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Human Cooperation among Kin and Close Associates May Require Enforcement of Norms by Third Parties

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Abstract

While our capacity for large-scale cooperation is striking, humans also cooperate with kin and close associates much more than most other vertebrates. Existing theories do not satisfactorily explain this difference. Moreover, mechanisms posited for explaining large-scale human cooperation, like norms, third-party judgments and sanctions, also seem to be essential in regulating interactions among kin and close associates. It is hypothesized that norms and third-party judgments are crucial even for small-scale cooperation, and that kin selection and direct reciprocity alone cannot generate the degree of small-scale cooperation needed to sustain the human life history.

Introduction

Human cooperation clearly differs from that observed in other mammals. Most striking, humans cooperate on much larger scales than other mammals, sometimes through a common cause generated in groups of thousands or even millions of people. To explain the evolution and maintenance of such large-scale cooperation, scholars have studied mechanisms that do not rely on kin selection or direct reciprocity, including indirect reciprocity (Nowak and Sigmund 1998; Panchanathan and Boyd 2004), punishment (Boyd et al. 2003, 2010; Brandt et al. 2006; Hauert et al. 2007), signaling (Smith and Bliege Bird 2000; Gintis et al. 2001; Hawkes and Bliege Bird 2002) as well as genetic (Sober and Wilson 1994; Choi and Bowles 2007) and cultural group selection (Boyd and Richerson 1985, 1990, 2002a; Henrich 2004a). Humans, however, are also exceptional cooperators at smaller scales compared to most other vertebrates.

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Division of labor and delayed exchange of valuable commodities, for example, occurs in virtually every human society whereas they are virtually absent in other vertebrates.

The fact that humans engage in more small-scale cooperation than other vertebrates is not satisfactorily explained by existing theories. It is generally accepted that large-scale cooperation, of the kind observed in humans, is not feasible in other vertebrate societies because the mechanisms that maintain large-scale human cooperation hinge on language and culture. However, the mechanisms that are thought to maintain small-scale cooperation—kin selection (Hamilton 1964) and direct reciprocity (Trivers 1971; Axelrod and Hamilton 1981)—should work equally well in many other vertebrates, and while a number of hypotheses have been advanced to explain the greater levels of human small-scale cooperation (Chapais 2008; van Schaik and Burkart 2010; Pinker 2010; Hrdy 2009), no consensus has been reached.

Here, we hypothesize that the enforcement of norms by third parties is crucial for the evolution of both large-scale cooperation *and* small-scale cooperation in humans. Not only do the distinct levels of small-scale cooperation in humans and other animals not follow from the existing theories, large-scale cooperation and small-scale cooperation in humans share much in common. This is particularly surprising if (a) small-scale cooperation evolved due to the effects of genetic relatedness and direct reciprocity and (b) large-scale cooperation evolved through the effects of reputation, sanctions, and cultural group selection. We posit that norms and the sanctioning of norm violators may have emerged to support small-scale cooperation, and that neither kin selection nor direct reciprocity on their own would suffice to produce the high levels of cooperation within families and among friends that is needed to sustain the human life history. This can account for the far greater degree of small-scale cooperation in humans than in most other vertebrates as well as the commonalities between small- and large-scale human cooperation. It also helps explain how, as the rate of cultural evolution accelerated, cultural group selection could have led to norm enforcement at the larger scales of cultural groups.

Insufficient Cooperation among Close Kin and Frequent Associates

There is compelling evidence that the human life history would not be possible without extensive cooperation within the nuclear family and across families (Kaplan et al. 2000). In three well-studied foraging groups, there is substantial net food transfer from husbands to wives, from parents to offspring, and from nonreproductive adults to breeding pairs with dependent offspring (Kaplan and Hill 1985a; Gurven et al. 2000; Kaplan et al. 2000; Hawkes et al. 2001; Gurven 2004; Marlowe 2004; Hill and Hurtado 2009). The high level of small-scale cooperation within foraging bands is essential to sustain the unique human

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life history traits of large brains, long life, low mortality, prolonged juvenile period, short interbirth intervals, and the utilization of the most nutrient-dense plant and animal resources in their habitats (Kaplan et al. 2000). Kin selection and reciprocity both play some role in supporting this cooperation (Gurven et al. 2000; Gurven 2004; Allen-Arave et al. 2008). However, in other vertebrates, close kin and social partners who repeatedly interact do not achieve similar levels of cooperation. This suggests that close kinship and reciprocity are not sufficient to allow the evolution of the extensive small-scale cooperation in humans.

Observed Levels of Small-Scale Cooperation Are Not Consistent with Kin Selection and Direct Reciprocity

If potential benefits from cooperation are widespread, the theories of kin selection and reciprocity suggest that close kin and frequent associates should cooperate to a much greater extent than they actually do. When we do observe cooperation, it is often among related individuals, consistent with kin selection (e.g., Jennifer et al. 1994; Silk et al. 2004 ; Silk 2006; van Schaik and Kappeler 2006; Langergraber et al. 2007; Hughes et al. 2008). However, a full test of the theory requires also evaluating the absences of cooperation, and not just the occurrences.

Cooperation in other vertebrates mostly involves behaviors that are low cost or even individually beneficial, because interactions are mutualistic or the result of coercion by a dominant individual (Clutton-Brock 2009; Clutton-Brock et al. 2001). Group hunting, alarm calling, joint predator mobbing, and territorial choruses that have been observed in nonhuman mammals and birds may provide direct benefits to the actor (Clutton-Brock 2009; Grinnell et al. 1995).

Reciprocity is rare in nonhuman animals (Hammerstein 2003). One of the few examples is grooming in primates (Frank and Silk 2009), a fairly low-cost activity. Models of kin selection and reciprocity, however, do not predict that cooperation should be restricted to low-cost interactions. It is the ratio of benefits to costs that matters, and so high-stakes forms of cooperation between close kin and regular interactants should be common. For instance, sharing food with a sick kinsman or close associate is costly, but can produce much larger benefits for the recipient. Illness and serious injuries are often fatal when individuals cannot feed themselves. Thus, it would seem that species in which kin provide such aid should be commonplace. Yet, humans are one of the few mammals that do this, and when they do, the benefits are large (Sugiyama 2004). More generally, specialization in food production coupled with food sharing seems to be highly beneficial, leading to lowered mortality, a long juvenile period, and high investment in learning that characterize the niche of *Homo sapiens* (Kaplan et al. 2000). In most animal societies, there is little food sharing even among close relatives.

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A few mammals (e.g., mole rats, callitrichid primates, wild dogs, wolves and meerkats) breed cooperatively (Solomon and French 1997; Jennifer et al. 1994; Clutton-Brock 2006), but they are the exception rather than the rule. Moreover, in many cooperatively breeding mammals, reproductive skew leads only to a redistribution of reproductive success in favor of the dominant without net gains in average fitness. Dominants suppress the reproduction of subordinates, who then are left with little choice but to help raise the dominant's offspring. In contrast, cooperative breeding in humans does not lead to increased female reproductive skew and, if anything, decreases the skew. Humans also manage to have exceptionally short interbirth intervals for our otherwise k-selected life history strategy—a clear sign that we actually reap the gains from breeding cooperatively.

Discrepancy Is Unlikely to Be Due to the Lack of Benefits from Cooperation

Our argument depends on the assumption that there are many opportunities for small-scale cooperation in nature that are not utilized in most vertebrates. However, it can be argued that other vertebrates lack extensive small-scale cooperation because cooperation is not beneficial in their ecological niches. While we cannot rule out this possibility, we do not think that it is very plausible. Several lines of evidence suggest that the potential benefits of cooperation—joint efforts, specialization, and trade—are omnipresent.

First, lineages that evolved division of labor and trade have had spectacular ecological success and have radiated into a vast range of habitats. Multicellular organisms arose when groups of single-celled creatures evolved specialization and exchange and, as a result, have occupied a dramatically large number of niches. Their success indicates that the benefits of cooperation among cells were present in niches as different as those occupied by plants and animals, ecologies as different as aquatic, terrestrial and subterranean habitats, and climates ranging from tropical to tundra to the ocean floor. Although the total biomass of single-celled organisms could exceed that of multicellular organisms, there is still extensive cooperation among single-celled organisms, including toxin production, aggregating to produce reproductive bodies, reduced virulence, and labor division (Rainey and Rainey 2003; Velicer and Yu 2003; Crespi 2001; West et al. 2006). Thus, cooperation among cells implies that if free riding can be tamed, cooperation would be beneficial in virtually every niche.

Similarly, eusocial insects are not restricted to a narrow ecological domain, but instead occupy a vast breadth of foraging ecologies ranging from carnivory to gardening, again suggesting that cooperation could provide benefits in a wide range of environments. Furthermore, eusocial insect colonies cooperate in multiple domains. For instance, army ants breed cooperatively, work together to build bridges, defend the colony, manage traffic, and have several

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castes of workers specialized for different tasks (Couzin and Franks 2003; Franks 1986).

The scope of economic exchange in humans also suggests that gains from specialization and trade are everywhere. Specialization within firms exists because it is more efficient to subdivide labor among individuals that specialize in one or a few specific tasks. This was recognized by the earliest economists (Smith 1776). Trade also offers a way to achieve division of labor and thereby increase efficiency in production. If one individual specializes in building houses, a second in farming, and a third in making music, and they trade their products, all three will typically enjoy better housing, food, and music than if they would produce everything themselves. Whether a firm or collective enterprise is small or large, and whether the web of exchanges is small and simple or large and complex, the fact that there are firms, as well as the fact that there is exchange, is evidence of the presence of gains from specialization.

Finally, people in small-scale hunter-gatherer societies cooperate in a wide range of activities, not just in cooperative hunting and meat sharing. The Aché cooperate in acquiring plant resources as well as in hunting, and both types of foods are shared (Hill 2002). Hill (2002:123) also notes:

> Non-foraging cooperation in Aché forest camps includes services such as clearing a camp spot for others; bringing water for others; collecting firewood for others; lighting or tending another's fire; cooking and food processing for others; building a hut that others share; making, fixing, and lending every imaginable tool; grooming others; keeping insect pests away from others; tending others' infant and juvenile offspring; feeding another's offspring; teaching another's offspring; caring for others when they are ill; collecting medicinal plants for others; listening to others' problems and giving advice; providing company for others who must stay behind in camp or go out to forage alone; and even entertaining others (singing, joking, telling stories) when requested.

Thus, the ecology of small-scale hunter-gatherers also contains the potential for gains from cooperation in myriad contexts. Given the rich variety of gains from cooperation that are captured by multicellular organisms, eusocial insects, and humans, we think it is unlikely that other vertebrates do not cooperate very much because there are no potential benefits to be had from specialization and exchange.

Discrepancy Is Unlikely to Be Due to the Detrimental Effect of Local Competition on Cooperation

We have posited that the differences between cooperation in humans and other vertebrates are not consistent with simple kin selection models. It could be that cooperation among kin is not more prevalent because local competition prevents the evolution of cooperation among relatives. If there is local competition, then even if large gains are possible from cooperation and relatedness between individuals is high, the conditions for kin selection to favor

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cooperation may not be met. However, local competition is unlikely to explain satisfactorily the *difference* in the levels of cooperation between humans and other vertebrates.

A local interaction model typically implies that neighbors not only face more opportunities for gains from cooperation than distant individuals, but also compete more intensely. With local interaction and local competition, interactants will be related. That is good for the evolution of altruism, but they will also compete more, which is bad for cooperation. In stylized, simple models, the two effects actually cancel out each other (Boyd 1982; Wilson et al. 1992; Taylor 1992a, b) and cooperation will not evolve at all. Thus kin selection will lead to altruism only if there is a discrepancy between assortment in interaction and assortment in competition. Measuring costs and benefits is typically hard, and determining who competes with whom and how intensely is even harder. There is no conspicuous reason why human social organizations and life histories are different from other mammals in a way that would alleviate the effect of population regulation and allow kin selection to favor cooperation in humans but not in other mammalian societies.

The ability to recognize kin and various dispersal mechanisms offers ways to get around the detrimental effect of local competition. If individuals condition their altruistic behavior on cues of relatedness, they confer benefits not just on anyone with whom they interact and whose offspring will compete with theirs relatively intensively, but on a subsample of those with whom relatedness is extra high. Many life cycles can do the same; after an interaction between relatives, for example, all offspring go to a migrant pool, where they compete with each other equally intensely. In addition, a species that cooperates in sporulating when the local food source runs out can be stable because the individuals locally can be related, whereas the spores compete more globally. Again, there is no obvious reason why kin recognition or dispersal is decisively different between humans and other vertebrates.

It is plausible that local population regulation prevents the evolution of cooperation among relatives in humans as well as in other species. Norms and cultural group selection then serve as an alternate mechanism that can allow cooperation to evolve in humans but not in other animals, because of the lack of language and cultural capacities in other species. Another possibility is that the conditions for kin selection are met in both, but norms help implement the behavior for which kin selection would select.

Discrepancy Is Unlikely to Be Due to Cognitive Constraints

One view holds that humans are able to gain the benefits of cooperation because we have more sophisticated cognitive abilities (Pinker 2010). However, complex strategies do not necessarily yield more cooperative outcomes, and thus human cognitive abilities do not explain the greater degree of cooperation in humans—at least not in any obvious way.

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In simple evolutionary models of repeated interaction, all positive equilibrium levels of cooperation require reciprocity, and strategies that reciprocate are more complex than ones that always cooperate or always defect. Therefore, every positive level of cooperation requires more complexity than no cooperation at all. Beyond that, there is not much of a link between complexity and the level of cooperation: equilibrium strategies can be very complex and only mildly cooperative, or only a bit more complex than unconditional defection, and already fully cooperative.

When there are multiple equilibria, a sequence of transitions between equilibria can take the population from a mildly complex, but very cooperative state to a very complex and only somewhat cooperative state (van Veelen et al. 2012; van Veelen and García 2010). In models of repeated interaction, which tend to have many equilibria (Abreu 1988; Axelrod and Hamilton 1981; Bendor and Swistak 1995; Fudenberg and Maskin 1986; van Veelen et al. 2012), each transition which increases cooperation increases complexity and vice versa. That seems to contradict the claim that a more complex state is not necessarily more cooperative. However, a possible sequence of transitions is that first a complex cooperative equilibrium is upset and replaced by a simple defecting equilibrium, which in turn is replaced by an extremely complex, but only mildly cooperative equilibrium. Thus the last equilibrium is more complex, yet less cooperative than the first equilibrium. Furthermore, if (genetic) assortment is added to the model, then even the relation between increases in cooperation and complexity for specific transitions between equilibria no longer holds—a transition from one equilibrium to the other can lead to an increase in complexity and a decrease in cooperation (van Veelen et al. 2012).

The predicted levels of cooperation also depend on the set of strategies considered in the model (van Veelen and García 2010), but allowing for more complex strategies does not imply an increase in average levels of cooperation. The likelihoods of transitions between equilibria are sensitive to the assumed distribution of mutation probabilities. Restricting attention to a specific set of strategies is a special and extreme choice for mutation probabilities; it sets all mutation probabilities from strategies within the set that is considered to strategies outside it to 0. It is, of course, not clear what the right strategy set is, or what the right assumptions concerning mutations are. However, if we allow for strategies of any complexity (and mutation is unbiased), the average level of cooperation is not necessarily higher than in models with smaller sets of strategies of limited complexity.

It is worth noting, however, that cooperation can require more complexity in behavior than defection for reasons that are abstracted away from in typical models. The cooperative behavior itself will involve performing some task, whereas the defecting behavior of not performing the task is typically simple by default. With human interactions, many cooperative behaviors would not be possible without linguistic communication. Coordinating who does what in collective efforts or negotiating terms of trade is very hard without language

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and impossible without communication (Smith 2010; Pinker 2010). Thus actual differences in complexity may come from things outside the model, depending on how involved the task is that would benefit the other.

Norms Affect Small-Scale Human Cooperation

Behavior between Kin in Humans Is Subject to Norms and Third-Party Enforcement

Many kinds of small-scale cooperation among kin are regulated by norms in human societies, including core domains like parent-offspring relations and pair bonding. Pair bonding is likely one of the earliest forms of cooperation that characterized our hominid ancestors. Yet this relationship is so regulated that almost every society has the concept of "marriage"—an institutionalized form of pair bonding with normative rights and obligations. Exogamy and endogamy rules are widespread. Such norms proscribe pair bonding with members within a social unit and prescribe pair bonding within another social unit, usually trumping the interests of potential marriage partners. There are additional layers of proscriptions regarding how the particular match is made between two individuals. Societies with arranged marriage prohibit the parties involved from choosing their own spouse and often restrict courtship or other forms of direct interaction between opposite-sex youth. Such norms are upheld not only by the community, but also by family members who may disown their noncompliant children. Norms specify how many persons one can marry. A man and woman cannot choose to marry polygynously in a society that is normatively monogamous, even if they think it is in their mutual, long-term best interest. Norms regulate the direction of wealth transfer at the time of marriage: in some societies, men pay bride price whereas in others the woman's family is expected to pay dowry. Postmarital residence is often regulated by norms. A man who hails from a patrilocal culture cannot decide to live at his wife's family's place for economic reasons without losing face. Sexual relations are regulated through norms that restrict the number of sexual partners people can have and norms that restrict premarital sexual behavior. Norms regarding premarital sex are cross-culturally so variable that in some societies a woman who has had sex before marriage can be stoned and killed whereas in other societies it damages one's reputation to be a virgin at the time of marriage.

Norms also regulate how individuals can raise their own offspring. In state societies, violations like child neglect, infanticide, and corporal punishment of children are within the purview of the law. There is much cultural variation in these norms, ranging from places where it is illegal for parents to beat their children to ones where parents who do not discipline their children are considered negligent. Foot-binding in China was strongly moralized even though it was a child-rearing decision. Community pressure maintained the norm and,

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correspondingly, condemnation of the norm from other societies led to its demise (Appiah 2010). Sending daughters to school, another child-rearing decision, was not normative in many societies until recently, causing a substantial fraction of women to be excluded from the market labor force. Parental investment is regulated by inheritance norms that specify how wealth should be distributed among one's children—only to sons or only to daughters, to the oldest, the youngest, or equal division among all the children. It would be wrong to practice primogeniture in a society where norms specified an even division or to deny daughters an inheritance in societies where all children should be given a share. The extent of paternal investment in offspring is also moralized. In societies where biparental care is expected, a father who abandons his children with their mother will be stigmatized. In other societies, uncles take up the paternal duties and absent fathers suffer no loss in status.

Pairwise Interactions among Nonkin Are Affected by Norms and Third-Party Interventions

Pairwise cooperation between unrelated people is also regulated by norms, and third parties often intervene to either mediate disagreements or to enforce norms through indirect sanctions. Thus pairwise exchange in humans often involves both direct and indirect reciprocity. In indirect reciprocity, cooperation in a pairwise exchange is maintained because defections damage the violator's reputation, allowing other people to defect when interacting with a violator without damaging their own reputation. In direct reciprocity, cooperation is maintained by the threat of defection by the partner herself.

Third-party monitoring and sanctioning govern many aspects of pairwise relations among the Turkana, a nomadic pastoral society in East Africa. For instance, if a woman refuses to give water to a man who asks for it, she can be criticized. However, if she heard that this man had abandoned his injured friend when the two of them went into enemy territory to steal cattle, then she can refuse him water without facing disapproval from her peers. The relationship between a man and his friend should be ideal for direct reciprocity—they are likely to have known each other for a long time and to have interacted often when herding, attending dances, patrolling, and raiding. Despite this, community approval and disapproval is vital scaffolding in sustaining the cooperation between these two men. In fact, the closer their friendship, the stronger the community's disapproval will likely be. Similarly, a herdsman who loses animals from his flock can expect to be hosted by a Turkana household when he travels in search of his stray livestock. Suppose, however, that this man stole his neighbor's camel. Then, rather than being invited in, he may be censured for cheating his neighbor and told to go his own way. Again, a relationship between neighbors, rather than being in the purview of direct reciprocity, is regulated by community sanctions.

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Furthermore, when there is a disagreement within a pairwise relationship, third parties often adjudicate the dispute. For instance, one of the primary functions of the judiciary of state societies and informal courts in politically decentralized societies is to handle disputes such as theft, homicide, battery, and violations of contractual agreements between two individuals. Among the Turkana, if a man's goat is stolen, he reports the matter to the elders or members of the respective families. They summon the alleged thief to determine what happened, and if the accused is at fault they instruct him to compensate the victim. Likewise, men often need to rebuild their herds after loss from raids, droughts, and epidemics, and they call on their friends to loan them animals. If a dispute arises later about repaying the debt, the donor is assured that people knowledgeable of their transaction will testify that he had indeed lent this friend an animal.

Culturally Evolved Norms May Have Enabled the Evolution of Small- and Large-Scale Cooperation in Humans

Thus far we have argued that:

- Levels of small-scale cooperation differ greatly between humans and other vertebrates. It seems hard to explain this difference by disparities in typical ingredients of kin selection models and/or models of direct reciprocity or as the result of ecological or cognitive differences.
- In human societies, culturally transmitted norms regulate many aspects of life, including kin relations and repeated pairwise interactions.

Given that culturally evolved norms are absent in other species, these observations lead us to explore the possibility that norms were essential to the evolutionary transition that led to cooperative breeding in humans. We hypothesize that culturally transmitted norms allowed for extensive small-scale cooperation in early human societies and may have been what helped bands comprising a few nuclear or extended families to seize benefits from social exchange. This led to the evolution of a moral psychology which then allowed the evolution of larger-scale cooperation through cultural group selection.

Cultural group selection models have typically assumed that individuals acquire complex normative behavior by copying successful or prevalent behavior; that is, they can use the same social learning machinery which they use to learn other kinds of locally adaptive behavior to acquire and implement the local moral rules. However, complex moral behavior may be hard to acquire without some kind of innate scaffolding already in place. Many of our normative concerns are somewhat abstract, as we recognize similarities in situations where there are aligned and opposed interests. That gives our moral machinery a grammar-like structure: we recognize common causes and conflicts of interest in novel situations never experienced, and we link them. We do not, for

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instance, just take turns in doing the dishes, but balance such duties over a larger set of chores. It may be difficult to maintain such rules with only a general cultural learning mechanism. However, if small-scale cooperation maintained by norms and third-party enforcement caused humans to already have an innate moral grammar, then cultural group selection can lead to large-scale cooperation more easily by exapting this moral psychology.

The transition we describe would not immediately yield large-scale cooperation. Our hypothesis is that moral sentiments are essential to supporting costly cooperation at the domestic scale and these then are exapted for larger-scale cooperation. However, simple misfiring of this psychology would be extremely costly. For instance, the Turkana mobilize hundreds of unrelated and unfamiliar warriors to participate in cattle raids against members of neighboring ethnolinguistic groups, and norms and enforcement shape behavior in this common endeavor (Mathew and Boyd 2011). Twenty percent of all male deaths in one of the Turkana territories along a hostile ethnic border are due to warfare (Mathew and Boyd 2011). From archaeological records, ethnographic accounts, and oral histories of various societies, we know that tribal-scale warfare is very old (Willey 1990; Bamforth 1994; Keeley 1996; Lambert 2002; Gat 2006). It is thus clear that if large-scale conflict resulted from a misfiring of mechanisms designed to regulate small-scale cooperation, there would then have been a long history of strong selection acting to correct this mistake. Instead, we think that the availability of a small-scale psychology, which can be extended if the needed adaptive pressure for large-scale cooperation exists, could make the transition to larger-scale cooperation far more likely.

This hypothesis predicts both that species with culturally transmitted norms will be more cooperative and that small- and large-scale cooperation in such species should rely on norms in similar ways. The absence of third-party enforcement of pairwise cooperation and adjudication of disputes should be detrimental to pairwise cooperation. Cooperation within the extended family unit should be sustained through norms and their enforcement through sanctions by family and community members. There should be cross-cultural variation in the norms dictating small-scale as well as large-scale cooperation. The psychology of norm compliance and enforcement for small- and large-scale cooperation will be sensitive to different cues as a consequence of the distinct selection pressures which shaped them. Norm compliance and enforcement in small-scale cooperation should depend on cues of family membership, or cues of repeated interactions. Such cues are rooted in individual identities: Should I help Joe? Is he my relative? Has he helped me when I needed him in the past? Negotiation, deliberation, and consensus among known individuals should be important in achieving norm compliance in small-scale cooperation. In contrast, cultural group selection on institutional variation should be more important in shaping norms governing large-scale cooperation. Norm compliance in large-scale settings should depend on cues of group identity: Should I help Joan? Is she a member of my ethnic group? Is she an American? In

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such settings, norm compliance can be achieved even without negotiation and consensus.

An alternative view of why we have norms concerning interactions between kin and repeated pairwise interactions is that they are just an after-the-fact reflection of equilibrium behavior. Such a view would be somewhat similar to the role of norms presented by Binmore (1994, 1998), and it would imply that if a norm or its enforcement were to go away, the behavior would not change.

Why Are Norms Necessary to Get the Benefits of Cooperation?

Our argument has thus far been empirical: humans exhibit many forms of small-scale cooperation not seen in other species, like specialization and exchange; norms play a crucial role in small-scale human cooperation; therefore norms potentiate the evolution of small-scale cooperation. However, it is not obvious how the evolution of norms and third-party enforcement should interact with ingredients from typical models assuming kin selection and direct reciprocity. One would expect that norm-enforcing strategies that support cooperation can invade more easily when there is relatedness in the social group, but also that norms are not absolutely necessary for cooperation to evolve. If the latter is true, we are still left with the question of why there is relatively little small-scale cooperation in other vertebrates. Below we sketch a few, admittedly speculative, possibilities of how the evolution of norms and kin selection or repeated interactions might relate.

Norms and Third-Party Enforcement May Resolve Problems of Errors

Errors may help account for why direct reciprocity may not lead to very much pairwise cooperation. Models without errors are typically much too positive about the possibilities for the evolution of cooperation (Hirshleifer and Martinez Coll 1988; Wu and Axelrod 1995). If norms could somehow reduce the detrimental effects of errors, then that could explain the higher levels of reciprocity among people. Still, it is not immediately obvious why this should be the case, because the evolution of indirect reciprocity is typically more sensitive to errors than direct reciprocity. With direct reciprocity actors only need accurate knowledge about the past actions of their partners; with indirect reciprocity they need accurate knowledge about the past behavior of all individuals in the group and whether that behavior was justified.

There are two possible resolutions of this conundrum, neither completely convincing. First, by linking the behaviors of many different individuals, indirect reciprocity increases the expected number of future interactions for each actor and therefore the opportunity costs of defection. However, given the density of pairwise interactions in small primate social groups, it is hard to see how this will have a big effect. Second, the evolution of reciprocity

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is especially sensitive to "perception errors" which occur when actors have different beliefs about whether a defection occurred. Strategies, like Pavlov's (Nowak and Sigmund 1993), can be stable when perception errors are common, but these strategies cannot easily increase when rare.

Adjudication by third parties can solve this problem, even if the adjudication process is also error prone (Mathew and Boyd, in preparation), because it aligns the beliefs of interactants. Adjudication of pairwise exchange is easiest if rules of behavior are shared within a community, and not restricted to a particular partnership. Otherwise third parties have no basis for evaluating deviations from these norms and arbitrating. However, adjudication does not necessitate enforcement, so why we end up with indirect sanctioning of defectors is unclear. Nonetheless, it can help explain the dearth of pairwise cooperation among frequent associates in other animals.

Norms Can Help Identify How to Get the Benefits of Cooperation in the Local Ecology

It is possible that the conditions for kin selection to favor cooperation are met in humans and other animals, but that different patterns of cooperation are favored in different environments and culturally transmitted norms are needed to adapt to local conditions. Most models do not explain how actors identify when and what to exchange with whom to reap the benefits from the exchange. In principle, this can be solved without norms—as has been done in cells, multicellular organisms, and eusocial insects through genetically evolved specialization, communication, and rules governing exchange. This solution allows extremely complex adaptations like those observed in social insects. However, the ability to adapt to different environments is limited to what can be acquired through individual learning and other individual forms of phenotypic plasticity. Humans occupy a very wide range of environments, and individuals may not have the ability to invent locally appropriate rules for governing cooperation. This problem will be particularly acute for contingent cooperation because sanctions require behaviors of others to be accurately judged.

Norms may solve this problem because cumulative cultural evolution allows rapid evolution of complex adaptations to local conditions. We know that cultural evolution leads to the gradual evolution of complex tools (e.g., kayaks and composite bows) which are superb adaptations to particular local environments, but beyond the inventive capacity of individuals. Norms are social tools that allow complex cooperative behavior in a wide range of environments with a wide range of behaviors, payoffs, and contingencies. Norms of Turkana society dictate, for instance, that one must share certain parts of the animal, lend a goat to a man who has lost his wealth in a raid, feed a traveler, ridicule a man who let his friend down, help your son acquire his first wife with part of your livestock wealth, offer water to a passerby who asks, or give a share of animals to your brothers and uncles after returning from a raid. The nature

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of cooperation and the conditions under which it would be favorable are quite different among the Aché or the Netsilik. These norms oblige certain behaviors and allow its practitioners to derive some benefits from mutual insurance, division of labor, and exchange. Practitioners may not necessarily recognize what the real benefits to each act are. However, as long as some process can make norms track the socioeconomic environment roughly accurately, norms, if not individuals, can recognize in which kinds of exchange the benefits of cooperation lie.

However, the argument that norms are needed to recognize where the gains from cooperation lie is not entirely convincing either. Vertebrates have repeatedly arrived at solutions to derive the benefits of mutualistic and low-stakes cooperation. For instance, herding, predator mobbing, and territorial chorusing have evolved in several lineages. Sexual reproduction is even a more complex coordination problem involving mate searching, consortship, signaling, and mate guarding. Yet, all mammals are able to orchestrate it carefully. Individuals can also easily identify social situations in which they can gain from engaging in self-serving behavior. Of course, people live in a wider range of environments and use a much wider range of subsistence strategies than any other vertebrate. This may make human cooperation more difficult to achieve without culturally evolved social tools.

Norms and Third-Party Enforcement Can Eliminate Inefficiencies Caused by Asymmetric Interests among Pairs of Individuals

Norms can enforce pairwise exchange that may be beneficial only at a scale larger than that of the dyad. For instance, parents have a greater interest in cooperation between their children than do the children themselves. Examples of sources of gains from cooperation are increased efficiency from labor division, transfers between individuals that are at different stages of their life cycle, and co-insurance. Suppose, for example, that two sisters agree to help each other, if the other sister gets hit by bad luck. Among siblings, Hamilton’s rule predicts that they will help as soon as the benefits of a transfer to the one are more than twice the costs to the other. Parents, however, have an interest in their offspring being more helpful than that, and if they could, they would bind their children to help whenever the benefit exceeds the cost. Conflicts of interest like that typically lead to a tug of war between parents and offspring, where the outcome depends on the mutations that both sides have at their disposal. However, a norm that siblings should help each other could work even better if it is shared by a larger community, as everyone ex ante is better off living in a group that has a higher level of between-siblings insurance. Such a norm could then later

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be exapted to also include nonkin. One could imagine similar scenarios for norms that concern labor division or delayed exchange within the family.

Norms and Third-Party Enforcement May Resolve Information Asymmetries to Inhibit the Evolution of Cooperation

In many situations, needy individuals must communicate their state of need to receive help, and this restricts the conditions under which cooperation can evolve, even among kin. There are situations in which reliable cues will allow potential donors to determine whether the benefits to their kin are sufficiently large. For instance, when the potential recipient is a newborn infant, the mother will have no doubt that the gains to the offspring from receiving care are much larger than the cost to the parent of providing care. Often times, however, the party that would benefit from a transfer is better informed about its state of need than possible donors. For example, it may be difficult for a mother to determine whether an older offspring is really ill or just malingering, because any signal used by a sick offspring to transmit information about its condition or needs can also be sent by a healthy offspring who just wants special treatment.

This problem can be solved if the cost of signaling is high enough to deter the less needy from dishonest signaling (Zahavi 1975; Grafen 1990a, b; Kreps and Sobel 1994; Bergstrom and Lachmann 1997, 1998; Lachmann and Bergstrom 1997). With such costly signals there can be transfers, but the cost of the signal consumes some (or even all) of the potential efficiency gains. When need varies continuously, “partially pooling equilibria” exist, in which ranges of neediness are lumped together under the same signal. These reduce, or even eliminate, the costs of signaling, but the information transmission becomes coarser. Moreover, there are also always equilibria where no transfer gets made (Johnstone 1999). In those equilibria either no signal is sent and no transfer is performed, or, if signaling is free, signals are sent but the reaction to all signals is to not transfer. This means that even if the combination of relatedness and the costs and benefits of the transfer is right, and kin selection suggests that not giving is not an equilibrium under perfect information, it can be that with information asymmetry, not giving is in fact an equilibrium.

Shared social norms and group enforcement may help resolve this problem. Without community monitoring and enforcement, a juvenile who signals to his mother that he is sick needs only to provide the right cues in her presence. He can go out and play when she is not looking. With community monitoring and enforcement, the cost of malingering will be much greater—he can’t play when anyone is looking. More generally, the coupling of this

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"tangled-web-of-lies" phenomenon to shared norms about appropriate behavior can reduce the cost of discriminating honest and dishonest signals, and this in turn can expand the range of conditions under which mutual aid can occur.

Conclusion

Theoretical work on the evolution of cooperation in humans has focused on how people maintain cooperation in large groups comprised of unrelated individuals, a form of cooperation that is rare in other animals. However, human cooperation stands out in yet another aspect: people engage in costly cooperation among kin and close associates to a much greater degree than is seen in other animals. We have argued here that current theories do not adequately explain this difference in levels of small-scale cooperation between humans and other animals. We posit that, like large-scale cooperation, cooperation among kin and friends also depends on norms and third-party judgments. We lay out tentative explanations for why this may be, but more theoretical work is needed to determine precisely how norms and third parties can aid the evolution of cooperation among kin and close associates, and why kin selection and reciprocity does not suffice to attain elaborate small-scale cooperation in many animals.

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