentives for reputation building?
- (2) How violent was the Pleistocene? And how much of this violence was intra-group rather than inter-group?
- (3) Was interaction with strangers frequent or rare?
- (4) What exactly would have been necessary for a psychology adapted to the Pleistocene to make sense of a much more frequent exposure to strangers in the Holocene? Was it just a matter of adjusting to a higher frequency of stranger contact or was it a qualitative shift?
- (5) What ensured that when agriculture arrived the social contract did not either (a) collapse, or (b) remain sufficiently robust to resist substantial increases in inequality?



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(6) In what sense, precisely, does the psychology we inherited from the Pleistocene continue to shape (either in the sense of enabling, or in the sense of constraining) the way we interact with strangers in modern societies?

I consider them now in turn.

How Transparent Was the Pleistocene?

All three of the commentators suggest in their different ways that TCOS underestimates just how much incentive hunter gatherers have to cooperate with each other even without pro-social preferences. This was likely to have occurred through some combination of mutual monitoring and punishment of defectors (GB and KS), desire to establish a reputation so as to be chosen as cooperative partners by other individuals (BF), and the undertaking of costly relationship-specific investments that are a credible commitment to cooperative behavior (GB). Importantly, if this claim is true it makes the transition to modern societies depend not on the presence of pro-social preferences but on the ability of modern societies to mimic the institutional arrangements of the Pleistocene for mutual monitoring, albeit at a vastly larger scale.

Evidence on this question is scarce but I think that what evidence we have points to social preferences being vital for hunter-gatherer cooperation. First of all, modern experimental evidence suggests that social preferences, notably for strong reciprocity, are very widespread in human societies, in the sense that significant proportions of strong reciprocators have been found in groups of experimental subjects drawn from populations all over the world (Bowles and Gintis 2011). Furthermore, it is rare that all individuals in a group are strong reciprocators, suggesting that social preferences exist in stable polymorphism with more standard self-regarding preferences. If social preferences were purely accidental by-products of natural selection and were not subject to selective pressures in their own right, their distribution over human populations would probably be much more variable. This suggests they must have had an adaptive function during prehistory.

In addition it seems unlikely, however well individuals in a forager society knew each other, that they can have engaged in sufficiently transparent mutual surveillance of one another to make redundant any considerations of character and intrinsic trustworthiness. Our practices of discussing others are filled with judgments of character and not simply catalogues of acts and omissions. We routinely try to decide whether others can be trusted in situations where they will not be monitored precisely. It's possible that these are entirely modern cultural practices, but as anyone who has brought up children knows only too well, even in the intense

atmosphere of family life, opportunities for cheating and free-riding are rife, and they go unpunished often enough for the punishments that do happen to be the occasion for endless argument over whether they are justified or not.

KS appears to recognize this when he writes that "small foraging communities are informationally transparent; the local group knows who is reliable and who is not." He does not write that the local group knows always who has cheated and who has not, in which case coordinated retaliation could ensure that the cheaters are always punished. In such circumstances there is no need for anyone to cultivate a reputation for reliability—that is, for not cheating even in circumstances where they would get away with it. It is not even clear how it would be possible to cultivate such a reputation, for in equilibrium no one cheats, whether reliable or not, since cheating is always observed and always punished. For there to have been sufficient selective pressure for the evolution of the capacity to judge character, character must have varied within the population, and this suggests that a stable polymorphism of character types (and ranges of competence for judging character) must have persisted for a long period during prehistory.

If character matters, if individuals differ substantially in the degree of their social preferences, how might these social preferences have evolved? Two broad families of explanation strike me as plausible. One is the idea that selection into cooperative groups (either pairs or more complex coalitions) on the basis of individuals' revealed cooperative character was important in counteracting the adaptive pressures for selfish behavior within such groups. I now think I may have underestimated the importance of this mechanism in TCOS, and BF has encouraged me to think harder about it (I discuss it at length in Seabright 2012a). It's important to note that this could only have worked if indeed there was substantial population variability in character, and if this character could be signaled in such a way as to affect decisions to include individuals within fitness-relevant groups (see Centorrino et al. 2011 for one such mechanism).

A second type of explanation appeals to multi-level selection, and requires there to have been large fitness costs to groups with few cooperators, to counteract the selective pressures against cooperators within groups. One possibility is that groups needed cooperators for fighting other groups (Bowles et al. 2003; Bowles and Choi 2007; Bowles and Gintis 2011). This is where the second question becomes important.

How Violent Was the Pleistocene?

Sam Bowles (2009) has recently estimated a mean rate of violent death among prehistoric foragers of 14 %, over ten times the rate of violent death in the twentyfirst century 170





world as a whole. Furthermore, he argues that much of this came from inter-group violence, and that at this rate there would have been strong pressures for the evolution of substantially altruistic preferences, notably a willingness to risk death for the defense of one's friends. KS is skeptical of this evidence, on two main grounds. First, it may be contaminated by conditions in the Holocene, which he admits to have been highly violent. Secondly, KS argues on a priori grounds that elimination of rival males is a public good from which all rivals benefit and which a good economist should therefore expect to be under-supplied.

I think we can agree that we need more and better archaeological evidence. But there is other indirect evidence that should not be ignored. I hope it does not caricature KS's view to summarize it as the idea that most human beings have no intrinsic motivation to violence ("violence is not the default"); when they do engage in violence they do so in pursuit of some other payoff, typically the theft of goods or land. Space forbids an exhaustive discussion of this here, but let me just note that (a) the highest rates of human violence in almost all societies are not against adults but against infants, who have nothing worth stealing; (b) the greatest violence among forager groups that have been studied tends to occur in raiding, when men collaborate to solve the public goods problem, and when the prize often includes rape and kidnapping of women; (c) reports of aggression being accompanied by male sexual excitement are too frequent to be treated as a minority pathology. I think we don't know enough about the relative strength of the sexual versus the acquisitive motivations for human violence, and I hope that future research will tell us much more. This is important because it affects what was required for initial human contacts between strangers to move towards the largely peaceful default that KS and I agree characterizes the modern world.

Was Interaction with Strangers in the Pleistocene Frequent or Rare?

GB believes I exaggerate the rarity with which foragers in the Pleistocene encountered strangers, and offers as evidence the importance of exchanging marriageable females. He may be right, but we need more evidence than this to settle the question. As with trading links between groups, for which there is evidence long before the Holocene, the issue is not whether foragers regularly encountered people outside their own group. The issue is whether these encounters with outsiders were largely confined to *familiar* outsiders or whether they included frequent meetings with complete strangers. It's quite possible for daughters to be exchanged regularly and repeatedly between geographically separated communities that are well known to each other over many

generations (the cross-cousin marriage system is based on this idea). It may also have happened regularly that trading links between groups made it possible for strangers to be introduced to each other without incident because one would travel in a party composed of the kin of the other. The really startling feature of the modern world that needs explanation is that I can walk out into the street and meet in safety with someone whom I have never seen before, who is not accompanied by a member of my family or a group of my friends. Did that happen in the Pleistocene—often, sometimes, seldom, never? I suspect, and conjectured in TCOS, that the answer is "seldom." But I accept that the evidence either for or against this hypothesis remains slender.

One of the many things I have learned from KS is that over long stretches of evolutionary time, apparently qualitative changes in cultural behavior can result from the accumulation of innumerable marginal changes in behavior that are each so tiny as to be invisible to the generations that undertake them. His book, The Evolved Apprentice (Sterelny 2012), is an eye-opener in that regard, and makes me already regret the confidence with which I assumed in TCOS that the remarkable flourishing of cultural symbolism by Homo sapiens in the last 40,000 years or so must have required significant genetic changes rather than an accumulation of cultural changes on a truly vast scale. (I still think that's plausible, but much less of a certainty than I thought before reading KS.) A similar point could be made about the frequency of meeting true strangers. If it happened at first almost never, then very rarely but with a frequency that increased with glacial slowness over the ages, then it may have required no psychological modification at all for humankind to adapt to the change. People could have told each other stories of the person grandpa befriended when he was a boy, who turned out to be a loyal support when the family needed him years later. The gradual increase in the frequency of such stories over generations might have made each new befriending seem a less hazardous act. Once again, this is something where the current state of our knowledge is seriously incomplete. It is hard to know exactly what evidence might settle the matter. However, if archaeological evidence were found (and it would have to be in Africa) of trade in a sufficiently wide and growing range of objects and foodstuffs dating back over, say, 200,000 years rather than forty or fifty thousand, that might make the gradualist hypothesis seem probable enough to become the default.

A Pleistocene-Adapted Psychology Coping with the Frequency of Meeting Strangers in the Holocene?

If meeting true strangers was no longer a rarity by the late Pleistocene, there is not much of a puzzle left. Given enough





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time, any adaptation can happen by unremarkable degrees. But suppose things were as I have conjectured? Once humanity began to settle down and was forced by sedentarism to face strangers instead of fleeing them, what would our psychology have needed to be able to do to shift gears so fast? First of all, BF is right to point out that strong reciprocity requires not just reacting in kind to the behavior of others but also a willingness to be generous, to make cooperation the default behavior. In a uniformly violent universe, that would not always or even often make sense. So we would need to explain why human psychology had evolved both to treat strangers with intense suspicion, and to be sensitive to small gestures that tipped the balance of advantage in favor of initial cooperation. The former is easy to explain, the latter much less so. The suggestion I make in TCOS—and my commentators are right to complain that it is insufficiently spelled out—is that it was a process of mimicry.

GB is right that honorary friendship in the sense I describe is not real friendship, but that is what mimicry does-it substitutes a simulacrum for the real thing in a context in which being the real thing is no longer strictly necessary. By smiling, making eye contact, avoiding carrying weapons in a threatening posture, I can behave as though I am your friend. If you have not had much prior experience of people who pretend to be your friend and are not, you may fall for the pretense (remember that you will typically be trying to identify me at a distance, and that foragers do not wear glasses). Of course, that may be a trap, but if I have genuinely put down my weapons and approach you over open ground, as only a friend would do, the danger is lessened. And you may not mind the mimicry too much once you discover your mistake, since after all I am not here to usurp your real friends but only to do this strange but ordinary thing: offer you a trade. Nevertheless, GB underestimates, I think, the riskiness of this mimicry when he says that he doubts there were any "deep additional problems in assessing the trustworthiness of strangers," since it has been plausibly argued (Bowles and Choi 2007) that the characteristics of altruism towards in-group members and hostility towards out-group members could have coevolved, each reinforcing the other. The challenge for mimicry would be to trigger the "friend" response in others before the others have properly recognized that we are strangers. But successful mimicry in all species involves challenges of just this kind.

GB's own suggestion that intermarriage might have provided a context for inter-group contact can also be a helpful hint here. Suppose that groups typically exchanged women with other groups they knew. It must often have happened that a group needed to find husbands for its daughters but that its usual sources of husbands had died or migrated away. Making contact with a truly strange group might be a gamble worth making, and groups willing to

engage in cautious dialogue with advancing but friendly strangers would have had an adaptive edge in such circumstances. Cormac McCarthy's novel The Road (2006) makes just such an encounter a pivotal moment in the story, and the reader who has come to share the characters' terror at the prospect of strangers can almost weep in relief at the recognition of a way around their mutual hostility. Intriguingly, suppose even that when such behavior began initially, all the men in the group that offered its daughters would be killed, but the daughters themselves would be incorporated into the victorious group. If the "peaceable" tendencies were influenced by genetic traits inherited via the female genome, the victorious group could become less aggressive and more prone to cooperate in future generations, in spite of the apparent success of its prior aggression.

What began as mimicry would evolve into a kind of symbiosis of roles: those who mastered the psychology of real friendship would benefit from their ability to signal honorary friendship, and vice versa. In order for that to happen, of course, a tipping point had to be reached in which the adaptive benefits from frequent and regular interaction with real strangers were much larger than they had ever been in the Pleistocene.

The Advent of Agriculture

What ensured that when agriculture arrived the social contract did not either (a) collapse, or (b) remain sufficiently robust to resist substantial increases in inequality?

Sterelny (2012) argues that we do not understand how hierarchy emerged in the Holocene, since the evidence suggests that Pleistocene foragers were intensely suspicious of empire builders (Boehm 1999), and until empires were actually built there would not have been the resources to fund the coercion on which the hierarchy of those empires depended (Trigger 2003, p. 265). KS makes the point here too, and I agree that it represents an important lacuna in the story. I (Seabright 2012b) suggest four possible answers:

- (a) that coercion might have been practiced by the threat of exclusion from the community;
- (b) that hierarchical innovations might have succeeded sometimes, and conditions in the Holocene have enabled for the first time groups with agriculture-plushierarchy to outnumber, and thereby outfight, groups based on forager egalitarianism;
- (c) that hierarchy might have appealed to evolved cultural tendencies that normally reinforced forager solidarity (admiration of noble fighters, say), rather as parasites exploit evolved features of their hosts;



I confess to being skeptical about (b) and (c), but I think a combination of (a) and (d) may get us a long way to an explanation. In particular:

The first hierarchies may well have been those in which indigenous farmers lorded it over slaves abducted from rival groups. It would then have been relatively easy to construct institutions of coercion aimed at creating and reinforcing hierarchy among the remaining farmers. Slaves could be offered as an inducement to those individuals who helped the first hierarchs to establish their dominance. This could have tipped the balance for many subordinate males between choosing to join a coalition to restrain an aggrandizer and choosing to join the aggrandizer. (Seabright 2012b)

Such a hypothesis suggests an empirical strategy: look for evidence of slave owning in small communities long before the emergence of large-scale slave-owning societies. We don't have such evidence yet as far as I know, but KS's identification of the problem gives us a good reason to look out for it.

The Psychology We Inherited from the Pleistocene

Finally, in what sense, precisely, does the psychology we inherited from the Pleistocene continue to shape (in the sense of enabling or of constraining) the way we interact with strangers in modern societies?

We do not yet know the answer to this question, but it provides a reason beyond pure scientific curiosity for trying to find answers to the other five. If our reactions to strangers are a relatively unproblematic extension of our reaction to fellow group members in the Pleistocene—a view I reject in TCOS but which has been shown by my commentators to have more life in it than I once thought—then solving the modern problem of cooperation among strangers is a matter of just continuing to build institutions that cement our incentives to cooperate. I have suggested a

somewhat more somber view: Cooperation is shaped by our emotions as well as by our capacity to calculate, and understanding our emotions is as important for cooperation as understanding our cognitive faculties. Our capacity for violence and mistrust may no longer be our default mode but may be easily triggered under conditions that resemble those in which it was our default. Our modern social equilibria could be a lot more fragile than if their foundations were more solidly institutional, since emotions are strange and wayward things. I think it matters which of these views is closer to the truth, and I am immensely grateful to my three commentators for helping to clarify the evidence that might help to establish that truth. I am grateful too, to the way books and their transmission to distant readers provide so gratifying an example of the institutions that transform strangers into at least honorary, and sometimes into very real friends.

References

Boehm C (1999) Hierarchy in the forest: the evolution of egalitarian behavior. Harvard University Press, Cambridge

Bowles S (2009) Did warfare among ancestral hunter-gatherer groups affect the evolution of human social behaviors? Science 324: 1293–1298

Bowles S, Choi J-K (2007) The coevolution of parochial altruism and war. Science 318:636–640

Bowles S, Gintis H (2011) A cooperative species: human reciprocity and its evolution. Princeton University Press, Princeton

Bowles S, Choi J-K, Hopfensitz A (2003) The coevolution of individual behaviors and social institutions. J Theor Biol 223: 135–147

Centorrino S, Djemai E, Hopfensitz A, Milinski M, Seabright P (2011) Smiling is a costly signal of cooperation opportunities: experimental evidence from a trust game. Discussion Paper no. 8374. Centre for Economic Policy Research, London

McCarthy C (2006) The road. Knopf, New York

Seabright P (forthcoming 2012a) The war of the sexes: how conflict and cooperation have shaped men and women from prehistory to the present. Princeton University Press, Princeton

Seabright P (forthcoming 2012b) The birth of hierarchy. In: Calcott B, Fraser B, Joyce R, Sterelny K (eds) Evolution, cooperation, and complexity. MIT Press, Cambridge, MA

Sterelny K (forthcoming 2012) The evolved apprentice. MIT Press, Cambridge, MA

Trigger B (2003) Understanding early civilizations. Cambridge University Press, Cambridge

