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On the Original Contract:
Evolutionary Game Theory and Human Evolution

Abstract

This paper considers whether the available evidence from archeology, biological anthropology, primatology, and comparative gene-sequencing, can test evolutionary game theory models of cooperation as historical hypotheses about the actual course of human prehistory. The examination proceeds on the assumption that cooperation is the product of cultural selection and is not a genetically encoded trait. Nevertheless, we conclude that gene sequence data may yet shed significant light on the evolution of cooperation.

Key words: evolutionary game theory, human prehistory, gene-sequences, lice, ancient DNA, Hadza, chimpanzees

Fehr, Fischbacher and Gächter conclude their paper, “Strong reciprocity, human cooperation, and the enforcement of social norms” thus: Strong reciprocity constitutes a powerful constraint for potential cheaters that *can* generate almost universal cooperation in situations in which purely selfish behavior would cause a complete breakdown of cooperation” (Fehr, Fischbacher and Gächter, 2002, p. 25, italics added). Bryan Skyrms employs the same verb in the conclusion of The Stag Hunt and the Evolution of Social Structure thus:

How much progress have we made in addressing the fundamental question of the social contract: “How *can* you get from the non-cooperative hare hunting equilibrium to the cooperative stag hunting equilibrium?” The outlines of a general answer have begun to emerge. Over time there is some low level of experimentation with stag hunting. Eventually a small group of stag hunters comes to interact largely or exclusively with each other. This *can* come to pass through pure chance and the passage of time in a situation of interaction with

neighbors. Or it *can* happen more rapidly when stag hunters find each other by means of fast interaction dynamics. The small group of stag hunters prospers and *can* spread by reproduction or imitation. This process is facilitated if reproduction or imitation neighborhoods are larger than interaction neighborhoods. As a local culture of stag hunting spreads, it *can* even maintain viability in the unfavorable environment of a large, random mixing population by the device of signaling. (2003, 123, italics added).

In fact we count five *can*'s in this passage. Fehr's and Skyrms' work, and that of the other evolutionary game theories offer the sort of "how possible" explanations that are common in evolutionary biology. In this paper we consider whether their models can be turned into "why necessary" explanations. That is, we ask how one can subject them to enough testing to decide whether they do or do not identify the actual causal forces at work in the emergence of human cooperative institutions.

Of course providing "why necessary" or "how possible" explanations may not be among the aims of evolutionary game theorists at all. There are several potential pay-offs to evolutionary game theory that have little or nothing to do with possible or actual human prehistory. It can for example help explain why there is so much cooperation in contemporary societies across the world, by showing that actual cooperation could be a stable equilibrium. It can help uncover particular mechanisms of reinforcement and punishment that can be employed by institution-designers to maintain cooperation in groups. Evolutionary dynamics can arguably provide better microfoundations for the stability of economic markets than those (if any) provided by rational choice theories. Surely, almost any replicator dynamics will be superior to Walrasian tatonnement. There may be other pay-offs to the how-possible explanations of evolutionary game theory. Indeed, the mere possibility that cooperation emerged in one of the ways evolutionary game theory suggests is actually a historically important achievement for biological science. Until the proof that cooperation, and in particular reciprocal altruism, could have emerged from the interaction of fitness-maximizers, evolutionary biology had only limited influence and application in the social and behavioral sciences. Once the bare possibility of fitness maximizers being selected for cooperation was acknowledged, evolutionary game theory had accomplished more than enough to vindicate itself.

Showing that one of the possibilities it envisioned is actual, is more than can be reasonably required to vindicate its research program. Nevertheless, its strongest vindication would be found in our confidence that human cooperation actually emerged in accordance with the strategies and structures advanced in one or another model evolutionary game theorists have offered. Of course, there are a large number of different games and strategies which have been developed and even tested among university students and people across a range of cultures (see for instance, Henrich et al 2004). Since many of these games have incompatible pay-off matrices, varying numbers of rounds of play, different choice strategies, and a variety of learning rules for changing strategies throughout the game's rounds, they cannot all be vindicated by evidence about human prehistory. But they could all be falsified by it.

1. Avoiding Panglossianism

It is tempting to argue that there is not much point questioning whether any model from evolutionary game theory, or some core shared by all models identifies the actual selective route for the evolution of cooperation. To begin with, the exercise might be deemed pointless owing to the fact that behavior is not among the hard parts left in the fossil record. Thus, there is no evidence that could possibly shed light on the actual course of cooperation in our prehistory.

A related but slightly less complacent argument concludes not that the task is impossible but that it is unnecessary. This argument begins with the observation that cooperation is ubiquitous among human societies even though the practice seems vulnerable at least in the short run to free-riders. So, cooperation must have been the best or even the sole satisfactory solution to a major design problem that all individuals, lineages and/or groups faced. In this respect, cooperation is like sex: the fitness cost to the selfish gene is so high, that there must be a very large design problem which sex solves for the selfish gene. If cooperation is ubiquitous and (like sex) apparently costly, then it had to be the result of natural selection, whether operating on strategies genetically or culturally transmitted. Thus, it might be inferred, one or another of the models evolutionary game theorists could advance must be right. The demonstration that cooperation could have emerged in one or more of the ways evolutionary game theory

describes is by itself sufficient to give us confidence that this is the way it actually happened, or at least as much confidence as many biologists have in their explanations for the appearance and persistence of many other animal traits that would leave no impressions in the muck of a river bed.

The conclusion that cooperation must have an adaptive function is overly complacent. It is generally a useful heuristic to assume that if an apparently costly trait, such as sex or cooperation, is widespread, then it most likely has some undiscovered adaptive function. However, to leave things there would be overly Panglossian.

Still another argument against bothering to test the theory suggest that we should not do so because the robustness of many of its models is so great that the course of evolution must have fallen somewhere within the parameters of the models. Consider the strong altruism models of Fehr and others, in which free-riding is punished even though punishment imposes costs on punishers, or Axelrod's nice, forgiving and clear Tit-for-Tat strategy, or again Skyrms' model of the imitation-structured stag-hunt. The three models are compatible, and for all we know the behavior of agents could have realized all three at various times and places in ways that selected for whatever it is about humans that leads them to employ these strategies. However, we know that in each and every one of these models the cooperative outcome is sensitive, sometimes extremely sensitive to even small changes in their parameters: the magnitude of benefits and costs, and other parameters that govern strategies, the rate of switching between them, which strategies are in play, how many iterations of a game agents play, and of course the rate of correlation between agents and/or the strategies they play. Is there independent reason to suppose that during the actual course of human evolution, all of the values for at least some of the models were satisfied for long enough to result in the cooperative outcome? Can common sense or biological anthropology provide this sort assurance? We suspect that at least some consumers, if not the producers, of these models will consider that the values employed to model paths towards cooperative outcomes are prima facie reasonable, just because they don't look like they were chosen with an eye to making the numbers come out right. Thus consider the pay-off matrix Skyrms has employed to get the stag hunt/hare hunt game started: the pay-off to successfully hunting stag cooperatively is 4, while the pay-off to successful hunting rabbit alone is 3. Surely this

seems a small enough difference for one to be confident that something no worse, from the point of view of cooperation, actually obtained in prehistory. But of course, as Skyrms himself notes (2004, chapter 3), it is easy to vary the values of the parameters and variables of these models in ways that produce non-cooperative equilibria. And arguments can be advanced for the plausibility of these values. Much the same can be said of Fehr's strong altruism models. Similarly, as Binmore (1994, p. 317, 320-23) notes, Axelrod's tit-for-tat has been tested against only a small number of competing strategies.

These three arguments for not actually subjecting historical hypotheses that emerge from the models of evolutionary game theory to some sort of test are all seriously vulnerable to the charge of Panglossian adaptationalism at its worst. But are these models really without testable implications for the record of human prehistory? Quite to the contrary, we suggest that there is much evidence which bears on them, and not all of it favorable. The next section of this paper describes considerable indirect evidence supplied by archeology, anthropology and primatology which renders some accounts of human prehistory more plausible than others. Furthermore, as we argue in the two subsequent sections, even more detailed data about the origins of cooperative behavior among our hominid ancestors might be extractable from the one place we have only begun to be able to explore: the human genome.

2. Evaluating the evidence from archeology, anthropology and primatology.

The applicability of at least some of evolutionary game theory's models could be supported by consilience with the orthodox account of the role cooperative hunting in long term human evolution. If big-game hunting characterized human and hominid life for long periods—say a million years-- before the present, archeological data about what game was killed, how it was killed and transported, prepared, shared and consumed, could shed light on the models of evolutionary game theory. Such a program of testing seems particularly to be suggested by models like Skyrms' stag hunt. The orthodox narrative of the role of big-game hunting as the crucial variable in human social evolution is associated with Washburn (Washburn and Devore, 1961): Climatic changes from the Tertiary period onward increased dryness and thus reduced the availability of plant-food

on the savannah, while increasing the density of large herbivores. This ecological change selected for hominid hunting especially in seasons when plant-food was unavailable. Large animal hunting selects for intelligence, weapons, and larger brains. Selection for larger brains, and so bigger crania, in turn, selects for shortened pregnancy (to allow the head to pass through the birth canal), and thus longer infant dependency, and a more sedentary female child care-plant-food gathering strategy, in short the sexual division of labor. Of course the longer childhood allowed for more (social) learning. The evidence for this scenario is largely archeological and dates from about 2 million years ago forward: the co-presence of simple stone cutting tools and large animal bone-remains (with hammer marks and cut marks from butchery and marrow extraction) at central camp locations which were identified by exponents of the Washburn hypothesis as ancient “living floors” (Leakey, 1971)--locations to which game too large for any one hunter to move--was cooperatively transported for butchering and sharing. The northern location of some of these sites could not have been inhabited, during winter months especially, without substantial meat-eating. Under these circumstances, and especially owing to the need for cooperation among several males in “stag-hunting”, there surely must have been strong selection for cooperation. What is needed to measure the force of selection for cooperation are estimates of the respective pay-offs in these settings of team vs. individual hunting.

However the forty year long consensus on the role of big-game hunting as the driver of human evolution, and the consequent selective pressure for cooperation has been called into question over the last decade. Two sources of non-archeological data are especially important: ethological observations of non-human primates (particularly chimpanzees) and foraging studies on isolated contemporary human societies still living as hunter gatherers (O’Connell, et al 2002). Conclusions drawn from these findings allow meat-provisioning several of the selective effects Washburn et al accord it, but not selection for cooperation. In fact, these studies accord big-game hunting an ecological role which does not select for cooperation or even needed caloric/protein provisioning at all, but something quite different, and incompatible with cooperation.

Observations of chimpanzee groups over the past 30 years reveal surprising findings about the foraging habits of this species, once thought to be exclusive

herbivores. Chimpanzees consume a considerable quantity of meat. For example, one community at Gombe National Park consumes over a ton of animal protein per year, rivaling some human societies (Stanford, 1999). In certain chimpanzee populations hunting involves a division of labor. For example, in the Tia National Forest some chimps act as drivers, pushing monkeys towards other chimpanzees who have climbed into the treetops to intercept them (Boesh, 1994). Once a kill is made monkey meat is shared among all members of the hunting party. Interestingly, however, this practice is not universal. At Gombe the hunt is more frenzied. Individuals are focused on the same goal of capturing prey, which is then shared nepotistically among close relatives and allies (Nishida et al, 1992). These differences suggest that hunting strategies vary among chimpanzee cultures (a point we return to below). Even more interesting, the amount of energy an individual hunter expends far exceeds his caloric return (Stanford, 1999). Chimpanzees usually hunt colobus monkeys - prey items weighing typically less than one kilogram - which are shared among up to twenty hunters, many of whom receive mere scraps. These are not the sorts of payoffs envisioned by the Stag Hunt model. It is as if chimpanzees are cooperating in order obtain rabbit, not stag, and this fact is especially perplexing given that chimpanzees have no apparent nutritional need for animal protein. Larger apes, like gorillas and orangutans, manage just fine without exploiting this available resource.

Findings such as these suggest to some primatologists that the function of hunting is primarily social in nature. Male chimpanzees engage in the hunt in order to reinforce dominance relationships, and females treat hunting prowess as an honest signal of a male's fitness (Stanford, 1999). This hypothesis gains support from the ritualized nature of meat sharing. Unlike other carnivores, who consume their kill immediately on the spot where it was landed, chimpanzees often transport their prey to a location distant from where it was caught and engage in a prolonged period of ritualized distribution. During this time dominant males carefully doll out scraps of meat to subordinates who engage in a characteristic "open handed" begging behavior. Meat theft is tolerated in accordance with an individual's social status. No less significantly, male chimpanzees will sometimes offer bits of meat to sexually receptive females in exchange for mating opportunities (Stanford, 1999). Thus, evidence from our closest living relatives suggests

that hunting has a competitive, not a cooperative function: as a venue for reinforcing dominance relationships and, ultimately, as a strategy for evaluating and obtaining mates.

A similar argument has recently been put forward to challenge the traditional Washburn hypothesis that big game hunting was the driving evolutionary force behind human cooperation. There is substantial evidence from the Hadza (of South Africa) and from other hunter-gatherer groups that successful hunting's evolutionary pay-off is by and large reproductive opportunities with females bearing fitter genes - much as seems to be the case in chimpanzees. If so, then not only is there no scope for reciprocal altruism with or without punishment, or other forms of cooperation in hunting. Rather there will have been some selection against cooperative hunting since it reduces the signaling clarity of successful hunting.

To begin with, anthropological evidence from the Hadza suggests that the acquisition of meat, hunted or scavenged, is a nutritionally poor strategy. Hawkes *et. al.* (1991) report that over a seven week period in the dry season of 1985, during which they acquired over 30 large animal meat sources providing more than a kilogram/consumer-day, the fifty members of her study group lost weight. Without access to non-meat resources, they would not have been able to remain in the habitat. In fact, in other studies Hawkes (1997) reports that there was no weight loss among these groups when large animal acquisition rates were lower!¹

¹ While these results are suggestive, the extent to which they undermine the traditional Washburn hypothesis remains unclear. Although meat represents a minimal proportion of a hunter gatherer's average caloric intake, perhaps this resource becomes indispensable during leaner times. Under drought conditions, for example, floral resources become scarce and competition for them intensifies. Perhaps big game hunting was a backup strategy our ancestors used when times got tough - without it, they might not have been able to survive at all. Moreover, paleoclimatological evidence suggests that our ancestors faced regular periods of drought from the past 500,000 years onward (Calvin, 2002). If drought conditions were sufficiently frequent --occurring every generation or two--and if meat consumption became imperative during these spells, there could have been sufficient selective pressure to sustain big game hunting and, possibly,

Hawkes' study suggests we look for alternative benefits, besides nutritional value alone, which might be associated with big game hunting. A further series of anthropological observations suggests that the provisioning of meat plays an important role in sexual selection - analogous to the role it seems to play in chimpanzees. As Deacon (1997) points out, the caloric demands on a female are at their highest precisely when she is least able to attain food from gathering - during pregnancy and while weaning offspring. If females become partly dependent on male provisioning during these crucial periods, there will be sexual selection on a male's provisioning ability. In turn, we would expect increased competition among males for their ability to provision and thereby gain access to mates. Interestingly, however, observations of Hadza meat sharing reveals that a) successful hunters simply bring their prey to a central place where it is shared among all members of the group and not controlled by the successful hunter, b) successful hunters do not regularly retain more of their prey for themselves and their families than other members of the group, c) persistently unsuccessful hunters do not secure a smaller quantity of meat, nor do successful ones keep track of one another's provisioning of meat for the group, and d) there is no quid pro quo exchange of meat for, for example, sexual access. What this suggests to biological anthropologists is the general reputational effects for the successful hunter who provisions meat to all comers "without any strings" confers greater fitness on him than a more direct provisioning strategy.²

cooperation. Thus, the fact that Hawkes' subjects lost weight during a period of drought, even though meat consumption was relatively high, does not undermine the significance of hunting over the long run. The important question to ask is, how much weight would these individuals have lost had there been no big game to fall back on.

² In fact, as Fehr and Fischbacher note,

Costly signaling theory also provides a reputation-based ultimate [i.e. adaptational] explanation for altruistic behavior. According to this approach, individuals signal favorable, yet unobservable, traits with altruistic acts, rendering them preferred mating partners or helping with the recruitment of coalition

Among the Hadza when big game is brought in, it takes on the character of a public good, as there is no exclusion, and individuals can consume as much as they want, regardless of their contribution to provision of the good.³ There is thus sufficient

partners in conflicts. The assumption behind this theory is that individuals with better traits have lower marginal signaling costs, that is lower costs of altruistic acts. Thus, those who do signal have better traits on average. The advantage of this approach is that it could, in principle, explain contributions to n-person public goods. The weakness is that the signal of unobservable traits need not occur by altruistic acts but can also take other forms. The approach, therefore, generates multiple equilibria, some equilibria, signaling occurs via altruistic behavior; in others, signaling does not involve any altruistic acts. Therefore the theory has difficulty explaining human altruism unless it is supplemented by some other mechanisms. One such mechanism might be cultural group selection. If groups where signaling takes place via altruistic behavior have better survival prospects, selection between groups favors those groups which have settled at a pro-social within group equilibrium. (Fehr and Fischbacher, 2003. p. 789)

³ Thus, O'Connell *et al* suggests the following non-cooperative meat-provisioning strategy as more likely than cooperative hunting:

As in East Africa today, carnivore calls and circling birds would have altered early humans to the death of a large ungulate in the neighborhood. Many would have been drawn to the scene, anticipating the change to eat meat. But displacing the initial predators would have been difficult. Modern Hadza (men, women, and children included) react to these opportunities with great alacrity, confident that the armed hunters among them will quickly eliminate the competition. For early humans, the absence of projectile weaponry and potential presence of more and larger predators would have made the odds less favorable and the exercise itself more dangerous. But the very danger and the presence of a large audience would also have created a sometimes irresistible opportunity for males to display their qualities as desirable allies and dangerous competitors. Depending on the size, number and hunger of the carnivores present, the size of

controversy about the adaptive function of hunter-gatherer big-game hunting that we can hardly be confident that human cooperation did in fact emerge in one of the ways outlined by the available models. Whether we model cooperative hunting as an iterated prisoners dilemma (with or without secondary reinforcement, punishment or what Fehr calls strong altruism) or as a stag-hunt, the prospect that hunting in the pre-Holocene was either solitary, or communal but competitive, makes the inference from could have happened this way to probably did happen this way very weak. Much the same can be said for models of fair division, including “cut the cake”, the ultimatum (or dictator) game, and strong altruistic versions of them. These arguments undercut any simple inference from “it could have happened this way” to “it must have happened this way.” Without some positive evidence at least for the approximate truth of the assumptions of one or more of these models, they must be treated as nothing more than suggestive “just-so-stories”, in the dismissive terms of the late Stephen J. Gould.

3. Testing cooperation as an optimal strategy

the carcass, the amount of meat already consumed, and the size and composition of the assembled human group, the contest may well have been protracted. Rock-throwing and/or stick wielding advances would have allowed males to distinguish themselves in a very public manner (Kortlandt, 1980). Where success was achieved, both actors and audience probably joined in consuming the prize, either right on the spot or in some shaded area near by. Increased archaeological evidence of carnivory, particularly involving large-bodied prey, would have been among the results. To the degree scavenging opportunities were differentially and redundantly associated with certain points on the landscape, as they would have been in increasingly patchy Plio-Pleistocene habitats and as they are in Hadza country today, such evidence would have become much more apparent. The sharp trend towards still greater aridity, seasonality, and patchiness after 1.7-1.8 Million years before the present] should have made that record even more prominent, *even in the absence of any real change in degree of reliance on meat* (2002, 861).

Now, we do not hold such stories in quite as much contempt as Gould did, but we do believe that if biology is to offer ultimate explanations, in the sense of Ernst Mayr, it has certain epistemic obligations. In particular it must establish that among the alternative adaptational mechanisms that could have resulted in a particular biological structure, the one offered as actual has some evidential advantage over others, or at least the possibility of securing such an advantage. There are a number of ways evolutionary biologists try to discharge this epistemic obligation. Let's consider whether any of them can be of use in the present connection.

Perhaps the most obvious strategy in converting a just-so-story into a testable and successfully tested hypothesis is one expressed in a slogan due to Elliott Sober (1987): "If optimality explanations are too easy, let's make the problem harder". An adaptational explanation tells us that the trait selected for is the optimal solution to a constrained maximization problem. It is too easy to offer such explanations, just because all the constraints and their dimensions are not known, indeed, most are unknown, so that it is hard to reject the explanation. Therefore, try to measure these constraints and calculate the optimal solution to the maximization problem given those constraints. Economists and linear programmers will recognize this as a version of the simplex problem. Finally compare the calculated optimum to the observed values.

How can this methodology work in the present case? If we could show that in the relevant environment, cooperative large-game hunting optimizes the net per hour calorie gain, compared to other strategies, there would be strong evidence that cooperation was selected for. If we could only show that large-game hunting, with or without cooperation, maximizes net per hour calorie gain, the evidence would be somewhat less decisive but still helpful in converting a just-so-story into a testable and partially confirmed hypothesis. What would the relevant environment be, and what would the competing strategies have to be, for this outcome to substantiate one or more evolutionary game theory models of selection for cooperative hunting? Well, the environment would presumably have to be the pre-Holocene sub-Saharan African savannah in which African eue and her forbearers lived; the obvious alternative strategies of calorie-gain are scavenging, small game (i.e. "rabbit" instead of "stag") hunting and vegetable-gathering. To the degree the contemporary sub-Saharan African environments of contemporary

hunter-gatherer groups provides the same constraints on their calorie-gain strategies that the environment of our prehistoric ancestors did, it represents an accessible evidential base to test hypotheses about optimal strategies. And of course the actual calorie-gain choices of the members of surviving hunter-gather groups in these regions may enable us to choose between alternative optimization-hypotheses. Of course contemporary hunter-gatherers are an imperfect source of evidence about our pre-Holocene ancestors. After all, they are our contemporaries and are influenced by their access to non-hunter-gatherer societies. But observing their behavior is the best we can do. Let us postpone for the moment whether it is good enough.

What does the evidence show about the optimal net calorie gain of strategies available among hunter-gatherers in contemporary African savanna environments? Alas, the evidence not only doesn't make us very confident that cooperation had to emerge the way evolutionary game theory models suggest. It does not even strongly suggest that hunting was selected for as a nutritional strategy at all. Take the case of Skyrms' stag-hunt. Here we'd like to know in particular if the ratio of the pay-off from successful cooperative hunting to the payoff from successful solo rabbit hunting is 4:3 or better. But research in biological anthropology suggests that the actual ratio may not even be in the required direction, let alone of the magnitude the model requires for the evolutionary dynamics to produce cooperative hunting. It appears that individual gathering of the sort women undertake (owing to their child rearing responsibilities) produces more calories more reliably than large-game hunting by their male mates. Consider the following data, reproduced from Hawkes *et al* (2001), comparing caloric intake among the Hadza (see Table 1).

Table 1.

	Acquisition rate in kilo-cal/hr. (avg.)	Provision per household (avg.)	Days between successful "kill"
Resource			
Big Game	1659	120	45
Plant Food	>>1000	>1000	0

The Hadza obtain significantly more calories from plant food, on a more consistent basis, than from big game (reproduced from Hawkes *et al.*, 2001, p. 687).

It is of course open to question whether gathering is a case of rabbit hunting, or more generally, to question the relevance of contemporary hunter-gatherer data or for that matter the data from chimpanzee behavior to the evaluation of hypotheses about pre-Holocene hominid evolution. One thing that must be said for the appropriateness of data from both groups for early evolution is the important similarity between them in respect of mate-competition. Among both the Hadza and chimpanzees, there is intense competition among males for a limited number of paternity opportunities, and there is substantial benefit in reproductive fitness to reputation secured by (individual) hunting success. That these two correlated traits should be homoplasies and not homologies is not something biological anthropology generally accepts. Denying the relevance of either to the test of hypotheses about human evolution would deprive us of most of the obvious sources of testing.

On the other hand, it has been argued that contemporary hunter-gatherers do not reflect formerly widespread adaptations to an environment most of humanity has left behind. Rather they occupy a new niche into which dispossessed third world cultures have been forced over the past several hundred years and bear little resemblance to hunter-gatherers of the pre-Holocene (see Stiles, 2001). It might be the case that the Hadza and other hunter-gatherers are being newly selected for adaptation to a new environment as a result of industrialization and agriculture in the regions from which they have been dispossessed. If so, little can be inferred from their current practices to those of hunter-gatherers who preceded them in Africa or elsewhere. It may be that, even though the Hadza remain relatively untouched by ecological changes due to industrialization and agriculture, that their ancestors long ago changed their own and their descendants' environment so much that nothing can be inferred from their hunting practices to those of their ancestors. There is at least some evidence that human hunters first kill off animals at the very top of the food chains, the other "top-predators" with whom they compete. This is apparently one reason why the western hemisphere is devoid of the largest game animals indigenous to the rest of the world. If attacking such top-predators requires cooperative hunting, then once they disappear, selection for cooperation will have

slackened. Under such circumstances, latter-day hunting strategies will have little bearing on pre-Holocene hunting.

Moreover, we may be taking a model like Skyrms' stag hunt too seriously. After all, perhaps 'stag hunt' is merely a name for a pay-off matrix in which individuals have to choose between cooperative and solo production, and not literally hunting. It is true that the accepted view among biological anthropologists has it that almost everything that is distinctively different between humans and other primates stems from the adoption of hunting as a strategy of protein provision: the large brain, the need for relatively high protein diet to support it, the long period of juvenile dependence due to short gestation (owing to maximum fetal cranium size), its consequent opportunity for learning, longer life-spans, nuclear families, reduced sexual dimorphism, but not necessarily non-kin-cooperation. There are well-known arguments among biological anthropologists which suggest that cooperation emerged first not among male hunters, but among female gatherer, not as a strategy for gathering, but for child-rearing, for protection against males, and most importantly across generations (cf. Hill and Kaplan, 1999; Hawkes *et al.*, 1998). The evolution of this sort of cooperation is less problematic than that among males owing to the scope for kin-selection to generate reciprocity. Why shouldn't women play the stag-hunt first or solely? Perhaps cooperation of the sort the stag-hunt models has its origins much later, perhaps as recently as the Holocene. One reason to think that "stag-hunt" style cooperation must have emerged no later than 10,000 years before the present is that such cooperation is required for agriculture when, but only when agricultural yields are sufficiently modest that rough egalitarianism in resources remains in force.

The shift to agriculture is the result of the domination of hunter-gatherer strategies, and the resulting overpopulation and over-hunting. It constitutes what very quickly becomes a strategy adopted by larger numbers of much less well off individuals. And where it began, in the near east, agricultural irrigation makes almost immediately adaptive a "stag-hunt" style cooperation. Notice that any model that result in egalitarian cooperation ("cut-the cake"-fair division for example) is the solution to a design problem which lasts only as long as agriculture does not produce a storable surplus. But once storable agricultural production arises, the pay-off matrix must cease to be anything like those that preferentially drive the evolutionary dynamics to cooperative egalitarian

equilibrium. For when storable surpluses emerge, unequal shares may all be large enough to make the smallest of them large enough for survival.

If cooperation kicks in only as late as 10,000 years ago, then it seems obvious that its appearance, persistence, and spread must be a matter of cultural and not biological evolution. Consequently, it will be held that seeking biological evidence to shed light on the actual course of the evolution of cooperation would be pointless. This conclusion is further supported by the primatological evidence that different chimpanzee societies have distinct, culturally transmitted hunting strategies. Indeed, even supposing that cooperation did emerge in the pre-Holocene among hunter-gatherers up to 250,000 years ago, there is a very strong temptation to deny that cooperation is a genetically encoded strategy. How could so complicated a strategy as Skyrms' "stag hunt", or Axelrod's "tit-for-tat" or Fehr's "strong altruism" be the result of a disposition recorded in gene sequences! This seems to some no more plausible than supposing chess could be genetically encoded.

Plausible or not, there is substantial evidence in the behavior of vampire bats and guppies that unlearned strategies of cooperation -- reciprocal altruism in the case of bats, tit-for-tat in the case of guppies -- is characteristic of these two species. But surely if unlearned, then there must be behavioral dispositions among these creatures which result from gene-complexes which have been evinced in behavior frequently enough to have been selected for. Still, even assuming that such gene complexes exist in guppies and vampire bats, no one can suppose that cooperation among Homo sapiens owes its proximate causes to a gene sharing a common ancestor with guppy or bat genes coding for cooperative behavior among guppies and bats. For were it to do so, then presumably the gene-complex would also be expressed up and down the phylogenic tree from our common ancestor with bats or guppies: cooperation would be widespread across most mammalian or even vertebrate species.

Of course the evolutionary game theory scenarios for the emergence of human cooperation are not claims about selection for genes encoding strategic choice rules, and their confirmation as why necessary hypotheses, as opposed to how possible hypotheses, does not require any adherence to strong versions of the genetic determination of behavioral dispositions. Thus the evolutionary dynamics that lead to cooperative outcomes in Skyrms' models of cut the cake or the ultimatum game will obtain no matter

whether strategies are transmitted from round to round or generation to generation by inherited genes, or by learning of the later generation from the earlier one. Of course, the more complicated models that involve imitation of the most successful strategies in a neighborhood clearly envision horizontal and oblique transmission of optimal strategies to non-kin. And all the evidence so far discussed will bear on the credibility of the models as scenarios of the actual evolution of cooperation whether it is genetically encoded or culturally transmitted.

4. Human and non-human genomes as a source of evidence for human prehistory.

Does the likelihood that if cooperation evolved, it did so as a culturally transmitted adaptation, instead of a genetically encoded one, make it more or less difficult to secure evidence for its actual evolutionary course? The presumption must surely be that, unlike artifacts, events, behaviors and social institutions in the pre-literate history of human kind leave no hard-parts, fossils, or other trances, and that therefore the answer is that there is only a small likelihood of finding evidence of the emergence of cooperation.

We think this conclusion is seriously premature. There is in fact a large and relatively untapped source of evidence that with ingenuity and good luck may tell us far more than we have learned hitherto about the evolution of cooperation. It is the only one that stands a chance of telling us if any of the models of evolutionary game theory are applicable to trace the evolution of cooperation. The source of data to which we refer is human and other animal gene-sequence data.

But wait. Didn't we just acknowledge that cooperation is almost certainly more the product of cultural than of biological evolution? Yes. So how can gene sequence data shed light on this matter? The way it can do so is better illustrated than described.

One classical problem of biological anthropology is the question of whether Homo sapiens evolved in one place (Africa) and then spread, displacing Homo erectus everywhere else without interbreeding, or whether Homo sapiens is the result of interbreeding everywhere with Homo erectus. The fossil record cannot decide this question, and it long seemed beyond the reach of evidential adjudication. Gene sequencing has changed all this. The African Eve hypothesis, that we are all descendant

from one woman and about a half dozen men living in the Kenya/Tanzania region 144,000 years ago among a very small (5000) population, is strongly supported by data from mitochondrial DNA (inherited only maternally) and by Y-chromosome data (inherited only paternally). Recent work on species of insects has enabled us to determine whether African Eve's descendants interbred with local populations of Homo erectus that preceded them out of Africa. The species in question are members of the head louse family, Pediculus humanus. Lice are highly specialized, they cannot survive more than a few hours without feeding from the bodies they inhabit, but beyond discomfort requiring grooming, head lice do not have significant fitness reducing effects on their hosts. Sequencing the mitochondrial DNA of head lice reveals however that the species consists of two distinct lineages, and further analysis of the amount of sequence difference reveals that these two lineages separated at least 1.8 million years ago, long before the appearance of Homo sapiens. The more widespread of these two lineages is to be found everywhere except the western hemisphere, to which the less frequent of these lineages is restricted. Since head lice move from head to head, the only explanation of this difference is that for a long time the two lineages were reproductively and so genetically isolated from one another, and evolved on distinct populations themselves reproductively and otherwise isolated from one another. The date of the lice-lineage separation matches the best date we have for the last common ancestor of Homo sapiens and Homo erectus: 1.8 million years ago. Had Homo sapiens and Homo erectus occupied the same environment for any length of time, there would have been much more gene flow between two lice lineages than has been detected. The inference drawn by those who have studied this data is that Homo sapiens completely disposed of Homo erectus wherever they found them, and did so in such a way as to allow the lineage of louse which evolved on the latter to switch hosts (Reed et al). The extirpation of Homo erectus has thus left some evidence behind after all.

Here is a more striking example of a relatively recent event in human evolution upon which louse gene sequences shed light: Consider the question of when Homo sapiens began wearing clothes. Not a question archeology can answer to an accuracy of several score thousand years. But a bit of clever gene sequencing seems to have done so. The head louse (Pediculus humanus capitis) lives only on the scalp; the body louse

(Pediculus humanus humanus) cannot live on the head, and needs to secure blood every few hours to survive. But the body louse cannot live on the body. It lives in clothes which cover the body. Employing mitochondrial and nuclear DNA, sequencing the head louse and the body louse genes reveals first, that the body louse evolved from the head louse, and second that it did so about 70,000 years ago. How do we know this? The nucleotide sequence differences between the two species is known, and the amount of nucleotide sequence difference can be compared to differences between sequences of other evolutionary lineages (usually other related species, in this case the chimpanzee louse) whose dates of separation from human lice (via chimp separation from humans) are known, and so provide a “biological clock”. The greater the difference between the nucleotide sequences of different species, the longer the separation between them. The greater the variation within a species, the older the species (since it has had more time to vary by neutral mutation). In this case, the nucleotide sequence differences tell us that since African lice show greatest sequence variation, human lice originated in Africa (as we should expect, since humans originated there as well), and non-African lice variation suggests a global expansion of humans and their lice out of Africa about 100,000 years ago. Moreover, the molecular clock tells us that the time of splitting between the head and body lice species was approximately 72,000 before the present. As the authors of this study report, “These results suggest that clothing was a surprisingly recent innovation in human evolution” (Kittler et al., 2003).

The moral of these two stories is that first, DNA sequence data can shed light on events, states, processes in human prehistory that otherwise leave little or no mark, including ones that are the result of cultural and other non-genetic factors; second, the relevant gene sequences are not always those of Homo sapiens, or even or closest relative, with whom we share over 98 % of our genomes, the Chimpanzee. On the other hand, there are a number of remarkable inferences about human prehistory that have been drawn from sequencing our mitochondrial and Y-chromosome DNA. Among them is the strongly confirmed conclusion that Homo sapiens co-inhabited Europe with Homo Neanderthalis for 30 to 40,000 years without any significant interbreeding between the two groups. This conclusion rests on the development of PCR (polymerase chain reaction) an important tool for amplifying small quantities of DNA into amounts which

can be reliably sequenced. By scraping small quantities of material from Neanderthal bones, extracting minuscule quantities of DNA, amplifying and comparing it to chimpanzee and Homo sapiens DNA it has been established that the probability of gene flow between Neanderthal and Cro-Magnon peoples was extremely low. The relatively narrow variation in mitochondrial and Y-chromosome data also suggests that Homo sapiens went through a narrow evolutionary bottleneck about 150,000 years ago, one which left about 5,000 individuals in the human population. What this near extinction was due to is unknown as yet, but what is striking is that very soon thereafter the modern human's habitat expanded to make it the dominant predator across the entire planet. Another conclusion drawn from sequence data about a still more recent event is that agriculture spread across Europe from the Middle East during the first half of the Holocene largely by the decimation of local populations, and not by imitation or other forms of cultural transmission. We can also date the arrival of Homo sapiens at most locations around the globe, date the independent emergence of most domesticated plants and animals, and determine the major waves of immigration and emigration across the old and new worlds.

The amplification of Neanderthal DNA to make comparisons with other species sequences reflects advances in the study of "ancient DNA", a line of research which in principle can provide sequence evidence going back far earlier than the last common ancestor of humans and chimps. Analysis of ancient DNA is limited only by the availability of DNA molecules (which in crystalline form can remain intact over many millions of years, and limited too by the risks of human experimenter-contamination when it is retrieved.

Could selection operating over the course of the period from just before African Eve and her half dozen Adams to the present result in significant gene sequence differences along lines of descent across a 100,000 years period, and reflected in extant human subpopulations? If the answer is no, then regardless of whether adaptations are encoded and transmitted genetically or not, their emergence and course of evolution will not show up in gene sequence differences. But, at least so far, the answer to this question is yes, local selection among human populations over periods of 100,000 years or less, does show up in gene sequence differences (Kayser et al 2003). This paper shows that

gene sequence differences among isolated human populations are greater than would be expected by drift, mutation, isolation, or other non-selective factors. It does not identify genes which contribute to local adaptations however.

5. Evidence of cooperation from the human genome.

Earlier we suggested that cooperation in humans is unlikely to be a genetically hardwired trait. For one thing, unlike guppies and vampire bats, human cooperation is more sophisticated, more conditionalized, and more domain-general than in either of these species. It seems unlikely that such a complex behavior could be coded in the genes. Secondly, cooperation seems to be too recent to be a genetically encoded behavior that has swept through our gene pool and become fixed. So, one might conclude, if there are no “genes for” cooperation, then human genetics will tell us little about how or when cooperation evolved.

This conclusion may be too hasty.

Begin with the hard data that gene-sequence differences and traditional archeology already provide: cooperation among Homo sapiens is universal, and all extant members of the species are descendants of an African population that was probably no larger than 5,000 or so 144,000 years ago. A body of their descendants left Africa about 80,000 years ago, and made extinct another species of hominid, Homo erectus which had flourished everywhere, but thereafter persisted perhaps only on the island of Flores. That is, across all the ecologies in which Homo erectus had subsisted if not flourished, from the African savannah to the central Asian steppe and the European forests, the Indian subcontinent, Siberia and the far east, as well as the accessible portions of Australasia, Homo sapiens killed them off, out-competed them, excluded from every occupiable niche, without interbreeding, even though archeological evidence shows that the two species cohabitated in Europe at least for 30,000 years. What design problem is to be found in all these niches, and in east Africa as well, that a relatively small and apparently unsuccessful species solved, and another much more populous species did not solve, sometime around or before the moment, 80,000 years ago, when Homo sapiens spread out of east Africa?

The answer that strongly suggests itself is that the design-problem was that of finding means, motive and opportunity reciprocally to cooperate. The design problem of cooperation has several features that scenario above suggests. First, it is a problem that obtains in all the ecologies Homo finds itself in—warm, cold, arid, wet, savannah, forest, steppe. Second, it is one that cannot be solved without those capacities that presumably distinguish Homo sapiens from Homo erectus: for example language and imitation learning. (Here the absence of complex tools among Homo erectus right down to 18,000 years ago provides independent evidence, as we shall see.) Third, there is independent anthropological evidence that Homo did not live in matrilineages that foster extended kin-altruism, but were solitary pairs for much of the preholocene period. For Homo cooperative opportunities would have to be reciprocal, not kin-altruistic (Maryansky and Turner, 1992). Fourth, as noted above, non-kin cooperation must have solved a very big design problem or equivalently, conferred a great adaptation advantage. For it has such substantial and obvious short term costs, that it would not have long persisted without a great pay-off: for example, the ability to exclude another species from every one of the varied niches in which they competed would be such a pay-off. Finally, since reciprocal cooperation among humans is presumably not coded by any genes, it must have spread horizontally, obliquely, and quickly on any evolutionary time scale. Again a solution to a design problem that can spread faster than any gene is just what we need to explain the rapid (50,000 year) spread of Homo sapiens populations into already occupied niches across the whole world.

Thus, we may treat the claim that Homo sapiens success is owing to its having hit upon the solution to the problem of attaining cooperative equilibria in some social interactions as a general hypothesis; and we may treat the models of evolutionary game theory as specifications of the particular structures that arrived at these equilibria. These are admittedly highly speculative hypotheses. Let us turn to the matter of how gene sequence data might test the general hypothesis and its specifications.

Consider the some of the capacities, dispositions, and traits which are required for one or another of the models of evolutionary game theory to obtain as the actual course of cultural evolution of cooperation. Among them are at least emotion—from jealousy and love to shame and guilt, reliable memories about other agents playing iterated games, the

strategies they employed and the game-pay-offs, a theory of (other) mind(s) or at least of goal directed behavior, and language—in which to exchange ex ante plans and ex post analysis of cooperative activities, and imitation learning—if as assumed, cooperation spreads by horizontal, oblique, as well as vertical cultural transmission.

Imitation learning is indispensable to models of the evolution of cooperation such as Skyrms'. For players must detect and imitate successfully strategies of other players, including players with whom one does not interact at all. So, in testing Skyrms' model or any other that depends on imitation-learning, the question arises, how long ago did imitation-learning emerge, and did it do so as a response to the environments' putting a premium on cooperation or some design-problem solution?

One clue that the sort of imitation required for learning appears rather late in hominid evolution is that the earliest date at which composite tools--axes with handles, for example, emerged was 250,000 years ago. For over a million years before that time, hominids were using roughly the same stone axes, their means of manufacture appears to have been repeatedly and independently discovered, it appears to show no cumulated improvement, and not to be widely transmitted. (The recently discovered Homo floresens, a putative member of the Homo erectus but living as late as 18,000 years ago, do not seem to have used composite tools). It's safe to assume that what was lacking was a suite of cognitive and communication capacities needed to preserve and disseminate technological discoveries. Before 250,000 years ago, there is no archeological record of Homo sapiens employing many of the obvious materials from which tools can be made—e.g. bones and antlers—before this date. If, as seems reasonable, the spread of such discoveries requires imitation learning, then we cannot date its emergence much earlier than 250,000 years ago, nor suppose cooperation of the sort which requires it to have appeared earlier.

Consider how selection might have acted on an organism that was capable of a moderate degree of imitation learning. The study of imitation in other primates, especially chimpanzees, is helpful here. What we find is that chimpanzees are relatively poor imitators. For example, when the chimpanzee Kanzi was instructed on how to fashion stone tools, he eventually, with considerable coaching, managed to produce a stone flake sharp enough to cut the string on a box containing a food reward (Mithen,

1996). However, this achievement was dwarfed by the number of details Kanzi failed to glean from his lessons. Kanzi never learned how to discriminate between different striking platforms on a stone to choose one that would produce the most effective cutting surface - his strategy was more to bang stones together until the flakes broke away. Nor did Kanzi manage to control his force in percussion (and this was not due to a lack of dexterity on Kanzi's part, either). It seems prudent to assume that our first tool fashioning ancestors were not much better than Kanzi at learning the subtleties of technique by watching one another. The basic idea of tool use might have gotten across, but many of the details were lost. This has been proposed as an explanation for why there was virtually no technological advances made to the hand axe for a million years, it is unlikely that innovations were not hit upon, the problem was that they failed to be passed along.

Suppose we can locate the suite of genes that subserve our imitation learning abilities, and locate their homologues in chimps, and with a lot of luck in Neanderthals, in ancient Homo sapiens remains in east Africa before and after the bottleneck period, as well as in the newly discovered Homo erectus from Florenes. We can then make sequence comparisons between them, and perhaps even more important, between their introns, promoters, and local non-coding regions. From these differences we may be able to theorize what mutations, translocations, duplications, etc. produced these differences in capacities, and perhaps order these molecular events, and even date the emergence of the capacities to learn and teach by imitation that they serve. We have assumed that non-kin cooperation really does solve a serious design problem that the Homo sapiens lineage solved when competing species did not, and that the solution continued to be selected for in all environments humans came to occupy. If the assumption is correct, there would have been very strong stabilizing selection among the genes which carry traits needed for cooperation, and probably more DNA-sequence stability and less drift than one might find in other genes for other sequences and for homologous sequences among the other species.

But suppose that, as seems overwhelmingly likely, the number of genes and the interactions among them that are necessary for the capacity to learn by imitation, or dispositions that underwrite cooperation and its evolution turns on, is astronomically

large? In that case how can gene-sequencing shed light on the actual course of evolution of cooperation. This question of course presumes a negative answer to a prior question: are the genes that subserve capacities needed for the evolution and persistence of cooperation large in number and complex in interaction? Consider linguistic ability and the ability to attribute strategies to con-specifics (part of a theory of other minds). These two traits arguably necessary for the several of the models of the evolution of cooperation we might seek to test. Although these are almost certainly polygenetic traits, there are well-known genetic defects associated with human incapacities in speech and strategic interaction, and gene sequence differences between us and our closest relatives at these loci. High function autism and Asperger's syndrome prevent normal cooperative behavior, are associated with anatomical and neurological abnormalities in the brain, and (in the case of autism at least) have a substantial hereditary component. There is reason to suppose that autism results from the interactive effects of at least three micro-rearrangements on genes some of which produce a serotonin transporter. These genes are probably located on Chromosomes 7 and 15, and they are implicated in some other rare genetically caused retardation. We know that normal children develop a "theory of mind"—the attribution of intentional states to others between the ages of two and four, and there has been some empirical investigation and good deal of debate about whether the primates show a similar capacity. If the capacity to treat others as having intentional states is one lost in autism (Klin *et. al.*, 2000), then we are on the way to locating the genes that are at least non-trivially necessary for the capacity in humans.

For another example, it has recently been shown that certain significant defects in speech assort in genetically familial patterns, and a technique of genetic localization known as positional cloning has enabled geneticists to locate the particular genes responsible for the defect. Mutatis mutandis, they have located some of the genes whose normal function is necessary for normal speech (Lai, et al 2001). Almost immediately it occurred to the researchers making the discovery of the "gene for" the hereditary speech disorder in question, that genomic comparisons to chimps could reveal important information about the evolution of language-competence, a vital necessity for the emergence of complex cooperative capacities. We know that chimps and gorillas have shown substantial communicative behavior in domestication, and ethological study of

vervet monkeys continues to increase our knowledge of their lexicon well beyond the well-known calls for eagle, leopard and snake. What infrahumans appear to lack is syntactic skills, and these skills are genetically hard wired in us is suggested not just by Chomsky's speculations but by Derrick Bickerton's studies of the transition from pidgins to Creoles (Bickerton, 1998).

Consider the idea that cooperation emerges earliest and differentially among hominid females. Suppose, for example, that reciprocal non-kin cooperation gets its start among females owing to the prior selection for dispositions and capacities which subserve kin-altruism. Selection for such dispositions and capacities among females, combined with neutrality or selection against it among males over a long enough period may be reflected in x-chromosome loci or even dose-dependent expression of genes on x-chromosomes. Such differences may support two quite different scenarios for the evolution of cooperation among males and females, which accord different roles to genetically transmitted and culturally transmitted traits in the emergence of cooperation in males and in females. And these scenarios might leave traces in gene-sequence differences.

Perhaps the genes underlying dispositions necessary for cooperation are not so hard to identify. But we don't need to assume the existence of such 'genes for ___', to show the relevance of DNA sequence data to testing the models in question. All we need is to identify loci that co-vary with these traits and their absence in other species or in Homo sapiens before the putative date cooperation emerged. And the technology to identify these sequences will soon exist. How soon depends in part on the rapidity and the declining costs with which gene-chip technology is improving. Gene-chip or microarray technology can enable the molecular biologist to identify and locate large numbers of DNA sequences whose expression subserves any particular somatic cellular activity and correlate these sets with dysfunctional human disabilities and incapacities, as well as differences between normal humans and our nearest extant relatives, chimpanzees. And this can be done without knowing exactly which genes subserve which capacities, how many do so, or how they do so. What is more, with good luck, it may enable us to pin point differences between DNA sequences known to have a significant role in human capacities and homologous sequences in Neanderthal, ancient Homo

sapiens recent Homo erectus or even older genetic material.

The gene chip, applied to gene expression in heritable human behavioral deficits, and to chimpanzee brain function, enables us to begin to identify sequences which covary with (and so are presumptively distinctively necessary) for the sort of complex behavior that constitutes social cooperation in normal environmental circumstances. These will be ones differentially expressed in the brain compared with other organs, they will be sequences in which there is less intraspecies sequence variation, owing to the pressure of selection for a function both specially restricted to humans, and under tighter selection than the homologous sequence among comparison species. The comparison will have to be three, four or even five way, including gene expression in the normally functioning brain, hereditarily malfunctioning brains, chimp brains, and ancient DNA from Neanderthal, and other Homo erectus remains.

Begin by using a microarray to identify the chromosomal locations of gene sequence differences between the normal and the large range of humans with hereditary neurological malfunctions. Given the location on the normal chromosome of these differences, use the same gene chip method to establish chromosomal locations of the homologous sequences, if any, in chimps. If the sequence is quite similar in size, copy number, relative location, etc., assume that it is not among those correlated with a distinctive human behavioral disposition chimps lack. If the gene-sequence is absent, different in number, location, introns, etc. in the chimp, then it is a candidate for being interestingly necessary for distinctive human dispositions.

It will take a very long time to identify all the gene sequences non-trivially necessary for complex cooperative behavior, and to learn the functions of the genes they are parts of. But it will not take as long to simply provide a list of locations, alternate sequences, introns, and copy numbers for these sequences without details about their biosynthetic products, and ultimately their combined behavioral consequences. And computational genomics will soon be able to provide hypotheses about the most likely macromolecular scenarios of how linkages, cross-over events, mutation, gene-duplications and translocations, and other events produced these nucleotide sequences from the common ancestor of humans and chimps. These genetic differences hold the key to our distinctive capacities and dispositions. For they were either selected for; or they

were along for the ride with what in the genome was selected for in the differential adaptation of the primate species. Despite the proportionately tiny quantitative nucleotide difference between us, the chimps and the gorillas, they are both relatively unsuccessful species, still restricted to a narrow and endangered niche geographically close to the one we started out in, while we bestride the globe. And then there will be the sequence differences between us and the various Homo erectus populations from Neanderthal to Florenses that we displaced everywhere without interbreeding. It is hard not to conclude that the sequences in which we differ from our common ancestors, other primates and other members of the genus Homo, must have been subject to selection (for or selection of, in Sober's phrase) in the environments we shared with them.

Once the list of locations and sequences for genes without a known function, but nevertheless implicated in distinctively human behavior, are given, the methods employed to date and order mitochondrial and Y-chromosome sequences can be employed to give the order of emergence and perhaps even the ages of these genes. Already, the comparison of human chromosome 21 and the homologous chimp chromosome 22 provides evidence that the genetic differences include rearrangements and duplications, and thus there is reason to think that within homologous sequences there will be sufficiently many single nucleotide polymorphisms — neutral point mutations -- to provide a molecular clock to date the emergence of each of the distinctively human gene these sequences are part of or lie near on the chromosome. This dating can proceed even before we know much more about the genes than that they produce a protein that functions in the brain cells. Of course once we have identified the proteins, we will be able to locate the DNA sequences which code for them. Then the homologous sequences, if any, which in other species are entirely missing or diverge beyond random point mutations, may tell us even more about the genes that figure in the production of these proteins.

What will the sequence chronology alone so established show us? It depends on what the chronology looks like. Consider some of the alternatives: the sequence differences enable us to order the chronology in which genes interestingly necessary for distinctively human dispositions emerges. It may show that they all emerge at roughly the

same date, that different sub-sets emerge together, or that each emerged at a different time and in no order to which adaptive significance can be attached.

Suppose all of the capacities that subservise cooperation can be dated to as far back as the time Homo sapiens began to make composite tools, say 250,000 years ago. That would disconfirm any scenario that made solving the design problem of cooperation the occasion for our spread out of Africa, or the competitive advantage which led us to extinguish Homo erectus. Nevertheless, if many of the capacities required — language, memory, the capacity for cognitive emotions, and a theory of other minds -- did emerge together with imitation learning-capacities, at the same time, and showed rapid spread and minimal drift (by little sequence variation at non-functional and functional sites respectively), this would suggest that cooperation emerged much earlier than 80,000 years ago. On the other hand, suppose imitation learning-abilities dates to the period 250,000 years ago, but some other capacity, such as language, appeared much later, spreading rapidly and without sequence-drift. We might then infer that game-theory models which rely crucially on learning and speech are more strongly confirmed by the sequence data than other models are. Similarly suppose it turned out that dispositions to have those emotions which we do not share with infrahumans — the desire for revenge, say, emerged together with speech, memory, and a theory of other minds. Then models like Fehr's that rely on reputation, secondary reinforcement or strong altruism, or other forms of enforcement that involve commitment problems, would be substantiated. And the sudden spread of sequences subserving such emotions, along with the concerted spread of memory-capacities, would confirm the importance of iterative play in the emergence of cooperation. On the one hand, models like Axelrod's tit-for-tat make far weaker demands on the players in a game having language than, say, Skyrms' stag-hunt. If the former models the evolution of cooperation more realistically than the latter, we may expect the appearance of the capacities it requires to emerge and spread together earlier than language. And these two scenarios should have left different marks in the DNA sequences of Homo sapiens.

Of course, if these capacities subserving cooperation appear to have emerged in various chronological orders among several lineages of Homo sapiens coming out of east Africa, if their spread was slow, and they showed average amounts of sequence-drift,

then doubt would be cast on all models from evolutionary game theory which treat cooperation as a culturally evolved outcome that solved a common design problem faced and was in fact solved by our ancestors better than those hominids they were in competition with. This sort of DNA sequence data would leave us with nothing more than a just-so story, a how possibly account, of why modern human beings are so prone to cooperation.

It is of course not for philosophers to speculate how this research once commenced will eventuate. The speculations here offered may be overtaken by events tomorrow, just as they were encouraged by front-page news (about Homo floreses) reported while we were writing. Good luck in recovering bone material and technological breakthroughs in reconstruction, amplification, and sequencing may provide imaginative scientists with tools to examine new evidence in entirely new ways that test these models. Cleverness in applying known tools and known evidence may enable scientists to do this as well. (Consider what our lice have already taught us about us). It will suffice for our purposes if we have shown that gene-sequencing at least holds out the best hope of combining with traditional archeology and anthropology to answer questions about the evolution of human cooperation and the relevance to it of the theoretically beautiful results of evolutionary game theory.

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