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CHAPTER 15

Evolutionary Selection and the Nature of Humanity

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Although the essentials of organic evolution have been understood for almost 150 years, evolution is still controversial as a general explanation of life and all its traits. It is particularly difficult for people to see evolutionary selection as giving rise to the more complicated aspects of life such as learned and other modifiable traits of humans. Evolution as a process is simple enough that many doubt it can be related in any explanatory way to human culture and history, regardless of the time available for it to operate. I consider this general problem and suggest possible connections between aspects of evolutionary selection and human performances in some difficult areas such as the arts.

CONNECTING LIFE'S SIMPLICITIES AND ITS COMPLEXITIES

More than two-thirds of a century ago, in *The Causes of Evolution*, J. B. S. Haldane (1932/1966) remarked that he would find it easier to be in sympathy with those who believed that consciousness could not arise from a nonconscious state were it not for the fact that this transformation happens in front of us all the time, in the development (ontogeny) of every normal child. The alternative is to imagine some

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kind of homunculus that could be carried in the sperm or the egg so that it would arrive fully formed in the newly formed single-celled zygote or would somehow be suddenly created there.

Others assume the problem to which Haldane alluded when they argue that humans are too complex to have evolved gradually from the simplicity of single-celled organisms. Of course, complex human individuals arise from single cells every time a fertilized zygote is successful. If it can happen during ontogeny, we may, like Haldane, be sympathetic to the idea that it can happen during evolution. Doubts paralleling those responsible for Haldane's observation continue to be raised regarding the background of the complexity of human culture and sociality, even—or maybe especially—among intelligent and educated people who may be intoxicated with the splendor of the arts, and of culture in general, and perhaps reluctant to entertain the possibility that reduction is a suitable tool for entering into the analysis of such grand human enterprises.

The process of organic evolution that underlies all life is dominated by the uncomplicated subprocess of selection, or the differential survival and reproduction of any and all heritably different and persistent units. Examples of such units are genes, chromosomes (which occasionally recombine), and asexual microorganisms that fission without genetic recombination. These units all persist for extremely long periods relative to the rates at which they are altered by mutation. Because the effects of mutations are random with respect to their usefulness for the organism, in the absence of selection mutations have extremely low likelihoods of generating complexity. Even that unique concentration of function, the sexual organism, can be viewed as a stable unit since, though by definition it lasts on average but a single generation, it still undergoes a vast number of cell divisions and thus many replications of genes (most of which, of course, are destined not to continue, dying with the individual as part of a disposable soma).

The claim by biologists that evolutionary selection per se can yield only traits that maximize the genetic reproduction of their bearers—and that therefore this must be the underlying basis for all human traits and tendencies—jarred sensibilities on a wide scale because it was unexpected and for many seemed from the start to be unlikely and even insulting. How could the massive and variable patterns of culture across the globe and the overall history of humanity, not to say the multiplicity of motives and meanings in the makeup of each of us as individuals, arise out of such a simple and ignoble process as maximizing the reproduction of our genes, more explicitly the reproduction of a few copies of those genes hidden away in our sex cells?

Objections to the claim take at least four forms. First there are those who seek to deny potentially unpleasant outcomes by denying evolution itself. But the process of organic evolution has become an easily observable fact; it is no longer theory. The theoretical nature of evolution today, the challenge for those who seek to falsify, is whether any traits of life—any at all—can be shown not to be outcomes of the process of evolution (Alexander 1978, 1979a).

Second, until recently there could be no broad evolved tendency (not necessarily conscious) to behave as if all human activities—and indeed all activities of all life—might exist because in some way they have served the survival (through reproduction) of unrecognized entities (genes), too small to be viewed even with the magnifying and analyzing devices we began to improve rapidly two or three centuries ago. The human opportunity to evolve to generate particular views on such matters is at least tens of thousands of years old; therefore, whatever views humans in general have held arose in the absence of an understanding of the reasons for those views existing, or any way of approaching that question. This situation is unlike that giving rise to the broad, correct, and apparently evolved intuition that individual interests tend to conflict, evidently arising out of the fact that sexual recombination has across our entire evolutionary history rendered genotypes unique. The enormous difficulty we (including those of us in science and medicine) have experienced in trying to understand the finiteness of individual lifetimes supports the notion that we have not evolved an intuitive understanding of the primacy of particles too small to observe directly.

Third, we typically recoil intuitively from the seeming banality that reproduction is the ultimate function of human activities. This reason is of special importance because, oddly, we are probably evolved to reject reproduction as an explanation for our own tendencies and capabilities, even though we are somewhat willing to accept it for other organisms (see below).

Fourth, evolutionists have not yet been able to describe in detail how evolutionary selection could take us, step by step from its effects on different genes to the appearance of cultural complexities such as the arts, without needing to claim, at one point or another, “Now here a small miracle takes place” (but see Alexander 1979a, 1989, 1993). Some biologists won’t like my using the word *miracle*, but until we bridge the gaps to our own satisfaction, the problem remains.

For some reason it seems to be more difficult for us to visualize a transition, via organic evolution, from the simplicity of differential genetic reproduction to the grandeur of the human scene in all its personal intellectual profundity and collective social drama, than to visualize a transition from absence of consciousness

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to presence of consciousness or from zygote to adult organism during ontogeny. At one time or another anyone will sympathize with the attitude that evolution simply cannot explain humans; such gloom has even descended on an occasional world-class evolutionary biologist.

During a recent discussion of the basis for the arts, one participant commented, “Maybe a person can have too much education.” He meant that it may be possible to know so much about human culture, in the various ways we have thought about it outside an evolutionary framework, that we reduce our likelihood of accepting a different (evolutionary) approach to the problem of its underlying basis or origins. Have human culture, knowledge, history, motivation, and thought been so elaborate and diverse—and have humans been oblivious to their probable basis and history for so long—that to become absorbed in the marvels of their manifestations is to become immune to recognizing or accepting their *raison d’être*? Can one indeed have “too much education” in the sense of being overwhelmed by the details of our collective history and achievements because of interpreting them without the guidance of potential causes so fundamental as to require stretching our knowledge and imagination into the logic of biology? Too much education to accept the reductionism necessary for explanation, for rebuilding and comprehending the story sensibly? Too much education in the arts themselves to allow sufficient effort to grasp the methods of science as a means of establishing facts, of reliably and demonstrably “getting it straight”? These questions are relevant to the extent that learning about culture or the arts occurs in the absence of a basic understanding of organic evolution as the only reasonable background of human activities and generates an attitude opposing the incorporation of any possible answers from the science of biology.

In the year 2000, Jacques Barzun published a remarkable 802-page volume titled *From Dawn to Decadence: 500 Years of Western Civilization*. A magisterial display of comprehension of many fields, including history, art, and literature, it deservedly won the National Book Award for criticism. Reading it through in admiration, one cannot doubt that some mentionable portion of Barzun’s intent was to understand and explain the basis for the arts. Yet he falters in all his brief mentions of the only likely ultimate and general underpinnings of culture: evolutionary selection. It is as if Barzun had written a book on sex without knowing about or accepting the existence of genes and meiosis—or perhaps anything at all below the level of the organism, even the genome as a whole. But the entire point of sex is to recombine those genes—and indeed to recombine only the particular copies that have a chance to be passed to the next generation, meaning the special ones residing in certain

places in the testes and ovaries, and scheduled to pass through the reduction division of meiosis and turn into sperm and eggs. It is fair to ask Barzun—and everyone engaged in parallel enterprises—what might be the corresponding “entire point” of culture, or whether there might be one, and how it might affect anyone’s interpretations of the arts. In 1979 I wrote on this issue as follows (Alexander 1979a, 68):

If human evolution, like that of other organisms, has significantly involved selection effective at genic levels, realized through the reproductive strivings of individuals, neither humans as individuals nor the human species as a whole have had a single course to chart in the development of culture but rather [because of the ubiquity and consistency of genomic differences among individuals as a result of sexual recombination] a very large number of slightly different and potentially conflicting courses. In this case it would indeed be difficult to locate “a function for” or even “the functions of” culture. Instead, culture would be, as Sahlins[’s] [1976] view may be slightly modified to mean, the central aspect of the environment into which every person is born and . . . must succeed or fail, developed gradually by the collections of humans that have preceded us in history, and with an inertia refractory to the wishes of individuals, and even of small and large groups. [Even if accumulated via cooperative efforts of members of human groups,] culture would represent the cumulative effects of what Hamilton (1964) called inclusive-fitness-maximizing behavior (i.e., reproductive maximization via all socially available descendant and nondescendant relatives) by all humans who have lived. I regard this as a reasonable theory to explain the existence and nature of culture, and the rates and directions of its change.

Flinn and Alexander (1982) pointed out that the adaptiveness of culture, as cumulative social learning, can be maintained by judicious imitation and anti-imitation of the behavior of others and decision making from direct observations of adaptive outcomes, including evolved proximate mechanisms such as pleasure and pain. Such evidence can also come from discussion with others about either proximate effects or adaptive outcomes. Eventually it can include analyses of long-term effects of actions: for example, painful or strenuous acts that nevertheless lead much later to positive effects can be interpreted accurately (adaptively). We are also capable of working out entirely in our own heads the likely outcomes of observed or even imagined actions through scenario building. (For discussions and examples, see Alexander 1979a, 131–33, and 1990b, 7–8.)

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On the surface there seem to be many problems with the argument that humans, and other forms of life, are evolved to maximize inclusive fitness: adoption, asymmetrical treatment and marriage of cousins, the so-called avunculate (or “mother’s brother” phenomenon), and the “demographic transition” are examples. A substantial literature shows that most of these seeming problems have been misinterpreted (e.g., Alexander 1979a, 1988, 1990b). Thus across history nonrelatives were rarely adopted except as workers or slaves; cousins identified as such by ethnographers are not necessarily cousins; asymmetries in arranged marriages between actual cousins tend to reflect the interests of powerful parents; there are reasons from cousin marriage patterns and confidence of paternity issues to expect men sometimes to tend a sister’s offspring more than a spouse’s offspring and to expect uncles to tend their future sons-in-law in order to control their behavior toward the uncle’s daughters later; and lowered rates of child production are not evolutionarily antireproductive when there are climbable ladders of affluence that can influence offspring success enough to offset using the resources to increase numbers of offspring less well tended (Alexander 1988).

Incidentally, I am deliberately vague or imprecise in my usage of terms like *culture* and *the arts* because I would rather err on the side of inclusiveness. I am not using either an anthropological view of culture or an impression from the humanities. Rather, I wish to assume the problem of somehow rebuilding the explanation of it all because, even if I cannot clarify all of the underlying forces, I think there are such forces general enough to apply to culture and the arts, however defined.

The problem we face in reconciling ourselves to reductionistic biology—and then mastering the synthetic chore of reexamining culture all the way from meme to magnificence—parallels the problem faced by molecular geneticists now that they have described the human genome. To understand the organism—the most important focus of our attention—molecular geneticists now must begin to comprehend ontogeny, progressive changes in the individual organism as it grows and develops—changes that are evolutionarily justifiable only if they increase the reproduction of the organism’s component genes sufficiently to overcompensate the delay and risk entailed by evolving a juvenile life. We onlookers tend not to deny that the molecular geneticists will eventually understand ontogeny; at least we don’t deny it in the way that we may tend to deny the prospect of getting from evolutionary selection to the arts. But we may doubt that anyone yet comprehends the complexity of the ontogenetic proposition. As organismal biologists, some of us may also wonder if molecular biologists are yet on the right track, one reason being

the misleading aspects of early concentration on rare gene effects correlated with rare disorders. Such rare gene effects may have immediate medical significance, but because they have had little chance to be integrated into the genome they probably have little general significance for understanding either the complexities of ontogeny or the human organism as a composite of adaptive (and incidental and not-so-adaptive) traits.

The genome biologists, in this new and obligate challenge of synthesis, must find out how to get from a paltry thirty-one thousand functional genes (or, controversially, a few thousand more) to an organism of many trillions of complexly divergent and organized cells—a organism that may be able to carry out many times thirty-one thousand different actions (physiologically and behaviorally) during almost any split second of its life. Further, whatever the mechanisms, all those actions have presumably been directed by evolution to serve a single function—a function brought into exquisite coordination by the unmatched and unified complexity of the organism, and commonsensical because of our realization of the organism's existence and nature (Alexander 1990a, 1993). By every logic the organism's singular function has to be an on-average equal reproduction of the genes that compose the genome and are variously and predictably represented in the genomes of its relatives. Molecular biologists have started the task—for example, working out the “proteome”—but the distance from proteins to the arts appears almost as incomprehensible as that from genes to the arts.

Given that this whole proposition appears to be so difficult, or even ridiculous, one might ask: Why even think about it? Why argue that humans, modular or not in their individual makeup, are evolved to do but one thing, to reproduce their genes? The underlying and seemingly irrefutable logic is that the genes of any unitary organism acquiring any traits that did anything else at all could not have competed across a single breath of history with others that did no such frivolous thing. In terms of everyday organismal mechanisms there may be no universal adaptation of the organism, only lots of flexible and not-so-flexible evolved and developed mechanisms or modules: lungs, heart, kidneys, liver—circulatory, alimentary, excretory, neural, and muscular systems—and a brain full of geographically localizable modules with separate although coordinated effects. It is worth remembering, however, that none of the individual adaptive mechanisms of the whole organism can be optimized in its particular subfunction. All are necessarily compromised to serve the unitary function of maximizing the success of transferring those paltry few germ cells into the next generation, in packages that, with parental assistance, will be able to do it all over again when their times come. Nothing else

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works. So it is worth trying to find out if the reproductive-end-all hypothesis has something to offer the students of meaning, culture, the arts, and all the rest.

Dobzhansky (1961, 111) said (so long ago!) that “[h]eredity is particulate, but development is unitary. Everything in the organism is the result of the interactions of all genes, subject to the environment to which they are exposed. What genes determine is not characters, but rather the ways in which the developing organism responds to the environment it encounters.” Every part of this thoughtful statement returns us to the suggestion of singular function, and simultaneously to the realization that ordinary genes (i.e., excluding effects of rare genes coincident with rare disorders) cannot be linked in any simple way to singular subfunctions of the organism. Dobzhansky’s statement challenges biologists with the staggering proposition that all genes well integrated into the sets of diverse genomes appearing in their population are somehow both pleiotropic and epistatic.

We are continually reminded of the enormity of the problem Haldane mentioned and Dobzhansky specified, that of ontogeny, of development, of understanding the whole organism and its fabulous phenotypic flowerings. Sir Charles Waddington (1956) called the break of understanding between zygote and organism the “Great Gap” in biology, and it still is that (Alexander 1990a). Ontogeny is not merely less trivial than distinguishing all the genes: its consequences make up the most astounding temporal and spatial concentration of complexity known in our universe. In terms of the size of the paper map of human genomic alternatives mailed out not so long ago by *Science Magazine*, we might wonder if a comparable map of normal ontogenetic alternatives in our species across any brief time period would, say, cover the surface of the earth.

UNDERSTANDING TENDENCIES TO DENY THE SIGNIFICANCE OF REPRODUCTION

Suppose we return to the question of skepticism. If we are evolved to reproduce and nothing else, why can’t we just accept it, even if we did not actually evolve to do such accepting? Why should our imaginations seem incapable of grasping the reproductive significance of every one of our acts, or at least be reluctant about it? Such feeling does not arise out of mere disgruntlement over reductionism—at least reductionism any more worrisome than that essential to all analysis. The most devoted student of meaning would not argue that difficult analytical problems can be solved without being temporarily reduced to manageable components (Alexander 1987).

Reproduction is a selfish act, meaning only that it serves the life interests of the reproducer. Surprisingly to us organism-centered observers, because reproduction refers to genes rather than organisms, reproduction (leading to survival of the genes) rather than mere survival (of the organism) is the ultimately selfish act.

Despite our human powers of observation—of our fellows if not ourselves—would any of us wish to be found guilty of a selfish thought or act—let alone a basically selfish nature? Who wishes to live or cooperate with either an avowedly or a sneakily selfish person? The very concept is intensely negative. Hence, perhaps, the occasional effort, still, to dismiss the messenger with the epithet “vulgar sociobiologist.” But why, after all, do humans have those keen powers of social observation that we know can ferret out the most minuscule evidence of selfishness, later to be exposed and brandished? Is it possible that we intuitively reject the reproductive end-all because we just don’t want to be the ones bringing up the possibility of pervasive selfishness? That we don’t want any soul imagining that we personally might be condoning selfishness in any way, shape, or form? Yet selfishness begins with the observable and entirely acceptable everyday process of simply staying alive and healthy. The incredible expense of medical science and practice, insurance, and all the rest attests to the magnitude of our concern with this problem. In terms of the reproduction of genes, selfishness also includes all the beneficence we extend judiciously (and comfortably and righteously) to our collections of relatives—beneficence that sometimes is virtually demanded by both morality and law for the selfish reason that the rest of us do not wish our tax monies or other resources to be utilized for the job.

As has been explained at length since Trivers (1971), reproductive selfishness also includes every act of beneficence to even nonrelatives if such beneficence has a sufficient likelihood of being reciprocated with interest, whether the return comes directly from the benefited parties or indirectly—for example, via the establishment of a reputation for beneficence that brings hopeful returns from observers not previously involved (Alexander 1975a, 1979a, 1993). It is difficult to imagine that anyone invests in the stock market for altruistic reasons; perhaps no one invests in anything at all (except relatives) without expecting (not necessarily consciously) phenotypic rewards that include some kind of interest on the investment. Perhaps, because reproductive selfishness in others is likely to be contrary to our own reproductive interests, and efforts at influencing others sometimes work, we could actually be evolved to reject reproductive explanations of ourselves (unconsciously), without knowing enough about such a possibility to accept its reasonableness consciously. The reason is that such rejection is one way of convincing others that we are good candidates as partners in social reciprocity—in other

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words, because such pretensions are a way of influencing the behavior of others in directions that serve our own reproductively selfish interests. All of these considerations must be judged with the knowledge that humans have, for some reason, evolved to live in groups, within which they both cooperate and compete, and outside of which they presumably failed consistently. They must also be judged by the realization that some acts of seemingly costly beneficence within human social groups may correlate with total reliance of individuals for their own reproductive success on the continued success of the group: that now and then individuals' interests correspond almost exactly with those of the group.

In the wake of having specified the human genome, the molecular biologists and their universities and the associated manufacturers of profitable medicinal molecules are currently constructing multi-billion-dollar research pathways called "life science initiatives." Their enterprise is the self-centered one of gathering the dollars to be derived from exploiting self-centered human urges to increase our individual and personal human life spans and our physical and emotional comfort. This is true even if we say that the entire enterprise arises out of the organizers' stated intents to help others (too). Without an underlying possibility that the research serves the interests of the (willing) sources of the funds, and the assenting taxpayers and voters, who can believe it likely that these projects would be so focused and so amply funded? As noted, these interests are defined around the concepts of personal survival and the right to generate and assist family. When happiness and good feeling are included in the formula, we have to consider that pleasure does not associate accidentally with actions that typically serve the above aims; neither pleasure nor pain has reason for having evolved to be expressed in any circumstance except when, in the environments of history, they lead to efforts to bring about acts that ultimately are reproductive (Alexander 1987).

If molecular biologists and universities can doggedly pursue their problems of synthesis, arising out of the reduction of the organism to a set of identifiable DNA molecules, then the rest of us—whether artists, humanists, economists, politicians, or social and biological scientists—can surely accept our own problem of synthesizing questions about meaning. Knowing our capabilities, we can surely be comfortable seeking the threads of connection between a fundamental reproductive motivation and the cathedrals of cultural splendor that have been generated across human history. At least we can accept others doing this, even if the effort seems to us unpleasant.

Science is for the most part the pursuit of broadly important facts, meaning facts that have the same or a similar meaning for large numbers of people—or all

people. In contrast, the arts are a pursuit of meaning, often in the sense of significance specific to individuals or small groups. As Barzun implied, poetry can be so personal as to be incomprehensible to virtually everyone but the poet (which, as we shall see, need not eliminate its importance for the status of the poet, hence his or her desirability as social or sexual partner). As already implied, there are good biological reasons for meanings often to be individual. In a sexual organism, every individual has a unique genome, therefore a unique composite of life interests (Alexander 1979a). That uniqueness of life pursuits happens to hold even for genetically identical twins only underscores the mechanism: because sexual organisms are overwhelmingly likely to have unique genomes, they can only evolve to behave as if their life interests are unique—even on the rare occasions when they are not. Disagreements between identical twins with different environments and environmental histories reflect that twins have been so rare, and so rarely successful, as to have little or no history of opportunity to respond to their genetic identity. Circumstances that are rare enough across history, such as successful twinning in humans, do not yield the ploddingly directional repetitions of selection that can elaborate distinctive traits.

In the end, do we not take whatever is known or assumed about every circumstance that can affect us and turn it to our own interests, however we interpret those interests? Sometimes, we accept that others (at least) even do it without conscious awareness.

To think about uniqueness of life interests, or of meaning, after accepting the framework of life interests being reproductive, think at first only of the unique collection of genetic relatives in the social realm of each individual. For humans, these collections of known relatives (kindreds) are huge. It is surely no accident that all human societies studied everywhere on earth are centered on extensive kinship systems that operate so as to match their circumstances to reproductive interests, no accident that humans everywhere know in amazing detail who their relatives are and how related they are and that they also have strong opinions about how much help they should be receiving—or giving (Alexander 1979a). The mechanisms of such knowing, when the knowing is coupled to differential nepotism, are in all cases known so far (in all animals) dependent on background patterns of social learning. There apparently are no magic cryptic mechanisms of differential nepotism, at least in humans, except those we can fool by modifying the situations of social learning (Alexander 1990a, 1991)—most of which are probably never conscious. That we use and depend on social learning to know and treat different kin appropriately in reproductive terms, and also the evolved finiteness of our

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individual lifetimes through senescence (e.g., Alexander 1987), should be every person's introduction to the evidence that genetic reproduction really is the evolutionary end-all.

Only humans distinguish a wide array of relatives; in the context of differential nepotism, most organisms appear to distinguish only relatives and non- (or distant) relatives, such as offspring and nonoffspring. Presumably, humans engage in extensive differential nepotism because (1) relatives are easily identified individually; (2) they remain near for life, or at least for long periods (at least across most of human history); (3) humans can use the kinds of beneficence relatives can supply; and (4) we have generated the mental mechanisms by which differential nepotism can be practiced in reproductively appropriate ways. The question is why this combination of features seems to exist in humans alone (see below).

What, then, can we do about the apparent absence of a satisfactory mechanism linking the lowest and the highest levels of function in human activities—linking, say, the operation of genes to the historical flow of the arts, and perhaps even Barzun's perception of cultural decadence? Our continuing ignorance of ontogeny means that we still have to start with the traits themselves rather than with the genes.

Supposed evolutionary analyses of human traits most often take one or both of two different forms: (1) efforts to explain the functional or phylogenetic origins of a trait (e.g., how—and perhaps when—did art or music or humor begin) and (2) efforts to explain how a trait functioned across some part of evolutionary history—so as to assume its present expression—as in the supposed “environments of evolutionary adaptedness,” sometimes curiously described for humans as (restricted to?) “the Pleistocene.”

A third perspective, assumed here and in most of my writing (e.g., Alexander 1979a, 1987, 1989), is to examine the current expressions and uses of a trait and from this effort attempt to postulate the function of the trait (in “the environments of history”) and relate the trait and the postulated function to parallel traits of other organisms by asking if a set of other traits or conditions correlate with the trait in a way that supports the presumed function. For an example including all three of these kinds of effort, see Alexander (1986, 1989) on humor.

A fourth approach, the one assumed by Alexander (1990b) and in the passage just below, is a comparative functional (reproductive) analysis of different and possibly related traits of the human organism—a kind of jigsaw puzzle or experimental-fit analysis of different unique or distinctive traits of a single species, all of which traits, because they are products of a natural selection elaborating a unified or-

ganism with the singular function of reproducing, are expected to work in concert and harmoniously (e.g., Alexander 1990b). This approach considers the human species—and in some ways its representative, the individual organism—as an N of 1 and in this sense parallels the efforts of theoretical physicists to identify and comprehend the nature and interplay of all the components of the single universe so far available to them for analysis. Students of the human species have two advantages over theoretical physicists: (1) occasionally homology with other organisms, because of phylogenetic relationships, remains useful (although the defining attributes of humans sometimes are so functionally distinctive that such comparisons lead instead to error); and (2) the immediacy, complexity, and predictability of evolutionary selection, absent in some sense from the physical universe, and leading inevitably to a kind of harmonious intricacy furthering the singular function of reproduction, yield a special kind of predictability for biologists. Biologists also have the disadvantages, compared to theoretical physicists, that (1) the human species, as with life in general, is immensely more complex than the physical universe as it is currently known; and (2) we are personally involved (thus different individuals and groups of humans sometimes have different and conflicting interests that are affected by particular findings or particular interpretations of the nature of the human species).

This fourth approach is also similar to an effort to understand any complicated novel machine, such as an internal combustion engine, which is also extensively modular and also has a single function—to produce certain torques at certain speeds on the drive shaft. With both the machine and the organism, if we can identify the function we can explore how each part contributes to that function and how the different parts work together to maximize it (Alexander 1993). As noted above, such an “experimental-fit analysis” of the traits of a single species can be combined with the better-known interspecific comparative approach using divergences or parallelisms (by phylogeneticists nowadays called homoplasies, as opposed to homologies) to discover the underlying selective reasons for traits (known as Darwin’s comparative method) (Ghiselin 1969; Alexander 1979a). This more usual interspecific comparative approach is difficult in analyzing humans because human distinctiveness—our singularity as a species and our phenotypic distance from our closest relatives—sometimes affords us few relevant comparisons. The second option, or approach, used in the final section of this chapter, calls for explanation via particular aspects or kinds of evolutionary selection, and that means we will need to classify different aspects or kinds of selection more effectively than before.

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No one should imagine that any effort to analyze human traits in evolutionary terms represents some kind of ideal cut-and-dried way to identify the truth, or, indeed, anything but a desperate effort. But desperate efforts can work, and if they are all we can muster we have no alternative but to use them whenever we think the questions are important enough to justify it.

TESTING FOR FITS IN REPRODUCTIVE SIGNIFICANCE AMONG UNIQUELY OR DISTINCTIVELY HUMAN TRAITS

If all of life function is understandable as reproductive, how might we discover that? Given the unique problems of verification in self-analysis and the impossibility of the usual kinds of repeatable, controlled experiments when humans are the test animal, one way is by first creating a list of uniquely and distinctively human traits, then seeking to describe, define, and connect these traits so as to demonstrate, if possible, that the only descriptions, definitions, and connections that make any sense whatever link their combined grandeur—which is us—inexorably and irrefutably to the genetic reproduction that modern evolutionary biology has helped us to despise. This is the kind of test attempted in this section. Some arguments that may seem skeletal here are more fully discussed in Alexander (1990b, 1996–97) and Alexander, Richards, and Lahti (in prep.); some will have to be filled in later by others.

We can begin with concealed ovulation (Alexander 1990b). If we have already postulated a plausible scenario for the reproductive function of this astonishing trait of the human female and then are able to show that under that explanation it connects reproductively to one after another of the other traits that distinguish the human species, so as eventually to create a network of interrelated traits that function in harmony with one another as reproductive adaptations, we will have provided a composite hypothesis that at least cannot be summarily dismissed. So long as everything continues to fit, and no other hypothesis has that same feature, we have generated the hypothesis (prediction) that still other traits of humans will fit the same construction. The more traits for which we find unexpectedly good fits, without ad hoc modification, the more likely we are on the right track. If the effort seems to fail with one or more traits, then one or more of our just-so stories is wrong and must be reconsidered, or else the entire proposition is in jeopardy. As long as we continue to succeed, however, we will encounter opportunities to falsify alternatives, particularly if the propositions that appear to combine

harmoniously around a reproductive function have a strong likelihood of being evolved adaptations.

Among mammals, concealed ovulation is either unique to the human female or extremely rare among other species. Most mammalian females do the opposite, advertising ovulation in what seem extreme ways. Some investigators, who believe that many mammal females conceal ovulation, are talking about something different from what is being discussed here. They are talking about ovulation concealed only incidentally from other species (such as human observers), as with ovulation advertised by odor alone, “concealed” from species like the olfactorily deprived human one, or about ovulation designed to be advertised across only short distances but nevertheless advertised, not concealed.

In undertaking this discussion there is no reason to worry whether concealment of ovulation ever became perfect: any evolution that seems to be in the direction of concealment is enough to startle the evolutionist. The human female conceals ovulation not only from human males but also largely from herself. If both facts were not true, human males—maybe even those merely “standing on the corner watching all the girls go by”—could sort ovulators from nonovulators; if that were possible, and if forced copulations could be thwarted, birth control by an ovulation-recognition method would be relatively easy and inexpensive.

Because ovulation is displayed elaborately in nearly all mammals, forms of it seen as cryptic may be evolving in the direction of concealment, perhaps in the sense of restricting its evidence to local males only. To show that evolution has achieved complete concealment one need only show that no one within the species is using ovulation as a social or sexual signal; that ovulation can be detected in test situations, or using modern technology—by either observers or by ovulating women themselves—is insufficient. If ovulation is not actually used in normal life situations, then, like a recessive allele in the heterozygous state, it can be assumed to be hidden from participants and thus from the action of selection.

What could possibly be the point of concealing ovulation? For starters, it disenfranchises the males whose strategy is to monopolize females only during ovulation and then to abandon them to look for still others that are also ovulating. A male’s only insurance of paternity is to stay long enough to ensure the female’s pregnancy. If she conceals her ovulation, this time may incidentally be long enough to establish at least the beginnings of a bond. If a male is remaining near a female, who for that reason is likely to produce his offspring, it may behoove him to protect her—at first, maybe, only from other males so as to give himself paternity, but eventually from all sources of danger because she, as the bearer of his children,

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has some likelihood of becoming for him the most important female—indeed, the most important other individual—in his species. Moreover, if there is any seasonality at all to ovulation, the longer he protects her the less his chance of accomplishing the same with another female. The benefits of staying and the costs of leaving each continue to grow. The male is increasingly placed in a position to be behaviorally as well as genetically parental. The “spousal” pair has an increasing chance of effective social cooperation, which increasingly raises the value of the female to the male, compared to other females. The opportunity thereby generates for a trend toward offspring having two tending parents. As more parental attention becomes increasingly important to the offspring’s success, for whatever reason, not only will males looking merely to identify ovulation lose in the race for successful reproduction, but so will females who advertise ovulation.

Does all of this fit with anything? Consider the human baby. It is by an astonishing degree the physically most helpless (or altricial) of all primate babies. Altriciality is one of its two most distinctive features, the other being the rapid expansion of its brain function. What is the point of the special human trait of infant altriciality? In other mammals and in birds it goes with either being hidden or being protected; in many birds and a few other mammals it goes with having two tending or protecting parents. An altricial baby is one that can afford to put all its calories into being a better individual later on—a better late juvenile or a better adult. By being altricial, a juvenile of any animal is telling us that throughout its evolutionary history it has not gained sufficiently by putting its calories into the alternative strategy of personal protection: it has not gained by being precocial. Something else has been taking care of that: two parents, an inaccessible or hidden nest (or both), a pouch on mama’s belly. Altricial babies grow faster (Ricklefs 1983, and discussion in Alexander 1990b). In particular the human baby, because of its altriciality, is able to grow an enormous and calorically expensive brain very rapidly. Consequently, and because of parental protection and teaching, it is able to turn a higher proportion of its expanding attention to learning about the social issues that some biologists believe responsible for the evolution of the uniquely complex human brain and therefore the unique human repertoire of social complexity. Perhaps we have gained a clue about the reason parental care became so important, therefore why concealment of ovulation evolved.

Human female and male parents not only share parental care, one way or another, but also tend the baby until it is an adult—today for life or longer sometimes (e.g., via inheritance). Correspondingly—and unlike altricial songbirds in dangerous nests and altricial parasites in temporary habitats (which use their al-

triciality to grow rapidly and escape the danger)—the human baby has evolved a *long* juvenile period, arguably with aspects extending beyond the second decade of life. Because of the expense of delaying reproduction, the consequent necessity of an overcompensating increase in reproductive likelihood, and the benefits of extended and multifarious social experiences for all young humans, the long juvenile life of humans fits easily into our chain of probable connections. Already we have causally linked—seemingly in a remarkably plausible way—several unique or distinctive human attributes: concealment of ovulation, biparental care, long-term spousal bonds, infant altriciality, rapid brain evolution, long juvenile life, and social complexity. Perhaps we are getting somewhere.

Another distinctive human trait is worthy of mention in this same context: menopause. Originally menopause was viewed as simple aging, as an antireproductive refraining from adding mutated offspring into the population, or as something that happened after the age when most women would have died. These arguments have been refuted or cast in doubt (Alexander 1990b), though the medical profession for the most part continues to view menopause as a pathological condition to be remedied by drugs, even when those drugs have deleterious side effects. In the human female, menopause is a programmed event that occurs almost midway during the average maximum adult lifetime. If it were incidental or accidental we should see its counterparts everywhere, and we do not. The most interesting postulated reason for menopause, which may also be the one most likely to succeed, is that it optimizes not merely parental care but the tending of the entire local collective of genetic relatives, which can profit in unusual ways from the wisdom and skills of an astute and diligent middle-aged female relative. Given intense and long-term maternal care, there will come a time in her life when the human female can profit by taking care of the variously dependent descendants she already has, in place of producing still more. At minimum she should stop producing children after producing the last one that she has a good chance of rearing to successful independence. At most she might be expected to use her postmenopausal period to tend all of her existing offspring, as well as other kin that need help she can give, to gain and use all the influence she can on who gets what from whom and why. In either case, the apparently unique human attribute of menopause, if indeed evolved, appears explainable only as a reproductive trait, closely connected to extensive nepotistic care. The greater the amount of parental care and other kin care given by a human female, and the longer it is important to the offspring, the more likely is the evolution of a cessation of ovulation long before the average maximum age of death.

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Kin care can be important only when sociality causes individuals to live in extended families in which close genetic relatives profit from continuing to associate throughout their lives. As noted, that is surely the situation in which complex kinship systems have always become established and maintained. It also provides a special situation demanding special parental and (other) kin care: complex social competitiveness within the social group, the force described earlier as possibly accounting for the evolution of a rapidly developing brain as a consequence of altriciality.

So to the above list of seven traits we can add menopause, extensive and complex kinship systems (meaning knowledge of them and actions with respect to them), and probably consciousness and extensive learning and social memory. This set of a dozen or so traits places us well along on the road to understanding the human species, assuming the traits are all functionally connected as implied. If they are functionally connected, in the way here suggested, then it is not surprising that we seem to understand each of them better than before. They not only start a description of the human species but are consistent with the idea with which we have conducted the analysis: that reproduction is the evolutionary end-all. The functional connections that seem to have dropped into place were generated from that beginning.

WHAT IS SPECIAL ABOUT HUMAN SOCIALITY?

The essential and underlying question keeps re-emerging: Why the complex human kind of sociality? Thus why a big social brain—including the elaborateness of this thing we call consciousness—and all the possible connections to it that have just been hypothesized? Complex sociality is the central question for the explanatory efforts of not only a Jacques Barzun but every student of human biology. Whatever causes it, or enables it, distinguishes our species and apparently has driven the evolution of many of our unique and distinctive features. What might have taken us in this particular direction? What has been different about the effects of selection on our ancestors—about the reproductive history of our species?

Selection cannot favor social abilities in the absence of social life. In all those life forms in which social organization resembles that of the genes in the genome, and in which the social group approaches the nature of the organism as a group of cells, sociality is relatively simple (e.g., all eusocial forms, with queens and workers typically in huge nuclear families). Conflicts of interest have been dramatically

reduced. In genomes, each gene (allele) almost always has an equal chance of being represented in a sperm or egg cell; in a eusocial form each worker usually has an equal chance of having its genes represented in the queen's eggs, and, as with the somatic cells in an organism, evidently a better chance than in having them represented in its own offspring. As with the incredibly numerous and divergent clonal cells of the body—each with the same complement of genes, and the same one as in the testicular and ovarian cells—agreement and cooperation are efficiently blind to details that might involve complicated decisions, conscious contemplation, and the building of alternative possible scenarios for future use. As human organisms, however, we are not blind to the details of complex and sometimes rapid decision making because they are central in our form of sociality. But why are humans so distinctively social, among all organisms, as to evolve a brain apparently uniquely capable of complex social learning and extensive scenario building, in the company of all of the other special, often related human features?

We can begin with the fact that the complexly social wasps, bees, ants, termites, naked mole rats, and all the other species that biologists call “eusocial” (Alexander, Noonan, and Crespi 1991) live in large social groups that are actually nuclear families: mother and offspring or both parents and their offspring. The large social groups of humans are not nuclear families—or faint divergences from such. Though we have generated huge governed units displaying various degrees of unity (patriotism), our nuclear families remain small within them. And we do not parallel the eusocial forms, or the genome, in allowing a few of our fellows (or cells) to do all the reproducing. Instead, as individuals we all begin our lives expecting to reproduce, and, significantly, we seem to treasure that right beyond any other. We have to be impressed by this often overlooked fact about human reproduction, which is responsible for maintenance of a high level of competitiveness within the group, no matter how unified it may be on occasions when the entire group is threatened.

But this fact alone describes nothing in human sociality that is even remotely close to being unique. The same is true of large numbers of social mammals and birds: they live in complexly social, often multimale groups in which all of the individuals “expect” to reproduce. So how are we different?

Consider again our first collection of apparently connected attributes—all the way back to concealment of ovulation and biparental care. Here is another human feature that is unique among mammals: we are the only mammal species that lives in more or less permanent multimale social groups in which considerable paternal care is directed at particular offspring of females. Said differently, we are

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the only such mammals in which males have a reasonable confidence of paternity and exploit it. So now we have targeted a new question: why we should have come to live in groups so potentially disruptive—thus costly to us—and how we manage it (cf. Alexander 1990b).

There is an enlightening side question. Many bird species—but not mammals—live as humans do, meaning in multimale groups in which both sexes give parental care to their particular shared offspring. How do they do it without being like us in other regards? Birds are unlike mammals in a central feature that is also revealing with respect to the original contention of the centrality of reproduction. In mammals, the female retains the egg after its fertilization and tends the embryo internally. As a result, fertilization takes place “high up” in the oviduct inside the mammal female and then moves farther “up” (meaning farther from the body opening that is the source of sperm) into the uterus, which implants the fertilized ovum and subsequently nourishes the embryo. In such cases we can speculate that, in mammals, compared to most birds and most arthropods, it is more likely that the first sperm (or ejaculate) in wins the race to the egg: first sperm in, that is, at particular times with respect to ovulation.

Birds, arthropods, and other egg-laying organisms are variously different, even though birds are so poorly studied in this regard as to leave open many questions about the nature and degree of their difference from most mammals (possibly excepting those, like bats, that store sperm). Arthropod eggs are typically fertilized just before being laid, and if sperm are stored, they are stored near the external entrance to the female’s genital tube; the last sperm deposited thus tend to be closest to the egg that is to be fertilized as it is being laid. In birds the fertilized egg acquires a hard shell and is deposited externally before much development of the embryo has taken place. It seems less likely to be the case in birds (generally) that, as in mammals, first sperm in wins the egg. Instead, as with perhaps most arthropods, it must often be virtually the opposite. With the expectation of many qualifications—and the certainty that there are significant unanswered questions about precise mechanisms—the last sperm (ejaculate) in can be more likely to win the egg. Apparently, a prospectively parental male bird can ensure paternity with more effectiveness by frequent copulation at the right times just prior to egg laying (or shell-ing), if another male has recently copulated with her, than is true for mammals. Males of monogamous songbirds, in which both sexes sometimes cheat, in fact tend to mate frequently with a female that has been out of contact even briefly; by being parental later on, males act as if they retain high confidence of paternity; male mammals, including humans, may often copulate with a mate that has just strayed,

but they are probably less likely than male birds to be devoted parents afterward. Whatever details are eventually worked out, we have good reason to believe that mammals and biparental social birds differ in ways like these, important to the difference between them with respect to paternal care in multimale groups. In this connection it is worth considering that in many birds the intromittent organ is very small or virtually absent.

So we are back to concealed ovulation, and it is appropriate to add one more to our list of distinctive human traits related to both reproduction and one another. Humans are also said to be the sexiest of primates—or perhaps mammals—because they copulate so frequently and seem almost constantly preoccupied with sex. One might say, “How else to ensure fertilization if ovulation is concealed?” That might be a suitable explanation early in the history of human evolution. But for modern humans we need to put a different slant on it: given the importance of a long-term pair bond in any species in which both parents tend mutual offspring with long juvenile lives to near adulthood, rates and patterns of copulation in modern humans may have evolved so as to have little to do with the actual production of babies—at least within bonded pairs. Instead, copulatory rate and pattern may have been shaped to initiate, elaborate, and maintain the parental bond. We can hypothesize that the human marriage, spousal, or mating bond is evolved as a parental bond, cemented and sustained—at least during the years of offspring production—to a significant extent by sexual activities. That a parental bond also sets up opportunities for cuckoldry, which lead to special aspects of copulation in social groups, can be left aside for the moment because we at least know that cuckoldry has not yet led to the disappearance of paternal care in multimale groups of either the human species or many bird species.

The parental bond function for copulation can work if such rates and patterns as sustain the pair bond incidentally cause fertilization and the production of babies at a maximal rate or in an optimal pattern. Certain trends and traits may not be explainable except from this hypothesis: examples are copulation during pregnancy and after menopause; ultimate replacement of copulation with other bonding mechanisms such as affection and social and emotional compatibility after the end of baby production; and the linking of copulation more to intimacy and bonding and less to orgasm, especially by the sex (female) that is more vulnerable with respect to receiving parental care from the other. Notice that these arguments assume that human life length is set so as not to interfere with the continuation of parental care and therefore also assume a continuing value for effects of bonding between the parents of any individual. It may at first seem paradoxical that the above

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argument is supported by parental behavior—and a parental bond—remaining important, and continuing, beyond active sexual behavior of the parents, either with each other or with other partners.

We can briefly address here the question of morality and contributions to its origin. If morality consists of somehow agreed-upon rules about how far any of us can go in serving our own interests within the social group (Alexander 1987, 1993), then we have to ask ourselves how and when the tendencies of human males to respect the pair bonds of others came about (Alexander 1990b). Because males are the sex more likely to be represented in defense of groups consisting of multiple families with dependent offspring, and because of the apparent urgency of paternal care within groups, it is appropriate to ask whether intermale honoring of within-group pair bonds arose in the context of group defense. The question has relevance here because it is clear that, despite concealment of ovulation, extra-pair copulations can lead to losses of paternity confidence and thereby disrupt the parental bond and reduce paternal care. The prominence of such issues in modern life, added to the ceremonial publicity given to weddings, attitudes toward children born out of wedlock, and actions that break up marriages in which there are children, cause us to wonder about the nature and antiquity of morality—rule-dominated patterns of social reciprocity—among potentially disruptive males. This question, as we shall see, is connected to a fundamental one that still remains.

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WHAT UNDERLIES THE DISTINCTIVELY HUMAN KIND OF GROUP LIVING?

We are returned to what has steadily become identifiable as a central question: Why should humans have evolved to live in their kinds of social groups when so many traits and tendencies apparently underwent such extraordinary evolutionary changes as a result—meaning, when the trade-offs involved were apparently extremely expensive? We need to discover an overriding importance for human social life that involved proximity of multiple breeding males but fostered a cooperativeness that allowed (or caused) extensive biparental care and all that has become associated with it.

Group living is always expensive, especially when all individuals retain the tendency to seek to reproduce, because it places individuals in more direct competition, engendering costly conflicts. There are not a great many different explanations for group living (Alexander 1974, 1975b, 1990b). Indeed, thwarting of predators in one way or another has gradually moved to the forefront among likely explana-

tions for many cases. There is little doubt that human social groups have been able to thwart predators that individual humans could not; they also hunted cooperatively early on. But, again, humans are in no way unique in these regards. Something more has to be involved.

We can approach the “something more” by thinking again about organisms as genes bundled into groups (genomes) that compete via their collectively produced phenotypes. Organisms compete with other organisms because they are sufficiently alike to use the same resources; as Darwin noted, the more similar two organisms are, the more directly they compete for resources. The same might be true of groups of organisms when they operate to gain resources as units, and it obviously is true of different groups of human organisms today. The reason for competition is that accessible resources will always be limiting in quantity, quality, or cost of acquisition, if for no other reason than because of the ways living creatures exploit them so as to maximize reproduction.

Suppose we start from the present and think backward through history. We can certainly say that the principal hostile force of nature for human groups today is other human groups. In various ways we humans have become “ecologically dominant” (Alexander 1989, 1990b), meaning that we have found ways to reduce the significance of the predators, food problems, and extremes of climate and weather that originally plagued us—at least in ways that affect the modes of interactions of different human groups with one another. Ecological dominance is not merely a way of repeating that we have been able to become the most ubiquitous and influential species across the globe: it also carries in it the explanation for that fact. For our arguments, the main question becomes when and how this situation arose, what form it took, and whether it happened far enough in the past to influence the combinations of human traits we have been discussing. To the extent that evidence can be garnered to prove the existence of multiple-male human groups with altricial babies in the oldest structurally modern humans, we can assume that neighboring human groups have treated each other as major competitors, thereby creating the necessary and sufficient conditions for our composite hypothesis (see also Alexander 1990b). In effect, humans have taken up a unique kind of within-species, group-against-group competition—an ongoing and perhaps endless balance-of-power race—that has led to a distinctive kind of sociality and huge nations. One serious question, then, is not whether, but when, this situation arose, with respect to all the causally intertwined human traits just discussed. The other is the extent to which competing subgroups and within-group alliances contributed to the effect we are considering, as opposed to adversarial relations between geographically contiguous groups.

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We can finish this section with a human tendency that may have received too little attention. Alexander (1979a, 1979b, 1987) described a seemingly unique feature of human societies, expecting that if he was wrong in calling it unique this would immediately be pointed out. It was simply that humans alone appear to compete in play, group against group. Other species either compete in play as individuals or, as in chimpanzees, compete as groups sometimes against a single individual. Group-against-group competition in play is evidently still viewed as unique to humans. It is potentially a very significant observation because play is generally interpreted as a way of practicing in low-cost situations for later full-cost social interactions. Thus predators such as cats play as if with prey, and all socially competitive animals that live in groups play, typically one on one, as they will have to compete later on. It is as if playing animals in general are building strategies of later responses in social situations, whether with members of their own species or members of prey species. These strategies, interestingly, parallel our own social scenario building, typically done consciously and later employed both consciously and unconsciously. The difference is that most animals that learn how to compete or deal with prey by playing are probably learning in the way humans learn to type, ride a bicycle, or shoot free throws. The repetition in the play renders the eventual response reflexive, thus quicker (and less open with respect to possible alternatives) than if it were conscious. We humans have had to play, with mental scenarios, in ways that enable us sometimes to use our consciousness later to compete. This situation (or race)—either novel in humans or at least uniquely complex—exists because alternatives are also dreamed up consciously and continually by our scenario-building human adversaries. (Alexander 1989 argued that humor, almost nonexistent in nonhuman species, evolved as social-intellectual play—see also Alexander 1986.) The multiplicity and novelty of ploys would devastate the organism with a repertoire of strategies involving little or no consciousness. Apparently uniquely, humans do all of this, including both physical and social-intellectual play, in preparation for both one-on-one competitions and group-against-group competitions, and including team play in preparation for the latter. We can interpret the intensity and complexity of intergroup competition in play as supporting evidence that humans evolved to compete in social groups within the species, almost as if the different groups were different species. Again, the only serious question about this unusual or unique tendency is when it became prominent, because we know it has been devastatingly prevalent across all of recorded human history. The existence, nature, and intensity of intergroup competition in play tend to support the argument that humans have been involved in their current distinctive kinds of social activities long enough to account for the combinations of traits examined here.

GENETIC SELECTION, PHENOTYPIC FLEXIBILITIES, AND CULTURAL RACES

Connecting genes to culture and its variations is a difficult exercise in terms of kinds and effects of selection, the nature and extent of heritability in trait differences, the functions of phenotypic plasticity, and the overall nature of the organism. At this point the most useful question seems to be whether we can identify aspects of selection that could be responsible for the human traits resulting in culture and the arts.

Some Features of Different Kinds of Selection

As already noted, differential reproduction of genetically different forms, or evolutionary selection, is the only candidate for principal guiding force of evolutionary change. Since Darwin, biologists have generally recognized two major forms of evolutionary selection: natural and sexual. Darwin described the causes, or hostile forces, of natural selection as climate, weather, food shortages, predators, parasites, and diseases. Members of a species—and sometimes members of different species—compete for limited resources affording relief from Darwin's hostile forces. Alleles residing in and transmitted by the particular (and relatively short-lived) individuals that happen to fare better in this competition outreproduce, hence outlast, other alleles located in individuals that fare worse. Faring worse or better can be owing to a single allelic difference. Sexual selection results from differential choice of mates by one or both sexes and from competition among members of either sex for the best partners of the other sex (cf. Bell 1997).

In *natural* selection we can begin with two kinds of interactions between living forms, predatory and competitive. In *predatory* interactions one participant (predator, parasite, disease) uses the other (prey, food, host) as a resource, and the other participant can only lose. In *competitive* interactions—competition for protection from Darwin's hostile forces and high-quality mates and other social partners—two parties strive for the same resource. As a result of a competitive interaction, which is expensive to both parties compared to its absence, one party typically wins and the other loses.

In the third kind of interaction, involving *mutualisms*, both participants can gain, and on average (in the population or species) must do so or the interaction will eventually disappear. Most if not all mutualistic interactions also include some competitive interactions. Thus, even in the sexual interaction, members of one sex compete for access to members of the other sex, or access to the better (more reproductive)

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sexual partners, and individuals less successful in this effort suffer in comparison to more successful individuals (Fisher 1958; Trivers 1972; Miller 2000). Of course, the interests of individual males and females probably never coincide exactly, so that one sex or the other can suffer reproductively compared to its mating partner or other reproductive competitors in the species. Nevertheless, both parties to a sexual interaction win in the sense that, when sex is the only vehicle of reproduction, successfully mating individuals will outreproduce any individuals failing to mate (excepting those with extensive knowledge of genetic kin and ability to help them). Even in a nonobligate social interaction, such as communication, it is also necessarily true that on average the individuals that communicate—both signalers and receivers—outreproduce those that do not. When this is not true, in both obligate and nonobligate interactions, the system is expected to vanish (Otte 1974): sexual organisms would become parthenogenetic or asexual, and efforts to communicate (or socialize in particular ways) would be dropped. Mutualistic selection thus differs from selection based on predatory or competitive interactions in that both parties in mutualistic selection can gain and must, on average, gain over nonparticipants.

Another way of expressing these ideas may be illustrative (modified from Queller 1994): whenever one organism begins to obtain costly and thus limited benefits (such as food) from another, at a net cost to the benefit giver, the benefit giver will evolve to reduce and eliminate the benefit. This is an effect of natural selection, the benefit takers being Darwin's hostile forces of nature. On the other hand, whenever benefit givers obtain a net reward for giving a benefit, they will evolve to give more of the benefits, and to do so at less expense to themselves, thereby gaining greater rewards. Benefit receivers will evolve to extract more of the benefits, and to use them more effectively, thus favoring the givers of more and greater benefits. This is mutualistic selection. The benefit givers in such selection, which can be either intra- or interspecific, might be labeled beneficent forces of nature. Beneficence need not be genetically altruistic because it can be extended at a reproductive profit to (1) genetic relatives, with the return solely genetic, in terms of the success of the relatives; and (2) nonrelatives, with the return (reciprocity) in beneficence with interest, which can then be used reproductively—for example, to produce offspring or help relatives.

Because of the ubiquity of the organism as evolutionary unit, we can hypothesize that on the whole the organism is an unusually good vehicle for maximizing reproduction among alternatives that might have been produced by all the different and conflicting forces of evolutionary selection in the history of life and also

that each particular kind of organism is the best vehicle for maximizing reproduction that could have been produced during its particular population's history, given its nature upon entry into that particular historical sequence.

Social Selection and Social Reciprocity

I will now focus largely on mutualistic and competitive aspects of selection. Further, I will ignore interspecific mutualism and restrict the discussion to social selection, which I identify as a form of mutualistic selection differing from most sexual selection (excepting hermaphroditic species) in that the partners in an interaction may alternate roles or assume the same roles in relation to one another. I will also restrict the discussion to those particular interactions that take the form of social reciprocity (Trivers 1971). Because social reciprocity is pervasive only in the interactions of humans, and because human cultural variations are our specific target, I will restrict the discussion even further to social reciprocity in the human species. My aim is to understand how evolutionary selection on genetic variations could account for the complexity and diversity of human culture—again, defined broadly, so that I am actually asking two questions: (1) how selection could have produced human tendencies to generate such a wide variety of activities, talents, competitions, and ways of life; and (2) the effects of all these activities, competitive races, and life patterns on the continuing genetic makeup of humans—how they affect evolutionary selection. It will be necessary to develop the arguments by considering various aspects of an evolutionary explanation.

Evolutionary selection on any trait can be directional, stabilizing, oscillating, or disruptive. Here I am concerned primarily with directional and stabilizing social selection. In directional social selection, traits exaggerated in a particular direction tend to be favored by prospective social partners (in the cooperativeness of reproduction or reciprocity). Although the resulting directional change may not have an obvious culmination, the amounts of genetic variation that continue to correlate with the trait variations will continually be reduced because selection tends to operate too fast for recurrent mutations to provide continuing new directional possibilities. In stabilizing social selection, a particular expression (or culmination) is favored, such that selection will tend to “fix” the trait at some point on its usual range of variation, removing from the population alleles that yield other expressions of the trait (or removing the relevant effect).

As noted earlier, *social reciprocity* can be said to take two forms, direct and indirect (Alexander 1977, 1979a, 1987). *Direct reciprocity* consists of exchanges of

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costly benefits of any kind, between parties, with no necessary involvement of third parties. Examples are all kinds of trading, barter, and directly reciprocal investments. *Indirect reciprocity* consists of benefit giving, or investment, with expectation of returns from parties other than the original recipient, as when benefits are given to relatives or partners of other persons, and the reciprocity is expected from those other persons—or even their relatives and associates in reciprocity. In both direct and indirect reciprocity, returns may be extensively delayed and still yield profit to the original donor. The currencies of giving and receiving are also frequently different.

Indirect reciprocity involves reputation and status, and when it is pervasive everyone in a social group is continually being assessed and reassessed by others. Examples of indirect reciprocity are donations to charity, giving of blood, heroism in defensive—or even expansive—wars, and expensive or risky assistance to any citizen of a close-knit group—all of these when there is a strong chance of the act becoming public. The return benefit to the originally beneficent party may come from individuals or groups that expect (not necessarily consciously) either subsequent benefits themselves from the original donor or benefits to others such as relatives or friends who will then have an increased likelihood of providing some benefit (genetic or phenotypic) to the giver of the return benefit. Eventually, merely enhancing the reputation of a benefit giver through public praise can be such a return benefit because of its likelihood of bringing further benefits to the benefit giver from still others. Indirect reciprocity thus contributes to selection of partners for direct reciprocity and binds together aspects of the sociality of an entire group. Thus a war hero who risked his life in defense of a group could receive many kinds of benefits, from increased access to potential mates to prestige and accompanying benefits to offspring and other relatives. Those who provide these benefits are more likely in the future to receive benefits from others who, observing the prestige afforded heroes, may more readily accept the challenge of being a protector of the group.

Humans introduce on a grand scale a special feature of social reciprocity that has given our intellectual race part of its nature: *risk taking*, or increasingly longer-term investments and increasingly greater willingness to invest extensively in the absence of immediate returns. Modern humans invest this way almost continually, often not expecting returns for decades, or even expecting returns only for their descendants after they themselves are dead. Such risky tendencies are likely to persist only as long as they continue to yield greater returns than less risky investments. They call for the evolution of increasing abilities to assess the social future accurately, thus continually reducing the risks of long-term investments.

Long-term and large investments provide countless opportunities for *deception and cheating* and create both evolutionary races and lifetime learning races among reciprocating individuals in abilities to recognize and deal with cheaters and otherwise to maximize investment effectively under increasing risks of being duped or cheated.

Since Trivers (1971) we have gradually learned that only in humans is there strong evidence of extensive evolution of complicated and multitiered potentials for *detecting and responding to deceptions and cheating*. Only in humans is *reputation* (status) likely to be of paramount importance, and, of course, we often say that “reputation is everything.” Improving ways to detect and respond to cheating, and to use reputations effectively, may have driven the evolutionary ratchet that created our enormous brains and our massive cleverness in social matters (Alexander 1989). One of the greatest advantages a human can have in social matters is superior ability at building mental scenarios that describe most or all possibilities in upcoming or ongoing interactions with parties having somewhat different life interests. Jack London said it pays to stay one idea ahead of the other fellow. This can be done by the equivalent of looking into other people’s minds not only by keen social observation and exceptional memory but also by emotional skills such as empathy and sympathy, thereby anticipating the possible and likely actions of important others in every circumstance that may arise. Many traits useful in human sociality—such as consciousness—reflect broad abilities in mental scenario building.

Consciousness can be defined as knowing what you are thinking about and being able to tell others about it and act on it as a matter of self-understood choice among envisioned alternatives in subsequent social or other situations. It implies the ability to think about times, places, and events separated from your immediate circumstances and the ability to use the understanding so gained to anticipate and alter the future, build further scenarios, plan and think ahead, anticipate different possible outcomes, and retain the potential to act in several alternative ways, depending on circumstances that can be only imperfectly represented at the time the plans or scenarios are being made. Language is a concomitant of consciousness, characterized by features that make communication of useful information about mental scenarios possible: signs, symbols, and displacement in time or space (Hockett 1960; Alexander 1979a, 1983; Pinker 1994, 1997).

How then do we model the probable manner by which evolutionary social selection might have resulted in the arts—or culture as a whole—as we know these features of modern human society? What do we need to say about social selection that has not been said before?

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Heritability and Phenotypic Flexibility

Perhaps we need to talk first about heritability of differences in traits and how heritability changes and sometimes virtually disappears. Selection cannot cause evolutionary change unless there are heritable differences in the traits involved in the selection. We need to understand how seeming flexibility in phenotypic expressions—what we oppose to heritable differences as “lifetime learning differences”—connects to evolutionary selection and heritability. Without this connection it is difficult for nonevolutionists to imagine how the learned variations of culture can be related to a history of genetic variations.

Differences in some traits of organisms are owing to differences in alleles, with little ability by the organism to modify the trait using environmental stimuli. Coat color in some mammals, such as horses, is a good example. In other traits, or species, nonheritable changes in coat color also occur; thus some Arctic mammals regularly change coat color between seasons. This ability presumably has to come about as a result of evolutionary selection in an environment that fluctuates with high predictability on a long-term basis. The heritability that allows evolution to occur results in an effect on the animal of a different kind with respect to the observable trait: alleles are favored that give the organism the ability to respond to environmental features such as day length, temperature, or substrate color, which predict the relevant environmental change, by altering coat color—probably by turning certain genes on or off, thus triggering changes in physiology. The genetic bases of all these abilities are most likely adaptive modifications from those yielding a single coat color for life.

In still another kind of coat color change, animals like the chameleon can change color quickly in response to differing substrate colors. This kind of change need not involve turning genes on and off; it could be mediated, for example, through the vision of the animal: what it sees is what it comes to resemble. This change in physiology is also most likely adaptive. All three of the abilities described so far have evolved to be present in the animal when it first encounters the relevant situations, probably effective when it is born or hatched.

The situation of most interest in trying to explain human social or cultural complexity and diversity is slightly different. Here the organism comes into the world unable to make certain responses and acquires the ability to make the responses during its lifetime, as by learning. It begins with abilities to start and continue acquiring responses, the nature of which depend on particular features of the conditioning or “teaching” environment. For example, blushing in humans might

be seen as a fourth kind of “coat” color change, which occurs even more quickly than even that of a chameleon, has social significance, is modified by social experience, and also must have a basis in evolutionary selection (Alexander 1993).

Sometimes we forget that learning is not a mere relaxation of the developmental or physiological circumstances of the animal. Each species learns particular kinds of things quickly and easily and other things with great difficulty or not at all. Ranges of learning as well as directions of learning also are more or less specified. The way experience affects the learning organism is therefore also surely a result of evolutionary selection. This means that when learned behavior is transmitted between generations as a result of learning and teaching, which is the way culture changes cumulatively, evolved capacities and tendencies are responsible (Flinn and Alexander 1982; Alexander 1990a).

When selection begins on a directionally changing social trait, variations in choosers and chosen may both be heritable, meaning they correlate with genetic differences. In this situation, both choosers and chosen will change evolutionarily (genetically): as Fisher (1958) noted (see also Lewontin 1970), the strength and rapidity of selection on any trait depend on intensity of the selection, amount of variation in heritable traits (meaning the differences are owing to genetic differences), and generation or cycle time. In reciprocity selection we can be referring to both (1) variations in choosing abilities and tendencies and (2) variations in the trait being chosen.

As with the coat color examples used above, selection changes heritability in traits that in various ways underlie the traits originally under selection. If the environment is like the social expressions of humans—that is, able to change very quickly, yet somewhat predictable—then selection is likely to favor quick abilities to alter responses, as in one-lesson learning, preparation through mental scenarios, and the use of rapidly changing behaviors in others to alter one’s own behavior profitably.

Phenotypic flexibilities can thus make us think that heritability of trait variations has disappeared, when it has actually become cryptic without disappearing, by influencing underlying physiological variations that are less apparent to us. They can make it too easy for us to accept oversimple interpretations of (supposed lack of) genetic contributions to complex trait variations in organisms. This error is made more likely by one of the simple-to-complex problems discussed in the introduction, that of understanding the ontogeny of the organism: the relationships between the particulatness of the genes and the unity of the organism to which the genes give rise via complexities of coordination and interaction that we as yet

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have no way of understanding sufficiently. This problem is exacerbated, but also sometimes clarified, by diversity in the ways in which choosers in mutualistic selection function. For example, Zahavi (1975) began the development of the so-called handicap principle, which describes how organisms choosing mates in mutualistic selection can use the amount and kind of expensive striving by potential mates as indicators of their overall good health and ability.

In other words, to some extent the heritability important for assessing effectiveness of evolutionary selection is transferred from the expression of the centrally important trait—which acquires flexibility in responses to environmental variations—to the effort exerted in its expression. Thus, in any race to be first—cultural or otherwise—heritable variations in, say, morphological or physiological traits affecting chances of winning can be outweighed by (potentially heritable) variations in determination or persistence. Only a broadly healthy individual may be able to win by increased determination or persistence, so that evolutionary selection may be transferred to heritable differences in these tendencies, and as well overall quality of the genome, which can be indicated by general health and thus immunity to diseases, ability to obtain high-quality food inexpensively, and many other traits. Included, for example, could be heritable variations in abilities to assess not only which races to enter but how hard to strive in particular kinds of races and in races with particular other kinds of individuals. Such shifts in the “locus” of heritability, significant for the changes that we observe occurring, can be virtually endless, as we can glimpse by thinking again of Dobzhansky’s implication of a universality of pleiotropy and epistasis. Giving short shrift to such potentials for continuing heritability in trait variations can make us think, too easily, that many of the traits we observe could not have (or may not have) assumed their present expressions as a result of evolutionary selection. The more complex the interactions of the genes in a genome, the more likely that some kind of significant heritability affecting any particular trait will crop up—a truism to be understood better by considering effects of the genetic recombinations of sexuality, including interbreeding between individuals from demes that have been separated for varying lengths of time in slightly different environments. Such interbreeding produces *novel combinations*—therefore *novel interactions*—of genes within genomes and must lead frequently to changes in selection with regard to epistasis and pleiotropy. This effect is not directly a function of relative amounts of variation within and between demes but of the production of novel genomes that include genes that may never have interacted before. Much of the heritability of trait variations in the world population of humans today is surely owing to increased interbreeding among individuals from

demes or populations that have lived in different places long enough to have genotypes that have integrated somewhat different sets of alternative alleles. Thus Dobzhansky (1961) and Roff (1994) may together have given much of the answer to why so much genetic variation remains in populations.

The point of this section has been to emphasize two things. First, there are many avenues by which significant heritability can arise, persist, or emerge in human populations. Second, there are so many levels and kinds of heritable variation in the physiological and behavioral hierarchies of animals like ourselves that it is risky to conclude from simple models of heritability that any particular trait is ever immune to evolutionary selection.

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STATUS AND THE ARTS

Status is central in human society (cf. Barkow 1989; Dickemann 1979; Henrich and Gil-White 2001; Hill 1984). It is important to every individual in society, hardly ever approaches being “complete,” and by its nature is always in short supply. For humans, unlike any other organisms, the numbers and kinds of differences in status in a complex society can be almost endless and constantly changing; in today’s societies, one individual can have different kinds of status in numerous different social circles. These facts create endless and elaborate performances and audiences, as well as endless opportunities and competitive races leading to narrow trends and fads about which little more can be said beyond “Second place is the first loser.” These things happen because, for various reasons (see below), audiences to artistic performance and competitive races can sometimes gain as much as or more than the participants. I would be surprised if any species has anywhere near as many performance-audience interactions as humans.

If status is, as seems evident, a measure of access to the resources of reproduction, we can grasp the importance of understanding it, and how to gain it, in a society like our own. How and why status has become so important in human society is another question. It can be complex and dynamic only when indirect reciprocity has become important. Reciprocity and nepotism are both investments that entail risk. Only a genetic return is required to make nepotism profitable, and unlike social reciprocity, much nepotism can occur regularly with a minimum of cognitive skill. Differential nepotism frequently takes the form of reciprocity, however, when two relatives reciprocally assist one other in times of special need for first one, then the other (see discussion in Alexander 1979a, 53–56). Success in reciprocity, with

CONNECTING THE ARTS TO EVOLUTION

People who are successful in the arts possess a set of basic skills that they use in relation to the social scene: observation, perception, appreciation, interpretation, imagination, prognostication, translation, and communication. They depict the social scene through faithful representations mixed with manipulation, exaggeration, and the parading of incongruity—all of which require extraordinary ability to understand the social scene in the first place. They use visual portrayals in art, dance, and drama. They use language in all forms, from oral narration and music to the literature of poetry and fiction. They use metaphor in every sense of the concept, and the race to catch up with all of the ways they do so will never be finished. They use humor, and to those who are sufficiently attentive they demonstrate its deadly seriousness. They combine most or all of these media, sometimes in a single stunning performance that creates novel comparisons and portrays relationships that enlighten and explain the social world as never before.

Audiences of the arts are accepting particular versions of the social scene secondhand from others whom they perceive to have better basic skills or broader experience. To do this effectively they must recognize the relevant talents and abilities in others. Basic to that task are universal and special features of the human brain: social capacity that includes a fertile imagination and all the talents necessary to use it. These traits are the same as those employed by the artists, leading us to wonder if they derive from a single machinery, even if not always equally functional.

The result of all this is that the arts are a glorious form of interpretive gossip, multifaceted, multilayered, and altogether still complex beyond anyone's comprehension. People in the arts are by definition the best storytellers among us. What they tell us is never superfluous, impractical, or trivial unless we, the audiences, allow it to be. We gain mightily from knowing how and when to listen, to whom to listen, and what to do with the experience afterward. For the arts are theater, and theater in all of its guises represents the richest, most condensed, and most widely understood of all cultural contributions to our patterns of social scenario building through consciousness and foresight. These scenarios, which we build, review, and revise continually every day of our lives, are obligate passports to social success, and perhaps the central evolved function of the human social brain. We use them to anticipate and manipulate the future—the ever more distant future in ever greater detail.

When Marshall Sahlins (1976) argued that modern hunter-gatherers are models of the original affluent societies because of the surprisingly small amounts of time spent hunting and gathering, he underplayed at least two things. First, time not occupied with securing food and shelter can only be occupied *otherwise*; and this can be done effectively only by engaging in activities that contribute to reproduction. Second, sitting around being social is not necessarily trivial or non-reproductive. Sahlins's comments, however, emphasize that the rise of art in its various expressions need not be restricted to recent societies demonstrating leisure time and affluence in some narrow modern sense.

Even if few could say it as well as Doris Lessing (1992, 35), artists are the people who understand that “[m]yth does not mean something untrue, but a concentration of truths.”

the simultaneous retention of social acceptance and harmony, requires the highest levels of cognitive skills (see, e.g., Trivers 1971).

From these assumptions it would appear that the underlying reason for direct reciprocity, followed by indirect reciprocity and an importance for status shifts in human society, is actually group living of the sort discussed earlier, which allows and promotes the kind of extensive differential nepotism apparently unique to humans and the most likely precursor of reciprocity.

The existence of status as an important variable in human society sets the stage for interest in any kind of contest or performance that assists in determining status accurately and in changing it to the observer's or participant's benefit. In Alexander (1979a), I hypothesized that much of the arts represents surrogate scenario building for audiences. I have also suggested previously that, for performers, all of the arts can provide opportunities for the elevation of status. Status and the ability to convey items of great importance to others go together. They may represent the key to understanding not only the arts but much of morality as well, because lowered status is effective punishment for behavior deemed immoral (Alexander 1987). Part of the reason this is possible, of course, is that coalitions and alliances capable of meting out punishment, as well as delivering rewards, can form within human groups and are aspects of indirect reciprocity. It is a large part of the complexity of human social life that, as part of the group-against-group aspect of human sociality, these coalitions can also shift and change in virtually every way imaginable.

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**THE CONTRIBUTION OF SOCIAL SELECTION TO HUMAN CULTURE:
IS IT A RUNAWAY PROCESS?**

We need now to engage more specifically the question of the particular flowering of the collective human phenotype usually called "culture." It is obvious that extensive learning abilities in humans, and the long and intimate overlaps of adults and juveniles in social groups, have created a situation in which learned activities are transmitted by learning, thus providing the background for the rapid accumulation of cultural innovations and change, consequently for rapid cultural divergence among variously isolated human groups. But without additional explication these facts seem frustratingly unable to account for the incredible races toward complexity and diversity of human social and cultural activities across the globe—not only the huge specialized human brain but the features that have led to such

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complex and diverse enterprises as the arts and, indeed, those leading to Barzun's label of decadence. Something more is needed—another step in our understanding of evolutionary process—to connect everything about the human organism to its complex cultural expressions. I ask now whether this “something more” may be considered appropriately under the label of runaway social selection, already introduced in this context by West-Eberhard (1983) and Alexander (1987, 1989).

Ronald A. Fisher (1930) used the adjective *runaway* to apply to a hypothetical selective process that he assigned to sexual selection (see also Trivers 1972; Miller 2000). I suggest that sexual selection and reciprocity selection are special forms of the broader concept of social selection. Social selection is a consequence of competition among individuals for rewards arising out of various kinds of social or mutualistic beneficence.

Fisher's runaway sexual selection has two special features. First is the tendency of the choosing parties to begin favoring individuals with traits that are extreme on some axis of desirability, rather than favoring some particular condition (other than extremeness) of the individuals to be chosen. This form of choosing can only occur in an organism that is able to compare an array of individuals and identify desirable extremes (e.g., Alexander, Marshall, and Cooley 1997). It can evolve to become the standard method of choice only if selection continues for a long time in one direction and the best choices continue to be beyond the previous expressions of the trait. Thus, if females that choose extreme males outreproduce those that do not, the choosing of extremes will spread. So will extremeness in males; otherwise the females choosing them would not gain. Spreading or fixing the choosing of extremes will inject a certain degree of inertia into the process. For this reason, once an “extreme-choosing” tendency is in place, extremes in the traits of the chosen individuals can pass beyond the form in which they are adaptive in any other sense and indeed can become disadvantageous in other contexts. Some such conflict actually exists among all the compromises of selection on different traits of the organism because the effect of selection can only be enhancement of the reproductive integrity of the organism as a whole rather than the state of any of its individual traits. When selection is social, however—when it is a matter of individuals choosing other individuals in a mutualistic or reciprocal social interaction rather than, say, competition to detect or capture food, or to escape enemies more effectively—overshoots in adaptiveness in other respects, because of choosing extremeness, will be more prominent

The second special feature of Fisher's runaway sexual selection is the feedback resulting from the genetic partnership between males and females in jointly produced offspring. Trivers (1972, 166) described it as follows:

[I]f there is a tendency for females to sample the male distribution and to prefer one extreme (for example, the more brightly colored males), then selection will move the male distribution toward the favoured extreme. After a one generation lag, the distribution of female preferences will also move toward a greater percentage of females with extreme desires, because the granddaughters of females preferring the favoured extreme will be more numerous than the granddaughters of females favoring other male attributes. Until countervailing selection intervenes, this female preference will, as first pointed out by Fisher (1958), move both male attributes and female preferences with increasing rapidity in the same direction.

We can note, first, that some aspects of human evolution that intrigue us, such as brain functions that result in cleverness in social interactions, including scenario building and testing the social future by weighing alternatives internally, could have evolved partly through sexual selection. In view of the tendency of the human brain to become larger across history, and of human behavior to become more complex—and seemingly ever more rapidly after these features had exceeded their counterparts in other species—we might be concerned to examine the likelihood that runaway sexual selection is involved. A related question is whether some or all features of runaway selection can also occur in nonsexual social interactions such as the high-risk forms of social reciprocity that are prominent only in the human species.

At first one may imagine that there are no parallels in social selection allowing it to become runaway. But the way an individual gains by selecting its social partners parallels the ways an individual can gain from cooperative interactions with a mate and from a mate's parental care. In both cases there is likely to be genetic change in both the ability to choose good partners and the background of the favored phenotypic attributes because a mutually beneficial interaction can be maintained only if, on average, both interactants gain.

Sexual selection is a distinctive kind of runaway selection because joint production of offspring by the interacting pair causes the process to accelerate (see above Trivers quote). The defining feature of runaway selection is not acceleration, however, but the tendency of the process to go significantly beyond adaptiveness in all contexts except within the particular selective race—much further beyond adaptiveness in other contexts than is ordinarily the case in the myriad compromises among the conflicting adaptive traits that create and maintain the unified organism.

This aspect of runaway selection may hold for reciprocity selection, in which, unlike in sexual selection, both parties can carry tendencies not only to choose

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extremes but also to display extremes. In social selection, again unlike in sexual selection (except in simultaneous hermaphrodites), an individual can play both roles, of chooser and chosen, with respect to the same traits, and alternations of roles can occur during extended interactions between particular partners. To the extent that social success in ecologically dominant humans (see earlier) becomes the central determinant of reproductive success, runaway reciprocity selection may be a more viable possibility than Fisherian runaway sexual selection.

Fisherian runaway sexual selection presumably begins with a likelihood of heritability (i.e., genetic variability) in both variations in choices and variations in chosen traits. It is easy to see that in this circumstance such competitions, or races, will lead to genetic changes, at first changing both the ability and tendency to choose extremes and the nature of the extremes available for choice. Continuing mutations and genetic recombination (outbreeding among temporarily isolated groups) will tend to offer the choosing parties increasingly extreme possible choices, though to a reduced degree as selection continues to remove heritable variations in trait expressions and the trait becomes sufficiently maladaptive in contexts other than sexual selection. From earlier arguments it is not easy to understand the extent to which relevant heritability is likely to disappear, or even become trivial.

Diminution (or disappearance) of heritability in variations will not necessarily change the tendency to choose extremes: in effect, if an ability and tendency to choose extremes in any of a variety of social races (at least in humans) could become genetically fixed in the population (including the ability and tendency to learn from others, or from observation, the values of such choosing), it could still offer advantages to the chooser of extremes (without evolutionary change in the trait *per se*) because of the usefulness of even nonheritable trait variations chosen in a social partner. Of course, there may be further evolutionary improvements in the ability to identify and use extreme traits even after all choosers are already choosing extremes.

On the other hand, heritable variations in *what is chosen* will result in a continued march toward greater extremes because this relative quality will not be fixed in the way the ability to identify and favor extremes can be fixed; extremes can be identified only by comparing whatever is available. In Fisher's version of runaway selection, extremes win reproductively at first because they are ecologically superior, meaning functionally superior outside the choice situation itself. Later they continue to win because they are sexually (or, here, socially) superior, even though, as a result of the progress of selection involving choice of extremes, they may have be-

come so extreme as to be otherwise functionally (ecologically) inferior. Here, “sexually or socially superior” means that the choosing parties will have acquired a genetic composition that will cause them to choose the extreme, the resulting choice of the extreme individuals itself causing the chosen individuals to outreproduce.

Extremes, however, will be chosen whether or not, as extremes, they represent heritable variants. If extreme social performances yield special social opportunities to those displaying them (e.g., via their reputations as achievers or winners), then regardless of the basis for the superior performances (i.e., genetic variant or not), winning performances can yield benefits to the kin or other social associates of the individual with the extreme traits. Thus merely joining social competitions or races can pay, though only heritable variations, including the (variant) ability to choose the best from among multiple available races *that might be entered*, will yield evolutionary change. Heritable variations in the ability to choose appropriate races—including not only those generally likely to be profitable but those in which the choosing individual, because of his or her special traits, has a special likelihood of competing successfully—may be all that is needed to drive runaway reciprocity selection. The more different ways that success can be achieved through reciprocity competition, the more robust will be this type of social selection. This is a kind of selection that will yield at least part of the human type of social intelligence, perceptiveness, and perseverance. As we all know, status (or “reputation”) can exist independent of the adoption of a *particular* extreme in behavior, so the importance of any behavioral extreme in changing some aspect of culture can also depend on whether a prestigious person adopts, favors, or approves of it.

Since Fisherian runaway sexual selection in nonhuman organisms has remained controversial (or theoretical), but social parallels to it may be robust in human society, one may wonder if Fisher actually derived his idea from observing human social situations rather than from thinking about sexual selection in the birds he ultimately used as his examples. If so, it is likely not the only instance in which an evolutionist was inspired by human traits and tendencies to develop a general evolutionary explanation (e.g., Darwin’s observations on human selection of variations in domestic animals and the fact that Hamilton’s rule applies in its fullest extent as extensive differential nepotism across multiple levels of relatedness only in humans). This suggestion is ironic in another way, in view of the success with which academic biology departments have managed to exclude the human species from their consideration, leaving its analysis to the almost exclusively nonevolutionary approaches of social science and medical departments, and surely delaying acceptable explanations of the human species in evolutionary terms.

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When extremes in particular directions are being chosen in social selection, new extremes never before experienced may be chosen above all other expressions of a trait. This behavior was originally referred to in European ethology as a “superoptimal stimulus” effect and is not specifically related to runaway selection. Whenever superoptimal stimulus effects can be identified, however, they suggest a history of choosing extremes, therefore the possibility of some form of runaway selection. If, for example, we perceive that during the past several centuries art—or even human sociality in general—has flourished and become an enormous and diverse enterprise compared to any “ancestral” condition it might have exhibited, we might suspect that this is evidence of a history of choosing extremes continually in short supply and consequently of some kind of runaway process in however artistry affects the securing of the resources of reproduction. Rather than evidence that evolution cannot be used to explain, say, the arts, explanations of recent flowerings of diversity and complexity in human enterprises can be sought by expanding our understanding of the various subprocesses of evolutionary selection. We should not be discouraged because the pathways to explanation become progressively more difficult and call for expansions of our understanding of the workings of the evolutionary process.

THE ARTS AND COMPETITION

Competitive races among humans, which include performances in the arts, can take either of two directions. They can change in the direction that enables individuals to give performances that are unique, not easily compared to those of others, and highly informative to observers about relatively complicated aspects of sociality. These are the races that we would most often term “artistic.” Their participants are likely to have carved out special life niches for themselves. In effect, a flourishing of the arts in its most diverse forms reduces direct and confrontational competitive races because it is more difficult to compare creative artists than to compare, say, athletes in the same sports, chess players who contest one on one, or people who try to best one another’s record in any uncomplicated or highly patterned and predictable game or contest.

Trends toward individuality in performance and meaning in the arts—as in poetry—can continue, paradoxically, because the value of gaining insight from the brilliance of others is so great to us. The more profound an insight, as well as the more personal or specific, the more difficult it is likely to be to absorb. This is the

reason that a poem can be so personal as to be understandable only to its author, yet the author can be accorded high status because of the poem. Because they expand and enhance our imaginations, poetry and art press continually at the boundaries of mystery and incomprehensibility, so that, as audience, we are always faced with the necessity of deciding whether the artist is incomprehensible because of telling us something unusually profound or because of telling us something trivial or wrong in an obscure way. It is a difficult decision because we know in our souls that the scoffer can lose as profoundly as the gull, whether the poetic message is used or rejected directly or attempts are made to use it indirectly during social interactions with the poet in some other context. The same challenge exists in the assessment and use of humor as insight into the social scene, as all those who have laughed too soon on at least one occasion will understand (Alexander 1986, 1989).

Socially competitive races that parallel those involved in the arts can also take a different form, changing instead in directions that progressively narrow the variations available to the performers and the nature of the prizes and diminish the social messages available to observers. Competitors in such races are forced into increasingly or more directly confrontational races.

Modern humans have generated almost endless possibilities of being “world class” in direct competitions, from championships in golf or boxing to first prize in poetry or painting or musical contests to making the largest pizza or longest hot dog in the world, flagpole sitting for the longest time, or establishing the fastest construction times for field latrines in the history of the military. When reputation comes to be based so strongly on relative achievement compared to other humans that the nature of the competition becomes trivial and the relative ranking of the competitor becomes paramount, extremeness in the competition may be represented by activities or “traits” so radical that, in all regards except the specific competition being considered, they are disadvantageous to the individual exhibiting them. Social messages for audiences, moreover, can be restricted to the identity of contestants that finished in particular rankings. Nevertheless, such rankings represent changes in social status or maintenance of social status.

I can give an example from horse competitions. Judged horse competitions are like other judged contests: they can reach maddening levels of faddishness. These endlessly competitive races involve a wide variety of things, including the details of the clothing worn during different competitive classes; precisely how a rider holds hands, feet, and head; minute details of the equipment worn by the horse; and exactly how the horse holds its head. To take only one example here, in certain breeds, in a competition called “Western Pleasure,” a tendency arose to favor horses

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that moved with their heads held somewhat lower than one is likely to see on the random horse galloping across the prairie or walking in someone's pasture. This favoring evidently began because it was undesirable for horses used in ranch work to hold their heads high enough to be in the way of the rancher's work. But lowered heads became a trend that reached such extremes that horses in these Western Pleasure competitions came to be called "peanut rollers" because their heads were so low they were jokingly regarded as able to roll peanuts as they walked or jogged along. Meantime, in breeds originally bred to move elegantly in parades and the like, and in others to show off unusual gaits, precisely opposite trends were set in motion in similar competitive classes. The horses were encouraged or forced to hold their heads higher and higher until the neck was essentially vertical. While some horse people were drugging their horses, starving them, or bleeding them (yes, I do mean those things) to get their horses to keep their heads down and move ever more slowly (and dejectedly!), those working with other breeds were letting their horses' fore hooves grow long so as to lift their front ends and their heads even higher. Eventually some of the latter people began placing plastic and other kinds of extensions on their horses' front hooves so that they appeared to be walking with their forefeet on boxes. And the riders began to sit farther and farther to the rear on the horse's back so that the horse would have a greater tendency to lift its front end in a fancy way while traveling around the show ring. This position became so extreme that riders began to wear capes that flowed over the horse's rump and to place bulky garlands across the saddle in front of them, both items evidently to conceal how embarrassingly far back the rider was sitting on the horse. Finally, some of the people with a certain breed of horses began to "sore" the tender portions of their horses' forefeet with acid or a knife, and to train the horses with heavy bruising chains around the tops of their hooves, in both instances so that they would lift their feet (and their heads) even higher. It seems sometimes that no judged contest of humans can maintain a happy medium in any one trait or action or fail to become narrow and faddish. Extremes appear, are quickly favored, and eventually become so ridiculously exaggerated as to discourage many people from participating. Perhaps only periodic dramatic changes in direction seriously retard such extreme trends.

Extremes of judging in narrow competitions are not restricted to small audiences or small-time events, as anyone knows who watches events such as figure skating or gymnastics in the Olympic Games. But for individuals or teams representing institutions (or nations), the social message has to do with competition between the institutions, meaning that, because of their symbolism, even narrow and

confrontational races with little relationship to social questions or broadly important qualities of the contestant can attract huge audiences and yield high status for excellence in performance.

The incredible tendency of humans to engage in competitive races and carry them to extremes tells us that such competitions must be a very old part of our makeup, and a part that somehow furthered our reproduction. A point with which such races are entirely compatible is that organisms do not evolve just to reproduce successfully but to *outrproduce* everyone like them.

Whenever tendencies exist to recognize and admire “winners,” whether they are outstanding artists, musicians, actors, dancers, poets or writers, shamans, humorists, athletes, war heroes, or thinkers, the tendencies may result in prolonged evolution, exaggerating the bases for the skills represented, perhaps producing the extreme skills and capabilities exhibited in the arts today. To the extent that such capacities tend to have a common genetic basis, the selection could be even more effective. Thus a wide variety of artists might achieve their special abilities partly through a common ability to construct and retain mental scenarios. Whether or not the most talented and specialized artists could use their special abilities to succeed in the social scene, their (genetically recombined) offspring might have superior skills in a variety of social situations. The favoring of seemingly different capabilities could have had common ground that led to the exaggeration of rather specific mental capacities, to which we have given labels such as “intelligence,” “genius,” or “perspicacity.” The prediction from this suggestion is that people unusually capable in one intellectual or other endeavor in the arts are likely to be unusually capable in others as well. To the extent that this generalization is accurate, and tends to involve the useful skills of humans very broadly, the concept of “maladaptive in other contexts” because of dramatic overshoot in particular traits is diminished. While reciprocity selection is evidently distinctive and influential in humans, the question of whether it involves a runaway process, at least in the Fisherian sense, remains unclear.

In the 1930s and 1940s, the newsreels that preceded showing of movies in theaters proclaimed that in the twenty-first century people would not have to work more than fifteen or twenty hours a week because technological devices such as robots and calculating or computing machines would take care of most of the mundane tasks humans had to do then. As a specific example, when the labor-saving three-point hitch was developed for small farm tractors (in England by Harry Ferguson), its glory was assumed to be that it would allow the small farmer to do all the necessary work on his 160 or so acres with considerably less time and effort,

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giving him extra leisure time. In both this special case and in general, the virtual opposite has happened. Today in the United States, in many or most families both parents work even more than one parent worked in the early part of the twentieth century, and children are—seemingly “necessarily”—relegated to day care and preschool. Farmers found that the three-point tractor hitch actually helped set off a new competitive race that required farmers to multiply the number of acres worked in order to make a living wage. Instead of having more leisure time, farmers were able to do more work in the same time, and, like everyone else in the same situation, they seemed to be essentially forced to do that to keep up with or forge ahead of everyone else. More recently, the advent of efficient hydraulic systems on tractors has largely superseded the three-point hitch and set off a new race in which a single family may find itself working one or two thousand acres while selling such products as corn and other grain at prices not too different from those paid when the three-point hitch was invented more than a half-century ago. All of this speaks again to the fact that, like other organisms, humans must be presumed to have evolved not merely to reproduce successfully but to outreproduce their most significant competitors, leading to the proliferation of unending competitive races. As implied in the above discussion of so-called labor-saving devices, we can perhaps be bold enough to ask whether concatenations of some human socially competitive races, because of their combined diversity, narrowness, and runaway and faddish effects, may even have value in comprehending why Barzun (2000)—and others—have felt it necessary to interpret both long- and short-term trends in human sociality as decadent.

Throughout the history of such narrow and frantic competitive races, something more properly called “art” has persisted, apparently because of a second attitude toward competitive races (both strategies can be witnessed being employed by children in that microcosm of the human social world that consists of competing for the approval of a single set of parents). One expression of this second attitude I have earlier described as avoidance of directness in competitiveness rather than the seeking of ever-more confronting forms or expressions of competition. Another similar expression may arise, not through avoidance, but through the incidental perception and adoption of new and appealing avenues of creativity. Whatever their origin, unique life niches are created by some humans for themselves, from which they are able to tell the world things that no one has ever known before. Perhaps, as individuals, these artists can indeed be said to have mounted the “single-minded effort to render the highest kind of justice to the visible universe” alluded to by Joseph Conrad (quoted in Barzun 2000, 791). Incidentally, they also

magnify the social diversity that we humans euphemistically refer to as “division of labor.”

CONCLUSION

In sum, I have tried to consider every relevant aspect of the topic I originally proposed. At least I don't think I left any gaps that might require miracles. If that is true, perhaps this essay helps make it more likely that some day we will know how to connect the entire array of human activities to a base in reproductive effort. The undertaking is important because it promises dramatic insights into our most precious thoughts and strivings, and those most stubbornly resistant to change. Such human self-understanding may be the most important change imaginable in our universe, not merely to promote happiness and well-being but to lengthen human lifetimes by reducing needless strife and aggression at all levels.

We think of the arts as differing from the sciences in seeking meanings—social facts that are often restricted in their usefulness, or personal rather than general. Part of the reason for the restrictions may be that the uniqueness of individual human genomes has resulted in each of us evolving to behave (in evolutionary terms, appropriately) as if, for each of us, the collection of our personal life interests were unique. We have evolved to use the myriad facts available to us in ways unique to ourselves, which in some sense is the meaning of meaning. Human social races are prevalent because of the importance of the prestige thought to be derived from doing well in almost any such race and the consequences of prestige that bring benefits (power) through the action of direct and indirect reciprocity. Evolutionary social selection, including nepotistic selection and mutualistic and reciprocity selection, may be the last important set of mechanisms required for the connecting of complex aspects of cultural phenomena, such as the arts, to a life basis in evolutionary selection favoring reproductive success. It leads to the exaggeration of all the capabilities that are displayed in artistic works and performances.

I recognize that all of my discussions are imperfect and incomplete. They will be worthwhile, however, if the shortcomings help point the way for those with the next round of insights. I conclude that we seem not to be lacking in mechanisms to approach analysis of our own activities in evolutionary terms, only in knowing how to use them. Perhaps the next generation can make sense of the rudimentary arguments that I and others have generated so far on these difficult topics.

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