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Runaway Social Selection in Human Evolution

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Darwin (1871) recognized that there could be important differences between selection occurring as a consequence of (1) interaction with ecological factors, such as predators, climate, and food; and (2) interactions among conspecifics (i.e., members of the same species competing with each other over resources such as nest sites, food, and mates). The former is termed "natural selection" and the latter, "social selection," of which sexual selection may be considered a special subtype (see Glossary for definitions of key terms). The pace and direction of evolutionary changes in behavior and morphology produced by these two types of selection—natural and social—can be significantly different (Alexander, 1974, 2005; Fisher, 1930; West-Eberhard, 1983, 2003).

Here we examine the process of "runaway social selection" and its importance for explaining the extraordinary sociality of humans and associated adaptations, including linguistic and sociocognitive skills such as language, theory of mind (ToM), creativity and imagination, self-awareness, foresight, and consciousness. We suggest that as our hominin ancestors became increasingly "ecologically dominant," a within-species arms race

involving complex coalitions based on extensive networks of reciprocity, including so-called "indirect reciprocity" (Alexander, 1987, 2006) emerged, facilitated by the use of socially transmitted information.

SOCIAL SELECTION

Organisms face many obstacles that potentially diminish survival and reproduction. Some of these challenges involve competitive social interactions among conspecifics for essential resources, such as nest sites, preferred locations at feeding sites and water holes, and mates. Social competition has produced a wide variety of adaptations. For example, weapons such as horns, teeth, and spurs are used in competition for mates across a wide range of taxa (Andersson, 1994). Males and females influence copulatory behavior of mates with a variety of behavioral, morphological, and physiological tools (e.g., Eberhard, 2004; Patricelli, Uy, & Borgia, 2003). Distress calls help recruit relatives to assist in social conflicts. Strategic positioning within aggregations facilitates the use of conspecifics as cover via the "geometry of the selfish herd." Complex, coordinated social behaviors appear necessary for successful coalitionary actions such as border patrols (Watts & Mitani, 2001) and displacement of dominant individuals (Conner & Whitehead, 2005).

Darwin (1871, p. 256) proposed sexual selection as a process that involved "the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction." Separating selective pressures involved with competition for mates from other aspects of social competition is difficult, in part because, as Williams (1966, p. 39) observed, "all adaptation must relate to reproduction." In effect, "reproduction is everything, and survival is nothing, except insofar as it contributes to reproductive success" (Ghiselin, 1997, p. 292). And from the other direction, mate choice can be based on assessment of social abilities, as well as survival components from natural selection, such as parasite resistance. Some aspects of reproductive competition, moreover, do not involve social interaction at the level of the individual vehicles, for example, gamete competition. Disentangling the components of social selection is not an easy task; perhaps this is partly why Darwin and subsequent evolutionary thinkers have not provided a widely accepted description. Another reason might be the relatively few species for which nonsexual social selection is a dominant evolutionary force.

Of particular interest here are information-processing capacities associated with social competition. We posit that runaway social selection was the primary pressure shaping several key human brain adaptations. Other social species, such as chimpanzees, dolphins, orcas, crows, and elephants, are less extreme examples.

RUNAWAY SOCIAL SELECTION: CONSPECIFIC RED QUEENS

Selection that occurs as a consequence of interactions between species can be intense and unending—for example, with parasite–host Red Queen evolution (Hamilton, Axelrod, & Tanese, 1990) and other biotic arms races (van Valen, 1973). Intraspecific social competition may generate selective pressures that cause even more rapid and dramatic evolutionary changes. Relative to natural selection, social selection has the following characteristics (West-Eberhard, 1983):

1. Because competition among conspecifics can have especially strong effects on differential reproduction relative to other ecological pressures, the intensity of social selection (and consequent genetic changes) can be very high.

2. Because the salient selective pressures involve competition among members of the same species, the normal ecological constraints are often relaxed for social selection. Hence, traits can evolve in seemingly extreme and bizarre directions before counterbalancing natural selection slows the process. If traits favored by social selection also provide benefits in regard to natural selection, as, for example, in the human brain's ability to design useful tools for contending with Darwin's traditional hostile forces of nature, then such constraints would be even further relaxed.

3. Because social competition involves *relative* superiority among conspecifics, the bar can be constantly raised in a consistent direction generation after generation, in an unending arms race.

4. Because social competition can involve multiple iterations of linked strategy and counterstrategy among interacting individuals, the process of social selection can become autocatalytic, with its pace and directions partly determined from within, generating what might be termed "secondary Red Queens." For example, reoccurrence of social competition over lifetimes and generations can favor flexible phenotypic responses, such as

social learning, that enable constantly changing strategies. Phenotypic flexibility of learned behavior to contend with a dynamic target may benefit from enhanced information-processing capacities, especially in regard to foresight and scenario building (Suddendorf & Corballis, 1997).

The conditions we have listed for social selection have been most extensively considered for mate competition. Fisher (1930) rekindled interest in Darwin's concept of sexual selection, identifying several key aspects of a directional runaway process that could result in seemingly bizarre or arbitrary traits such as elaborate visual (e.g., peacock tails) or auditory (e.g., warbler songs) displays. Such traits would have no evolutionary function in solitary species that were selected in regard to their abilities to contend with strictly ecological factors. But species in which reproduction was determined in part by social competition are a different evolutionary story (e.g., Iwasa & Pomiankowski, 1995). Social competition over mates may be indirect, as in the case of a gray tree frog choosing males on the basis of their call characteristics (Gerhardt, 2005). Mate choice preferences for the relative extremes of a trait (e.g., the longest tail) can drive a runaway process of sexual selection (Andersson, 1994; Eberhard, 2004; Fisher, 1930). The links between social selection from mate choice and natural selection have been difficult to determine. Mate choice for traits such as resistance to pathogens could have important advantages, although assessment of honest advertisement of heritable true fitness is problematic (Hamilton, 1999). The intensity of selection for pathogen resistance could be enhanced by social selection involving mate choice (e.g., Borgia, Egeth, Uy, & Patricelli, 2004). Increased predation risk and other ecological factors, however, may constrain such displays (e.g., Endler, 1988).

CONCLUDING REMARKS

Within-species Red Queen dynamics can generate especially strong social selection. Decreasing constraints from natural selection, combined with increasing social competition, generate a potent runaway process. Human evolution appears to be characterized by such circumstances (Flinn, Geary, & Ward, 2005). Humans, more so than any other species, appear to have become their own most potent selective pressure, via social competition involving coalitions (Alexander, 2005; Geary & Flinn, 2002; Wrangham, 1999) on the one hand, and dominance of their ecologies involving niche construction (Laland, Odling-Smee, & Feldman, 2000) on the other. The

primary functions of the most extraordinary human mental abilities—language, imagination, self-awareness, ToM, foresight, scenario building, and consciousness—involve the negotiation of social relationships (Allman, 1999; Flinn, Ward, & Noone, 2005). The multiple-party reciprocity and shifting nested subcoalitions characteristic of human sociality may generate especially difficult information-processing demands for these cognitive facilities that underlie social competency.

GLOSSARY: DEFINITIONS OF KEY CONCEPTS

Ecological dominance: The relative lack of selection from extrinsic causes compared with the relative importance of selection from interactions with conspecifics. From this perspective, the term does more than indicate a species' success in contending directly with Darwin's hostile forces of climate, predation, and resource scarcity. Although rhinoviruses, kudzu, and many species of beetles are highly successful in their respective ecologies, they are not ecologically dominant in this sense. Their phenotypes have been, and continue to be, primarily designed by selection involving extrinsic forces, rather than by interactions with members of their own species.

Taking another example, although part of ecological dominance involves relative lack of selection from biotic interactions including predation, this is not sufficient. The top guild predators themselves, such as eagles, bears, lions, tigers, and orcas, and large animals with effective protection, such as elephants and sperm whales, are relatively free from predation. But resource scarcity (e.g., getting food) and pathogens may still be significant selective pressures relative to contending with conspecifics, particularly in regard to evolution of the brain. The critical factor in ecological dominance is the extent to which a species has become its own selective pressure, its own principal hostile force of nature.

Natural selection: Selection occurring as a consequence of forces "in nature." Adaptations are produced as a consequence of success or failure in dealing with aspects of the abiotic and heterospecific biotic environments. Examples include Darwin's hostile forces of food shortages, predators, pathogens, and harsh climate.

Runaway social selection: Sir Ronald Fisher (1930) identified the potential for positive feedback loops in sexual selection involving mate choice for the relative extreme of a trait. Females benefit from heritable choice biases because their sons (and grandsons) are more likely to be chosen. Richard Alexander (2003) extended this concept, recognizing that choice of social partners for reciprocity can also involve a directional, runaway process. We suggest a further generalization to all aspects of social selection in which competition favors a relative extreme in a positive feedback loop. In this vein, one might identify a process of runaway cultural selection for relative extremes (e.g., faster cars, better weapons).

Selection: Differential success of phenotypic variants that result in differential success of organic germ-line replicators (heritable genetic units; for reviews, see Dawkins, 1982; West-Eberhard, 2003; Williams, 1966).

Social selection: Selection occurring as a consequence of interaction among individuals of the same species. It is useful to distinguish sexual and nonsexual social selection (for reviews, see Alexander, 1974, 2005; West-Eberhard, 2003). Adaptations are produced as a consequence of success or failure in dealing with the social environment. Examples include competition among conspecifics for food or nest sites (nonsexual), or mates (sexual selection; Darwin, 1871).

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The Evolution of Mind

Fundamental Questions and Controversies

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