

HOW DID HUMANS EVOLVE?

Reflections on the Uniquely Unique Species

Richard D. Alexander
Museum of Zoology and Department of Biology
The University of Michigan
Ann Arbor, Michigan 48109-1079 USA

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MUSEUM OF ZOOLOGY, THE UNIVERSITY OF MICHIGAN
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This essay is dedicated to Theodore H. Hubbell
who for more than thirty years criticized willingly and thoroughly
whatever ideas I was brave enough to present to him.

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INTRODUCTION

The most mysterious and compelling unanswered question about ourselves is how we came to be. What caused us to evolve our marvelous intellects and our unsurpassedly complex social life? Why are we so different from our closest relatives? What happened to all of our extinct ancestors? Why is it that during the several million years since hominids diverged from the ancestors of modern apes, while other rapidly evolving forms of life were speciating prolifically, no part of the evolving human line has survived as—or possibly even became, contemporaneously with other incipiently human species—a different species? Why are we all alone at the pinnacle of the particular direction of rapid evolutionary change that led to the combining of such traits as a huge brain, complex intellect, upright posture, concealed ovulation, menopause, virtual hairlessness, a physically helpless but mentally precocious baby, and above all our tendency and ability to cooperate and compete in social and political groups of millions? What, precisely, was happening to the evolving human line in different parts of the world 50,000, 500,000, or (among our prehuman ancestors) 5 million years ago?

Interest in such questions is shown by the attention given to newly discovered fragments of human ancestors. Every piece of bone or tool, every ancient campsite or other bit of information about how our ancestors lived, excites the imagination and reveals how much we care. Perhaps we care partly because we know intuitively that to understand how we came to be may tell us things of value about modern human activities, especially those that perplex and frighten us.

Given the woefully incomplete knowledge of our long and distant past, the public has had to satisfy its thirst for self-understanding however it could.

Some have accepted religious answers involving creation by a Supreme Being, and the idea that moral and social rules come from the same source. Others have simply resigned themselves to living with only a vague notion of how it all might have come about.

Biologists and biologically-minded anthropologists, in particular, who take it as given that all forms of life have come about through an organic evolution guided primarily by natural selection, are not satisfied with either vague or supernatural arguments. Even if their theories do not easily yield convincing or comprehensive answers, they keep probing and questioning—trying, it might be said, to construct a “rough draft” of a scenario or theory of how humans evolved. Such a rough draft—even based on no more than speculations not easily dismissed—has been difficult to complete. Natural selection implies reproductive advantage. But there are whole suites of human activities that seem to have nothing to do with reproduction, and that no one has been willing to tackle in such terms. How does one explain art, music, opera, literature, humor, politics, science, or religion, using arguments from biological evolution? Conversely, why should we take evolution seriously, in trying to understand ourselves, if such important activities seem immune to its probings?

These problems can be discussed in three parts: (1) what general selective forces drove the evolution of hominids, while for the most part keeping them a single species, (2) what combinations of selective forces caused the appearance of the various unique or distinctive features of humans and their social life, and (3) how can the answers to these two sets of questions be combined to yield an overall synthesis?

A NOTE ON METHOD

How does one test grandiose hypotheses of the sort I am trying to review and develop here—hypotheses about the large picture of the evolution of the human species? Everyone would like straightforward and easy-to-understand Popperian falsification procedures for every important hypothesis, whatever the field. No realistic person, however, expects that such tests for hypotheses about the generalities of human evolution will be easily discovered. Indeed, such tests are rare for all broad or general biological questions, and very few writings about human activities are scientific, in the sense of being immediately and objectively testable. The more important is a biological hypothesis, the less likely we are to find simple, satisfying tests, and the more likely we will have to be ingenious in finding ways to adjust the probability—perhaps only in minor fashions at first—that we are on the right track.

With these difficulties in mind, I have attempted to develop the narrative of this essay as a testing procedure. First, I discuss two independently derived hypotheses that bear on the general question of how humans evolved: (1) the so-called “balance-of-power” hypothesis for human evolution, generated piecemeal by a succession of authors and perhaps first made explicit by Alexander and Tinkle (1968), Bigelow (1969), and Alexander (1974, 1979), and (2) Humphrey’s (1976) hypothesis about the evolution of the brain as a social tool. I take the stand that considering whether such independent hypotheses are compatible represents a test, even if not a definitive one. In this case I find the hypotheses not only compatible but apparently mutually reinforcing; had it been otherwise one or both would have been cast into doubt.

Next, I review and update discussions of several distinctive or unique human attributes, explicitly to consider their compatibility with the introductory general hypothesis. Sometimes I have been able to describe procedures that appear to falsify some of the alternative hypotheses generated to explain these human attributes.

I also consider aspects of human uniqueness—

human attributes and tendencies—that have not previously been considered in an evolutionary light, apparently because no one had a way of beginning analyses of these traits in such terms. I assume that exploring all such topics—with the question explicitly in mind whether they seem compatible or incompatible with the general hypothesis generated from the combination of the balance-of-power hypothesis and the evolution of the brain as social tool—is also a method of beginning to test the general hypothesis. I think it is important to think of all these topics together—to create a completed rough draft—because it is their fit as a combination that constitutes the best test of the general hypothesis.

No doubt critics will regard my “tests” as woefully inadequate, and I cannot disagree. I think, however, that the subject is sufficiently important, and that it has been virtually untouched by science long enough, to justify developing discourse that has to be regarded initially as only partially scientific. I base this opinion on these perceptions: First, even if most of the readers of this essay see themselves as fortunate, life obviously is not always good for all people. The world is filled with misery from actions such as murder, rape, terrorism, abuse, deception, and discrimination. I think it obvious that these actions are often not simply pathological or owing to either obvious or easily eliminated proximate causes. As a result they must be dealt with in part through deeper human self-understanding, sometimes as aspects of competition and conflicts of interest. Second, our planet’s life-sustaining capacity is threatened by the combination of human population growth and continual efforts to raise the quality of human life in ways—such as through technology—that paradoxically reduce rather than increase the probability of long-term human survival. This trend too seems most likely to be halted or reversed only as a result of deeper human self-understanding.

If, as I believe has been amply demonstrated, organic evolution is the explanatory background for all traits of life, then human self-understanding adequate to the proposition of long-term survival

depends to some extent on self-analysis in evolutionary terms. Yet evolution is a process studied extensively and seriously by a miniscule proportion of the earth's population, and it has been applied extensively to human self-understanding by an even smaller group of individuals. Additional efforts may literally be a survival imperative. If tests

of the hypotheses reviewed and developed here are inadequate, their presentation at least has the potential to stimulate others to devise better tests. The task seems sufficiently important to warrant even a painfully slow step-by-step development toward the goal of scientific status and real or statistical probabilities.

WHAT GENERAL SELECTIVE FORCES HAVE DRIVEN HUMAN EVOLUTION?

A PARADOX

In the late 1950's, while trying to understand speciation in field crickets, I began to believe that the human species has evolved in an unusual, perhaps unique fashion. The evolutionary line giving rise to the human species separated from that giving rise to chimpanzees, our closest living relative, 5–8 million years ago (Ciochon and Corruccini, 1983; Ciochon and Fleagle, 1987; Caccone and Powell, 1989). During these several million years the hominid line diverged far from that of the apes, especially in regard to brain size and function, and the accompanying complexities of behavior—particularly social behavior. Additionally, evidence from the fossil record, especially of hominid skull cavities, indicates that evolution of the human brain accelerated as it diverged from the ape line (Kurten, 1971). Hominid brain evolution has for this reason been termed an autocatalytic process (*e.g.*, Godfrey and Jacobs, 1981; Stringer, 1984).

Two things are surprising, or puzzling, about this description of hominid evolution. First, despite the long time since separation of the hominid line from that of the great apes, and despite the apparent rapid rate and acceleration of its evolutionary divergence, there are few if any clear instances of species multiplication, and only a single species remains today. Current arguments on this question concern whether or not more than a single species ever occurred together geographically and temporally (*e.g.*, Foley, 1989), but we might have expected that numerous similar species would have co-existed. Among organisms in general, rapid evolution and rapid multiplication of species tend to go together, but evidently not in this case.

This puzzle is exacerbated by a second problem, represented by the degree of divergence between the human line and that of the great apes (actually, all other forms of life), especially in regard to brain size and function. What selective challenge could drive the hominid line so far away from that of other primates, and, even more puzzling, what sort of challenge could have caused this divergence to accelerate in its later stages? It did not seem to me that any combination of what Darwin called the "hostile forces of nature," or the forces of natural selection—food shortages, climate, weather, predators, parasites, and diseases—could represent a challenge adequate to explain human evolution (one may also include sexual selection and sexual competition among the hostile forces of nature, as "mate shortages").

Because the hominid line evidently evolved away from its closest relatives, and at an increasingly rapid rate, the human species cannot be described as a "living fossil" whose close relatives have simply become extinct while it alone lingered through evolutionary time. Even if it did not speciate prolifically, there is the problem of why all the intermediate stages became extinct across this very long period of dramatic change and dramatic divergence from ancestral forms.

A POSSIBLE SOLUTION

Across the years these problems remained in my mind, and I eventually published a brief comment on them from a 1965 lecture in a symposium on systematics (Alexander, 1967), following this with additional hypotheses in a review of Konrad Lorenz' (1966) *On Aggression* and Robert Ardrey's (1966)

The Territorial Imperative (Alexander and Tinkle, 1968). Subsequently I developed the idea from these initial comments in papers and books published in 1971, 1974, 1977, 1979, 1987(a,b,c), and 1989b. Robert S. Bigelow, also a cricket biologist, with whom I had co-authored a paper on field cricket speciation in 1960, independently developed a parallel idea, published initially in his widely cited 1969 book, *The Dawn Warriors*. Our arguments were not as new as we initially thought, for Charles Darwin (1859, 1871, 1872), Sir Arthur Keith (1949), and Raymond Dart (1954) had developed parts of the same ideas long before. Others have continued to develop the general propositions involved (e.g., Carneiro, 1970; Hamilton, 1975; King, 1976; Pitt, 1978; Strate, 1982; Wilson, 1973, 1975; Ghiglieri, 1985–1989; Reynolds *et al.*, 1987; Shaw and Wong, 1988; Manson and Wrangham, in press).

The hypothesis these various authors have developed gradually and collectively is that perhaps only humans themselves could provide the necessary challenge to explain their own evolution—that humans had in some unique fashion become so ecologically dominant that they in effect became their own principal hostile force of nature, explicitly in regard to evolutionary changes in the human psyche and social behavior. At some point in their evolution humans obviously began to cooperate to compete, specifically against like groups of conspecifics, this intergroup competition becoming increasingly elaborate, direct, and continuous until it achieved the ubiquity with which it has been exhibited in modern humans throughout recorded history across the entire face of the earth. Such a scenario can account not only for the degree of divergence of humans from other lines but also for the absence of surviving intermediate stages and the acceleration of the divergence in later stages. This unique kind of within-species balance-of-power race—involving, eventually, virtually all levels, or group sizes, within societies—would be a perpetual or unending one, in which the losers, in selective or reproductive terms, would always be but a step behind the winners (because they would, in general at least, be members of the same interbreeding populations), and in which rapidly

appearing differences in culture and technology could become significant unbalancers that could accelerate the process even further. It could be termed a case of “runaway social selection,” paralleling the runaway sexual selection discussed by Fisher (1930, 1958) (see also West–Eberhard, 1983; Alexander, 1987a, 1989b). Rather than simply the other sex—and competitors within one’s own sex—representing the environment of reproductive competition, it calls for adversarial and competing groups of humans to be central in creating the environment of brain and psyche selection. Unprecedented levels of cooperation within groups could thereby be generated, as well as unprecedented kinds of between-group adversarial relationships.

THE BRAIN AS A SOCIAL TOOL

The kind of selection described above does not necessarily call for other humans to be the most important overall source of human mortality or reproductive failure, but it does call for other humans to be the principal source of such failures which affected the evolution of the brain, the psyche, and the complexity of social behavior. A necessary concomitant would be that the human brain has evolved in the context of social cooperation and competition.

In 1976, a young Cambridge psychologist, Nicholas K. Humphrey, published a paper titled “The social function of intellect” in which he argued that the human brain and psyche evolved as a social tool (see also Humphrey, 1978–1983). He referred to humans as possessing a “runaway intellect” and argued that the human intellect evolved as a means of dealing with the uncertainties of social life. Humphrey meant that the real challenge in the human environment throughout history that affected the evolution of the intellect was not climate, weather, food shortages, or parasites—not even predators. Rather, it was the necessity of dealing continually with our fellow humans in social circumstances that became ever more complex and unpredictable as the human line evolved.

This argument is a very special one. Consider intelligence tests or the writings of philosophers

and others about “artificial intelligence.” Consider “brain-twisting” problems, and other models and descriptions of what the human mind, in its most remarkable forms, is able to accomplish. Consider the reverence we show for great mathematicians, chess players, and masters of memory who strut their stuff on television quiz shows. Where in all of this is even a hint that the humans who succeeded most dramatically throughout most of our evolutionary history might have been those best at socially manipulating, using, or besting their fellows? It would seem perverse even to imagine “intelligence” tests designed to give high scores explicitly for such abilities. We would probably all like our personal lawyers, and the politicians who represent our interests against those of others, to be ultimately clever in social manipulation; but whom, one also may ask, do we hold in greater suspicion and distrust than such social experts? Such attitudes may have confused us about the forces that have molded our intellectual capacities, and caused a considerable misdirection of efforts to understand the design of our brains and our social abilities and tendencies. Together with our desires to emphasize the cooperative and “brighter” sides of human nature, they still confuse us and cause us to speak and write about, and read, only what we want to hear.

Humphrey was not saying that the behavior of other humans is unpredictable in the sense that the weather is unpredictable. We can't do much about the weather, but we can influence the behavior of our associates. The evolutionary problem would have been to influence others' behavior in ways most beneficial to our own interests. Humphrey was suggesting that variations in the ability to predict and manipulate others' behavior gave advantages to some, and resulted in the step-by-step changes in intellectual complexity that eventually yielded modern humans. Biologists would wish to specify that the advantages given in the situation just described were, ultimately, advantages in reproductive success, for that is how evolution proceeds.

Humphrey's hypothesis quickly caught the imagination of many biologists and philosophers, who have repeated and developed it since (*e.g.*,

Blakemore and Greenfield, 1987; Byrne and Whiten, 1988; Alexander, 1987a, 1989b). Humphrey did not refer to the ideas and arguments about cooperation to compete, described earlier, and he evidently saw no connection between them and his own hypothesis. In other words, he provided no mechanism by which selection would cause humans, alone, to continue their brain evolution toward the extreme condition represented today. Nor did he, or those who were attracted to his idea, appear to realize that for his idea to work some scenario of the sort described above would have to be the case; indeed, a balance-of-power hypothesis seems to lead necessarily to the conclusion Humphrey reached.

In other words, if natural selection caused increasingly rapid directional changes in the human brain and psyche across a long period as a result of social interactions, it becomes necessary to account for the continuing elaboration of the competitive situation leading to the changes. When selection is intense, there are not only winners but many losers, and one has to explain why the losers, or incipient losers, did not tend at every stage simply to retreat from the social competition. Why did the human species continue to become increasingly elaborately social and cooperative during times when so many of its members were suffering, with respect to both survival and reproduction, as a direct result of the sociality? If humans became potentially the most detrimental force with respect to the lives and success of their fellows, then why didn't humans evolve to live apart from one another so they wouldn't have to contend with competitive, aggressive, manipulative associates? After all, thousands of species do not live socially. With humans, ecological dominance and social competition seem instead to have become involved in a vicious cycle in which each exaggerates the importance of the other. What could have caused this?

It would seem that the answer has to be that they could not withdraw from the particular kind of society that was evolving without losing even more dramatically. To understand why this should be the case, we are returned to the question of what challenges could have continued to force an ever more complex and elaborate sociality. It seems

to me that we are returned to the hypothesis of cooperation-to-compete within the species; of humans as their own hostile force of nature; of a balance-of-power race accelerated by the increasing intelligence, cooperativeness, and cultural cleverness of the increasingly ecologically dominant human line.

THE IMPORTANCE OF ECOLOGICAL DOMINANCE

Anthropologists have long described humans as the species that, rather than simply living in a certain environment, or choosing one, most explicitly creates its own environment. And they have also noted that, as a result, humans have long been able to live almost anywhere they pleased on the face of the earth. In other words, the human species is so ecologically dominant that it can mold, manipulate, or even remove aspects of its environment—including other living forms—more or less at will. This is just another way of saying that humans have so reduced the significance of what Darwin saw as the external “hostile forces of nature,” or the forces of natural selection, that other humans very well could have assumed the role of the principal “hostile force of nature,” at least most of the time and insofar as evolution of the intellect is concerned (see also Alexander, 1989b).

Once humans began to use social cooperation as a principal means of competition they began to compete socially not only as individuals but in coalitions of every imaginable size and variety. We all know that humans do this today, and they have apparently done it throughout recorded history. The implication is that our ancestors did it for thousands of generations. Moreover, once humans started living in groups (or continued group-living) explicitly because this enhanced their ability to compete with other neighboring groups of humans (as surely is the case today), then the possibility of living nonsocially virtually disappeared—even if predators were removed, and food and shelter became abundant—because humans themselves would not allow it. Even today, when we like to think of ourselves as civilized, ethical beings who respect the rights of others, there is great difficulty in living as a hermit, and hermits who try to rear

families (reproduce) and still remain isolated have even more trouble; small groups, such as communes, within or near larger ones, have this same difficulty, as do nations near enough to one another to represent mutual threats.

We usually think of cooperation as the opposite of competition—as an alternative to it. It's true that in any given situation one individual can either compete or cooperate with another. But if cooperation works, the evolutionary effect is to cause a kind of indirect competition with everyone else who didn't cooperate quite as well. Regardless whether one individual ever interacts with another, the two are inevitably competing in regard to which will leave more copies of its genes. And, over the long run, those who are better at it become the ancestors of whoever remains. In this sense, cooperation is always competition as well, and competition thus is not only inevitable but in evolutionary terms has no alternative. If a species simultaneously becomes so ecologically dominant that no other aspect of the physical or biological world is as important to the success of its members as are other members of the same species, and if its members also take up cooperation as a principal means of social competition—as the various authors cited above have argued—then Humphrey's scenario becomes a reality. Social cleverness, especially through success in competition achieved by cooperation, becomes paramount, and the race toward intellectual complexity—a particular kind of intellectual complexity—is on. This process is evidently unique to the human species. It seems to me that it would lead precisely to the kind of organism we are, and I can think of no other process that would. The apparently mutualistic relationship between the two hypotheses of a balance-of-power race and the brain as social tool—hypotheses that were generated independently—may not be an adequate test of either hypothesis, but it causes each of them to be more difficult to dismiss.

These thoughts are worth careful contemplation. They mean, for example, that if we argue that the emotions have evolved to produce “harmony” in human social interactions (*e.g.*, Gibbard, 1990), our understanding of the emotions will not be

complete until we understand the selective reasons for the promotion of harmony. If all our cooperation across history had been merely to fend off nonhuman or even nonliving threats, then the only paradoxes in moral issues would be those engendered by within-group efforts to compete. Even these might be sufficient to perplex moral philosophers indefinitely. But if the hypothesis is correct that the complexity of our modern, world-wide, within-species, between-group strife is ancient, and a driving force in structuring human sociality and cooperation, then the dissection of intentionality and the understanding of morality becomes infinitely more convoluted.

SOCIAL COMPETITION AND SCENARIO-BUILDING

What kind of intellectual complexity would be generated by the type of evolutionary race described above? Human mentality has several components, but consciousness is probably central. The concept of consciousness is related to other ideas like foresight, planning, awareness, self-awareness, fantasizing, and dreaming. All of these are part of anyone's description of human mentality. Among other things consciousness implies the ability to think about times and places and events separated from our immediate personal circumstances. It implies the ability to use information from the social past to anticipate and alter the social future, to build scenarios—to plan, to think ahead, and to anticipate different possible outcomes and retain the potential to act in several alternative ways, depending on circumstances that can only be imperfectly represented at the time the plans or scenarios are being made.

Language is tied closely to consciousness as scenario-building, because it alone enables us to communicate with others about events "displaced" in space or time or both (Hockett, 1960)—a requisite characteristic of social (or other) scenarios. We can use signs or symbols to designate places, events, objects, and individuals, and then, through the use of tenses, talk to others about events, objects, or individuals in different times and places. In no other way can detailed information about mental scenarios, which necessarily involve different times

and places, be transferred between individuals (see also Alexander, 1989b; Gibbard, 1990).

What circumstances should we expect to be most challenging, with respect to accurate and complete building of scenarios *via* consciousness? Surely, the answer is: those involving other organisms doing exactly the same thing in preparation for their competitive and cooperative interactions with us. In other words, nothing would select more potently for increased social intelligence—for better ability to look ahead and survey the alternatives accurately—than a within-species co-evolutionary race in which success depended on effectiveness in social competition. In effect, consciousness is a way of seeing ourselves as others see us so that we may cause competitive others to see us as we wish them to, rather than as they might like to (that is, with our "defenses" down).

I think that this view places cognition, as a part of problem-solving ability, in a clearer light as well, because it implies that the problems that have driven the evolution of cognitive abilities have been social problems. I have argued that other aspects of human mentality such as the expression of the emotions and personality traits are also parts of our supply of tools for social cooperation and competition (Alexander, 1989b). Psychologists and anthropologists have already suggested independently of the theories discussed here that mathematical ability is a special case of linguistic ability (Lenneberg, 1971), and that linguistic ability is likely explainable as serving a social function (Burling, 1986).

Scenario-building, including dreaming and day-dreaming as well as serious or purposeful planning, has seemed to many a kind of social-intellectual play. The most widely accepted theory of play is that it represents practice for the future, which occurs under circumstances that make it inexpensive compared to real-life, full-cost episodes of social competition (Fagen, 1981; Humphrey, 1983). Such practice can take many forms. It can merely improve physical, social, or intellectual skills. It may involve producing and trying out alternative scenarios. It may also involve acquiring status, or learning how to deal with dominance rankings that may be difficult to change as the playing individu-

als grow and develop and begin to compete in earnest for the actual resources of reproductive success, such as mates, jobs, and status (Alexander, 1989b). The term "thought experiments," as used frequently by scientists, suggests the centrality of scenario-building. It refers to an initial, internal process of testing and rejecting possibilities, and in that sense I regard it as responsible for the generation of virtually every reasonable hypothesis. To the extent that useful ideas represent a limiting factor in the advance of knowledge, this process may be central in even the most conservative and rigorous aspects of science. Einstein completed the general theory of relativity in his brain and tested it there so thoroughly that he was confident that "The result could not be otherwise than correct. I was only concerned with putting the answer into a lucid form. I did not for one second doubt that it would agree with observation" (Clark, 1971, p. 259).

Every human continually builds hypotheses and initiates their testing within his own mind, whether he is dealing with high-level scientific questions or everyday problems like how to start a car or whether or not to cross the street in some particular place or time. Such thought-experiments work because every human already has some relevant data in his head when he generates an hypothesis. The skill with which the process of internal testing is undertaken, and the data that already exist in the theorist's head against which he can test his idea, are what determines whether the hypothesis, when it is finally communicated to others, will be reasonable and useful, or will immediately be seen as false or unacceptable because of someone else's thought experiments. Reviewing possibilities and probabilities, and mentally playing out step-by-step either physical or mental challenges that lie ahead, are widely believed to be sometimes more important than more direct forms of practice. Even the actual experimental testing of an hypothesis, after all, is itself nothing more than a mental scenario brought out into the external world.

ARE SOME ASPECTS OF HUMAN STRIVING IRRELEVANT TO EVOLUTION?

Many human attributes have previously seemed inaccessible from the evolutionary viewpoint of biology. Free will, for example, is one of the provocative issues argued across the history of philosophy that any universally applicable theory of human evolution ultimately must explain. How does it fit here? In *Darwinism and Human Affairs* and *The Biology of Moral Systems*, I argued that the concept of free will is not a question of whether or not our acts are physically determined, but of whether or not individuals believe they have the ability to act on whatever personal intellectual scenarios they happen to choose, among the several or many they might have generated. I think that any individual with the freedom to act on his own scenarios, according to his own interests as he sees them, believes that he has "free will," and vice versa. In other words, I believe that the concept springs from an interaction between our ability to generate and use alternative scenarios, and the imposition of rules and restrictions by society. I restate this argument here because it seems useful to be reminded that even a difficult or extreme topic such as free will need not be incompatible with the adaptive view of human mentality here supported. The fact that the question of free will continues to be thought of as whether or not some behavioral alternatives are selected in the absence of physical causation is in my view an intriguing mistake of human thought—a mistake worth reflection because it shows how difficult it sometimes is to eliminate particular kinds of fuzziness from our intellectual ruminations.

Because of our social competition, and because of the importance of reputation in reciprocal interactions, deception has also become a prominent aspect of our social lives. Sometimes it is effected through self-deception that prevents us from knowing our own true motives and allows us what the psychologist Donald T. Campbell (1975) calls "sincere hypocrisy." The pervasiveness of decep-

tion in our everyday lives (both self-deception and the deception of others) can be glimpsed by anyone willing to reflect on how often (and for what reason) he or she does one or more of the following things: bathes, shaves, puts on deodorant or makeup or artificial eyelashes, chooses clothes with concealing and flattering effects such as shoulder pads, dons shoes with elevated heels, pops a mint into the mouth, and enters the work place wearing a polite smile. We seem not to like to dwell on the deceptive aspects of human sociality, except in fun or as part of the behavior of those we think we have reason to disparage and to imagine as utterly unlike ourselves. But such reluctance will not make deception go away or solve the problems of dealing with its prevalence in the world. Our efforts at self-analysis must include more than just the "brighter" side of human nature if we expect to solve the truly pressing human problems (see also Trivers, 1985; Mitchell and Thompson, 1986).

If scenario-building, in connection with social cooperation and competition, becomes as central in the life of a species as it apparently has with modern humans, then it may also become important to observe the scenario-building of others, as well as their "real-life" efforts, and learn from them. Ability to anticipate social situations and the reactions of others to them might enable a person mentally to imitate or parody their possible actions and thereby assist himself in developing responses most self-beneficial when the necessity for social interaction arises. Perhaps his predictions will be improved if he acts out the possibilities and involves others in such explorations. These others, upon observing the performance, will themselves gain by having some parts of scenarios useful to them acted out for them. From such imitation it is only a short step to taking advantage of superior scenario-building abilities of others, and even reimbursing them to build scenarios for us. Individuals who are particularly good at such acting out (and analysis or teaching) may be rewarded in various ways, perhaps at first only by elevation of status. Eventually, the rewards may become formalized, so that the unusually good actor becomes a professional, and some significant proportion of

society attends the sessions in which he performs and pays him handsomely for the privilege.

It seems to me that some such idea can be developed so as to involve nearly all of the seemingly inaccessible suites of activities mentioned earlier (see also Alexander, 1986, 1989a, b)—humor, art, music, myth, religion, drama, literature, theater, preaching, teaching, and the magnetism of television soap operas and team sports. Our ancestors—as with many but not all humans today—literally existed within the "soap operas" of their extended family's or clan's daily social and political activities. Modern humans more frequently are able to do the same vicariously in the surrogate situations afforded them by literature, radio, television, opera, and other similar forms. We reimburse others (lawyers, politicians, teachers, novelists, actors, physicians, coaches, plumbers, electricians, horse trainers) to build scenarios for us (make diagnoses, represent us in competitions, work out repair procedures, teach and demonstrate routes to success and failure) because they can do it better than we can—more inexpensively, more elaborately, or more quickly—just as we hire others to do for us jobs that we cannot do as well, or from which we wish to be freed so that we can do other things at which we think we are more effective. Such surrogate scenario-building appears to be a unique-to-humans kind of occupational speciality of the general sort we call "division of labor."

Team sports seem to me especially significant to the arguments presented so far. To the observer they represent not only the physical and mental "how to" of intergroup competition and intragroup cooperativeness but as well a way of participating in the ceremonial and reinforcing aspects of own-group success. The equivalents of fans and cheerleaders have surely been important for a very long time in the group competitions of humans, and it is no accident that the "home court" gives a significant advantage. It is also not incidental that both extensive mental scenario-building and the resolve of "team spirit" have come to be essentially formal aspects of training in sports and other group-competitive events.

This view of human thinking, then, seems not

only compatible with the centrality of social competition by cooperative groups as a general theory of human evolution and human brain evolution but strongly supportive of it.

ALTRUISM, KINSHIP, AND RECIPROCITY

In general, humans tend to help their relatives against other groups of less closely related individuals. A little thought shows that this particular kind of cooperation to compete will yield rewards in terms of genetic survival, for closer relatives by definition carry proportionately greater numbers of one another's genes, as compared to more distant relatives or nonrelatives (Darwin, 1859; Fisher, 1930; Haldane, 1955; Hamilton, 1964). Anthropologists have for a long time known that humans everywhere have kinship "systems," in which different relatives have different labels and are treated in special ways. Close kin tend to cooperate against distant relatives and nonrelatives.

Philosophers and social scientists have often written as if evolution had been causing us to become indiscriminate altruists who continually sacrifice our own life interests for those of others. Similarly, ecologists and animal behaviorists once supposed that the individuals of nonhuman species evolve to do things for the good of their populations or species, even at the expense of their own "genetic survival." Now we know that evolution cannot produce such tendencies (which does not mean, however, that it cannot produce a thinking organism that can consciously create such tendencies in itself as an incidental outcome of its evolutionary past). It only seems that way—in humans partly because of the enormous importance of nepotism, social reciprocity, and reputation in social success, and partly because the interests of individuals within groups are often identical, at least for short periods of time or in particular circumstances. Self-beneficial reputations can also be acquired through beneficence to others, and humans alone have sorted out their common interests within groups and translated them into extensive cultural or moral rules (Alexander, 1987a).

Owing to the probability that relatives are primarily "recognized" by being learned about and

remembered through social relationships (for a review and defense of this idea, see Alexander, 1990a), and because continuing nepotism takes the form of reciprocal assistance, nepotism converts easily into social reciprocity (Trivers, 1971; West-Eberhard, 1979). This is the reason that modern human sociality assumes a form similar to that of small hunting-gathering groups composed almost entirely of actual relatives and relatives by marriage (who produce actual relatives for their "in-laws"), even though modern sociality sometimes almost entirely involves reciprocity between non-relatives.

DISCUSSION

So now we at least have an hypothesis for why the populations most like our evolving ancestors failed to survive alongside us in the way that many similar species of animals and plants do co-exist. Evidently they were extinguished—the collections of traits that identified them disappeared—as a result of the cooperative group-against-group competition that we conduct so frightfully well. Even our distant relatives suffer today. Primatologists estimate that human predation on primates is more severe than that from any other source (*e.g.*, Cheney and Wrangham, 1987). This is probably true for only a few other mammals, for example some ecologically dominant species like lions, elephants, and rhinoceroses. The reasons for killing our closest relatives, moreover, are not always the same as those involved in killing, for example, game animals. I speculate that our closest relatives—chimpanzees, gorillas, and orangutans—have not only been severely restricted by human predation and competition, but may have had many aspects of their social structure virtually determined by their human competitors and enemies (Alexander, 1974). If they had been even more like us, or perhaps less able to diverge from us in the face of evolutionary competition, they too would probably be extinct. On the other hand, if we were to disappear from the planet even now, and leave them to their own devices, I have little doubt that chimpanzees, at least, would evolve many attributes paralleling those of modern humans. Chimpanzees have already evolved specialized group-against-

group competition (Ghiglieri, 1988, 1989; Manson and Wrangham, in press). Their brains are most like ours, and they and orangutans alone share with us the ability to recognize themselves in mirrors, suggesting a kind of conscious self-awareness (Gallup, 1970). At least among males, chimpanzees show signs of the extraordinary and complex within-group cooperativeness that, in a primate, probably represents the adequate "initial kick" for the runaway social process here envisioned (Alexander, 1989b). Of course significant changes in chimpanzee social life would have to occur before an evolutionary pathway resembling that of the hominid line could be taken (see below).

In an earlier paper I argued (Alexander, 1987b) that science differs from the humanities in that "Scientists typically pursue topics within which there exist cores of factual discoveries—within which statements can be made that approach undeniability" and that practitioners in the humanities, in contrast, "are preoccupied with meaning, or value . . . concepts [which] are interpreted individually—or at least not universally—and therefore lead toward diversity and disagreement rather than universality and undeniability." I suggested that "Practitioners of the humanities are concerned with what literature, art, music, aesthetics, religion—and even ethics and history sometimes—mean to different individuals or different groups. They are preoccupied with variations in interpretations, which arise out of differences in interests." I also suggested that "Whatever bodies of facts do underlie the activities of humanists, they are typically not regarded as the central issue" (p. 319). I did not, however, indicate how to identify superior works in the humanities, although how to do so in the sciences seems obvious. Moreover I failed to examine the question of what things might be common among all those humanities-oriented works (of art, literature, music, or whatever) that are widely or essentially universally considered great.

Bruner (1986), in an essay close to mine in some of the above regards (but distressingly more incisive and eloquent), has taken up these questions, in a way that I believe bears on the ideas discussed above about scenario-building and surrogate sce-

nario-building as an aspect of the evolution of the human psyche or intellect. Bruner suggests that literature (or art or music) attracts huge and enduring audiences—becomes great or classic—when it bears on problems of broad or universal significance and provides unusually rich opportunities for scenario-building for a broad array of readers (or viewers), allowing them to develop and interpret meaning for their own individual purposes. He notes that not merely the topic but the particular forms of language involved in works of literature are crucial, since through language the reader is provided opportunity to use his own scenario-building capacities to participate in what the author (artist) has constructed—to maximize the number of alternative mental pathways ("possible worlds") stimulated by the work. A further contrast between science and the humanities is thereby emphasized—that scientists are expected to write in an effort to be unequivocal, while their counterparts in literature and the arts strive to produce works that yield maximal potential meaning through subtlety, ambiguity, and the possibility of interpretation according to the particular interests or wishes or enjoyments of different parts of the audience (thus, the success of a recently popular song was attributed by its author-performer to its having included "something for everyone.") When the audience, implies Bruner, can make much more from a work than meets the eye, then the work has some likelihood of being judged superior. He remarks the profound difficulty of bridging the gap between science and the humanities, so defined, and thereby stresses the difficulties that beset the discipline of anthropology, which straddles the two sets of enterprises, the various aspects of biological anthropology on one side and those branches most recently called interpretive or symbolic anthropology on the other. Anthropology thus seems to range from hypothesis construction and testing, on the one hand, to literature on the other. But Bruner's exposition of textual construction and analysis as exercises in creating and extracting richness of surrogate scenario-building at least seems to me to point the way toward an analytical compatibility among all aspects of the human enterprise, and, as well, a way of resolving some of the

many difficulties that have prevented us from completing a "rough draft" of how modern human activities may all have generated from a back-

ground in differential reproduction of genetic materials.

HOW HAVE THE VARIOUS UNIQUE AND DISTINCTIVE FEATURES OF HUMANS AND THEIR SOCIAL LIFE APPEARED?

INTRODUCTION

Combining the cooperation-to-compete hypothesis with the notion of the brain as social tool allows us to pursue more effectively the understanding of both unique and unusual human traits. Examples of such traits are: menopause, concealment of ovulation, altriciality of the human infant, the extended duration of juvenile life, relative hairlessness of both juveniles and adults, evolutionary increases in the hominid lifetime, long-term pair bonding, frontal copulation, postmenopausal sexuality, and extensive paternal care, all of which seem to relate to general increases during hominid evolution in the amounts and durations of parental care or social tending (which we now realize we must explain in detail). Also included are the generation and maintenance of intricate and unified kin relationships, group-against-group competition in play, prominence of play throughout adult life, language, consciousness, music, art, humor, the aesthetic sense, complex abilities and extreme propensities to engage in social reciprocity, and the concepts and practice of morality and ethics. We are seemingly in a much better position than ever before to analyze such unique or unusual traits so as to understand better how the human species evolved—how it attained its present general nature, and why it diverged so far, in the particular directions it took, from all other species (I am not claiming that all of the above traits are unique to humans—for example, consciousness, which seems likely to exist in some form in several other species, in particular, apes, and may even include in such forms aspects of behavior that have been excluded from consciousness in the hominid line).

Conversely, if we cannot connect the special traits of humans to the general scenario just described, then we are justified in being skeptical of

its accuracy or usefulness. In this section I draw some connections partly through hypothesizing some new conditions of early human social life. For this presentation I have chosen a few human attributes, and an arrangement of them, which facilitate my arguments.

MENOPAUSE

Menopause is that time in middle age when the human female stops producing fertilizable eggs and therefore stops having children. In no nonhuman species are females known to undergo an evolved menopause. Sometimes very old females in zoo animals or domestic species become incapable of becoming pregnant a few years before they die, but this is not the same as a complex programmed cessation of ovulation in approximately the middle of the maximum lifetime, as happens in human females (Lancaster and King, 1985). In a few other species—such as elephants (see below) and pilot whales (Kasuya and Marsh, 1984; Marsh and Kasuya, 1986)—some females seem to live several years beyond their last production of offspring, and to do so in connection with assistance to relatives; these appear to be the closest approaches to menopause as demonstrated in humans.

Prior to modern selection thinking the opinion was widespread that menopause happens because older women are more likely to produce defective children and menopause prevents pollution of the gene pool. It was one of the most important changes in selective thinking that we now realize that selection cannot ordinarily favor attributes that assist the population or species at the genetic expense of the individual (Williams, 1966). In this case, ordinary common sense (and a modern view of natural selection) is sufficient to understand that, if pollution of the gene pool were all that was

involved, genes that tended to cause women to continue having babies despite the risk involved would certainly outreproduce those that influenced women to stop having babies, thereby (in this argument) canceling all future chances of improving their reproductive success.

It is also a common assertion that menopause happens simply because women live longer now. The presumed average age of prehistoric women has been used to back up the statement. Average ages, however, are not appropriate, first because they are powerfully influenced by infant and juvenile deaths and, second because it is not how many individuals live past a certain age that counts in selection but what proportion of their reproduction is thereby affected. Of a million codfish eggs only one may live to become a mature fish, but this does not mean that selection on the adult stage is ineffective. This is another example of a failure in selection thinking about humans that has persisted for decades.

There is another important source of error here: despite repeated arguments that medical research will eventually double or triple the human lifetime, there is no evidence that maximum human life spans have been significantly altered by the entire history of medical research (Fries, 1980). Reducing accidental and premature mortality has changed the average human lifetime, but the existing maximum life span is a product not of modern technology but of hominid evolution (Sacher, 1975; Lovejoy, 1981; Turke, ms.).

Still another argument has been that menopause is not an evolved phenomenon, but a product of senescence (Symons, 1979). Menopause seems to me too complex and to come too early in the human female's life to be regarded as other than a product of natural selection. These arguments need not be the only evidence. Comparing life lengths of modern primates indicates that the distinctive maximum human lifetime of a little over 100 years represents an approximate doubling of lifespan since hominids diverged from the ancestors of the great apes (Smith, 1989; Turke, 1989, ms.; Lovejoy, 1981). This doubling was caused primarily by adding to the length of adult life. Unless older humans were somehow contributing, directly or

indirectly, to the reproductive success of their genetic materials, no such alteration could have occurred as a result of natural selection. It is relevant that the human female, despite her early cessation of production of gametes, on average outlives the human male, who continues to produce viable gametes throughout his life.

Three different investigators independently postulated almost exactly the same reproductive or adaptive function for menopause (Williams, 1957; Alexander, 1974; Dawkins, 1976). The reason for the independence is not admirable. Rather, it was because I did not read (or remember) Williams' paper carefully enough, and Dawkins evidently did not read (or remember) either Williams' or my paper carefully enough. All three of us, however, postulated that menopause is a system whereby the human female turns her effort from adding new objects of maternal care to tending those she has already produced. Rather than introduce into her life another object of investment that may require an investment of 15–20 years, she has evidently evolved to turn her effort toward assisting the offspring she has already produced, and perhaps other relatives as well. In addition (see below), postmenopausal women may be even dramatically more capable at contributing to the success of their offspring and other kin than younger women, simply because success in social and political matters is to a large extent a consequence of gradually acquired knowledge, wisdom, and power.

Dawkins (1976) quantified what might be called the simplest version of this hypothesis in the following way (p. 135–136):

“... the difference between the abrupt change of life in women and the gradual fading out of fertility in men suggests that there is something genetically ‘deliberate’ about the menopause—that it is an ‘adaptation’. It is rather difficult to explain. At first sign we might expect that a woman should go on having children until she dropped, even if advancing years made it progressively less likely that any individual child would survive. Surely it would seem always worth trying? But we must remember that she is also related to her grandchildren, though half as closely.

“For various reasons, perhaps connected with

the Medawar theory of ageing, women in the natural state become gradually less efficient at bringing up children as they get older. Therefore the life expectancy of a child of an old mother was less than that of a child of a young mother. This means that, if a woman had a child and a grandchild born on the same day, the grandchild could expect to live longer than the child. When a woman reached the age where the average chance of each child reaching adulthood was just less than half the chance of each grandchild of the same age reaching adulthood, any gene for investing in grandchildren in preference to children would tend to prosper. Such a gene is carried by one in two children, but the greater expectation of life of the grandchildren outweighs this, and the 'grandchild altruism' gene prevails in the gene pool. A woman could not invest fully in her grandchildren if she went on having children of her own. Therefore genes for becoming reproductively infertile in middle age became more numerous, since they were carried in the bodies of grandchildren whose survival was assisted by grandmotherly altruism.

"This is a possible explanation of the evolution of the menopause in females. The reason why the fertility of males tails off gradually rather than abruptly is probably that males do not invest so much as females in each individual child anyway. Provided he can sire children by young women, it will always pay even a very old man to invest in children rather than in grandchildren."

In general, one cannot fault Dawkins' calculations (although, as Martin Daly pointed out to me, the point at which genes for investing in grandchildren would "tend to prosper" depends on the point at which the actual investment yields a greater genetic return, and this depends on such things as what other investments are available to grandchildren). I wonder, however, if his general view of this trait, and of the reproductive effort of middle-aged women and men, is not too simplified. First, as already noted, the human lifetime probably could not have doubled during hominid evolution if his argument is correct and complete: older adult

humans appear to have been contributing too extensively to reproduction to explain menopause as no more than a side-effect of senescence. Moreover, any evolutionary shift toward some kind of reproductive effort other than child-bearing would make it look as though the middle-aged female's child-bearing ability was deteriorating through senescence rather than through the evolution of alternatives, and thereby confuse the issue in the direction of Dawkins' "baby-sitting" view of the reproductive effort of postmenopausal women. Dawkins' view does not allow for any improvement or change in the nature of either a man's or a woman's reproductive effort; it relies instead upon a deterioration that forces a change. Yet we know that older men and women increase their social knowledge cumulatively, acquiring capabilities that are either absent or uncommon in younger adults and called by such terms as "wisdom," and that they continue to increase their control of resources, or their effective power, through increases in more proximate devices such as status or reputation and, more recently in human history, wealth. Across the entire world, wealth and power are heavily concentrated among people of both sexes who are near or beyond the age of menopause in women. The simple view that reproductive output is greatest near the usual first age of reproduction evidently does not apply to humans, as it does not apply to many other organisms such as those with indeterminate growth (*e.g.*, fish) and the queens of some eusocial forms that grow and improve (even multiply many times) their ability to produce gametes after they have reached adulthood and begun to reproduce (Wilson, 1971; Alexander *et al.*, 1991).

Perhaps Dawkins' calculations can be combined with the notion that women as well as men increase their social-political power and interests such that their reproductive effort in regards other than direct baby-production and -care may become so valuable to their reproductive success that it pays them to turn their efforts entirely in different directions. Children and grandchildren may not be the sole recipients of such reproductive efforts, which

often may affect the entire collection of a woman's (or a man's) genetic clan. Older people with status, power, wealth, and wisdom may act in ways that simultaneously benefit all of their close relatives as a collectivity.

Dawkins' comments about older men siring children also seem incomplete. An older man may profit from retaining the ability to produce children not because he consistently invests less in each child but because the nature of his investment means that he can produce children which will survive, more or less independently of his age. Any such effect may combine with the facts that (1) young children may survive better with a woman's care alone than with a man's care alone and (2) access to resources (through status, power, wealth) is among the more valuable contributions of human males to their offspring throughout human history. One needs to understand not only the kinds of investments men make in their children, but at what ages, and if such investments involve endowing children with status and transferring to them the kinds of resources that may virtually always have been controlled lopsidedly by older men.

If the above hypothesis about menopause is correct, then we should expect to find starts toward menopause in those species in which older females protect or guide or tend not only their own offspring but additional relatives. As suggested by Alexander (1974) and Sherman (1978), elephants—which live in groups of female relatives dominated and apparently led by the oldest female—seem to be one of the best prospects. Apparently independently of such considerations, Douglas-Hamilton and Douglas-Hamilton (1975) reported of one old dominant female that she exerted so much effort protecting her herd of offspring and relatives that she caused her own last offspring to starve to death, apparently because it simply did not have sufficient nursing time. Moss (1988) reported an old female that did not produce an infant for nine years, then at age 58 produced an infant that did not survive; Moss also reported that this female was remarkably close socially to one of her grandoffspring.

Unlike these possible incipient menopauses, in humans menopause occurs in every female that does not die from accidental or "premature" causes. Several predictions about possible adaptive variations in ages of onset of menopause in humans are also possible from the above hypotheses, none of which I believe has been tested sufficiently (Turke, 1989 and *ms.*, summarizes much of what is known about menopause, and provides an excellent account of the recent literature).

Several problems remain that prevent our understanding of menopause from being satisfactory. Thus, the human female's ability to produce babies diminishes rather sharply, and in several ways, across approximately the decade prior to menopause. Why does this capability not remain approximately the same right up to the time of menopause? There is an implication that women have typically reproduced but little during this period. That could come about either through senescence or because they have already started to turn their reproductive efforts, perhaps gradually, in alternative directions. Whatever the reason for a diminution of the tendency to produce babies during this period, it should also correlate with a diminution (or change) in sexual interest in males. Similarly, there should be a reduction of sexual interest in such women by males who do not already share offspring with them.

An interesting question is why sexual interest continues at all in postmenopausal women and in men toward postmenopausal women. An obvious possibility is that pair bonds are thereby continued that are important in maintaining social relationships which bear upon the distribution of resources controlled by males and females who jointly share offspring and other relatives. One might predict that when concern for relatives by older men and women who are paired with one another remains more or less symmetrical with respect to the particular individuals being supported, then the pair bond and sexual interest (and kissing and affection and cooperation and all kinds of evidence or promise of continuing attention and confluence of interests) will be maintained. The pair becomes a social-

political coalition in the context of tending resources (including status) and passing them to relatives. When concern for relatives becomes asymmetrical between a bonded male and female one might expect a loss of interest by both parties, and in extreme cases dissolution of the pair bond.

CONCEALMENT OF OVULATION

Despite some confusion on this topic, it is probably correct to say that humans are the only mammal for which it is known that neither the female nor the male can reliably detect ovulation; and humans are at least unusual in engaging in sexual behavior during all parts of the ovulatory cycle, sometimes at random with respect to it, and during pregnancy as well. They are probably unique in engaging in such sexual behavior in long-term pair bonds that sometimes eventuate in lifetime monogamy. They are almost certainly unique among all animals in having these various behaviors and as well living in multi-male social groups in which males show extensive paternal behavior.

In most mammals, females advertise ovulation widely and fairly precisely during an "oestrus" or "heat" period that is, however, somewhat longer than (and for the most part precedes) the actual period of ovulation. In a smaller number but still a wide variety of mammals, females are sexually receptive during considerably longer periods and evidently deceive males to a greater degree concerning ovulation, even engaging in copulation during pregnancy (*e.g.*, Hrdy and Whitten, 1987; Berger, 1986; Andelman, 1987). This description implies that all females may conceal ovulation in one fashion and to one degree or another, and there seems no reason to believe otherwise: females rarely share every interest surrounding ovulation and pregnancy with a single male or a group of males. The most likely cases of such sharing would be species in which lifetime monogamy occurs, with parental care shared equally between the sexes and mated pairs fairly well isolated from one another. Among primates, gibbons would seem most nearly to qualify. Humans may often be deceived about whether or not ovulation is advertised in other species unless they use patterning of copulatory behavior as the

indicator. Thus, modern dairy farmers notoriously find it difficult to tell when cows are ovulating so as to call the artificial inseminator, and mistakes are costly; but bulls have little difficulty in knowing when to copulate. Determining if ovulation is signaled is more difficult even than this example might suggest: one needs to observe not only when any males copulate with a female but when the dominant males copulate with her. Nevertheless, even if human females who have various kinds of medical information and technology available to them can derive reasonable ideas about when they ovulate, there has been some kind of virtually complete turn-around in the evolution of external evidences of ovulation in humans.

A widespread assumption in the older literature was that continuous sexuality evolved because it keeps the male at home through the sexual pleasure it affords him. Many people have mentioned some version of this idea, such as Morris (1967) and Pfeiffer (1969). Hrdy (1979, 1981) discusses it, although perhaps not clearly distinguishing it from the paternal care hypothesis (below). Alexander and Noonan (1979) argued that this hypothesis fails (see also Datta, 1987): If only sexual pleasure were involved, human males would have evolved to be interested in sex only at ovulation time, and females would have evolved to give a brief signal of use only to their spouse. Sex except at ovulation time would be a useless risk and effort; and, as expected from this argument, continuous sex and concealed ovulation do not occur in gibbons and other species that live in separated monogamous pairs, or in gorillas in which troops are essentially one-male polygynous bands. To understand humans we have to explain what would evolve in multi-male bands in which paternal behavior became increasingly valuable during evolution. Human males give much paternal behavior now, in multi-male groups, and much concern is shown over paternity; this is not the case in our closest relatives, chimpanzees and bonobos, which also live in multi-male groups (Smuts *et al.*, 1987).

For a long time it was also argued that ovulation is not obvious in human females because it was simply not needed once sexual receptivity became more or less continuous; but this implies that if

human females began to advertise the timing of their ovulations, the way most mammal females do, or if they began to copulate with any and all males, there would be no particularly important changes in human social life. This prediction is not credible.

Concealment of ovulation in humans was first considered as such in 1979, and that year five different hypotheses were published by evolutionary biologists and anthropologists to account for it. I think that all but one have been falsified.

1. *Prostitution Hypothesis* (Symons, 1979).—Females prolonged oestrus (receptivity) because males gave them meat (or other resources) in exchange for sex. This hypothesis does not explain why females cannot detect their own ovulation. Indeed, under this hypothesis one expects that they would be extremely good at it. With such knowledge, regardless how many or which males they mated with (and secured food or other commodities from), they could choose the males they wished actually to father their children (for example, males able to produce disease-resistant offspring, or sons capable of securing many mates).

2. *Cuckoldry Hypothesis* (Symons, 1979; Benshoof and Thornhill, 1979).—Concealment of ovulation enables a female to cuckold her mate, thus securing his paternal care while bearing the baby of a genetically superior male. This hypothesis has the same problem as the prostitution hypothesis; if females alone knew precisely when they ovulated they could really cuckold successfully.

3. *Smart Woman Hypothesis* (Burley, 1979).—Concealment of ovulation prevents the intelligent female from reducing her own reproduction by failing to copulate while ovulating (*i.e.*, its primary function is to deceive the woman herself), thus avoiding the discomfort of pregnancy and the pain of childbirth. This hypothesis seems to fail on several grounds. Why did females not evolve either to be "stupid" (rather than smart), at least in this regard (thereby not being required to conceal ovulation from themselves)—or simply to forget quickly the pain of childbirth and discomfort of pregnancy? Also, why did females who failed to conceal ovulation from males not outreproduce others who did evolve to conceal it from males? This

hypothesis thus fails to explain why ovulation came to be concealed from men.

4. *Paternity Confusion or Infanticide Prevention Hypothesis* (Hrdy, 1979).—Concealment of ovulation and promiscuity combined to confuse early hominid males about paternity and averted infanticide by males.

Apparently, chimpanzee males have no way of identifying their own offspring, because of promiscuity of females, and they tolerate the offspring of females in their group. Infants of strange females are killed; presumably these females have not mated with any of the local males. Male behavior of this general sort is not restricted to chimpanzees (Bygott, 1972) but occurs as well in langurs (Sugiyama, 1967; Mohnot, 1971), a wide variety of other primates (Hrdy, 1979; Hausfater and Hrdy, 1984), and other mammals ranging from ground squirrels (Sherman, 1981) to horses (Berger, 1986). These animals, however, are unlike humans. They have extended the period of sexual receptivity without inducing much in the way of paternal care beyond a tolerance of juveniles within groups (see also Andelman, 1987; Datta, 1987). Promiscuity by females does not seem likely to lead to increased paternal care. Comparing humans with other primates, however, indicates that paternal care has increased dramatically in the human line, even though the multi-male nature of human social groups has evidently increased opportunities for cuckoldry.

Concealment of ovulation of the human sort, in which females restrict their copulations to certain males and nearly everyone is powerfully concerned about paternity, thus does not seem a requirement for elimination of infanticide within the social group, so long as ovulation is advertised and females are promiscuous. Those cases in which increased male attention to a female and her offspring (and even some kinds of assistance) associate with tendencies for females to mate promiscuously may be better interpreted as efforts to secure subsequent matings (*e.g.*, baboons: Smuts, 1985) than as paternal care, and as pseudo-reciprocity rather than reciprocity (Connor, 1986). In the human line, the trend toward increased paternal care seems to require high confidence of paternity, which in turn

seems to require restriction of mating to the presumptive father. These features seem opposite to those suggested by the infanticide prevention or promiscuity hypothesis. Even if at some point the evolving human line did behave more or less as chimpanzees do today, events that occurred subsequently, and of a different nature, are necessary to understand human sexuality and sociality.

Marmosets may seem most likely to be concealing ovulation while employing promiscuity to garner paternal care (Goldizen, 1987). In these primates, two (or more) males sometimes accompany and mate with a single reproductive female, and carry her twin offspring more than she does. Data on whether or not males detect ovulation, however, are ambiguous, and paternity of the offspring has not been ascertained (Goldizen, 1987). If the female conceals ovulation and mates with both males as effort that gains parental care from both of them, the evident value of increased parental care causes us to wonder why dominant males do not monopolize females and why births have not evolved to be single offspring rather than twins so that a single male can carry out adequate paternal care. This interesting case seems unlikely to be understood thoroughly until relatedness of males and parentage of the twin offspring are ascertained, and further observations on social behavior are carried out.

5. *Paternal Care Hypothesis (Alexander and Noonan, 1979).*—This hypothesis notes that continuous readiness to copulate is a necessary part of concealment of ovulation and proposes that the human kind of concealment of ovulation evolved because it reduces a male's options by increasing the amount of time he must stay with one female to ensure her pregnancy. This increased time could then cause profit to him (in circumstances when it would not otherwise do so) from helping (directly or indirectly) to rear the female's offspring rather than abandoning her in the interests of more polygyny, less confidence of paternity, and no paternal care. In other words, concealment of ovulation—probably first by increasing the duration of behavioral oestrus—created a circumstance in which males were drawn into a degree of female-helping that was not in their interests before the female began to change in this way, but which was

in their interests once the female did begin to change, because it forced a change in the way males competed with one another. This hypothesis assumes that increased amounts of parental care were important to the juvenile and to its mother, but not sufficiently to the male until the female tipped the balance by increasing (not decreasing) confidence of paternity and soliciting and using male mating effort that was easily convertible into parental investment.

This paternal care hypothesis was improved by Strassmann (1981), who noted that the process described by Alexander and Noonan would likely have tended to cause subordinate males to become pair-bonders (Alexander and Noonan had suggested that dominant males would be the first to change), and would have most severely disenfranchised dominant males by taking away their ability to monopolize females only at ovulation time and still be confident that they were siring those females' offspring.

Daniels (1983) emphasized the significance of lowered disruption of social life when ovulation is concealed (males cannot easily gain from fighting over females at ovulation time), and the facilitation of cooperative efforts among males; this is also consistent with the paternal care hypothesis, and with the intergroup competition hypothesis for human evolution (see also the comments of Alexander and Noonan [1979] on the significance of socially-imposed monogamy).

Alexander and Noonan argued further that females evolved to conceal ovulation from themselves (*i.e.*, they typically are not consciously aware of ovulation and cannot tell when not to copulate so as not to get pregnant, with any degree of reliability) because this deleted the requirement that they continually deceive a long-term or life mate. Concealment of ovulation from one's mate virtually demands that there is a conflict of interest and that the concealment serves the interests of the concealer; the only way to delete from the female's psyche a requirement of continual or repeated deception is for the knowledge involved to be kept out of her consciousness.

The hypothesis of concealed ovulation has also been called into question because women some-

times know when they ovulate. Some women are able to tell when they ovulate only with devices or information from modern technology, such as thermometers and/or information from modern medicine. In other cases, however, such kinds of information seem not to be required (thus, some women say that they experience headaches or other sensations each time they ovulate). Assuming accuracy in such statements, selection that might have been reducing women's ability to detect ovulation appears to be incomplete, although complete enough to make the manufacture of contraceptives a lucrative business. It also seems necessary to take into account that the importance of knowing when ovulation actually occurs has been made more explicit recently than probably ever before. Nevertheless, this evidence has seemed to some to cast doubt on the entire notion of concealment of ovulation. Dr. Bernard J. Crespi (pers. comm.) has noted, however, that women may have been selected primarily to convey the impression to their males that they do not know about their ovulation, and that being able to do this may require that, in general, they in fact not know about it—or not know that they know (it may require, for example, that they are less conscious of cues, which can nevertheless be made conscious with some effort, than we might have expected otherwise). The reasons for his suggestion are, first, that a pair-bonded male expecting to invest heavily in his mate's offspring, and living in a multi-male group in which he does not always have the possibility of 24-hour surveillance of his mate, might be uneasy about a mate who is keenly aware of those brief times when she can be made pregnant by an insemination. He would "know" (*i.e.*, behave as though he knew, or respond to selection as though he knew) that opportunities for cuckoldry would be enhanced by such knowledge. Second, it is difficult to deceive a close and more or less continually intimate associate about conscious knowledge sharply contrary to the associate's interests and sharply coincident with one's own interests.

This is an argument, then, for a woman tending not to have any knowledge of ovulation time in her consciousness, or not in general being especially attentive to cues about such (otherwise reproduc-

tively crucial) aspects of her physiology. Because it is possible for a woman bonded to a particular male to be certain that she will be inseminated at reproductively appropriate times simply by behaving in a particular way that in other respects will help keep him attentive to her (including mating with him at sufficiently frequent intervals), conscious knowledge of ovulation could become an expense, and perhaps even a severe risk.

From this argument, it follows that women would not necessarily have been selected to eliminate all cues that they might be able to use if they become intellectually tuned to the question of when they ovulate—only that they become relatively insensitive to any such cues and generally not work up a conscious understanding of (or a great interest in) precisely when they ovulate, or behavior that would give the impression of such an understanding or such interest. Under this argument, even noticeable and consistent changes in the sexual receptivity of his mate during the ovulatory cycle might provoke resentment or uneasiness on the part of a human male. This argument, then, may account for several aspects of behavior associated with human sexual activity that the hypothesis as previously stated did not include. At the least, several testable predictions are involved.

Mitchell (1986) and Gray and Wolfe (1983) criticized Alexander and Noonan's discussion of deception and self-deception in connection with concealment of ovulation as 'a confusion of a lack of information with deception.' Our argument, however, was that if an event as central to reproduction and as physiologically profound as ovulation—and as available to both sexes as it is in perhaps all other mammals—is not conscious (and cannot be made conscious) in an animal that possesses consciousness, then there is a strong implication that it has been kept out of the conscious by selection. We meant that any item of information that appears easily available to consciousness yet is not there is perhaps not there because evolution has designed the animal not to accept that particular bit of information into consciousness, even when similar kinds of information in other contexts are readily accepted into consciousness. This view of self-deception may at first seem confusing to those who

define self-deception as refusal to acknowledge information that is nevertheless possessed. We do not argue that women necessarily possess knowledge of ovulation, only that they have evolved not to express it, whether or not they possess such knowledge in one form or another; in other words, selection for failure to express some particular kind of knowledge may lead to its possession also being suppressed to one degree or another.

Discussion.—By combining concealment of ovulation with a pattern of more or less continuous willingness to copulate with a male of her choice—presumably thereby favoring males who were willing to engage in extended consortships and to attend to the female in ways important to her—the human female created a situation in which her mate could enjoy a high confidence of paternity, even when other males were in the vicinity. She thereby created, as well, a situation in which pair bonds and paternal care had a greater likelihood of evolving, even in the complex and close-quarters social situations that prevail in modern human society. The argument made here presumes that during human evolution both continuous sociality and paternal care were becoming more important, the latter to both the human baby and the human female, and that the human female's ability to draw the male into extended consortship, and her concealment of ovulation, tipped the balance so that paternal care also became reproductively important to the human male. The entire combination, including the associated evolution of menopause and extreme altriciality in the human neonate (see below), is evidently unique to humans. Eventually we must dissect the different components of parental care (or social tending) and determine which were important in early hominid evolution and why, and the effects of such aspects of parental care on the evolution of social life, and on the evolution of the intellect and the psyche in each of the two sexes.

ALTRICIALITY: WHY ARE HUMAN BABIES HELPLESS?

Altriciality, or physical helplessness, is widespread among juvenile animals, but the human neonate, which is distinctly more helpless than any

of its primate relatives, is probably the most famous of all altricial juveniles (Zeloff and Boyce, 1982, and Dieneske, 1986, survey an extensive literature). Although I concentrate here on the human juvenile, I have tried to consider how to account for altriciality wherever it occurs.

The words "altricial" and "precocial" are used primarily in the ornithological literature and are defined in most dictionaries in terms of their application to newly hatched birds (see also Gill, 1990). Altricial hatchlings, as with sparrows, starlings, and pigeons, are more or less naked and helpless; they may be blind and are usually ectothermic. Food is brought to the nest for them by their parents. In contrast, precocial hatchlings—as with chicks, ducklings, pheasants, and quail—typically are covered with down, agile, homeothermic, have their eyes open, and are more or less ready to move out alongside their mother and pick up their food themselves. There are degrees of intermediacy (for example, goslings are somewhat more helpless than ducklings, the eyes of owl hatchlings are closed but not those of hawks, etc.). Gill (1990, pp. 369–70) exemplifies and illustrates eight different categories of hatchlings originally established by Nice (1962) based on "primary criteria of mobility, open or closed eyes, presence or absence of down, and the nature of parental care . . ." The extreme differences between (1) most songbirds and (2) mound-builders and most ducks, shorebirds, and "fowl-like" birds is probably the reason why the terms altricial and precocial were applied so readily to birds, as well as studied there more extensively than in other organisms.

As Nice (1962) and Case (1978) noted, other animals also display variations paralleling those found in birds. Newborn mice and rats are naked, blind, and more or less helpless. They are born in a nest where they remain for some time. In other mammals, such as some ungulates, on the other hand, newborn often are able to stand alone within a few minutes, and some, such as horses, are able to gallop alongside their mother in less than an hour. Newborn ungulates may travel considerable distances with their mothers, who are following a herd in more or less normal movements. Again, there are intermediates: canine and feline babies are

blind when born but not naked, and not as helpless as most newborn rodents; and some ungulate newborns are physically less capable than others.

It is useful to apply the concepts of altricial and precocial even more widely, for example to insect juveniles. Maggots, and the maggot-like larvae of some insects with complete metamorphosis (*e.g.*, honeybees), can be regarded as altricial (in a broader application of the term, so can all insect larvae). In contrast, the nymphs of insects with incomplete metamorphosis, such as grasshoppers and crickets, are precocial in the same sense as some baby mammals and birds. Again, there are intermediates. For example, within the Family Gryllidae (Order Orthoptera), including all crickets, most juveniles would be seen as precocial. Their exoskeletons are hard, and they are agile, quick, and seek out their own food right from hatching; there is no parent alive to assist them. But in genera such as *Anurogryllus*, in which the female cricket prepares a closed burrow with a food cache before she lays her eggs, and then tends her babies until she dies—feeding them small, apparently unfertilized trophic eggs—the hatchlings are soft and fat, resembling termite juveniles (West and Alexander, 1963). Many other examples could be given: thus, caterpillars may be soft and helpless or quick-moving and covered with urticaceous hairs or other defenses. Many internal parasites, especially those living in the alimentary tracts of their hosts, have some of the features of altricial juveniles. Certain adult insects, such as queens in large-colony eusocial forms, possess some of the characteristics of altricial juveniles (Alexander *et al.*, 1991).

Ricklefs (1974, 1975, 1979a, 1979b, 1983) has contributed extensively to the development of theory that helps explain altricial and precocial juveniles. Initially he showed that altricial nestlings of birds grow faster than the more precocial nestlings of related species, and he eventually concluded (1983, pp. 11–12) that “The overwhelming advantage to altricial development seems to be rapid growth Although adoption of the altricial condition may increase vulnerability to predation and enhance the effects of exposure to bad weather, these are presumably more than compensated for

by the brevity of the development period.” Faster growth may actually be the adaptive function of altriciality in a wide variety of species. The human embryo and neonate both grow faster than do the embryos and neonates of their primate relatives (Sacher and Staffeldt, 1974). It is difficult to believe, however, that this is the full explanation for the altriciality of the human infant. Unlike altricial birds, for example, the human juvenile has a juvenile life as long or longer than those of the closest relatives of humans whose juveniles are all less altricial (Smith, 1989). As Montagu (1961, p. 156) notes, “. . . man is born and remains more immature for a longer period than any other animal.”

Dienske (1986) has reviewed and criticized previous theories about human altriciality, giving good reasons for doubting that human newborns are altricial simply because more advanced neonates could not pass the pelvic passage, and pointing out that although apes have pelvic passages that are larger in relation to their babies' heads than are those of rhesus macaques, the apes' babies are more altricial. It does not seem likely either that the human baby is simply born at an earlier stage through shortening of the gestation period, since the great apes have about the same gestation periods as humans, or slightly shorter (Schultz, 1956; Sacher and Staffeldt, 1974), and the 12-month gestation briefly postulated for Neanderthal because of a presumed larger pelvic opening has since been discounted (Rosenberg, 1986; Greene and Sibley, 1986; Trevathan, 1987; Trinkaus, 1987).

Dienske also doubted that altriciality occurs because the human baby's brain is small in size, since it is comparable in size, in relation to the body weight, to that of other primates. Dienske summarized the evidence that in humans the adult brain is much larger, in relation to its size at birth, than those of other primates, and he wondered if this might not have something to do with altriciality, supposing that this difference might mean that the neonate's brain is less developed. As he put it: a neonate brain that is smaller in relation to the adult brain “. . . implies a greater immaturity if many parts of the neonatal brain are still in a [rudimentary] stage of functioning.” Although this hypothesis is probably correct, it need not imply that

this aspect of altriciality is explainable simply as a result of a physiological or developmental constraint or that human neonates are "embryos," simply born at an earlier stage of development (*e.g.*, Kuttner, 1960). That view would not account for the early mental precociality of the human juvenile compared to ape juveniles or engage the question of the pattern of development of function in the human brain.

Zeveloff and Boyce (1982) seek an adaptive hypothesis for human altriciality. Concordant with the arguments developed here, they suggest (p. 540) that "... monogamous pair-bonds and concomitant opportunities for paternal investment may contribute to the evolution of human altriciality," and that monogamy and paternal care were made more likely by increased confidence of paternity. They also argued that increased time for learning, from an increased length of the juvenile period, is the main benefit of altriciality. My arguments here differ from theirs in that (1) they sometimes seem to be suggesting that monogamy and paternal care evolved because of altriciality ("an altricial neonate will offer greater potential for male parental care"—p. 537) rather than vice versa and (2) they seem to assume that altriciality (a) depends on a shorter gestation period and (b) is responsible for the longer learning period (see also Case, 1978; Zeveloff and Boyce, 1980). The extensiveness and profundity of learning and maturational changes in human juveniles following ages 11–13 indicates that it is appropriate to refer to the human juvenile period as lengthened in comparison to those of related primates even if the earliest time of possible reproduction is about the same for chimpanzees and humans (Smith, 1989). This extended juvenile period may have evolved for the same reasons as human neonate altriciality and not simply as a necessary or incidental result of it—that is, because it contributed to the long learning period, or period of plasticity, that enables human juveniles to absorb and cope with the complexities of culture and human sociality.

In general, we are not hard-pressed to provide adaptive hypotheses for precocial organisms having the attributes that cause us to label them as precocial. It seems obvious why a baby ungulate would

gain from being able to run alongside its mother soon after birth. Precocial birds are often tended only by their mothers, are usually hatched in vulnerable nests on the ground, and typically eat the kinds of food that can be captured by moving about on the ground or in the water (Nice, 1962). Juvenile insects in species with incomplete or gradual metamorphosis (that is, the precocial sort) live without parents in dangerous locations, and they are usually able either to run or leap, or else they produce various kinds of poisons or other deterrents to predators. Their abilities to do these things are what causes us to see them as precocial. The same is true, more or less, of relatively precocial larvae in insects with complete metamorphosis (that is, larvae with urticaceous hairs, unusual locomotory abilities, or other special defensive features), even though the larva itself, and the form of metamorphosis ("complete") that it typifies, can be seen as an evolutionary trend toward an altricial feeding stage.

The question that remains is: Why, when extrinsic sources of mortality are removed, do juveniles become soft, fat, helpless, and maggot-like? Is there a general answer, other than the unsatisfying or incomplete one that particular selective pressures are relieved or removed, or that there is some advantage to the parents rather than to the juvenile itself? Case (1978), for example, offers several possibilities for the latter, but all seem to depend on shorter gestation periods and young being smaller in altricial forms. Although some cases of altriciality may fit one or more of the arguments invoking advantages to parents, neither shorter gestation periods nor smaller young is always associated with altriciality; thus, altricial neonates of humans are larger than less altricial neonates of their relatives (Sacher and Staffeldt, 1974). Because some altricial organisms seem to have evolved shorter juvenile periods (*e.g.*, songbirds), and others longer juvenile periods (*e.g.*, humans), any general explanation will have to take both conditions into account.

In seeking a broad explanation, we may first note that juvenile life has two main functions: to get to the adult stage without dying and to become the best possible adult. For our purposes the latter need have no more precise definition than to be

maximally capable of doing whatever an adult has to do in one's own species to reproduce as well as or better than anyone else. Presumably, the only selective reason for the existence of a juvenile stage is that it gives rise to an adult that is sufficiently better at reproducing to more than offset the disadvantages of juvenile life such as longer generation time and investment of calories in other than reproduction *per se*.

The traits and tendencies that make one a better adult are not likely to be synonymous with traits that enable one to bypass or deal successfully with particular hazards along the pathway to adulthood. In other words, the two functions of juvenile life are not likely to be achieved by precisely the same directions of selection. What we call precociality evidently represents expensive ways of dealing with hazards that may terminate juvenile life—expensive in the sense that they interfere with selection that otherwise could cause the juvenile to use more of its life effort in preparing to be a more reproductive adult.

In the course of becoming satisfactory adults, juveniles must do two things: grow and develop. Growth enables the juvenile to reach an appropriate adult size at the appropriate time or season. Development, which can be defined as differential growth or change in different tissues or organs, involves changing from the form or function that best serves the juvenile to that which best serves the adult. But this description is still far too simple. Juvenile life is not necessarily unitary: in different forms it can be subdivided into multiple stages, each of which takes its own form, growth rate, developmental rate, and way of functioning. Obviously, all of these things may be affected by changes in the nature or emphasis of the forces that affect the juvenile's success, such as sources of mortality.

Complex metamorphoses—as illustrated by parasites (especially those with multiple hosts), anuran amphibians, and insects—presumably evolve when appropriate forms and functions for different stages of the life cycle vary widely. The larval stage of insects with complete metamorphosis lives in habitats that are suited to feeding and growth. Development is primarily restricted to the

pupal stage, which follows the larval stage. The adult does not resemble either of the two juvenile stages or, in general, live in the same habitat. A similar pattern is exhibited by anuran amphibians, with the feeding, aquatic tadpole eventually transforming during a relatively short period into an adult that is dramatically different in form and function and lives in a different range of habitats.

Such patterning during the juvenile life may be considerably more subtle, yet require understanding if we are to explain the nature of the human juvenile and the patterning of its life. Thus, the altricial juveniles of songbirds for the most part live at first in a nest hidden from predators or inaccessible to them but shortly become capable of flight and leave the nest (songbird nests must often become increasingly vulnerable to predation as the juveniles grow and the parents visit the nest increasingly frequently to feed them). Following fledging, the juvenile songbird's life soon becomes that of an independent flying bird which lives more or less in the adult habitat. As Ricklefs (1983) specified, his description of altriciality as a way of providing more calories for the growth process thus applies only to the earliest part of juvenile life—the time spent in the nest. That period, moreover, necessarily includes not only rapid growth but the development required to transform an altricial hatchling into a feathered, coordinated fledgling capable of flight and with keen sensory apparatus enabling it to avoid predators and locate its own food. In precocial birds these parts of development largely precede hatching. We are required to assume that altriciality, involving only a brief initial part of a songbird's juvenile life, provides sufficient advantage in growth rate to more than compensate for the delay in initiating the dramatic developmental changes necessary for transformation into a suitable fledgling, which in at least some cases might appropriately be described as having achieved a certain precociality.

In some senses songbird hatchlings parallel certain altricial juvenile insects, such as the fly larvae called maggots that occur in dung, carrion, fungi, and other short-lived and vulnerable habitats. These larvae do not seem well protected from predation, weather, or deterioration of their mi-

crohabitats. Why, then, do they take on the aspect of being altricial? I would guess because they cannot do anything about the serious threats in their habitat, so that their best strategy is to get through the dangerous feeding stage and out of the larval habitat as fast as possible. As with internal parasites, who may be protected, their particular form of altriciality has caused them to evolve to become mere "sacks" of efficient nutrition-grabbing ability. In their temporary and dangerous hatchling environments they load themselves with nutrients as fast as possible and drop off or crawl out of the dangerous place where they have secured their food to grow and develop in safer locations. One might suspect that they are highly precocial in terms of their ability to ingest their medium rapidly.

Songbird and insect patterns of altriciality are not easily compared to those of humans. First, neither songbird hatchlings nor maggots have evolved coincidentally altriciality *and* a longer juvenile life as have humans. Second, unlike songbirds, in humans parental care remains extensive not only throughout the juvenile's life but well into its adult life.

The general adaptive explanation for the evolution of altriciality seems to be this: to the extent that a juvenile is relieved of the necessity, or any importance, of evolving to protect itself from extrinsic hostile forces of nature (such as predation), it is freed to devote a greater proportion of its calories to improving its performance at some later stages of juvenile life or to becoming a better adult. This will be true, regardless of the means by which the relief is effected, whether by direct or continual parental solicitude or by having been placed in a safe location by a now deceased or departed parent. It will also be true regardless of the means by which the improved later performance is effected: whether primarily by growth or development. Protected juveniles are also free to bring back into their juvenile life—further in time and to a greater extent—traits, tendencies, and events (learning or practicing)—that are devoted to enabling their survival or competition as older juveniles or as adults.

On this hypothesis allowing more calories to be devoted to growth is, as Ricklefs (1983) main-

tained, surely a widespread advantage of altriciality. In songbirds this is possible because the nest is either hidden or off the ground and inaccessible to predators, and because in general both parents provide food. In some rodents and subterranean crickets, as well as larvae injected by their mothers into safe locations such as inside wood, parallels in degrees of security from predation and the physical environment have evolved.

Prior to parturition the human embryo grows faster than do the embryos of other primates (Sacher, 1975), and the neonate is considerably larger in both body weight and brain weight (Sacher and Staffeldt, 1974). Accordingly, it seems possible that the altricial nature of the human neonate yields a significant part of its advantage as an increase in growth rate during the embryonic stage. The human brain, however, also changes in mass during postnatal juvenile life several times as much as the brains of other primates (Sacher and Staffeldt, 1974). Postnatal body size changes in primates are considerably more variable, with gorillas adding much more to their mass than humans or other apes and humans adding more than chimpanzees (Sacher and Staffeldt, 1974). Effects of early altriciality on growth rates during juvenile life—even as a consequence of the unusual intensity and duration of parental solicitude—thus do not seem likely to explain the distinctiveness of the entire pattern of human development.

The overall problem in understanding the adaptiveness of altriciality and precociality is thus one of trade-offs between different life stages, whether similar or different activities or structures are being compared. Precocial birds have larger brains than altricial birds (Gill, 1990), but the altricial human infant's brain is larger than those of its less altricial relatives (Sacher and Staffeldt, 1974; Dienske, 1986). In birds, the larger brain of the precocial bird is presumably used to protect it from predators and other more or less immediate threats—that is, to provide it with skills that increase the likelihood it will reach the adult stage. In humans, however, the size and construction of the neonate's brain has likely evolved for a different reason—in a way that enabled it eventually to develop into an

extraordinarily large and complex brain that functions primarily in the complex social activities required for reproductive success in the adult stage.

I hypothesize, then, that early physical precociality has been sacrificed in human juveniles partly in favor of later mental precociality. I suggest that early physical precociality was expendable because human parents became almost entirely responsible for the survival of the juvenile to adulthood, and for its failure to survive when this outcome occurs. This responsibility could only evolve, of course, if the parents were capable of giving sufficient parental care of the appropriate type and if their interests very broadly overlapped those of the offspring. On this theory, the characteristics of the brain of the human infant are investments toward the development of a better adult (or late juvenile) brain and are less involved in the survival of the (early) juvenile than the enlarged brain of a precocial bird or other animal.

If the general idea about altriciality presented here is correct, then to understand the altriciality of human babies thoroughly we will need to understand what kinds of attributes make the best possible adult (or late juvenile) human. I think the answer is, generally speaking, intelligence and social capability. If Humphrey's (1976) argument about the evolution of the human intellect is correct, we should expect the physically altricial human juvenile to become, at some point, intellectually and socially precocial, as suggested by Alexander and Noonan (1979) in their discussion of parental care and the concealment of ovulation. We should expect that the juvenile human begins practicing to be socially successful much earlier in life and on a much more massive scale early in life than is possible for less altricial primate juveniles. I think that this prediction is consistent with the seemingly inordinate attention given by humans to the concept of so-called "intelligence quotients," with their connotation of intellectual precociality, attempting to measure mental development, or "age," in relation to physical or chronological age. It is also consistent with the efforts of many human parents to parade their offspring as socially and intellectually precocial. Many aspects

of human juvenile life also give the appearance of social-intellectual precociality—such as early smiling, humor, language acquisition, and engagement in reciprocity. Throughout human history even young adult humans probably depended on their parents and other relatives for success, emphasizing the importance of considering that even aspects of early human juvenile life may take their form and function because of events that will transpire many years later in late juvenile or adult life.

I also think of humans as having brought far back into their juvenile life many kinds or instances of social-intellectual-physical play, as practice, and of them having done so as part of what we usually have termed evolving increasing degrees of altriciality. I think as well that they have been able to do this because of the dramatic increase in the amount and effectiveness of parental care during human evolution. For humans, explicitly, it seems to me that the question is moot as to what extent the general increase in parental care took place because it allowed human juveniles to devote more calories to becoming better adults, and to what extent it occurred because it literally saved juveniles from death, thereby incidentally allowing the juveniles to devote more of their calories to becoming better adults. In either case, my hypothesis requires that in young juvenile humans more calories are now devoted to better performances later in life, including adult life, and I think this means being socially more effectively cooperative as a way of being reproductively more competitive, than was the case in the days of, say, *Homo erectus*, or of species ancestral to *Homo*.

The intellectual-social precociality of the human juvenile was probably responsible for two prominent evolutionary theorists, G. Evelyn Hutchinson (1965) and George Williams (1966), making independently the intriguing suggestion that the creative intellect of adult humans is an incidental effect of selection for high intellectual capacity in juvenile humans. The only way this argument seems to me to have credibility is if it is applied only to the late juvenile (or early adult) stages, when juveniles are actually striving to enter the breeding population. Even with this qualification, it seems

to me that the length of adult human life and the evidence of rather dramatic increases in control of resources during adulthood, together with the fact that the juvenile survives and succeeds primarily at the behest of its parents and other adult close relatives, tends to deny the argument that human brain complexity functions primarily during juvenile life.

Discussion.—Altriciality apparently evolves, then, when an infant gives up on protecting itself and turns its protection over more or less entirely to extrinsic forces. This protection may come about through continued attention by the parent or because the juvenile lives in a protected situation, where it may have been placed by its parent. If the extrinsic force is long-term care by parents or a permanently safe location, the offspring is also free to evolve an extended juvenile life, if by this it improves its adult performance sufficiently to compensate the added time and expense involved. Altriciality in some attributes may even evolve in an unsafe situation if thereby the juvenile can grow at the fastest possible rate and escape the unsafe situation. In such cases, obviously, juvenile life will decrease in duration. Or, as in the case of internal parasites protected by being inside their host or eusocial queens protected by their workers and soldiers, physical "altriciality" may continue for the entire life of the organism, in the interests of turning all effort to activities more directly reproductive than (useless) protection. Although two parents (or any tending parents) are not required for the evolution of altriciality, biparental care is a common situation, explaining the association with monogamy in birds and mammals.

The human baby appears to be the only highly altricial mammal, other than marsupial infants which are carried in pouches and the young of some bats, that are carried by the mother, as opposed to being hidden in a nest while the mother gathers food (Walker, 1975). The human baby is evidently safer when with its mother (or some other close relative) than when bound to a particular spot or hidden. The reason for this being true seems not yet to have been made obvious, although increasing altriciality obviously caused weather, predators, and infanticide by other humans all to be possibilities.

HAIRLESSNESS IN LATE JUVENILE AND ADULT HUMANS

I have not taken up the question of why humans remain relatively hairless as juveniles and adults, and I confess that I do not have a convincing hypothesis. Nor, evidently, does anyone else. Some comparative discussion around this question, however, may be useful.

The argument has been made repeatedly that "... the evolution of human hairlessness was somehow associated with temperature regulation in a tropical environment" (Kushlan, 1980, p. 727; see also Campbell, 1966; Leakey and Lewin, 1977). Morris (1967) suggested that hairlessness enabled humans to lose heat more efficiently, as when chasing large game. Schwartz and Rosenblum (1981, p. 10) noted that "As the ratio of surface/volume decreases in a static series of adult primates, the advantage of an insulating coat diminishes as well." The human baby, however, is both the smallest human and the least hairy, and the human female, smaller than the male, is next. Neither juveniles nor females do much chasing of large game. As Darwin (1871) noted "... other members of the order of primates ... although inhabiting various hot regions, are well clothed with hair." No other predator that captures its prey after chases in the hot areas of the world has lost its hair. Nor has any other species at all taken up the particular pattern of hairlessness that the human species exhibits, in which there is (1) a single naked infant rather than a litter of naked infants and (2) a naked infant that is carried as opposed to being hidden in a nest or a marsupial pouch. It is at least possible that in the hominid line a hairless baby evolved first, followed by older juveniles, the adult female, and finally the adult male.

It has also been argued that humans lost their hair because parasites were such a problem, but then we have to ask why parasites were more of a problem with humans than with other species. None of these or other hypotheses given so far for human hairlessness (clothing, fire, and shelter made hair superfluous: Glass, 1966; early humans were aquatic: Napier, 1970; sexual selection, spe-

cies identification, social appeasement, neoteny: Darwin, 1871; Keith, 1912; Guthrie, 1970; see also Kushlan, 1980) seems to have gained much momentum.

It appears that other relatively hairless mammals have lost their hair for reasons that cannot be used to explain human hairlessness. The following arguments on this topic are modified from Alexander (1991b), a chapter written for a volume on naked mole rats. The prevalence of ectothermy among altricial mammal and bird juveniles, and the ability of human babies to survive extreme lowering of the body temperature for long periods, suggest a general connection between ectothermy and altriciality, and raise questions about the apparent connections between ectothermy and nudity in some cases.

Mammalian Variations in Hairlessness.—Mammals are the organisms that have hair and produce milk. There are analogues for both traits in other organisms (pigeons produce a milk-like food for their young—see discussion in Gill, 1990—and many organisms have hair-like structures), but no homologues.

The amount and kind of hair varies extensively among different mammals. Relative hairlessness occurs in a variety of mammals, rarely for reasons that are entirely obvious (Lyne and Short, 1965; W. J. Hamilton, 1973; Jarvis, 1981). For some aquatic mammals, both marine and freshwater (*e.g.*, cetaceans, sirenids), a layer of fat beneath the skin seems to have proved a more appropriate correlate of homeothermy than a coat of hair, partly because hair causes drag in an aquatic environment, reducing the efficiency of locomotion, and partly because trapped air in pelage or plumage can be lost through compression, for example as a result of diving. Although a variety of aquatic mammals have retained a hair coat (seals, walruses, polar bears, otters, mink, beaver), these seem invariably to be either species that live in cold climates or species that spend a significant amount of time out of the water. Some mammals have replaced part or all of the hair coat with armor of one sort or another (armadillos, pangolins, ant-eaters—in some armadillos abundant ventral hair is retained); such forms

also live in mild or tropical climates (Walker, 1975). Several large, entirely terrestrial (elephant, rhinoceros) or primarily terrestrial (hippopotamus) mammals have lost a hair coat in favor of a thick, leathery skin. It has been postulated that these tropical forms have a low body surface area in relation to their body mass and therefore have gained by increasing their ability to lose heat through the skin. As predicted from this hypothesis, temperate zone, montane, and rain forest-dwelling relatives of these forms have more hair, and juveniles of these forms have more hair than adults (Walker, 1975). A few mammal species (suids and some primates) are somewhat intermediate, having lost much of their hair (Lyne and Short, 1965). Many mammals that bed down or nest in contact with their young, or carry infants on their venters, have lost much of the hair on their venters and around the mammary glands (*e.g.*, suids, rodents, some primates). In such cases the young juveniles are also either virtually hairless (rodents), relatively so (suids), or only lightly haired on the particular parts of their anatomy that regularly contact the mother (primates) (birds that brood altricial young also sometimes have bare patches on their venters).

Only two mammal species additional to the above groups have virtually hairless adults and older juveniles: naked mole rats and humans. Each of these species appears to have evolved nudity independently of any other mammalian forms, since their close relatives are all relatively hairy. The exception to this statement is that nearly all rodent newborns are naked, so that in fact only the older juveniles and adults of naked mole rats have diverged in this regard from other rodents. The hairlessness of non-newborns in naked mole rats and humans is also similar in that in neither case is there either a dramatically thickened skin or armor (although relatively more in naked mole rats); it differs, of course, in that adult humans have retained abundant hair on the head, in the pelvic region, and in the armpits. The nudity of non-newborns in these two species, representing two of seven or more independent origins of relative hairlessness, seems more reminiscent of the kind of hairlessness of newborn altricial mammals; these

two species may also be the only mammals in which nudity in newborns (probably) preceded nudity in older juveniles and adults.

Hairlessness in newborns is widespread in mammals, as is absence or near absence of feathers in newly hatched birds (see discussion of altriciality above). This is probably the reason hairlessness has been regarded as part of a neotenic trend, which may be a correct view in terms of developmental processes but does not provide an explanation in evolutionary or selective terms. Phenomena such as neoteny and allometry may represent inertial or constraining forces, in the sense that natural selection must always operate on "last year's model," but in the same sense all genetic, developmental, physiological, and morphological attributes of organisms represent inertial elements for selection. Unless one assumes that natural selection is helpless in the face of such inertias, the search for evolutionary (selective) explanations continues in approximately the same fashion as in the absence of information about such inertias. The general assumption of such searches is that selection is the *principal* (not the sole) guiding force of evolution.

Hairlessness and Ectothermy.—Newborn mammals that are both naked and sometimes left by the mother in a nest also tend to be ectothermic, as do altricial vertebrates in general, and this implies that there is merit in attempting to relate the evolution of hairlessness to that of altriciality (see also Case, 1978). The human baby is not ectothermic, but it is often said to be unusually capable of surviving periods of lowered body temperature, and this feature may not be entirely independent of its extreme altriciality.

An ectothermic organism is one that relies for its body temperature largely or entirely on external sources. Such organisms are often described as having "poor" or "inadequate" means of thermoregulation. This view is not productive of hypotheses as to the origin and basis of the trait, unless one imagines, again, that selection has somehow been ineffective and a trait that is disadvantageous has evolved. Such traits do evolve, as in senescence (Williams, 1957), but only under special conditions such as pleiotropy, with beneficial and deleterious gene effects continuing in concert whenever

they derive from the same indivisible chunk of genetic material. Such deleterious traits are saved only because their inevitable companion traits are sufficiently beneficial to overcome the deleterious effects and no way of divorcing the two effects has yet appeared. In no organism, apparently, has a reason been generated for regarding ectothermy as a deleterious pleiotropic effect, and, contrary to the situation with senescence, no circumstances seem to exist that make such an explanation likely. Accordingly, it seems parsimonious to assume that ectothermy evolved in altricial juveniles and naked mole rats because it is somehow directly advantageous, or because it allowed some other change that was advantageous.

One correlate of ectothermy is a rather low metabolic rate, and it has sometimes been assumed that this is the source of the advantage (reviewed by Case, 1978). A lowered metabolic rate, for example, might allow naked mole rats to subsist on fewer calories and therefore suggests a continuing problem in caloric intake that is greater or of a different nature than that encountered by the usual homeothermic mammal.

A potentially profitable way to start thinking about the evolution of ectothermy in a previously homeothermic animal is to consider that it has evidently become more efficient, for whatever reason, for that animal to rely upon an external source of warmth. This situation would seem to prevail whenever such external sources are so reliable and effective that the expense of homeothermic machinery is superfluous. To understand when such conditions might exist, one must consider not only the external source of heat itself, but also the nature of threats, such as inability to obtain food when it is crucial and inability to escape from predators that are able to maintain a high rate of metabolism and predatory ability when external heat sources are minimal or absent. Naked mole rats, preyed upon largely by snakes in their burrows (Sherman *et al.*, 1991), have apparently been largely relieved of homeothermic predators, and their tropical burrow systems are relatively stable in both temperature and humidity.

Hairlessness and Altriciality.—Altricial juveniles that have given over virtually all protection from

predators and supplying of food to their parents (as with naked, ectothermic forms) are in a position to retreat from homeothermy and use their parents as the (primary) external heat source. Such a juvenile might gain from refraining from use of nutrition provided by the parent to maintain a high metabolic rate when the parent is absent, and instead conserve ingested calories for later growth by maintaining a high metabolic rate only when external heat (parent, sun) is available. In this fashion parents become suppliers of calories through not only food itself, but also through providing heat for metabolism. This set of attributes correlates with both nakedness in the juvenile and nakedness in at least the part of the anatomy of the parent that most emphatically contacts the juvenile during brooding (brood patches of birds, naked bellies and mammary glands of mammals). It is probably significant that most naked juvenile birds and mammals occur in litters, and single offspring are rarely naked. Nakedness allows extremely rapid absorption of heat from extrinsic sources such as the sun, bodies of other individuals, and warmed

soil on sunny days and into the night. Coincidentally, it also causes or allows rapid heat loss to other individuals, which are always close relatives in the case of parental birds or mammals or colony members in naked mole rats.

Discussion.—These comparative arguments provide a background for thinking about hairlessness, altriciality, and tendencies to be ectothermic in juvenile mammals and birds, including the human baby. They leave unanswered, however, as I suggested would be the case, precisely why older juvenile and adult humans are relatively hairless. They also fail to answer in a satisfying way the questions why the human baby is (1) apparently the only singly produced mammalian or bird offspring that is naked, and (2) the only nonmarsupial mammalian offspring that is both highly altricial and carried by the parents (newborns of apes are more altricial than those of other primates, but much less so than the human baby: Dienske, 1986; some bat neonates are carried by the mother: Walker, 1975), as opposed to being hidden and left, as with altricial rodent newborns and songbird hatchlings.

SYNTHESIS: PARENTAL INVESTMENT AND THE UNIQUENESS OF THE HUMAN SOCIAL SITUATION

PATERNAL CARE IN MULTI-MALE SOCIAL GROUPS

I have been arguing that several attributes of humans—actually more than I have discussed—show that parental care was increasing during human evolution. The reader may realize that this fact was generally known before. But it is important that the argument be reviewed and verified because increased parental care is required for the more general hypotheses being advanced here for the evolution of human sociality and of the human psyche.

Moreover, more has happened in the hominid line with respect to parental investment than a simple increase. I have referred to the human species as the “uniquely unique” species, and here is a good illustration of my meaning. The human species not only evolved an increasing amount of parental care, it evolved several unique features in

the process. Many animal species have evolved increasing amounts of parental care, and many have evolved altricial juveniles, but none is known to have evolved either menopause or the particular kind of concealment of ovulation typical of humans. Certainly in no other species are all three of these attributes evident. Nor does any other primate produce an infant nearly as helpless and naked as the human infant, although apes produce infants judged more altricial than the infants of other primates.

To me this suggests that humans were evolving increased amounts of parental care in an environment that was somehow unusual or unique. What part of the environment was involved?

To make an unusual comparison, it is not surprising that the ancestors of whales, dolphins, and porpoises changed dramatically when they entered the sea. Likewise, the naked mole rat evidently

evolved its remarkable and unique attributes after shifting into a unique kind of subterranean life in which it is confined to burrows and feeds on tubers located beneath the soil surface (Sherman *et al.*, 1991). But humans do not seem to have moved into a dramatically different ecological niche. Why, then, did they evolve so many unique attributes while they were increasing the amount of parental care? What was the source of infant mortality or reproductive failure that made increased parental care so valuable?

Again, it would appear to be the social environment of evolving humans that was unique—at least unique for their kind of animal—and that increased parental care was adaptive in this unique social environment.

What is unique about the human social environment? Here at least is a beginning: Humans are the only mammal that lives in multi-male groups, in which confidence (likelihood) of paternity is high (probably, in general, above 90%), and the males are both extensively and complexly parental and also extensively and complexly cooperative with one another (and in which, I speculate, the males with the highest confidence of paternity also tend to be the most cooperative).

Comparative biologists know that hundreds of bird species live in huge colonies in which the males show extensive parental care, even if they do not cooperate in the way human males do. Birds and mammals differ, however, in a way crucial to this social difference.

In mammals the sperm travel more or less straight toward the egg, which waits, as it were, in the upper reaches of the female's genital tract near where it will be implanted in the uterus once it is fertilized. Not so with birds, who lay eggs, and who are more like insects and reptiles than like mammals. In insects, reptiles, and birds, the female gains from being able to control when the egg is fertilized because she is going to lay it at a particular time and in a particular place that may have little relationship to when copulation takes place. The egg tends to start development right after it is fertilized, and the correlate is that the female fertilizes the egg just before it is laid, rather than immediately following copulation with the act of

fertilization leading to uterine implantation. So the female has evolved to store the sperm in what amounts to side shunts—sometimes elaborate chambers where the sperm may remain for days, weeks, months, or even years, depending on the animal (Birkhead and Hunter, 1990). A consequence is that, while in mammals the first sperm to arrive in the female's genital tract during the appropriate ovulatory window have the best chance of fertilizing the egg, in insects, reptiles, and birds, the last sperm in—up to a certain time before fertilization—have the best chance of fertilizing the egg (Parker, 1970; Smith, 1984; Birkhead *et al.*, 1987; Birkhead, 1987; Birkhead and Hunter, 1990). A male mammal cuckolded near ovulation can reduce his problem primarily by outnumbering the sperm of his competitor as soon as possible after being cuckolded. A cuckolded male insect, reptile, or bird, however, can reduce the problem to a greater extent (or in a different fashion) by mating after cuckoldry because sperm precedence is to some extent reversed between mammals and birds. To the extent that the last sperm inserted into the female have the greatest likelihood of fertilizing the egg, a male insect or bird's confidence (likelihood) of paternity can remain relatively high even if the female had mated previously with another male. Moreover, unlike anything yet known in mammals, the deposition of the sperm in special holding chambers renders it vulnerable to being expelled by the female or scooped out by males that subsequently mate with her (Birkhead and Hunter, 1990). (In oviparous animals that do not tend their nests constantly, as with many birds, both parents suffer an additional confidence of parenthood jeopardy not likely in mammals, owing to the fact that it is generally more difficult to recognize an alien egg than an alien infant.)

The human species thus evolved its peculiar attributes related to parental care in a peculiar social situation, involving multiple cooperative males and females in close enough proximity to cause paternal confidence to be in jeopardy. Probably they evolved increasing amounts of parental care partly because of jeopardies to the juveniles in connection with those social situations. What might

that kind of parental care have been, and what changes allowed them to develop their unique social situation?

To understand the evolving brain of humans we evidently must identify a reason for their continuing to become more elaborately social rather than avoiding competition by becoming nonsocial. To explain how the increasingly elaborate sociality of ancestral humans could have led to the unique features of modern humans such as menopause, concealment of ovulation, and altriciality, we must understand the reconciliation of male cooperation in multi-male bands with increased tendencies to male parental care, which in turn requires high male confidence of paternity. Much evidence indicates that competition over women is a central theme in male-male sociality in humans (*e.g.*, Chagnon, 1977). How can males reconcile their competitiveness over women, while continuing to enhance their cooperativeness, so as to produce the unique tendencies and skills that are expressed in almost innumerable ways in all societies? Several other authors have already hinted at the significance of this question in understanding the general selective situation that gave rise to the peculiarities of human sociality (*e.g.*, Daniels, 1983; Lancaster and Lancaster, 1983).

Male confidence of paternity can be high in multi-male bands only when each female restricts her matings to one male, and that male has a way of knowing it. Chimpanzees and bonobos have never attained this condition. They have bands containing multiple males who cooperate against other bands of male chimpanzees, but female chimpanzees advertise ovulation very prominently and usually mate promiscuously. No one, evidently neither humans nor chimpanzees, can draw a chimpanzee pedigree with both sides represented (*e.g.*, Goodall, 1986). In consequence, chimpanzee infants evidently have no social fathers, or at least no particular ones within the social group. Within social groups there could be little significance for a term or a signal meaning "bastard" in chimpanzee language. Humans in contrast make much of terms meaning bastard in virtually every society (Alexander, 1977). In humans, fathers are important—perhaps often essential—to the well-being

and eventual reproductive success of their offspring. In both humans and chimpanzees, infants are in jeopardy when mothers transfer between groups (Goodall, 1986), and in humans they are also in jeopardy when mothers transfer between individual males (Daly and Wilson, 1981).

RECIPROCITY AMONG MALES AND COMPETITION FOR FEMALES

Social reciprocity may not be unique to humans, but it is certainly uniquely prevalent in their social life today. I believe that the way to turn a chimpanzee-like situation into a human social situation is to cause respect for the social, sexual, reproductive relationship between a male and a female, or the honoring of that relationship, to become a part of the system of social reciprocity by which males continue to evolve enhancements of their cooperative (hence, group-competitive) interactions. No such situation exists in chimpanzees, but it clearly does exist in all human societies. It seems to me possibly to represent at least part of the beginnings of morality—the establishment of rules that provide rights and privileges to the individuals in a group that they will be able to sustain only because some kind of coalition within the group defends the rules and their application.

Once this situation exists, then the establishment of such male-female relationships should tend to become public events, as weddings are public, evidently in all extant societies. Socially imposed marriage or mating systems become possible, as with the unique system of socially imposed monogamy that prevails in most parts of human society the world over today, which, when it works, represents a kind of ultimate in the honoring of male-female relationships. Socially imposed monogamy seems to have spread across the world largely as a result of military advantages of the peoples promoting this particular marriage system. It's difficult to ignore the potential for a relationship between this fact and the general balance-of-power argument with which I began this essay.

How can concealment of ovulation evolve in multi-male groups, from a beginning in which ovulation is advertised? How can it evolve while

the tendencies of males to maintain their coalitions at the level of the whole group are being retained and even reinforced? Concealment of ovulation might have begun as concealment of copulation—or more narrowly as copulations sneaked by males otherwise subordinate, and possible because females agreed to them (one can observe such interactions between ovulating female chimpanzees and subordinate males in the movie, "Family of Chimps," made of the chimpanzees in the Arnhem (Netherlands) Zoo (*cf.* de Waal, 1982); in wild chimpanzees they appear to take the form of male-female consort pairs leaving the vicinity of the other males: Goodall, 1986; Smuts *et al.*, 1987).

Suppose a male invites a female to consort with him, and to copulate outside the view of the dominant male and she agrees. He accepts that she is hiding the relationship and the copulation too, partly because afterward she does not rush screaming from him and incite the dominant male to persecute him. Next, the female may offer herself repeatedly in secret to a particular male. Presumably she now holds a secret with which she can coerce the male: if he does not help her she will not copulate with him again, and if the male with which she has initiated secret copulations does not continue to help her she is in a position to subject him to the ire of the dominant male—she can do it easily at any time by pretending to allow him one more furtive copulation and then exposing him abruptly.

Whenever a male helps a female who secretly copulates with him, and the female continues to allow that male secret copulations, then copulation itself moves toward general secrecy (a general attribute of human sexual behavior today), and a special kind of pair bonding has begun which is in some sense tied to this secrecy—perhaps the only kind of pairing that can work when both parents invest in the offspring in social groups containing multiple adults of both sexes (and multiple related adults of both sexes). Males are helping females who copulate secretly with them and females are secretly copulating with males who help them. The next step is that the females simply conceal ovulation from the other males, and eventually start resisting them in copulation. At the same time they are

presumably copulating sufficiently with their bonded male to cause themselves to become pregnant as often as is optimal. And, eventually, the pair bonds are recognized and accepted by other adults in the group, so that consortships are no longer necessarily secret, although copulations appear to have tended to remain private and most people are made uneasy—even angry—by public displays of affection that go beyond affirmation of a pair bond, especially if they become explicitly sexual.

Presumably, the above scenario would appear only when males really could help females and their offspring. Presumably also, there may have been increasing ways males could contribute to offspring success during human evolution. Perhaps some of these ways of helping females and offspring only came into being as the changes here described began to take place. Prevention of infanticide, for example, would be a massively important way that a male might help his female and the offspring he sires. Suppose a female begins to restrict her copulations, excluding certain males or excluding all but a single male. In a primate resembling chimpanzees we are justified in assuming that such a female would place her offspring in jeopardy of infanticide by the disenfranchised males within her own group. Because of her loyalty to the male who mated with her, it would profit him to defend her offspring against attack, at least under circumstances where this would not have been the case before, and assuming that his loyalty had some chance of being effective in preventing infanticide. If unity among males is sufficiently important, then rudimentary social reciprocity among males in connection with defense of the group or the "exporting" of aggression (Manson and Wrangham, *in press*) could cause a male's importance to the group, and the importance of overall amicability among males, to prevent males who could not copulate with a particular female from attacks on her offspring or on the male who undertakes to defend them. Obviously, respecting the right of the offspring of other individuals or families to exist and go about their business is also a part of the social cooperativeness—the moral systems—of humans today.

None of this will work unless a sufficient proportion of the males is thereby obtaining access to females. Because there is no reason to suppose that sex ratios ever varied much from their present condition, this suggests to me that a strong tendency toward monogamy occurred early in human history, a unique kind of monogamy because it existed under social life in groups containing multiple males who cooperated with each other against males from other groups. It suggests that paternal care became important early in human evolution, and that extreme polygyny and domination of females within groups by subgroups of old males as occurs in some modern societies may actually be a derived feature of human social life, associated with extremes of social power developed by older males.

I think this scenario of monogamous tendencies under complex and intensive social cooperativeness, especially among males, includes some possible answers to questions that were not even

recognized as such by Lovejoy (1981), in an analysis otherwise harmonious with that generated here, because he did not deal with the question of how humans continued to enhance group cooperation while evolving paternal care and concealment of ovulation. Similarly, Humphrey (1976) did not deal with the question of why humans continued to live in groups such that selection could continue to favor increasing intelligence as a social tool. Virtually no moral philosopher has ever considered why humans have continued to live under conditions in which conflicts of interest among individuals often become acute. Such lapses may seem trivial. Perhaps the central message of this essay is that they are not: to develop an adequate view of how natural selection has produced humanity, and therefore to be able to use selection and evolution to assist in understanding ourselves, requires that we take into account all aspects of the selective picture.

CONCLUSIONS

The ideas developed here are an effort to combine in an integrative way theories constructed by different authors about cooperative group-living, competition between groups, the evolution of the human brain and intelligence, the rise of parental care, and the appearance of monogamous tendencies in the hominid line. This combination of theories seems to predict several things about how humans will interact in groups. It suggests for example that, over long periods, consistent overlaps of interests among members of cooperating groups and conflicts of interest between members of different groups will cause a correlation between a sharing of conviviality within cooperating groups and the sharing of enmity toward members of other competing groups. It may imply that our enthusiasm over the conviviality that we share restrictively will cause us to ignore or dismiss opposite kinds of emotions that in other circumstances become over-riding, and even to vilify those who call them to our attention.

The theory also implies that there will continually be balance-of-power races between competing

groups, and scarcely anything better describes the economic, political, and social interactions of internally cohesive human groups. It implies that humans should have evolved to practice competitively group-against-group; play that meets this criterion is of course a central theme in our lives and evidently we are the only species for which this is true. At the same time, partial differences of interest within groups will cause continual efforts at manipulation and deception there, as well as cooperation.

Everyone puzzles over the insanity of our current group-against-group competition and the international arms race with its threat of mutual extinction or the loss of civilization. Yet the ideas discussed here seem to predict—perhaps to require—just such a tendency. They seem simultaneously to account for the rise of nations and the runaway aspects of the international arms race. Indeed, the runaway social process invoked here would seem unstoppable except as a result of either calamities resulting from large-scale aggression or irreversible damage to the environment as a result of resource

competition. In the modern world these two possibilities in fact loom as increasingly likely catastrophes, and one or both has in recent years come to be discussed virtually every day in the news of the world. Humans serve their interests by cooperating in groups—but not as a single group—not as a world population. Instead they continue to cooperate as groups against other similar human groups or populations.

The urgency of human self-understanding seems to grow as population growth, technology, communication, and economic interdependence continue to shrink the effective size of the planet, and to exacerbate the severity of the effects of our general inability to control terrorism, arms races, and other forms of potentially or actually deleterious competitiveness over exploitation of the earth's resources. Designed for the most part to improve the current quality of life, our technological races and our strivings as individuals seem also to threaten the quality of life and sometimes the very survival of our descendants.

Perhaps the ideas discussed here, through their effect on human self-understanding and self-images, will eventually assist us in dealing with not only the traumas of conflicts between individuals and small groups but our bizarre international competitions and our stubbornness in seeking pleasures that threaten the long-term future of our planet as a human environment. We hear increasingly the suggestion that to save future generations from disaster will require lowering the current quality of life—even “massive altruism”—by our

own generation. What is suggested is a virtual reversal of current directions of striving, and that will not be easy to effect. How do we decide if any such thing is necessary, and how do we bring about such changes if they are ultimately deemed inevitable?

If human self-understanding were easy, then unraveling the cumulative effects of natural selection would be trivial. But self-analysis has proved the most perplexing and convoluted of all human challenges. Some of the reasons may become more accessible through understanding our evolutionary background. It seems appropriate to expect that the ideas of evolutionary biologists, about “ultimate” causes and the cumulative forces and changes that explain them, can eventually be combined usefully with the analyses of other scientists who focus on more immediate causes, such as everyday physical and mental pain and pleasure, and why we seek and use them in particular fashions. No part of biological theory has ever legitimately implied that humans cannot use their evolution-given traits to set and accomplish goals that are entirely incidental—even contrary—to their history of natural selection.

“ . . . there is no alleviation for the sufferings of mankind except veracity of thought and of action, and the resolute facing of the world as it is when the garment of make-believe by which pious hands have hidden its uglier features is stripped off.”

—Thomas Henry Huxley, 1909, p. 13

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REFERENCES

- Alexander, R.D. 1967. Comparative animal behavior and systematics. In Anonymous. *Systematic Biology*. National Academy of Science Publication 1692: 494–517.
- . 1971. The search for an evolutionary philosophy of man. *Proceedings of the Royal Society of Victoria, Melbourne* 84: 99–120.
- . 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5: 325–383.
- . 1977. Natural selection and the analysis of human sociality. In C.E. Goulden (ed.). *Changing Scenes in the Natural Sciences. 1776–1976*. Bicentennial Symposium Monograph, Philadelphia Academy of Natural Sciences Special Publication 12: 283–337.
- . 1979. *Darwinism and Human Affairs*. Seattle: University of Washington Press.
- . 1986. Ostracism and indirect reciprocity: the reproductive significance of humor. *Ethology and Sociobiology* 7: 253–270.
- . 1987a. *The Biology of Moral Systems*. Hawthorne, NY: Aldine de Gruyter.
- . 1987b. The evolutionary approach to human behavior: What does the future hold? In L.L. Betzig, M. Borgerhoff Mulder, and P.W. Turke (eds). *Human Reproductive Behaviour: A Darwinian Perspective*: 317–3. London: Cambridge University Press.
- . 1987c. The real origin of the species. *Washington Post*, June 28, p. C3.
- . 1989a. [Why aesthetics?] *LSA Magazine*. Ann Arbor, MI: The University of Michigan College of Literature, Science, and the Arts 12: 22–24.
- . 1989b. Evolution of the human psyche. In P. Mellars and C. Stringer (eds). *The Human Revolution. Behavioural and Biological Perspectives on the Origins of Modern Humans*: 455–513. Princeton, NJ: Princeton University Press.
- . 1990a. Epigenetic rules and Darwinian algorithms: the adaptive study of learning and development. *Ethology and Sociobiology* 11(3): 1–63.
- . 1991b. Unanswered questions about naked mole rats. In P. Sherman, J. Jarvis, and R.D. Alexander (eds). *The Biology of the Naked Mole-Rat*: 446–465. Princeton, NJ: Princeton University Press.
- and R.S. Bigelow. 1960. Allochronic speciation in field crickets, and a new species, *Acheta veletis*. *Evolution* 14: 334–346.
- and K.M. Noonan. 1979. Concealment of ovulation, parental care, and human social evolution. In N.A. Chagnon and W.G. Irons (eds). *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*: 436–453. North Scituate, MA: Duxbury Press.
- , ———, and B. Crespi. 1991. The evolution of eusociality. In P. Sherman, J. Jarvis, and R.D. Alexander (eds). *The Biology of the Naked Mole-Rat*: 3–44. Princeton, NJ: Princeton University Press.
- and D.W. Tinkle. 1968. Review of *On Aggression* by Konrad Lorenz and *The Territorial Imperative* by Robert Ardrey. *Bioscience* 18: 245–248.
- Andelman, S.J. 1987. Evolution of concealed ovulation in vervet monkeys (*Cercopithecus aethiops*). *American Naturalist* 129: 785–799.
- Ardrey, R. 1966. *The Territorial Imperative*. New York: Atheneum.
- Benshoof, L. and R. Thornhill. 1979. The evolution of monogamy and concealed ovulation in humans. *Journal of Social and Biological Structures* 2: 95–106.
- Berger, J. 1986. *Wild Horses of the Great Basin. Social Competition and Population Size*. Chicago: University of Chicago Press.
- Bigelow, R.S. 1969. *The Dawn Warriors: Man's Evolution toward Peace*. Boston, MA: Little, Brown.
- Birkhead, T. 1987. Sperm competition in birds. *Trends in Ecology and Evolution* 2: 268–272.
- , L. Atkin, and A.P. Moller. 1987. Copulation behaviour of birds. *Behaviour* 101: 101–133.
- and F.M. Hunter. 1990. Mechanisms of sperm competition. *Trends in Ecology and Evolution* 5: 48–52.
- Blakemore, C. and S. Greenfield (eds). 1987. *Mindwaves*. London: Basil Blackwell.
- Bruner, J.S. 1986. *Actual Minds, Possible Worlds*. Cambridge, MA: Harvard University Press.
- Burley, N. 1979. The evolution of concealed ovulation. *American Naturalist* 114: 835–858.
- Burling, R. 1986. The selective advantage of complex language. *Ethology and Sociobiology* 7: 1–16.
- Bygott, J.D. 1972. Cannibalism among wild chimpanzees. *Nature* 238: 410–411.
- Byrne, R.W. and A. Whiten (eds). 1988. *Machiavellian Intelligence. Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Oxford: Clarendon Press.
- Caccone, A. and J.R. Powell. 1989. DNA divergence among hominoids. *Evolution* 43: 925–942.
- Campbell, B.G. 1966. *Human Evolution. An Introduction to Man's Adaptation*. Chicago: Aldine Publishing Co.
- Campbell, D.T. 1975. Conflicts between biological and social evolution and between psychology and moral tradition. *American Psychologist* 30: 1103–1126.
- Carneiro, R.L. 1970. A theory of the origin of the state. *Science* 169: 733–738.
- Case, T.J. 1978. Endothermy and parental care in the terrestrial vertebrate. *American Naturalist* 112: 861–874.
- Chagnon, N.A. 1977. *Yanomamo: The Fierce People* (2nd Ed.). New York: Holt, Rinehart, and Winston.
- Cheney, D. and R.W. Wrangham. 1987. Predation. In B.B.

- Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (eds). *Primate Societies*: 227–239. Chicago: University of Chicago Press.
- Ciochon, R.L. and R.S. Corruccini (eds). 1983. *New Interpretations of Ape and Human Ancestry*. New York: Plenum Press.
- and J.G. Fleagle (eds). 1987. *Primate Evolution and Human Origins*. New York: Aldine de Gruyter.
- Clark, R.W. 1971. *Einstein. The Life and Times*. New York: Avon Books.
- Connor, R. 1986. Pseudo-reciprocity: investing in mutualism. *Animal Behaviour* 34: 1562–1566.
- Daly, M. and M.I. Wilson. 1981. Abuse and neglect of children in evolutionary perspective. In R.D. Alexander and D.W. Tinkle (eds). *Natural Selection and Social Behavior. Recent Research and New Theory*: 405–416. New York: Chiron Press.
- Daniels, D. 1983. The evolution of concealed ovulation and self-deception. *Ethology and Sociobiology* 4: 69–87.
- Dart, R. 1954. The predatory transition from ape to man. *International Anthropological and Linguistic Review* 1: 201–213.
- Darwin, C.R. 1859. *On the Origin of Species*. A facsimile of the first edition with an introduction by Ernst Mayr, published in 1967. Cambridge, MA: Harvard University Press.
- . 1871. *The Descent of Man and Selection in Relation to Sex*. Two vols. New York: D. Appleton and Co.
- . 1872. *The Expression of the Emotions in Man and Animals*. New York: D. Appleton and Co.
- Datta, S. 1987. The evolution of concealed ovulation in vervet monkeys. *Trends in Ecology and Evolution* 2: 223–224.
- Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford University Press.
- Dienske, H. 1986. A comparative approach to the question of why human infants develop so slowly. In J.G. Else and P.C. Lee (eds). *Primate Ontogeny, Cognition, and Social Behaviour*: 147–154. London: Cambridge University Press.
- Douglas-Hamilton, I. and O. Douglas-Hamilton. 1975. *Among the Elephants*. New York: Viking Press.
- Fagen, R. 1981. *Animal Play Behaviour*. New York: Oxford University Press.
- Fisher, R.A. 1930 (rev. 1958). *The Genetical Theory of Natural Selection* (2nd Ed.). New York: Dover Publications.
- Foley, R. 1989. The ecological conditions of speciation: a comparative approach to the origins of anatomically-modern humans. In P. Mellars and C. Stringer (eds). *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*: 298–318. Princeton, NJ: Princeton University Press.
- Fries, J.F. 1980. Aging, natural death, and the compression of morbidity. *New England Journal of Medicine* 303: 130–135.
- Gallup, G.G. 1970. Chimpanzees: self-recognition. *Science* 167: 86–87.
- Ghiglieri, M.P. 1985. The social ecology of chimpanzees. *Scientific American* 252: 102–113.
- . 1988. *East of the Mountains of the Moon: Chimpanzee Society in the African Rain Forest*. New York: The Free Press.
- . 1989. Hominid sociobiology and hominid social evolution. In P.G. Heltne and L.A. Marquardt (eds). *Understanding Chimpanzees*: 370–379. Cambridge, MA: Harvard University Press, in cooperation with the Chicago Academy of Sciences.
- Gibbard, A. 1990. *Wise Choices, Apt Feelings*. Cambridge, MA: Harvard University Press.
- Gill, F.B. 1990. *Ornithology*. New York: W.H. Freeman.
- Glass, B. 1966. Evolution of hairlessness in man. *Science* 152: 294.
- Godfrey, L. and K.H. Jacobs. 1981. Gradual, autocatalytic, and punctuational models of hominid brain evolution: a cautionary tale. *Journal of Human Evolution* 10: 255–272.
- Goldizen, A.W. 1987. Tamarins and marmosets: communal care of offspring. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (eds). *Primate Societies*: 34–43. Chicago: University of Chicago Press.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behaviour*. Cambridge, MA: Belknap Press.
- Gray, J.P. and L.D. Wolfe. 1983. Human female sexual cycles and the concealment of ovulation problem. *Journal of Social and Biological Structures* 6: 345–352.
- Greene, D.L. and L. Sibley. 1986. Neandertal pubic morphology and gestation length revisited. *Current Anthropology* 27: 517–518.
- Guthrie, R.D. 1970. Evolution of human threat display organs. *Evolutionary Biology* 4: 257–301.
- Haldane, J.B.S. 1955. Population genetics. *New Biology* 18: 34–51.
- Hamilton, W.D. 1964. The genetical evolution of social behaviour I, II. *Journal of Theoretical Biology* 7: 1–52.
- . 1975. Innate social aptitudes of man: an approach from evolutionary genetics. In R. Fox (ed.). *Biosocial Anthropology*: 133–155. New York: Wiley.
- Hamilton, W.J. III. 1973. *Life's Color Code*. New York: McGraw-Hill.
- Hausfater, G. and S.B. Hrdy. 1984. *Infanticide: Comparative and Evolutionary Perspectives*. New York: Aldine Publishing Co.
- Hockett, C.F. 1960. Logical considerations in the study of animal communication. In W.E. Lanyon and W.N. Tavolga (eds). *Animal Sounds and Communication*. Washington, DC: American Institute of Biological Sciences, Publication No. 7: 392–430.
- Hrdy, S.B. 1979. Infanticide among animals. *Ethology and Sociobiology* 1: 13–40.
- . 1981. *The Woman That Never Evolved*. Cambridge, MA: Harvard University Press.
- and P.L. Whitten. 1987. Patterning of sexual activity. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (eds). *Primate Societies*: 370–384. Chicago: University of Chicago Press.
- Humphrey, N.K. 1976. The social function of intellect. In P.P.G. Bateson and R.A. Hinde (eds). *Growing Points in Ethology*: 303–318. New York: Cambridge University Press.

- . 1978. Nature's psychologists. *New Scientist* 78: 900–903.
- . 1980. Nature's psychologists. In B. Josephson and B.S. Ramchandran (eds). *Consciousness and the Physical World*: 57–75. New York: Pergamon Press.
- . 1983. *Consciousness Regained: Chapters in the Development of Mind*. Oxford: Oxford University Press.
- Hutchinson, G.E. 1965. *The Ecological Theater and the Evolutionary Play*. New Haven, CT: Yale University Press.
- Huxley, T.H. 1909. *Autobiography and Selected Essays*. New York: Houghton Mifflin.
- Jarvis, J.V.M. 1981. Eusociality in a mammal: cooperative breeding in naked mole rat colonies. *Science* 212: 571–573.
- Kasuya, T. and H. Marsh. 1984. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Report of the International Whaling Commission*, Special Issue 6: 259–310.
- Keith, A. 1912. *Man, A History of the Human Body*. New York: H. Holt and Co.
- . 1949. *A New Theory of Human Evolution*. New York: Philosophy Library.
- King, G.E. 1976. Society and territory in human evolution. *Journal of Human Evolution* 5: 323–332.
- Kurten, B. 1971. Time and hominid brain size. *Commentationes Biologicae*. Helsinki: Societas Scientiarum Fennica 32(36):3–8.
- Kushlan, J.A. 1980. The evolution of hairlessness in man. *American Naturalist* 116: 727–729.
- Kuttner, R. 1960. An hypothesis on the evolution of intelligence. *Physiological Reports* 6: 283–289.
- Lancaster, J. and B. King. 1985. An evolutionary perspective on menopause. In J.K. Brown and V. Kerns (eds). *In Her Prime*: 13–20. South Hadley, MA: Bergin and Garvey Publishers.
- and C.S. Lancaster. 1983. Parental investment: the hominid adaptation. In D.J. Ortner (ed.). *How Humans Adapt: A Biocultural Odyssey*: 33–65. Washington, DC: Smithsonian Institution.
- Leakey, R.E. and R. Lewin. 1977. *Origins*. New York: Dutton.
- Lenneberg, E. 1971. Of language knowledge, apes, and brains. *Journal of Psycholinguistic Research* 1: 1–29.
- Lovejoy, C.O. 1981. The origin of man. *Science* 211: 341–350.
- Lorenz, K. 1966. *On Aggression*. New York: Harcourt, Brace, and World.
- Lyne, A.G. and B.F. Short. 1965. *Biology of the Skin and Hair Growth*. New York: American Elsevier Publishing Co.
- Manson, J. and R.W. Wrangham (in press). The evolution of hominoid intergroup aggression. *Current Anthropology*.
- Marsh, H. and T. Kasuya. 1986. Evidence for reproductive senescence in female cetaceans. *Report of the International Whaling Commission*, Special Issue 8: 57–74.
- Mitchell, R.W. 1986. A framework for discussing deception. In R.W. Mitchell and N. S. Thompson (eds). *Deception: Perspectives on Human and Nonhuman Deceit*: 3–40. Albany: State University of New York Press.
- and N. S. Thompson (eds). 1986. *Deception: Perspectives on Human and Nonhuman Deceit*. Albany: State University of New York Press.
- Mohnot, S.M. 1971. Some aspects of social changes and infant-killing in the Hanuman langur, *Presbytis entellus* (Primates: Cercopithecidae) in western India. *Mammalia* 35: 175–198.
- Montagu, A. 1961. Neonatal and infant immaturity in man. *Journal of the American Medical Association* 178: 56–57.
- Morris, D. 1967. *The Naked Ape*. London: Cape Publishing Co.
- Moss, C. 1988. *Elephant memories. Thirteen Years in the Life of an Elephant Family*. New York: William Morrow and Co.
- Napier, J.R. 1970. *The Roots of Mankind*. Washington, DC: Smithsonian Institution Press.
- Nice, M.M. 1962. Development of behavior in precocial birds. *Transactions of the Linnean Society of New York* 8: 1–211.
- Parker, G.A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biological Reviews, Cambridge Philosophical Society* 45: 525–567.
- Pfeiffer, J.E. 1969. *The Emergence of Man*. New York: Harper and Row.
- Pitt, R. 1978. Warfare and hominid brain evolution. *Journal of Theoretical Biology* 72: 551–575.
- Reynolds, V., V. S. E. Falger, and I. Vine (eds). 1987. *The Sociobiology of Ethnocentrism*. London and Sydney: Croom Helm.
- Ricklefs, R.E. 1974. Energetics of reproduction in birds. In R.A. Paynter, Jr., (ed.). *Avian Energetics*. Cambridge, MA: Publication of the Nuttall Ornithological Club No. 15: 152–297.
- . 1975. The evolution of co-operative breeding in birds. *Ibis* 117: 531–534.
- . 1979a. Adaptation, constraint, and compromise in avian postnatal development. *Biological Reviews, Cambridge Philosophical Society* 54: 269–290.
- . 1979b. Patterns of growth in birds. V. A comparative study of development in the starling, common tern, and Japanese quail. *Auk* 96: 10–30.
- . 1983. Avian postnatal development. In D.S. Farner, J.R. King, and K.C. Parkes (eds). *Avian Biology*. Volume 7: 1–83. New York: Academic Press.
- Rosenberg, K. 1986. The functional significance of Neanderthal pubic morphology. Ann Arbor, MI: University Microfilms.
- Sacher, G.A. 1975. Maturation and longevity in relation to cranial capacity in hominid evolution. In R.H. Tuttle (ed.). *Primate Functional Morphology and Evolution*: 418–441. The Hague: Mouton Publishers.
- and E.F. Staffeldt. 1974. Relation of gestation time to brain weight for placental mammals: implications for the theory of vertebrate growth. *American Naturalist* 108: 593–615.

- Schultz, A.H. 1956. Postembryonic age changes. In H. Hofer, A.H. Schultz, and D. Starck (eds). *Primatologia. Handbook of Primatology. I. Systematik, Phylogenie, Ontogenie*: 887-964. Basel: Basler Druck-und Verlagsanstalt.
- Schwartz, G.C. and L.A. Rosenblum. 1981. Allometry of primate hair density and the evolution of human hairlessness. *American Journal of Physical Anthropology* 55: 9-12.
- Shaw, R.P. and Y. Wong. 1988. *Genetic Seeds of Warfare: Evolution, Nationalism, and Patriotism*. Boston: Unwin Hyman.
- Sherman, P.W. 1978. Review of *Among the Elephants* by I. and O. Douglas-Hamilton and *Elephants and their Habitats* by R.M. Laws, I.S.C. Parker, and R.C.B. Johnstone. *Journal of Mammalogy* 59: 453-454.
- . 1981. Reproductive competition and infanticide in Belding's ground squirrels and other animals. In R.D. Alexander and D.W. Tinkle (eds). *Natural Selection and Social Behavior. Recent Research and New Theory*: 311-331. New York: Chiron Press.
- , J.V.M. Jarvis, and R.D. Alexander (eds). 1991. *The Biology of the Naked Mole-Rat*. Princeton, NJ: Princeton University Press.
- Smith, B.H. 1989. Dental development as a measure of life history in primates. *Evolution* 43: 683-688.
- Smith, R.L. (ed.). 1984. *Sperm Competition and the Evolution of Animal Mating Systems*. New York: Academic Press.
- Smuts, B.B. 1985. *Sex and Friendship in Baboons*. Hawthorne, NY: Aldine Publishing Co.
- , D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (eds). 1987. *Primate Societies*. Chicago: University of Chicago Press.
- Strassmann, B.I. 1981. Sexual selection, paternal care, and concealed ovulation in humans. *Ethology and Sociobiology* 2: 31-40.
- Strate, J. 1982. *An Evolutionary View of Political Culture*. University of Michigan Ph.D. Dissertation, Department of Political Science. Ann Arbor, MI: University Microfilms.
- Stringer, C. 1984. Human evolution and biological adaptation in the Pleistocene. In R. Foley (ed.). *Hominid Evolution and Community Ecology. Prehistoric Human Adaptation in Biological Perspective*: 55-83. New York: Academic Press.
- Sugiyama, Y. 1967. Social organization of Hanuman langurs. In S.A. Altman (ed.). *Social Communication among Primates*: 221-236. Chicago: University of Chicago Press.
- Symons, D.A. 1979. *The Evolution of Human Sexuality*. New York: Oxford University Press.
- Trevathan, W. 1987. *Human Birth: An Evolutionary Perspective*. New York: Aldine de Gruyter.
- Trinkaus, E. 1987. On Neandertal pubic morphology and gestation length: reply to Greene and Sibley. *Current Anthropology* 28: 91.
- Trivers, R.L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46: 35-57.
- . 1985. *Social Evolution*. Menlo Park, CA: Benjamin/Cummings Publishing Co.
- Turke, P.W. 1989. Evolution and the demand for children. *Population and Development Review* 15: 61-90.
- . (Ms.). Evolution of the 100 year lifespan.
- Waal, F. de. 1982. *Chimpanzee Politics*. New York: Harper and Row.
- Walker, E.P. 1975. *Mammals of the World* (3rd Ed.). Baltimore: The Johns Hopkins University Press.
- West, M.J. and R.D. Alexander. 1963. Sub-social behavior in a burrowing cricket *Anurogryllus muticus* (De Geer). *Ohio Journal of Science* 63: 19-24.
- West-Eberhard, M.J. 1979. Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society* 123: 222-234.
- . 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* 58: 155-183.
- Williams, G.C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11: 398-411.
- . 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Wilson, E.O. 1971. *The Insect Societies*. Cambridge, MA: Harvard University Press.
- . 1973. The queerness of social evolution. *Bulletin of the Entomological Society of America* 19: 20-22.
- . 1975. *Sociobiology: The New Synthesis*. Cambridge, MA: Belknap Press.
- Zeveloff, S.I. and M.S. Boyce. 1980. Parental investment and mating systems in mammals. *Evolution* 34: 973-982.
- and ———. 1982. Why human neonates are so altricial. *American Naturalist* 120: 537-542.