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## Social Selection and the Origins of Culture

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Something extraordinary happened on the evolutionary path that gave rise to creatures capable of culture. The changes are so profound it is as if we humans were somehow domesticated. Levels of violence are drastically lower than for the other great apes. We are born helpless, we require extended care, and we actively teach each other. We pay exquisite attention to each other's wishes and emotional states. We not only cooperate in ways other great apes cannot, we also form deep attachments to nonrelatives and groups that result in altruistic behaviors obviously harmful to fitness. Even our bones are different from our ancestors in ways typical of a domesticated species (Leach, 2003).

Domestication does not require planning. Self-interested behaviors are sufficient. Chasing away aggressive wolves allows friendly ones to gain an advantage by scavenging scraps. After only a thousand generations, this has transformed wolves into the prosocial, loyal, and helpful dogs we now love. Of course, humans were not domesticated by choices made by some other species. Nonetheless, many human social characteristics would be easy to understand if we had somehow been domesticated. Aspects of culture now select for prosociality and capacities for complex social cognition. But what happened before there was culture? What got the process going?

We are understandably curious about what happened on our evolutionary path that made us capable of culture. The sequence likely involved so many interacting factors and recursive causal cycles that any description that satisfies our evolved minds will inevitably oversimplify the actual process. Nonetheless, as illustrated by the chapters in this book, an enormous amount of thought and research has advanced our understanding of how selection shaped capacities for culture. Old arguments pitting evolution and culture as alternatives have been replaced by formulations that recognize both as essential to any full explanation of human

behavior (Alexander, 1979; Axelrod, 1984; Boyd & Richerson, 2005; Hammerstein, 2003; Lehman, Chiu, & Schaller, 2004; Levinson & Jaisson, 2006; Norenzayan, Schaller, & Heine, 2006; Ridley, 1997). Furthermore, it is increasingly recognized that the causal pathways are multidirectional; selection forces shape capacities for culture, and culture gives rise to new selection forces that further shaped our ancestors in a cascading process that runs away to vast complexity (Henrich & Henrich, 2006; Lumsden & Wilson, 1981; Richerson & Boyd, 2005).

This general framework is uncontroversial, but the details are perplexing at best. To begin with, there are so many of them! Selection has shaped many traits closely related to culture, including bipedality, hunting, language, tool making, manual dexterity, agriculture, cooperation, emotions, facial expressions, foresight, inhibition, guilt, conformity, imitation, social learning, norm enforcement, morality, empathy, and theory of mind, among others (Levinson & Jaisson, 2006; Norenzayan et al., 2006). Many selection forces have been proposed to shape these traits, including kin selection, group selection, sexual selection, cultural group selection, and the benefits of exchange relationships (Hammerstein, 2003; Lehmann & Keller, 2006). This chapter builds on this knowledge that human capacities for culture result from many selection forces shaping many traits, but it proposes that these factors, even taken together, are insufficient to account for some aspects of human social cognition and cooperation.

Some of these aspects may be explained by social selection. Social selection is the subtype of natural selection in which fitness is influenced by the behaviors of others. The benefits of being preferred as a sexual partner are well recognized in sexual selection, as are the resulting extraordinary traits. The fitness benefits of being preferred as a social partner are also well recognized in basic evolutionary biology, but the effects of social partner selection in shaping human social cognition is just now being explored systematically (Alexander, 2005; Nesse, 2007). This chapter reviews the basic principles of social selection and applies them to the origins of human capacities for social cognition, several of which are essential prerequisites for culture.

## COOPERATION, MOSTLY EXPLAINED

Social selection shapes many human capacities in addition to prosociality, but its special contribution is explaining some uniquely human phenomena that are otherwise difficult to account for. So, we begin with a brief overview of evolutionary explanations of cooperation, the limits of those explanations, and what social selection offers that is new.

That human capacities for cooperation are central to culture, and explained in part by culture, is not controversial. No other species demonstrates complex relationships and exchange networks on the scale of humans (Stevens, Cushman, & Hauser, 2005). Explaining such capacities for cooperation has become a major focus at the intersection of biology and social science. The problem and solutions will be familiar to many. Prior to 1966, capacities for cooperation were explained as obviously beneficial for groups, but everything changed when Williams (1966) pointed out and Dawkins (1976) emphasized that selection would tend to eliminate

genes that resulted in greater fitness benefits to others than the self. The problem this insight created has now been mostly solved by kin selection, mutual benefits, and various versions of reciprocity theory.

Kin selection explains much individual sacrifice that benefits others (Hamilton, 1964). Genes that harm individual fitness can nonetheless be selected for if they give a sufficient benefit to relatives who share genes in common. How much benefit is sufficient depends on the genetic closeness of the relationship. For siblings (who share 50% of genes in common), a behavior will increase fitness if its costs to the actor are half or less than the benefits to the sib. This principle is the key to explaining much costly cooperation among kin of all species, not just humans.

Cooperation between nonrelatives has a different evolutionary explanation (Trivers, 1971). Most of this cooperation arises from mutually beneficial exchanges that are easy to explain because no enforcement is needed. For instance, birds benefit directly from picking parasites from the hide of a rhinoceros. Trading favors or exchanging goods yields more than the investment for both parties; when exchanges are delayed, however, the system changes because there is a danger that the other will defect, leaving the cooperator at a disadvantage. This has been extensively modeled using an artificial game called the prisoner's dilemma, in which players on each move choose to cooperate or defect. Mutual cooperation yields maximum net benefits, but on any given move, a player who defects gets a large reward while the cooperating player gets none (Axelrod, 1984). Hundreds of studies based on this model have yielded remarkable insights into how cooperation works (Axelrod, 1997).

Mutual exchange is ubiquitous in human interactions. It was originally thought that such reciprocal exchange was also common in animals, but new attempts to document the same process in animals have come up remarkably empty-handed (Stevens et al., 2005). This is very important for the present thesis. Human patterns of exchange, and the associated fitness benefits, are not found in other animals. They may be crucial steps on the road to culture.

Another conclusion from recent research is that most people do not play behavioral economic games according to the strategy that maximizes their payoffs. Instead, they cooperate too much at the start, and if others defect, they tend to impose spiteful punishment (Fehr & Fischbacher, 2003). Yet another important conclusion is that cultures differ dramatically in the extent of cooperation individuals demonstrate on related behavioral tasks (Henrich et al., 2005).

These basic models for the origins of cooperation have been extended and investigated to create a spectacularly fast-developing area of human knowledge (Hammerstein, 2003; Henrich, 2006). There is no way to review this huge area of work here, but it is essential to describe both the success of some main directions in this enterprise and its inability to provide fully satisfactory explanations for some human traits.

Many mathematical models outline how selection can shape traits that give advantages to groups without necessarily framing the process in terms of group selection (Lehmann & Keller, 2006; Queller & Strassmann, 2006; West, Griffin, & Gardner, 2007). Another useful line of work has modeled how cooperators can identify and selectively associate with each other (Noë & Hammerstein, 1994).

Closely related is work on how reputation effects can maintain tendencies to sacrifice, and much recent work has been done on how social systems (and natural selection) can maintain tendencies to punish defectors (Axelrod, Hammond, & Grafen, 2004; Henrich & Boyd, 2001). Many of the most profitable directions have investigated how social norms that benefit groups are preserved and transmitted (Fehr & Fischbacher, 2004). Cultural group selection models also describe how complex exchange networks within groups create new selection forces that shape human capacities for culture (Boyd & Richerson, 1985, 2005). Extensive behavioral economic investigations have explored human behavior in laboratory settings generally characterized by anonymity and small cash payments, and they are allowing initial investigations about brain mechanisms for social capacities (Fehr & Fischbacher, 2003).

Despite all this progress, there is a consensus that something is missing. Simple economic and biological views predict that individuals will maximize their personal and genetic interests, but observations from the laboratory and everyday life reveal much difficult-to-explain human generosity, moral behavior, and spitefulness. Investigations about the possible role of strong reciprocity (Gintis, 2000) and commitment strategies (Nesse, 2001) address only a tiny fraction of the problem. Two leaders in the field summarized by saying, “At the ultimate level, the evolution and role of altruistic rewarding for cooperation in larger groups remains in the dark” (Fehr & Fischbacher, 2003). Gintis, Bowles, Boyd, and Fehr went further:

We suspect, on the basis of the many studies completed over the past several years, that the new knowledge obtained will give us a picture of prosociality (and its obverse, antisociality) that is fundamentally incompatible with the economist’s model of the self-interested actor and the biologists’ model of the self-regarding reciprocal altruist. (Gintis et al., 2003, p. 169)

This chapter proposes that social selection offers an important part of the answer.

## SOCIAL SELECTION

Social selection is the subtype of natural selection in which choices made by other individuals influence fitness and change gene frequencies. The next few pages outline the history of the concept and where it stands now.

To prevent confusion, note that social selection has a different meaning in sociology and epidemiology, where it refers to factors that result in overrepresentation of certain kinds of individuals in a group or neighborhood. For instance, the prevalence of schizophrenia tends to be higher in low-income neighborhoods because many people with this disease cannot afford to live elsewhere. Note also that recent use of social selection as an alternative to sexual selection is confused (Roughgarden, Oishi, & Akcay, 2006); social selection is not an alternative to sexual selection but the superordinate category of which sexual selection is a subtype. The question of whether social selection for social partners can explain traits previously attributed to social selection for sexual partners remains interesting.

The full range of social selection's applications is increasingly recognized and modeled (Frank, 2006; Simon, 1990; Tanaka, 1996; Wolf, Brodie, & Moore, 1999), but it was first explored in depth in a pair of papers by West-Eberhard (West-Eberhard, 1979, 1983). She defined social selection in relation to its exemplar and subtype, sexual selection:

Sexual selection refers to the subset of social competition in which the resource at stake is mates. And social selection is differential reproductive success (ultimately, differential gene replication) due to differential success in social competition, whatever the resource at stake. (West-Eberhard, 1979, p. 158)

In sexual selection, females choose males with extreme displays, giving them a fitness payoff of increased matings, which shapes yet more extreme male displays and stronger female preferences for mates who can muster extreme displays. As already noted, social selection is the same, except both sexes choose, and the payoffs are social resources other than matings.

Geoffrey Miller argued that sexual selection shapes capacities for morality and culture along with extreme displays of prowess and fitness (Miller, 2000, 2007). This seems plausible, and it is surprising that the idea is not more widely discussed. Miller emphasized, however, the dominance of sexual selection over other kinds of social selection, saying, "Other forms of social selection are important, but mostly because they change the social scenery behind sexual selection" (2000, p. 13). In contrast, the thesis here is that nonsexual forms of social selection are independently powerful whether or not they influence mating success. Being preferred as a social partner can give manifold benefits that increase fitness by routes other than directly getting more or better mates. The relative importance of sexual and nonsexual social selection is an empirical question.

Darwin recognized sexual selection as a kind of social selection resulting from mate choices, and he attributed moral and cognitive capacities to this process (Darwin, 1871), but it took a long time for this lead to be further developed (Cronin, 1991). Wynne-Edwards offered many examples of social selection, especially those related to hierarchy, although he misidentified many as results of group selection:

The hierarchy is a purely internal phenomenon arising among the members of a society, but it can nevertheless enormously affect their individual expectations of life and reproduction. Its establishment places in their own hands, therefore, a powerful selective force which can conveniently be described as social selection. It is similar in character to the process Darwin believed to apply in the more restricted field of sexual selection. (Wynne-Edwards, 1962, p. 139)

The idea was further developed by Crook (1972), who mentioned it only briefly:

Social selection, then, is that process leading to the evolutionary enhancement of morphological allesthetic and behavioral characteristics that function within a social system to provide biological advantages to the individual in relation to survival prior to reproduction, the formation of zygotes, and the birth and rearing to maturity of young or the progeny of close kin. Direct

competition, often by means of ritualized display, is usually involved. Social selection results from (a) the effects of competition between the subject and others of either sex with respect of commodities essential to survival in a situation that will allow an attempt at reproduction, (b) competition for access to preferred members of the opposite sex for mating, and (c) effects of competition between subjects for access to commodities of the environment and social for the rearing of the young in the troop below reduction age. Of these b is the process most commonly referred to as sexual selection. Social selection is undoubtedly one of the main evolutionary processes responsible for the emergence of both individual and group behavioral characteristics. (Crook, 1972, p. 264)

West-Eberhard was the first to explore the power of social selection to explain many traits in plants and nonhuman animals. For instance, she noted that the extraordinary diversity and colorful profusion of floral extravagances result from competition for pollinators. She also attended closely to the runaway characteristics of social selection:

Social characters—the weapons used in fighting, and the signals used in ritualized combat and competitive display—should evolve rapidly, for they are under a special strong selection (slight variations in these characters are associated with great variance and reproductive success). ... There is a potential for mutually accelerating selection for attractiveness and choice whenever one class of individuals is in a position to choose the winners among those competing. (West-Eberhard, 1983, pp. 158, 160)

In the earlier paper, she suggested that this runaway process could explain primate intelligence:

It is tempting to speculate that the explosive evolutionary increase in the proto hominid brain size, which had the appearance of a “runaway” process, was associated with the advantage of intelligence in the maneuvering and plasticity associated with social competition in primates. (West-Eberhard, 1979, p. 228)

Thus, the evolution of higher levels of social integration can be an “emergent” and result of selection on competing individuals. ... As Wilson (1975) has foreseen, a major synthesis regarding social behavior and natural selection is in the making. I believe, and the intuitions of other authors confirm, that it will develop along the lines crudely sketched in this essay. The main theme is competition within groups, and its special consequences: competitive rituals and displays, “runaway” specialization in traits contributing to social success, intraspecific character divergence (the evolution of alternative strategies), mutually exclusive specializations, divisions of labor, mutual dependence, and social integration. (West-Eberhard, 1979, p. 233)

Competition within groups, rituals and displays, divisions of labor, and social integration—this list could hardly be more germane to the origins of human capacities for culture. Almost 30 years later, a full application of social selection to the evolution of human behavioral characteristics is a project still getting underway.

## SOCIAL SELECTION FOR PARTNERS

There seems to have been some tipping point beyond which human social cognitive evolution took off fast. Once beyond this point, some process entered a positive feedback cycle that increased the strength of selection. Although many traits evolved together to make advanced sociality possible, one candidate for a tipping point is the moment when the number and quality of relationships began to strongly influence fitness. In chimpanzees, alliances influence mating success (de Waal, 1982; Smuts, 1987), and bonobos seem to spend much of their time negotiating less hierarchical but more complex relationships (de Waal & Lanting, 1997). Laboratory studies find that chimpanzees consistently prefer a cooperative partner in a task that requires mutual action (Melis, Hare, & Tomasello, 2006). Only humans, however, get major fitness benefits from exchanging multiple different resources with many other individuals with time delays that make defection a potential problem. Humans are, consequently, exquisitely sensitive to social rejection (Maner, DeWall, Baumeister, & Schaller, 2007). Once fitness is significantly influenced by one's desirability as a social partner, individuals with the best displays of resources and generosity will get increasing advantages. At this point, social selection for displays of partner value and generosity could enter a runaway cycle that shapes extreme human social traits not found in other species.

What kinds of traits should we expect social selection to shape? It should shape traits that make an individual preferred as a social partner, including (a) high levels of resources (health, vigor, personal skills, powerful allies, status, territory, and other resources), (b) tendencies to share those resources reliably and selectively with relationship partners, (c) accurate intuitions about what others are seeking in a partner, and (d) strong motivations to please partners and other in-group members.

These characteristics are not culture itself, of course, but they are traits that make humans capable of culture. Note that the goal here is not to explain culture itself. Culture emerges from human cognitive capacities and takes on a life of its own. It could emerge, however, only after humans gained the requisite cognitive and motivational capacities. As already noted, social structures, from dyads to groups to cultures, create new selection forces that further shape capacities for social cognition. Our goal here is to assess the role of social selection at the initiation of that process, and its subsequent role after culture itself influences the fitness of variations in cognitive capacities.

Social selection offers an explanation for the central role of display of resources and generosity in every culture. From potlatch ceremonies to conspicuous consumption (Veblen, 1899), they are often referred to as "status displays," but they may increase fitness by attracting and keeping the best possible social partners. The importance of reliable resource sharing is reflected in the ubiquity of social norms (Fehr & Fischbacher, 2004), gossip about violators (Dunbar, 1996), and preoccupation with group boundaries, conformity, and the rights and responsibilities of group members.

The motivation to please others is obvious and ubiquitous, but selfishness and norm violations get more attention. We are attuned to detect such violations for the very good reason that deception is ubiquitous (Cosmides & Tooby, 1992).

However, social selection and prisoner's dilemma models highlight different risks. In models based on the prisoner's dilemma model, every interaction involves a risk that the other will defect. Constant vigilance is warranted, as is constant assessment about whether one's interests are served best by cooperating or defecting. In contrast, social selection shapes extreme vigilance about how others are judging you. This is not only to preserve reputation to maximize personal gain, but also because selection has directly shaped intense wishes to please others by acting in whatever ways will make one a preferred partner. This should not be pushed too far. Cultures, and individuals within cultures, vary greatly in strategies for maintaining cooperation (Henrich et al., 2006) and how much they care about what others think about them. There is no one essential human nature to be explained. Nonetheless, social selection may have played important roles in shaping human capacities that make us capable of culture.

## SOCIAL SELECTION FOR CAPACITIES FOR CULTURE

I have emphasized the importance of social selection as an explanation for human prosociality. This is congruent with tendencies to emphasize the role of cooperation in aspects crucial to culture including getting mates, hunting, agriculture, warfare, or tool making. In contrast to approaches that emphasize one or another product of selection, however, social selection calls attention to one process that shapes a whole suite of traits. It pulls the focus away from the products of selection and their utility and toward the process that influences fitness for individuals who vary on certain behavioral traits. Although this process depends on an individual's behavior, fitness is directly influenced by what happens in the brains of other individuals. Fitness changes depending on whether others choose to accept or reject, help or walk away.

This suggests that we should expect extraordinarily pervasive, subtle, and expensive attempts to influence others to prefer one as a partner. I use the word *influence* instead of *manipulate* because others are on the lookout for self-serving manipulators. The perspective from social selection is, in some respects, the opposite of that from the prisoner's dilemma. An appearance of being Machiavellian toward relationship partners dramatically decreases one's value as a partner. Conversely, the appearance of genuine caring about the welfare of partners increases one's value and should be selected for. Although false displays and deceptions are inevitable, when partner choice has high payoffs, deception strategies will be especially risky. For every sociopath in modern Western societies, there are 10 overly conscientious, socially anxious individuals who are constantly preoccupied with pleasing others and maintaining relationships (Grant et al., 2005).

In short, social selection can shape tendencies to genuine altruism, by which I mean helping motives shaped directly by selection, with calculation of costs and benefits as a secondary, not a primary, consideration. Such genuine altruism can give a net long-term payoff, offering a possible solution to the "mystery of altruism." If a relationship gets badly out of balance, altruistic motivations tend to fade, as expected. The perspective from social selection, however, emphasizes that inexpensive decisions made by others have major influences on an individual's fitness.



The result may be motives to try to discern what will please others and to provide it if that is possible at reasonable cost—the very model of prosociality.

As noted already, prosociality is but one trait expected from social selection for social partners. Deep enduring relationships are something beyond cooperation, and having powerful motives for creating and maintaining enduring close relationships is distinctly human. Individual relationships in baboons and chimpanzees can be important (Smuts, 1985), but they are nowhere near the intensity or importance seen in humans (Mills & Clark, 1994). Likewise, chimpanzees and baboons chose alliance partners based on kinship, size, strength, and social status (Smuts, 1987). Only humans, however, make discerning choices among potential partners based also on their ability to help with special skills or knowledge, their wealth, and their moral character. Although studies of human relationships tend to neglect the role of simple alliances, many relationships involve much more than mere alliance (Mills & Clark, 1994). Displays of power and resources are ubiquitous among animals, and, as noted by Wynne-Edwards (1962), they are important for competing in hierarchies that exist because of patterns of social choices. But only humans invest heavily in costly displays of generosity and conformity to social norms.

A variety of other mental traits give advantages when social selection influences fitness. Ability to recognize and remember other individuals is essential, thus helping to explain specialized mechanisms for face recognition and for remembering cheaters (Mealey, Daoud, & Krage, 1996). The benefits of knowing others' expectations and needs should shape close attention to others' preferences and a theory of mind to anticipate what will please or annoy them (Povinelli & Giambrone, 2001; Wellman & Cross, 2001). The benefits of being able to predict how complex social relationships will play out have been proposed as an early engine of social evolution (Humphrey, 1976). Because the costs of being rejected or excluded are high, strong motivation to inhibit selfish and impulsive behavior will give advantages in most situations. Social anxiety inhibits and punishes actions disliked by others (Nesse, 1990). A tendency to conformity may arise by social selection if individuals prefer to associate with those like themselves and if they discriminate against outsiders. Social selection magnifies the benefits of language skills for communicating and understanding others, especially by making promises and threats effective means of social influence (Nesse, 2001).

Social selection shapes much more than prosocial tendencies. Flares of temper, for instance, give a selective benefit by influencing the behaviors of others. Others can be strongly influenced if they can be convinced that an emotional individual will act in ways contrary to his or her self-interest. This shapes emotions that are extremely emotional and unpredictable. Likewise, spiteful behavior gives advantages by influencing the behavior of others who quickly recognize that defecting from such a partner will be costly. These examples are at the intersection of social selection and commitment theory (Nesse, 2001).

## SOCIAL SELECTION AND HUMAN DOMESTICATION

I began with the observation that humans are so exquisitely attuned to the wishes of others that we seem almost to have been domesticated. Of course, no other

species domesticated us. It seems useful, however, to consider the possibility that we domesticated ourselves (Leach, 2003). Self-interested social choices gave selective advantages to those of our ancestors who were less aggressive, more generous, and better able to intuit what others wanted. Preferred partners got advantages, those who preferred the best partners got advantages, and the preference and displays ran away to shape extreme prosociality that is otherwise difficult to explain.

Adam Smith's (Smith, 1759/1976) "invisible hand" offers an interesting parallel. It refers to how self-interested individual choices give rise to mutually beneficial economic systems. Sellers who charge too much lose customers. Employers who pay too little lose employees. Goods in short supply command increased prices that induce increased production of those goods so supply meets demand. The result is mutually beneficial cooperation beyond what any planning process can create. Such capitalistic systems are, of course, notable for their unfairness and inefficiencies. The large picture, however, is one of remarkably efficient and smoothly operating markets that emerge from the actions of individuals pursuing their own self-interest.

Markets work because the self-interested choices of agents create incentives that shape markets to the mutual benefit of most participants. The role of market models in social biology and the crucial role of partner choice in fostering cooperation are just now being recognized (Noë, 1990, 2001), but antecedents go back a long way. Adam Smith used the phrase "invisible hand" only once in *The Theory of Moral Sentiments* (Smith, 1759/1976), but his idea offers a remarkable parallel to how social selection can shape human capacities for cooperation and culture.

Individuals advertise what they have to offer in relationships, and others make choices among potential partners. Those who offer others the most, while asking the least in return, are chosen more often by better partners and gain correspondingly increased benefits. Deceptive displays and defection are always possible, but reputation monitoring and the ability to switch partners limit their utility. Trustworthy individuals are preferred not only because defection is less likely, but also because they reduce monitoring costs. If individuals can convince each other that their mutual commitment goes beyond mere exchange to genuine friendship, they get considerable additional benefits by having help available when it is most needed (Nesse, 2001).

On the individual level, this process also unfolds during development. The dog owner rewards desired behavior and punishes disobedience. By simple reinforcement, the dog's behavior maximizes not only its own interests but those of its owner as well. Children are socialized not only by such rewards but by their evolved tendencies to conform and to take in cultural norms as their own. The cascading effects of culture have been through so many iterations that it is hard to even describe how selection shaped the mechanisms that facilitate enculturation. It is easy, however, to see that it did, and it is remarkable to observe the reliability of these mechanisms.

Viewing human social evolution as domestication by social selection offers a perspective quite different from that of economic models that must confront costly cooperation as a mystery. Individuals pursuing self-interest make thousands of social choices. These choices are the invisible hand that domesticated our species. Each lifetime recapitulates the process; tiny social cues act on mechanisms shaped by selection to detect and respond to them, steadily but firmly rewarding increasingly prosocial behavior.

Of course, it does not always work. Some people have few relationships; others get trapped in unsatisfactory relationships. Some people spend so much time and effort trying to please others that their life is a burden. Others mistrust others so completely that their relationships can make use of only crude exchanges. Understanding the origins of such individual differences is a task different from trying to understand the selection forces that shaped human social capacities. They are related, and the perspective of social selection should illuminate phenomena such as sociopathy and excess scrupulosity, but these are topics for another occasion. For now, it is important mainly to note the wide variation of human social phenotypes, the good evolutionary reasons for this, and the implication that attempts to explain essentialized human nature are inconsistent with biology.

## CONCLUSION

Social selection is an important subtype of natural selection that can explain some human traits that are otherwise difficult to understand. Its focus on the role of partner choice calls attention to the fitness effects of decisions made by other individuals and thus to the fitness benefits of trying to understand what others want and how to get them to prefer one as a partner. The benefits of such displays and choices create escalating positive feedback cycles that result in extreme traits with high costs. These traits, such as strong motives to please others, give a net long-term benefit on the average, but like the peacock's tail, they can also have substantial negative effects. Sexual selection increases the magnitude of a display until its fitness advantages from increased matings are balanced by other costs such as energy expenditures and increased vulnerability to predation. Social selection increases the magnitude of prosocial traits until the benefits of getting more and better partners are balanced by personal costs incurred by creating displays, following norms, fulfilling commitments, and helping others. The positive feedback in this process offers an explanation for how selection could have shaped such extraordinarily costly social traits.

Culture is by no means explained by this process alone. It seems likely, however, that social selection was of particular importance at the transition point where culture became possible. Once complex culture emerges, it becomes, as many have noted (Barkow, 1989; Boyd & Richerson, 1985; Dunbar, Knight, & Power, 1999; Durham, 1991; Henrich & Henrich, 2006; Lancaster, 1975; Lumsden & Wilson, 1981; Norenzayan et al., 2006), a force of selection in its own right, shaping yet more complex social capacities that result in yet more complex cultures in which social selection becomes even more important in shaping "endless forms most beautiful and most wonderful" (Darwin, 1859).

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