Runaway Social Selection in Human Evolution

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Darwin posited that social competition among conspecifics could be a powerful selective pressure. Alexander proposed a model of human evolution involving a runaway process of social competition based on Darwin's insight. Here we briefly review Alexander's logic, and then expand upon his model by elucidating six core arenas of social selection that involve runaway, positive-feedback processes, and that were likely involved in the evolution of the remarkable combination of adaptations in humans. We discuss how these ideas fit with the hypothesis that a key life history innovation that opened the door to runaway social selection, and cumulative culture, during hominin evolution was increased cooperation among individuals in small fission-fusion groups.

> "There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection"
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> Charles Darwin [1871: 166]

> "Why are we all alone [in]... our tendency and ability to cooperate and compete in social groups of millions?"
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> Richard Alexander (1990: 1)

INTRODUCTION

In 1871–2 Charles Darwin tackled two major challenges to his theory of evolution: costly displays and weaponry used in courtship, and the descent of humans. He proposed that mating competition among conspecifics — sexual selection — was a potent evolutionary force that could explain the apparent enigmas of bright plumage, antlers, even the great horn of the Rhinoceros beetle. Sir Ronald Fisher (1930) furthered Darwin's concept of sexual selection by positing that intraspecific competition could involve a process of "runaway" selection if choice was based on comparisons favoring relative extremes. Crook (1972) and West-Eberhard (1979, 1983) expanded Darwin's and Fisher's concepts to include selection from all aspects of social interaction among conspecifics, termed "social selection." Humphrey (1976) and later Dunbar (1993) and Tomasello (1999) suggested that intelligence could evolve in the context of social competition and cooperation among conspecifics: cleverness in the "social chess game." Alexander (1990); (see also Alexander, 1974, 1979, 1989) integrated these ideas into a comprehensive model of "How humans evolved" involving a process of "runaway social selection" where hominins "increasingly became their own principal hostile force of nature," with cooperation and coalitions posited as crucial and complementary aspects of hominin social environments (Alexander, 1987, 2006; Wrangham, 1999).

We use the term "runaway" selection here to refer broadly to selection that involves either: (1) arms races within species, whereby competition-based selection between individuals and groups leads to reciprocal, escalating trait expression and elaboration across evolutionary time, or (2) positive feedback between the selection pressures and evolutionary changes in one trait (e.g., a phenotype subject to choice), and selection pressures and evolutionary changes in a second trait (e.g., choice of the phenotype), such that evolutionary changes in both traits become mutually reinforcing across generations (e.g., Nesse, 2007; Nakamaru and Dieckmann, 2009; Piantadosi and Kidd, 2016; Bailey and Kölliker, 2019). As such, runaway selection can apply to a wide variety of sets of phenotypes, including aspects of social interactions, in addition to those involved in female choice and sexual selection (e.g., Bailey and Kölliker, 2019). Alexander focused on a process of "runaway social selection" involving arms-race competition among individuals for "social cleverness" (including language abilities, social skills, aptitudes for cultural information, coalition building, and multiple other types of intelligence) that became increasingly important in human evolution (Alexander, 1990; Flinn and Alexander, 2007). There are other plausible models of human evolution involving social competition (e.g., Hrdy, 2009; van Schaik and Burkart, 2010; Wrangham, 2019); our main objective here is to describe, extend and expand upon Alexander's runaway social selection model, which connects to both Darwin's (1871) ideas about selection associated with competition among conspecifics and his model of human descent. As such, we consider runaway social selection involving both competitive arms races, and positive feedbacks driven by mutually reinforcing selection during choice-trait coevolution.

DARWIN AND THE DESCENT OF HUMANS

Darwin (1871) suggested an evolutionary scenario for humans involving a positive feedback loop between tool use and intelligence. Initially a "smart ape" began to use tools; this advantage led to further selection for intelligence and more sophisticated tools, and eventually to upright bipedal locomotion, precision hand control, reduced dentition, social cooperation, morality, and other human traits. Evidence from hominin paleontology and archeology over the past 150 years has not supported Darwin's tool use model as he presented it. Fossils indicate that Australopithecines and perhaps even earlier hominins were habitual bipeds for >2 MY prior to significant changes in brain evolution (McBrearty and Brooks, 2000; Antón et al., 2014; Almécija et al., 2021). Tool use also predates increases in cranial capacity by at least 1 MY (McPherron et al., 2010), it is not restricted to hominins and it is not subserved by specialized neurobiological mechanisms (Geary and Huffman, 2002; Geary, 2005; Sherwood et al., 2008; Bruner, 2021). Although technology is clearly a significant part of the human evolutionary story (Osiurak and Reynaud, 2020), it apparently does not account for our extraordinary social mental aptitudes including such traits as empathy, language, mental

time-travel, consciousness, and mind-reading (Herrmann et al., 2007; Haber and Corriveau, 2020), or for the uniqueness of the hominin evolutionary trajectory.

Darwin recognized that culture — socially transmitted information and materials — was also a key selective pressure in human evolution. Indeed, he noted (1871, pp. 78–79) that "the formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel." Aptitudes for language, learning, and the sociality underpinned acquisition of information were increasingly important for hominin survival and reproduction, eventually resulting in the extraordinary Anthropocene niche that we inhabit today. Why humans are "the uniquely unique species" (Alexander, 1990) who developed such extraordinary cognitive and cultural abilities remains an elusive evolutionary puzzle (Tomasello, 1999; Henrich and McElreath, 2003; Laland and Seed, 2021). The problem is further complicated by inherent biases of humans trying to understand themselves (Alexander, 1987; Varella, 2018).

ALEXANDER AND RUNAWAY SOCIAL SELECTION

An important universal trait of mammals is maternal care of altricial (helpless) offspring. Many mammalian species, including most primates, also have varying levels of alloparental support and protection by relatives. Beyond these shared features, however, humans exhibit a suite of highly unusual traits (Alexander, 1990; Chapais, 2009), many of which appear adaptively responsive to variable conditions. Humans are the only species characterized by the *combination* of stable breeding bonds; flexible and extensive alloparenting and considerable male parental effort within multi-male groups; lengthy childhoods; cryptic ovulation; extended bilateral, multi-generational, and affinal kin recognition; grandparenting; influence of relatives over mate choice; language; variable group composition and inter-group relationships; and a suite of other human-elaborated traits.

Alexander's model of how hominins evolved this combination of traits is based on the concept that hominin evolution became an increasingly autonomous and self-reinforcing, runaway process. A key selective pressure on hominins was thus interactions with other hominins, particularly with regard to its selective effects on brain evolution (Alexander, 1990; see also Flinn et al., 2005). Concomitant with the increased importance of competition and cooperation among conspecifics was an increase in "ecological dominance," whereby predation and competition from other species became weaker and weaker selective forces on hominin phenotypes.

We describe a set of revisions and extensions to Alexander's model, in the light of recent work on human social and sexual evolution and behavior. First, we discuss an explanation for the initial split in the evolutionary trajectories of hominins and *Pan*, and how it underpinned the divergence of the two lineages. Second, we operationalize Alexander's model of runaway social evolution by explicitly describing the relevant arenas of social selection and social competition, what traits were selected for

and how, and how different arenas and forms of social selection contributed to runaway effects.

HOMININ ORIGINS

Hominins and Panins last shared a common ancestor about 6.5–9 MYA (Andrews, 2020; Almécija et al., 2021). From an orthograde last common ancestor, Hominins and Panins initially diverged into distinct niches, with associated changes in locomotion leading to upright bipedalism in hominins, and knuckle-walking in *Pan*, similar to *Gorilla*s. Arguably, the shift to bipedalism implies a more terrestrial niche, with different foraging opportunities and predation pressures (Harcourt-Smith, 2007; Almécija et al., 2021). Early hominins likely developed a fluid sociality similar to that characteristic of contemporary hunter/gatherer societies, involving tolerance of, and interaction with, individuals from other small, local, low-density groups (in contrast to chimpanzees and gorillas; more similar in some but not all aspects to bonobos as discussed below), eventually encompassing flexible alliances and coalitions in their fission-fusion context (Walker et al., 2011; Apicella et al., 2012; Macfarlan et al., 2014; Migliano et al., 2017, 2020). Such alliances may have been beneficial, at least initially, in terms of cooperative foraging, food-sharing, and protection from predators (Allen-Arave et al., 2008; Smith et al., 2016). This initial difference, possibly linked to the gradual shift to a more open and mobile, terrestrial niche, would have enabled a series of subsequent evolutionary changes: (1) a flexible, distinctive pattern of extended family relationships that supported longer periods of child development (Washburn and Lancaster, 1968; Lovejoy, 1981; Hrdy, 2009, 2014; Hawkes, 2020); (2) critical aspects of the fluid and complex coalitional sociality posited above (Gavrilets et al., 2008; Chapais, 2009, 2011; Hawkes et al., 2018); and (3) an environment in which cultural innovations were increasingly important for foraging, defense against predators, and success in cooperation and competition with conspecifics (Hill et al., 2011; Lotem et al., 2017; Flinn, 2021; Garg et al., 2021).

Early hominins also diverged from *Pan* in which other sets of individuals were most important to them. For female hominins, relationships with mothers, sisters, daughters, aunts, and grandmothers were of increasing importance. But so too were fathers, mates, brothers, and sons. From the male hominin perspective, relationships with paternal relatives — fathers, brothers, and sons — were of increasing importance for cooperative defense and foraging. As posited above, female relatives — wives, mothers, sisters —, and children benefited from this crucial support from males.

Hence the conundrum, analogous to the "matrilineal puzzle" proposed by Richards (1950); (see also Irons, 1983; Macfarlan et al., 2014; Dyble et al., 2015) emerges. How can males and females be with kin who reside in different places? How to help both your sister and your wife? And how to effectively avoid inbreeding problems if male and female relatives — father-daughter, brother-sister — co-reside? The solution is found in most hunter-gatherer foraging-band societies: flexible, fluid camp residence and social networks. Individuals can choose to stay or visit with whomever is most useful to them at a particular time. With inter-camp group tolerance and cooperation, hominins got the best of both worlds; help from maternal and paternal kin, mates and affines. This pattern of "exploded fission-fusion" sociality (Marlowe, 2004; Foley and Gamble, 2009; Macfarlan et al., 2014) stands in stark contrast to that of all other hominids.

A key consequence and benefit of this fluid interactive social system was an open door for cumulative culture and language. Socially transmitted information could move easily and rapidly across the hominin social landscape (Hill et al., 2011, 2014; Walker et al., 2011; Gowlett et al., 2012). A good idea ("meme") would spread fast and far (go "viral"). "Good ideas" were not limited to tools, engineering, and technology, but include social tactics and strategies (e.g., Coward and Grove, 2011). And, as described below, such a complex matrix of self-selected interactions provides excellent opportunities for social selection to exert its runaway effects, by the various mechanisms, in the various contexts, that typify human cognition, behavior and culture.

PSYCHOLOGICAL MECHANISMS OF SOCIAL SELECTION

Selective arenas represent specific contexts within which social selection mediates variation in inclusive fitness among individuals. The primary psychological mechanisms of social selection, within these contexts, are cognitive and emotional. Thus, an individual will benefit the most in inclusive fitness under social selection if they can:

(1) Individually recognize all of the persons in their group;

(2) Discern the relationships of kinship, friendship, and sexuality among all interacting individuals in their group;

(3) Figure out, consciously or unconsciously, how each individual person who they interact with could best be manipulated, cooperated with, or competed with, in what way, to maximally increase their own lifetime inclusive fitness;

(4) Discern and infer, consciously or unconsciously, how any other individual would be expected to respond to these possible actions toward them, from being able to take their mental perspective regarding their strategies and abilities to maximize their own inclusive fitness.

Each other person in a group thus has some potential inclusive fitness value to a focal individual, that could be maximized by success in providing benefits, imposing costs, or taking control of behavior away. Ability to achieve this potential will be some function of asymmetries in information, physical and intellectual power, alliances, and leverage (control of a resource or service that cannot be taken by force; Strassmann and Queller, 2010; Watts, 2010; Bissonnette et al., 2015). An individual would also benefit tremendously from knowing their own abilities and best strategies for increasing inclusive fitness, in this complex

multidimensional web of social interactions and their mental representations.

The cognitive challenges of being able to most-effectively maximize inclusive fitness *via* the four steps described above are open-ended and almost unimaginably complex, for any extended human group of reasonable size, such as 50 to 150. As a result, social selection and responses to the selection, in the context of evolving human social-cognitive-emotional abilities, can proceed virtually without limit, being constrained only by human neural computing power, manifest in brain size and modular specializations, and being driven by multiple forms of runaway social selection, as described in detail below.

The psychological mechanisms of social selection can be applied in a wide variety of specific contexts, or arenas, whereby pairs and larger sets of humans interact. These arenas can, in turn, delineate the different forms of runaway social selection that lead to accelerated human evolution for cognitive and cultural traits, and the remarkable suites of adaptations that result.

ARENAS OF SOCIAL SELECTION

Arenas of human social selection exemplify the different contexts of human interactions that contribute to runaway human social evolution under the broad umbrella of Alexander's (1989; 1990) model. These arenas have been discussed before, but not integrated together, and they have not been considered in the framework of how humans evolved since their divergence from a shared ancestor with the genus *Pan*. The "runaway" component of runaway selection is especially important because it can help to account, *via* positive feedbacks, for the extraordinary rapidity of human cognitive and social evolution.

Arenas of social selection help to indicate the mechanisms of social interactions that can lead to the enhanced brains and more-complex social cognition and emotion that characterize humans. They represent pairs or larger sets of human interactions, ordered by sex and age and number and nature of groupings, that have been postulated to involve runaway effects. The key question in particular is how runaway social selection is expected to work in fluid populations of early humans, in terms of how increased social abilities can translate into higher inclusive fitness of individuals, and enhanced survival and proliferation of groups, and in terms of evolutionary dynamics across generations.

The First Arena: Arms Races

Most generally, runaway social selection effects within generations can be driven by social competition, social cooperation or social choice. The first arena of social selection described here is *direct, symmetric and asymmetric arms-race competition within a group*, whereby two or more individuals are engaged in some fitness-related conflict where the individual with better social skills (social "weaponry") wins. Such competition represents a classic arms race, where the selective pressure is

autocatalytic across generations, because the selective cause is persistent and self-reinforcing. Arms races are normally thought of in physical terms, where they become limited, across many generations, by the costs of armament and tradeoffs with other components of fitness. This limitation may apply to brain size, over the long term, due to the high costs of neural tissue. However, psychological arms races *per se* should be subject to no such constraints, since they are governed by "software" — neural organization — that can, in principle, complexify indefinitely, and involve cumulative learning and culture. In hominins, brains concomitantly evolved to become both larger and more "socialized" (specialized for social cognition), with material culture lagging behind (Geary, 2005; Gowlett et al., 2012; Rilling, 2014), as expected under autocatalytic models driven by social selection.

Possible examples of psychological arms races would be enhanced abilities to read emotions and intentions in others, levels in metacognition and theory of mind ("I think that they think that I think," etc.), ability to gain status (and recruit partners in reciprocity, as discussed below) through displays of cognitive abilities, and skills involved in strategically "out-thinking" adversaries in conflicts (e.g., Byrne and Whiten, 1988; Dunbar, 2014). The arsenal of social weapons would also include a broad range of cognitive and emotional phenotypes whose expression reciprocally selects on each other within and across generations, mainly in the general context of motivating other individuals to behave more, and more often, in the inclusive-fitness interests of the actor. A number of studies have examined coevolutionary arms races in the context of social selection and intelligence (e.g., McNally et al., 2012; dos Santos and West, 2018; Coen, 2019), and have supported the conclusion that such arms races can drive higher levels of intelligence, cooperation, and social complexity. Indeed, as noted by Darwin (1871, p. 97) "natural selection, arising from the competition of tribe with tribe, would, under favorable conditions, have sufficed to raise man to his high position."

Among males, psychological arms races should be most prominent where males are evenly matched physically, such that simple muscular dominance cannot determine competitive outcomes. Among females, it may commonly involve indirect forms of (non-physical) aggression, such as manipulations of social status and abilities in competition for allies (friends) and social support. Competition for useful allies is also likely to have been very important to males.

Mental arms races are the psychosocial equivalent of Darwin's (1871) sexual selection by male-male competition. Such simple, one-on-one psychological arms races should ramify easily into one-on-multiple and multiple-on-multiple interactions, given the fluidity of human groups and kin-structured and reciprocity-structured organizations. Indeed, the high fluidity and organizational complexity of human groups are likely, in part, end products of such arms races as well. The "multiples" of these interactions are presumably allies of some sort, who can join psychological and physical forces to better increase their inclusive fitness at the expense of others. Once a competitive dyad expands, however, the dynamics

necessarily change. Indeed, a pair of competing individuals may themselves be allies in some domains and adversaries in others. How they became so is a matter for the next selective arena.

The Second Arena: Partner Choice

The second arena of social selection is *partner choice* in the context of cooperative traits, which can lead to runaway choice-trait coevolution under a variety of conceptual and mathematical models (e.g., Nesse, 2007, 2010; Debove et al., 2015). Here, "partner" refers to social partners, with whom one preferentially interacts, over a relatively long period, due to various benefits that accrue especially *via* mutualism and reciprocity, sometimes combined with kinship. In the same way that classical sexually selected mate choice is driven by attractive displays by one individual to others, social partner choice is driven by attractive social displays, usually involving demonstrations of prosocial traits such as honesty, reliability, cooperative cultural and religious beliefs, and generosity through social, informational and material assistance in times of relative need or potential for benefit (Nesse, 2007, 2010). There are some interesting parallels here between social selection and classical Fisherian runaway selection (typically involving choice of a few "top-ranked" individuals) and "complementary" mate choice (such as for immune system gene compatibility). Thus, for example, social selection may entail tradeoffs between choosing the "best" partner (i.e., individuals that are highly socially intelligent or skilled in some area), versus choosing individuals who will remain committed to, and focus on, the relationship, even when mutualistic reciprocal relationships demand consistent effort and attention, limiting the ability to engage effectively in many of them. The latter type of relationship should also be promoted by complementarity of different social (and other) abilities between members of a dyad, which increases the benefits accruing to both.

Social partners are, of course, conventionally regarded as "friends," who in evolutionary terms represent allies who both gain inclusive fitness benefits, over the longer term, from their continued association. The partnerships can be of any dyadic combination of the two sexes, or can involve larger groups united through multiple partner choice events, merging into and overlapping with other such groups in complex social networks. Choice of partners in various contexts can also generate "markets" for partners, with complex dynamics that can enhance the competitive nature of the processes involved (Barclay, 2016; Eisenbruch and Roney, 2017). Smith and Apicella (2020) describe how partner choice, for traits that include generosity and foraging ability, mediates campmate preferences among Hazda hunter-gatherers.

The long duration of the human lifespan makes social partnerships, in principle, highly beneficial to inclusive fitness, especially if they involve complementary abilities, knowledge or resources (Nesse, 2007, 2010). In humans, choices regarding memberships in coalitional groups, based on the traits of the group and its leader, should also be notably important (Boyd and Richerson, 2009), and could themselves synergize with group against group arms races, as discussed in more detail below.

Partner choice, like arms races, can result in the runaway evolution of socially selected traits. By this process, the expression of the chosen trait, and the choice of the trait, come to be positively genetically associated with one another across generations (Sachs et al., 2004), as they both increase rapidly in frequency. Cultural analogs of this process can also lead to culturally inherited patterns of association that do not require genetic change, although such changes can themselves impose selection for genetic change and gene-culture coevolution (Richerson and Boyd, 2005; Lotem et al., 2017).

Nesse (2007, 2010) described how runaway partner choice may have promoted a whole suite of uniquely human or elaborated-in-humans traits, including theory of mind, extreme forms of cooperation, capacities for morality, the importance of building and protecting one's reputation, and self-domestication of the recent human species as a whole. Most generally, partner choice, and choice of leaders and groups, should select for finer and finer abilities to discriminate the socially salient qualities of other individuals and groups, in terms of if and how much interacting reciprocally with them, compared to alternatives, will result in gains to inclusive fitness. In humans (and possibly dolphins) the complexity of cooperation (and the intelligence required to negotiate alliances) increased dramatically in the context of triadic interactions among groups in nested hierarchies (Connor, 2007; Gerber et al., 2021). The risk/reward ratio and the number of options (and potential outcomes) were probably critical with regard to selection for enhanced intelligence, and these increased dramatically with expansion in the number of levels in a nested hierarchy of interacting entities (individuals, groups, groups within groups, etc.) and associated potential alliances. As such, this arena of social selection should result in notably enhanced abilities to judge character, truthfulness, morality and social abilities, as well as the ability to display and communicate these sorts of traits, even if they sometimes conflict with one's ability to maximize inclusive fitness by alternative, relatively selfish, and self-serving means.

The Third Arena: Mate Choice

The third arena of social selection, human mate choice, was, of course, originally formalized by Darwin (1871). It represents a subset of partner choice that is sufficiently special and distinct to warrant its own domain. Classical Fisherian mate choice by sexual selection (Fisher, 1930; Lande, 1981; Kirkpatrick, 1982) involves a process whereby choice by one sex (in animals, usually females) for one or more fitness-related traits in the other sex (usually males) results across generations in a positive genetic correlation between stronger choice for the trait (typically in females) and higher level of trait expression (typically in males) — a runaway process that stops only when the trait is so highly developed that it incurs strong costs in terms of some other component of fitness, typically survival. This dynamic appears responsible, at least in part, for the rapid evolution and high diversity of sexually selected, mate-choice-related traits among many non-human animal groups (Arnold, 1983).

Human mating systems have diverged substantially from the Fisherian paradigm, in that (a) females, as well as males, exhibit forms of sexually selected "beauty," that may be chosen by the

opposite sex; (b) mate choice is commonly more or less joint and reciprocal, with both sexes engaging in choice of a partner based on some criteria (though often with social constraints on choice); and (c) mate choice engenders relatively long-term pair-bonding, with mutual contributions to the rearing of offspring (e.g., Miller, 2000; Buss and Schmitt, 2019; Geary, 2021).

For human mate choice, the main considerations in the second arena apply, specifically, to the situation where males and females each choose one individual of the other sex by some criteria. Individuals are thus under selection to display socially selected traits (e.g., intelligence, cleverness, humor, conversational ability, kindness, a variety of social skills), and to choose some overlapping constellation of such traits in others (Etcoff, 1999; Miller, 2000). Choice of a good opposite-sex partner for mating, reproducing, providing, and parenting is probably a much more challenging task than making and maintaining a same-sex friend, and thereby should represent a stronger socially selective filter. Pair-bonded males and females are thus selected to be able to successfully navigate the psyche of their mate, in a much more intimate, cognitively complex, and fitness-salient way than for friends. Indeed, among animals, comparative analyses by Dunbar and Shultz (2007) have demonstrated that among carnivores, artiodactyls and bats, larger relative brain size is associated with pair-bonding, and that in primates it is linked with complex, enduring social relationships even more broadly (as well as with larger group size); they argue that these findings reflect "the cognitive demands of the behavioral coordination and synchrony that is necessary to maintain stable pair-bonded relationships." Humans appear to represent an extreme of social selection and bonding effects on relative brain size and behavioral coordination, especially given the partially divergent optimal mating and parenting strategies of the two sexes, and the complex mixtures of confluence and conflicts of inclusive-fitness interest that ensue.

From an evolutionary perspective, mutual mate choice in humans becomes subject to runaway dynamics due to genetic correlations of socially selected pair-bond related traits with choice of these traits; for example, females choose kind, caring males, males with genes for these traits are selected for, and the genes for the choice and the traits become associated and rise in frequencies across generations. For this type of sexual-social selection, it remains unclear if there are evolutionary brakes on the process equivalent to those operative during natural selection by predation against, say, too-large of a train in peacocks. Possibilities for such "brakes" might be over-expression of choice (such that no or few individuals are deemed suitable for a mate), or expression of prosocial, altruistic, or parenting-related traits to such a degree that they became maladaptive in the context of maximizing inclusive fitness as a whole.

The Fourth Arena: Caregiver-Offspring Choice and Signaling

Runaway coevolution between social signals and their choice includes not just cooperation partners, and female-male pairs, but also offspring interacting with their caregivers, specifically mothers, alloparents, and fathers (West-Eberhard, 2003,

p. 467; Hrdy, 2013). By this mechanism, offspring benefit from producing signals, such as high levels of subcutaneous fat, vigorous crying, smiling, eye contact, and other social interactions with caregivers ("other-regarding" in Hrdy's term), that represent indicators of their phenotypic and genetic "quality" (inclusive fitness value) and that prompt increases in feeding and engagements that enhance social-emotional cognition and learning. Such signals are expected to be predominantly honest indicators of offspring value, but may include manipulative elements (West-Eberhard, 2003), as in other models of signal-receiver interaction, that could reinforce increased discriminability of cues by receivers. Social selection and evolution should thus increase maternal, alloparental, and paternal sensitivities to offspring cues (to better reward higher-value offspring, invest less in lower-value ones, and tell honest from dishonest signals), and increase offspring aptitudes and success at solicitation. As for the other forms of signal-choice system, the result is genetic and/or cultural correlations and coevolution by a self-reinforcing runaway process (West-Eberhard, 2003).

Runaway social selection between caregivers and offspring represents an integral component of the human life history evolving toward increased alloparental and paternal care, shorter interbirth intervals and higher reproductive rates, larger-brained offspring (which are more expensive to produce and rear), and neural precocity and plasticity combined with physical altriciality (Alexander, 1990; Hrdy, 2009; Piantadosi and Kidd, 2016; Sherwood and Gómez-Robles, 2017). Neural precocity, in turn, forms part and parcel of social precocity and the evolution of greatly enhanced human social and emotional cognition, the acquisition of which is inherently developmental and centers around the elongated human childhood and adolescence (Bogin, 1990; Flinn et al., 2011; Ponzi et al., 2020). This selective arena is especially important given that infant mortality has long represented such a substantial component of variation in fitness among humans, and that such mortality can be reduced in a variety of socially salient ways, including effective offspring solicitation, alloparental contributions to maternal nutrition and infant care, paternal augmentation of food supplies, and broader social support in the group for mothers who warrant or earn it. For example, in many human groups, there is evidence of strong positive associations of lower child mortality with higher cognitive abilities of the mothers (e.g., Sandiford et al., 1997; Piantadosi and Kidd, 2016).

The Fifth Arena: Cultural Traits and Social-Cultural Learning

A final arena of within-group social selection is culture, the human-created material and information-based aspects of the environment that underpin tools, customs, religion, arts, and beliefs (Flinn and Alexander, 1982). All human phenotypes derive from interactions of genes with environments — especially cultural and social ones — but culture is special because it can be transmitted both vertically (like genes, or language as noted by Darwin, 1871) and horizontally (as memes), with horizontal transmission potentially proceeding

at a very rapid pace. As such, human traits can evolve due to "gene-culture coevolution" (interactions of genetically based human phenotypes with cultural aspects of environments; Laland and Seed, 2021), commonly due to differential human adoption and perpetuation of different cultural phenotypes and culture acting as a causal agent for selection (Whiten et al., 2017; Richerson et al., 2021).

Cultural change can proceed under a runaway process, whereby increases in cultural complexity and sophistication (the "traits") generate environments that select for enhanced social-cultural learning and more-effective adoption of cultural behaviors (the "choices"), especially by young individuals, leading to runaway coevolution (e.g., Alexander, 1979; Flinn and Alexander, 2007; Boyd and Richerson, 2009; Rendell et al., 2011; Legare and Nielsen, 2015; Legare, 2017; Lotem et al., 2017; Muthukrishna et al., 2018; Markov and Markov, 2020). This process, coupled with "arms race" elements of cultural change, may have been especially effective in driving the recent and accelerating human cultural change that has so complexified human social environments. As such, and given the cumulative nature of human cultural change, this arena of social selection should be exerting stronger and stronger effects on human evolution as time proceeds, relative to the other four (Birch and Heyes, 2021; cf. Wadley, 2021).

The Final Arena: Between-Group Competition

The five arenas of runaway social selection described above all operate within human groups, where groups may be delineated by various terms including families, bands, villages, tribes, or ethnic, linguistic, or cultural groups, of any sizes, that each has some conception of "us" in relation to "them." Whereas social selection and competition occur extensively within such groups, their evolution should be constrained by demographic, ecological and anti-cooperative effects that weaken the group in the context of their competitive interactions with other groups (Lahti and Weinstein, 2005). As such, a final, higher-level arena of social selection operates between groups, as described by Darwin (1871) in terms of competition between human "tribes," and by Alexander specifically in terms of runaway imbalances of power. In particular, Alexander posits, following from Darwin's (1871) views that conflict between tribes selects for within-tribe cooperation and morality, that human social evolution has been driven, in large part, by group against group competition that selects for enhanced within-group cooperation as a means to counter external threats (Alexander, 1979, 1987, 1990, 2006). Alexander's balance/imbalance of power model represents a form of arms race, with both cognition and culture as weaponry, that selects for larger and larger, more and more cooperative groups, with better and better ways to compete, though larger group size may also exacerbate within-group variation and conflicts and dilute the benefits of winning. Such between-group conflicts would have originated in hominins on small scales (indeed, presumably reminiscent of the "warfare" of common chimpanzees; Mitani and Watts, 2001), as represented now in some extant human societies (e.g., Berndt, 1964; Chagnon,

1977; Macfarlan et al., 2014), but escalating as populations increase in size.

Perhaps the most telling evidence in support of Alexander's model is the observation that human history is, in considerable part, the history of human warfare based on groups defined by culture, language, and ultimately, genes (Bowles, 2009; Turchin et al., 2013; Bauer et al., 2016; Turchin, 2016). Warfare may, however, represent only the most extreme, obvious and effective form of between-group human competition, since humans compete, and cooperate to compete, in fluid, dynamic groups at all levels from families to nations, and based on biological kinship, ethnic markers of diffuse long-term ancestry, and cultural differences represented by kinship that can be mainly or purely psychological (Jones, 2003). Groups may also form on the basis of complementary skill sets or interests. In this context, the fluidity of human groupings, with shifting of alliances across time and space as a universality rather than exception, may connect the early evolution of hominids, lost in prehistory, with the recent evolution of modern, historic humans — and all points in between.
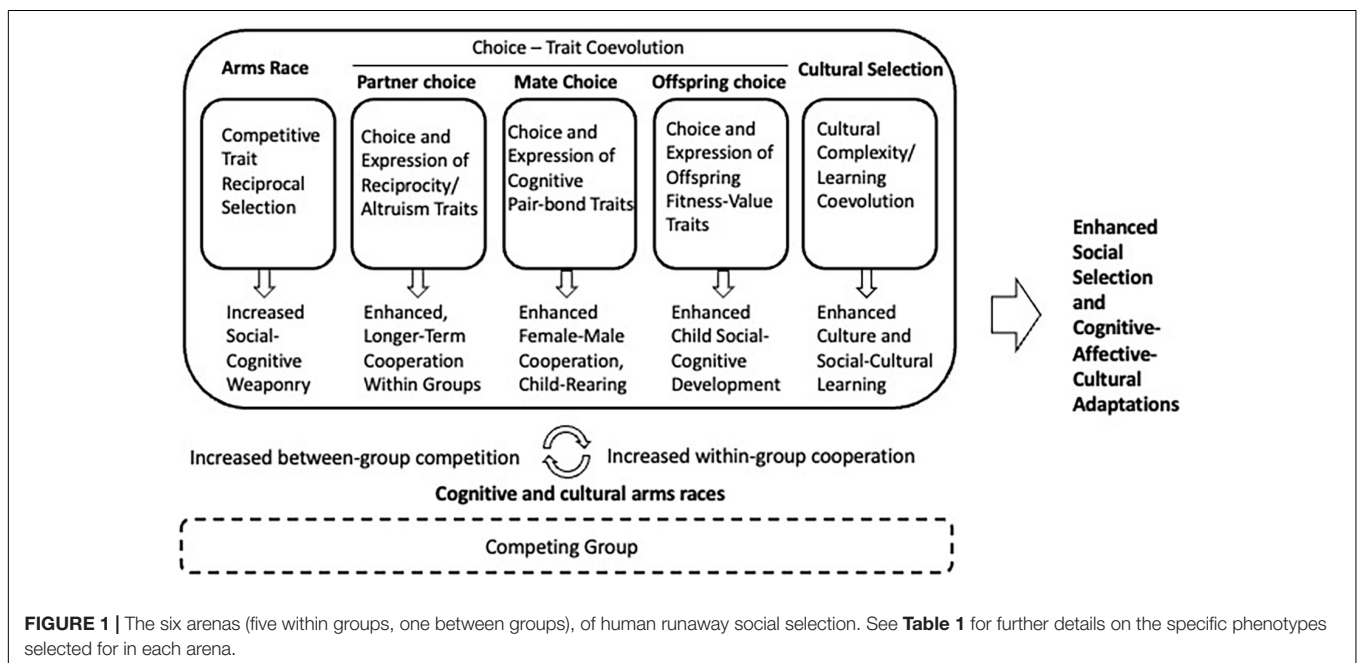
The six arenas of social selection described here each generates, given any degree of heritability, social evolution of sets of psychological traits and abilities that have collectively "made us human" (**Table 1**). What is striking about these sets of phenotypes is that they encompass a tremendous range of human-elaborated psychological and social traits, many of which are expected to be reinforcing across arenas (e.g., honesty and morality in partner choice and among-group arms races), transferrable across domains (e.g., finer-scale social discrimination in caregiver choice, partner choice, mate choice), or complementary (e.g., abilities to compromise with, lead, persuade, or control other individuals). The effects of these interacting arenas of social selection echo the emphasis of Laland and Seed (2021) on "dynamical feedbacks between mutually reinforcing aspects of cognition," with human cognitive uniqueness arising from "trait interactions and feedbacks," with the salient traits evolving squarely in the context of complex sociocultural landscapes (see also Dean et al., 2013; Whiten, 2018; Lombard and Högberg, 2021; Spikins et al., 2021). As such, runaway social selection and evolution appear to exhibit the breadth, power and scope to help explain, in principle, how modern humans evolved psychologically from chimp-human ancestors.

DISCUSSION

Uncovering the selective pressures that gave rise to the first hominins, and to modern humans, has been a perpetual challenge ever since Darwin drafted the first clear hypotheses of human origins in 1871. From a broad perspective, it makes sense that the most exceptional human features, large social brains, complex cooperative and competitive interactions, and elaborate culture, should themselves reflect the selective pressures that guided their evolution. The logic of runaway social selection suggests that humans generated and became their own primary selective pressures, through diverse forms of arms races within

TABLE 1 | Phenotypes and abilities postulated to be selected for, in six different arenas of human social selection and evolution.

Arms races within groups	Partner choice	Mate choice	Caregiver-offspring relationship	Cultural traits – social learning	Arms races among groups
Joint attention; Scenario-building; Theory of mind; Leadership; Manipulation of status; Social creativity; Persuasion; Coercion	Loyalty; Honesty; Reputation; Social status; Sustained reciprocity; Fine social discrimination abilities	Fine discrimination of cognitive, emotional, physical traits and abilities; Ability to navigate psyche and behavior of mate Enhanced physical, reproductive and survival abilities	Infant, child eye contact, smiling, laughing, early language development, secure attachment; Social development, maturation in childhood, adolescence Fine discrimination of offspring traits	Enhanced sophistication and efficiency of social learning about cultural norms, including aspects of language, religion, customs, arts, rules and laws, institutions, technology, and resource acquisition methods	Parochial altruism; Ingroup morality; Heroism; Xenophobia; Complex within-group cooperation; Dehumanization of other groups

FIGURE 1 | The six arenas (five within groups, one between groups), of human runaway social selection. See **Table 1** for further details on the specific phenotypes selected for in each arena.

and between groups, and through choice-trait coevolutionary-dynamic interactions involving allies, mates, and offspring with caregivers. By the hypotheses presented here, each of these arenas of social selection drove the evolution of different, interacting dimensions of human sociality and culture, that merged to create the humans inhabiting our world today (**Figure 1**). This hypothesis is by no means incompatible with those based on other selective pressures postulated to be important in human evolution, such as alloparental care (Hrdy, 2009; van Schaik and Burkart, 2010) and self-domestication (Wrangham, 2019), but it stresses the importance of runaway social selection as a potential key factor in how and why modern humans evolved.

Tracing the selective history of humans relies on one part evolutionary logic, one part ecology, one part psychology and neuroscience, one part anthropology, and all parts grounded in phylogeny and evidence from archeological remains. An enduring part of the puzzle, the initial divergence of the eventual *Homo* and *Pan* lineages, is addressed here with the hypothesis that the divergent evolution of hominins was "kick-started," in an ape with a small (i.e., 400 cc) brain living at relatively low densities, by ecological conditions that favored increased fluidity, connectivity, tolerance, and especially local cooperation within and between small social groups. At first, such cooperation need not be sophisticated or complex, and need not involve larger brains. But when conditions eventually arose that allowed the evolution of larger and more complex brains (e.g., cooking of foods, and use of more energy-dense foods), and the first manifestations of culture, such early humans would have been poised to enter a socio-ecological niche characterized by increased population densities, larger brain sizes, enhanced competition and cooperation, cumulative culture, and strategic social choices, that collectively encompassed the multiple mechanisms of runaway social selection described above.

Increases in understanding of Darwin's (1871) "insensible grading" from an apelike form to humans requires clear and specific hypotheses that make testable predictions. Indeed, a primary criticism of the runaway social selection model is that it lacks concrete empirical support, in terms of the specific processes involved. The mechanisms that underpin the

hypotheses described here, especially those relating to choice-trait coevolution among allies, mates, and offspring-caregiver interactions, can, however, be evaluated in extant human groups, and ecological benefits from relatively simple primate alliances can be evaluated in field populations using the most relevant taxa. In particular, empirical evaluation of the hypotheses described here regarding social selection in human evolution will require testing for evidence of the operation of each proposed process and link in the causal positive-feedback cycles, especially in small-scale human societies. The hypotheses would thus be falsified by robust findings that the within-generation processes that underpin runaway social selection, in any given arena, do not occur in human societies or, if they occur, do not impact upon variation in inclusive fitness. Neurology and neuroendocrinology may also provide salient evidence of mechanisms for social competition (Dunbar and Shultz, 2007; Rilling, 2014; Shultz and Dunbar, 2014), and the evolutionary transitions of brain evolution (Sherwood et al., 2008; Sherwood and Gómez-Robles, 2017; Stout and Hecht, 2017; Bruner, 2021). Although the challenges inherent in all analyses of the broad scope of human evolution are daunting, the intellectual rewards remain profound, in better comprehension of just what we as a species are, and how we came to be.

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All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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