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EVOLUTION AND HUMAN SOCIETY

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Note to HBES members from Richard D. Alexander: For various reasons, all my own fault(!), I was unable to finish my keynote lecture at Kyoto in a way that I regarded as satisfactory. To help correct this insufficiency I have written out the materials I expected to cover in the talk, for anyone who might wish to know more about what I intended to say. I have included three items: first, a slightly expanded version of the Abstract (or Introduction) to the talk with its original (and the overall) title (*Evolution and Human Society*), second, the text of the talk (Understanding the Human Species and Its Immediate Ancestors); third, the Lecture Handout is included after the text of the talk. These documents can also be read or downloaded at: <http://insects.ummz.lsa.umich.edu/pdfs/Alexander2008HBES.pdf>

EVOLUTION AND HUMAN SOCIETY

June 2008 Kyoto, Japan, meeting of the Human Behavior and Evolution Society

Richard D. Alexander

1. Abstract (or Introduction to the Lecture)

(Comments in brackets were inserted after the abstract was published in the meeting program)

Darwin's fabulous intellect implanted the concept and general nature of evolution permanently in the minds of humans willing to think seriously about it. His several challenges included demonstrating that evolution tends to save only traits that contribute to reproduction, that evolution produces "complex organs" only via "numerous, successive, slight modifications," and that traits carried by sterile individuals can be furthered if relatives of the sterile individuals are sufficiently and appropriately aided.

In 1930, Sir Ronald A. Fisher elaborated on Darwin's arguments by explaining factors affecting rates of evolution, how such traits as allelic dominance, sex ratio selection, heroism, and runaway sexual selection could evolve, and how kin selection can be quantified.

The arguments of Darwin, unfortunately, were not sufficient, and those of Fisher were too late, to cause the social and medical sciences, and of course religion [which developed answers to its pressing questions centuries ago], to accept the evolutionary process, combined with the succession of evolutionary environments, as the key to profound explanations of virtually everything about life. The building blocks were there, but the willingness and necessary vision were not.

As a consequence, the human-oriented sciences generated and elaborated the strategies, practices, and principles of their societies in a virtual absence of contributions from evolution-based science. For more than a century evolutionary biology was largely restricted to studies of pattern rather than process, amassing data from fossils and comparisons from phylogenies and genealogies of species. [Evolution was often defined then, even by biologists, as simply "change with time." Many who

are for one reason or another skeptical of evolution continue to see it almost entirely as a skimpy record of long-term changes with large unexplained gaps, and remain unfamiliar with the generation-to-generation process of evolution and how it meshes with the fossil record]. In the early and middle 20th century, mathematical versions of the evolutionary process, via population genetics, primarily considered the evolutionary process to be focused on increasing the average fitness of populations, until Alice Brues, in 1964, explained as J.B.S. Haldane's "Dilemma" his claim that too many rare beneficial alleles would render the average fitness of a population so low as to threaten its extinction [The mistake was made because the most beneficial allele was always given an arbitrary "fitness" of 1.0 to prevent fitness measurements from rising in a mathematically cumbersome way; as a necessary result the more abundant (therefore more influential) long-present alleles received lowered fitnesses because of the presence of the new, rare, more beneficial allele(!)].

This general state of affairs was not alleviated until George C. Williams (1966) put together the arguments that (1) life is organized hierarchically, (2) selection can operate at many levels simultaneously, (3) selection can be reversed at different levels, and (4) selection is most likely to be potent at the lowest levels of organization [within species, only genes and (inter-generationally transmitted) results of learning persist reliably, generation after generation] [Given the last phrase, I think this is still correct!].

The resulting chaos of conflicts was most traumatic for the already established human-oriented disciplines. Social scientists, medical scientists, philosophers, religious people, and those in the arts and literature for the most part vigorously rejected (or avoided) the intrusive [to their disciplines] revival of Darwinian and Fisherian arguments, and, even more forcefully, the establishment -- by such as George C. Williams, Robert L. Trivers, and William D. Hamilton -- of a "new" science of evolutionary adaptation with consequences for human understanding apparent in every direction.

The objections will continue. They are bolstered by ideological, moral, and ethical systems that, because of their tendencies to utilize authority-based absolutism, seem to conflict with evolution as an approach and with science as the method. They are aided immensely by our continuing -- and, unfortunately, to-be-long-continued -- ignorance of the incredibly complex, largely uncharted, and all-too-often unyielding processes of ontogeny, including tendencies, capacities, and constraints on learning. [The adjectives just used are appropriate mainly because of the nearly complete cooperation of the 20,000 or more genes in the human genome. This cooperation has evolved because the genes typically cannot change groups (genomes) except as a result of the generational meiotic events; hence genes in a genome approach having interdependent identical fates via roughly equal chances of getting into a successful gamete. This situation is resistant to being unraveled and explained because it necessarily involves an enormous number of genic interactions (and virtually uncountable and un-assessable sequences of micro-environments) -- leading to probably thousands of trait-expressions for individual genes). As a result we have not yet been able to explain entirely the ontogeny of a single behavior of any animal, no matter how seemingly simple.]

It is easy to be hostile toward evolution as the background of adaptive forces that conflict with current ethical views. It is easy to be skeptical, or even fearful, of oversimplified ontogenetic and experiential hypotheses, assumptions, and biases. It is tempting to assume or accept that human

society is doing just fine, and that if it is not, an evolutionary perspective is not likely to help matters.

During the last century, between 50 and 150 million people were reported killed in warfare and genocides – an incredible average of somewhere between 1400-4000 per day across 100 years. If data on current conflicts are accurate and relevant, up to hundreds of times as many people as were killed were also maimed physically, mentally, or emotionally, often permanently. On this single basis, we can make no claim to be doing “just fine.” We are now beginning to face global problems that will require global cooperation to be solved. There is reason to believe that we have not evolved to solve global problems by global cooperation, and to believe that we have never accomplished such [even when “global” was not actually global but merely involved multiple adversarial human groups]. Indeed, the most important and frightening of all human adaptations is likely our stubborn and perhaps unique manner of alternating our most intense emotional expressions between the two extremes of amity and enmity within our own species [I have argued across some 40 years that this feature of human life, more than any other, has shaped and elaborated the other outstanding or massively important human traits that I will discuss here.].

[Humans are uniquely preoccupied with between-group competition and aggression (warfare and patriotism) within their own species. The results of this preoccupation are reflected in virtually every unique or distinctive major trait of humans, including biparental care, concealment of ovulation, menopause, altriciality of the human juvenile, kin recognition and differential nepotism, intensity of patriotism, and perhaps every aspect and concomitant of human intelligence and imagination, from the size and complexity of the brain to cognition, consciousness, language, absorption and retention of knowledge, imagination, and the future-seeking of mental scenario-building.]

We need every tool available to understand such things about ourselves. These are reasons why the Human Behavior and Evolution Society has the potential to become the most important scientific organization in the world.

A hydrogen bomb is an example of mankind’s enormous capacity for friendly cooperation. Its construction requires an intricate network of human teams, all working with single-minded devotion toward a common goal. Let us pause and savor the glow of self-congratulation we deserve for belonging to such an intelligent and sociable species. (Robert S. Bigelow, 1969. *The Dawn Warriors*)

The challenge of Darwinism is to find out what our genes have been up to and to make that knowledge widely available as a part of the environment in which each of us develops and lives so that we can decide for ourselves, quite deliberately, to what extent we wish to go along. (Richard D. Alexander 1979. *Darwinism and Human Affairs*) [Not all evolved adaptations are likely to be deemed desirable in today’s world.]

Heredity is particulate, but development is unitary. Everything in the organism is the result of the interactions of all genes, subject to the environment to which they are exposed. What genes

determine are not characters, but rather the ways in which the developing organism responds to the environment it encounters. (Theodosius Dobzhansky 1961. In: *Insect Polymorphism*, John S. Kennedy, editor)

Kindness and generosity arise spontaneously when the otherness of others goes away. (Barry R. McKay, 3 August 2007 letter to the *Ann Arbor News*)

2. Understanding the Human Species and Its Immediate Ancestors (The Lecture)

(Bracketed statements in this version have been added since publication)

Introduction

In 1990 I published a paper titled *How did humans evolve? Reflections on the uniquely unique species*. In that paper I developed arguments about how humans might have evolved to be so strikingly different in certain regards from their current relatives among the apes, and why, given the apparent speed of evolutionary change in humans, there are so few clear instances of species multiplication, with only a single human species remaining today. In the years following, I generated a list of 34 distinctive or unique human traits and sought to develop hypotheses regarding their functions (see materials in the Kyoto talk handout in this document, and the three additional papers for which online addresses are given in the Handout).

My intent in the Kyoto lecture was to consider two of the 34 human traits (menopause and concealment of ovulation) in some detail because questions have been raised about whether they even exist, and whether they can be regarded as adaptations, and also because I think they can be regarded as especially important in the effort to understand ourselves. I expected to continue my talk by discussing the importance of menopause and concealment of ovulation as indicators and enablers of the other 32 traits, then complete the talk by discussing how the functions of the 34 traits in the handout could be recombined in various ways, so as to contribute to reconstructing some of the stages through which hominid lines passed on their way to becoming the modern human species. I was unable to carry out this continuation. Here I present a condensed version of the entire talk.

Menopause

The human species has essentially doubled its average maximum lifetime compared to its ape relatives, roughly from 40-45 years to 80-90 years. I am not aware of any suggestion that ovulations were added during the added 40-45 years. As a result the menopausal years have typically been referred to as a post-reproductive period. This label, however, applies only if reproduction is restricted to production of offspring. Evolutionary biologists today understand that the reproductive process also includes tending not only offspring, but, according to the amount of their genetic overlap with a potentially beneficent helper, any genetic relatives that can be aided in reproduction (Hamilton 1964).

Darwin (1871, vol. 1, p. 319) said the following: *The only check to a continued augmentation of fertility in each organism seems to be either the expenditure of power and the greater risks run by parents that produce a more numerous progeny, or the contingency of very numerous eggs and young being produced of smaller size or less vigorous, or subsequently not so well nurtured.*

In the above statement, Darwin was telling us what can now be translated thus: The evolutionary process, guided principally by natural selection, changes organisms adaptively solely by increasing the persistence of genetic materials (e.g., genes, alleles), sometimes more or less indefinitely. This

fact, which does not entirely please us, nevertheless describes the meaning of reproduction, or reproductive success, as used by modern biologists.

A fundamental question is whether or not the menopausal period – and the equivalent 40-45 added years in men -- have been added as adaptations. It is obvious that both women and men contribute to the reproductive success of genetic relatives during the second half of their lives. To my knowledge, however, no one has demonstrated a sufficient positive effect to prove adaptiveness (i.e., to prove that neither removing the added 40-45 years nor adding ovulations would be as reproductive as the existing situation). [This failure is surely at least partly a consequence of difficulty in identifying and locating societies with social structures – kinship systems, group sizes, etc. -- comparable to those during which human life lengths were being doubled.] But we can settle this question by referring to another of Darwin’s remarkable challenges. In 1859 Darwin said this: *If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down.* To my knowledge this wonderful challenge has never been met, and we can carry it even further by noting that numerous instances of inter-specific hybridizations, including backcrosses and successive crossing of hybrids, demonstrate that differences between individuals of different species are of exactly the same sort that exist among genetically different members of the same species: numerous, successive, slight modifications [e.g., Alexander in press]. This fact shows that “Intelligent Design” advocates cannot claim that species differences are either so great or of such specific kinds as to demonstrate that species had to have been created separately.

It is instructive to turn Darwin’s challenge around and thereby realize that any accumulation of numerous, slight, successive modifications yielding directional change (the kind that can produce Darwin’s “complex organs”) is necessarily adaptive. Sequential saving of genes that produce cumulative effects is a positive indication of adaptive change. There seems to be no evidence that the human species added 40-45 years to its lifetimes via a single mutation. Even if this were true, such a mutated gene would be lost unless the added years were a pleiotropic effect that happened to be ineradicable because of other inseparable and more adaptive effect(s) of the gene involved. But pleiotropic effects of genes that are, for example, favorable early in life but responsible for later senescence (Williams 1957), have essentially no likelihood of resulting from numerous, successive, slight modifications yielding years of additional lifetime.

Accordingly, investigators failing to find sufficient evidence of adaptiveness in the additional years of the human lifetime have only the options of either looking more carefully for adaptiveness in modern environments or else identifying recent environmental changes that have reduced the previous adaptiveness of the additional years. I suggest that both men and women approach meeting, in somewhat different ways, Hamilton’s broad statement that we expect organisms to evolve so as to help relatives according to their degree of relatedness. I also suggest that, in the more obviously cohesive and cooperative kin groups of [early or] pre-technological human societies, older women and men evolved toward the adaptive “ideal” of kin helping that Hamilton’s Rule describes. As a result I am inclined to view competent older individuals in human societies, such as postmenopausal women, as evolved super-nepotists.

Why should such an extension of life have occurred in humans and not in their closest extant relatives? We know the context of extended lifetimes in fish, turtles, termite and naked mole rat

queens, and numerous other forms of life. Fish continue to grow, and live longer, because large fish eat smaller fish and the reverse is typically not true. Large fish thus not only lay more eggs but probably enjoy a wider range of accessible food and also become less vulnerable to predators – i.e., as individuals, they continue to become increasingly reproductive. Turtles are similar except that they add the benefit of armor, with effects so striking that some biologists have viewed them as dying without even having a period of senescence. Termite queens and naked mole rat queens also grow, thereby becoming able to lay more eggs, and they too live much longer than their “sterile” workers and soldiers. They are protected, not by their sizes or any armor, but by the workers and soldiers that surround and guard them in their niches inside logs (termites) or beneath the ground (both termites and naked mole rats). It is obviously possible to evolve a longer adult life if the rate of reproduction can be sufficiently increased as to delay or reverse senescent trends caused by late-acting deleterious pleiotropic effects of genes having their advantageous effects primarily in earlier life.

How have humans accomplished this? They do not grow continually. They are not armored or surrounded by individuals sufficiently devoted to protecting them. We need only consider a set of human traits that menopause also demonstrates: living in kin groups under conditions that have spawned the huge brain that causes the human baby’s head to be the limiting factor in successful birth, and later becomes the most calorically expensive – and the most remarkable -- organ of the human body. I will argue that the unique human brain accords with all of at least the first 32 traits I have numbered on the handout. The human brain and all of its correlates in learning, cognition, consciousness, extensive and elaborate scenario-building, memory, and other intellectual features enable human individuals to increase their reproductive output via kin help and make evolution of longer lifetimes adaptive. The collection of mental adaptations in humans – and their continued elaboration late in life -- can be so significant that individuals that have become seriously senescent in physical attributes can nevertheless remain important, or even essential, to the survival of families and kin groups. It is thus not surprising that [in humans] age is so often venerated, and that some kinds of leaders are desired or required to be as old as, or older than, the usual age of death in non-human primates (e.g., presidential candidates in the USA). Despite suggestions that the altriciality of the human baby is incidentally responsible for the extension of the adult human lifetime, and adult intelligence [e.g., Hutchinson 1965; Williams 1966; see also Alexander 1990], the reverse may be more likely: that selection favoring the collection of mental capabilities of adults has caused those capabilities to be further enhanced by beginning and increasing their elaborateness and their earliness of development (including learning capability) in the human juvenile.

Menopause could not be identified as a broadly kin-based adaptation without lengthened lifetimes in the absence of additional ovulations. What we have to explain now is how the kinship systems of humans have taken forms enabling the kin help that is essential in adaptive lengthening of adult lifetimes, and what is the role of concealment of ovulation in bringing about these changes.

Concealment of Ovulation

If menopause is an indicator of how human ancestors generated the situation that resulted in many distinctive and unique traits of the modern species, concealment of ovulation may be the essential enabler of all of those same traits. Without concealment of ovulation there can be no generation of extensive [bilateral] kinship systems in multi-male groups, in which differing degrees of relatedness

can be used in the way Hamilton envisioned -- therefore, no traits that can appear only as a result of extensive and complicated kinship systems. Humans, chimpanzees, and bonobos all live in multi-male groups, but of these only humans, in which females conceal ovulation, discriminate nepotistically among a wide variety of genetic relatives. In multi-male human groups, only with appropriately concealed ovulation can there be confidence of paternity, strong and lasting parental bonds, and biparental care. Only in humans with concealed ovulation can the bonds of parental care and differential nepotism provide the extensive kinship contributions that have resulted in the altriciality of the human baby, the lengthened life of juveniles, menopause, and the adaptiveness of lengthened adult life. Perhaps, as well, concealment of ovulation in multi-male groups has, at least indirectly, enabled the collection of human traits that include extensive language, art, music, humor, morality, and religious tendencies.

Confusion about concealment of ovulation seems to have existed for two reasons: (1) concealment is probably never complete and (2) concealment takes different forms, even within species. We should not expect concealment to be complete, first because evolution is unlikely to achieve or maintain perfection, and, second, because even if conscious awareness of ovulation and use of modern methods of detecting it work today, earlier in our history it may have been outside consciousness, and more nearly complete. As with all traits, our investigations and conclusions should therefore be focused on demonstrating the *directions* in which evolution is proceeding -- or has proceeded -- rather than expecting a visualized ultimate state or expression of traits. Even the cooperativeness of genes while they are functioning within the genome is not complete, despite the commonality of their fates in that situation, evidenced by the near-unity of ontogeny, including the near-randomness of allelic success during meiosis, responsible for the survival of the concept of Mendelian ratios.

Second, concealment of ovulation varies, within as well as between species, because it is directed at different individuals. Female mammals that exhibit prominent features of estrus for periods significantly longer than the period of actual ovulation are concealing ovulation within the period of estrus and thereby gaining opportunity to favor one or more potential fathers for their offspring. For example, female horses (mares), which live in one-male herds, display estrus "extravagantly" (long distance, both chemically and visually) for 3-7 days (with ovulation occurring near the end of this period), thereby inviting outside stallions as well as the herd stallion. But this happens only when they are not accompanied by a foal of the year. When mares have new foals by their sides they ovulate approximately nine days after foaling (the gestation period is approximately eleven months and ten days, and the ovulatory cycle is approximately 21 days; therefore, unless the events of becoming pregnant are always ideal, a mare is unlikely to produce foals annually and during the appropriate season). By displaying estrus locally, quietly, briefly (usually 1-3 days), only near the herd stallion, and sometimes only at night, mares with new foals are strongly favoring the herd stallion, excluding potential rivals that may be lurking near the herd, and thereby protecting the young foal from stallions that may either accidentally or "intentionally" injure or destroy a foal produced by another stallion. Not surprisingly, the herd stallion seems to cooperate with the mare's postpartum muted and brief version of estrus (the endangered foal would be his own offspring and in a widely advertised estrus the next foal might not be). Finally, when a mare has for some reason become separated from her herd and must join a strange herd, she often displays estrus (encourages and accepts copulations from the herd stallion) immediately as she attempts to enter the herd, and

then (typically) remains in estrus until ovulation, even if that is not “scheduled” to arrive for two or more weeks.

All female horses thus conceal something about ovulation during each of their three distinctive estrus periods. Manipulation of estrus in the concealment of ovulation is probably well described as a centrally important feature in the sociality of all mammals. In the multi-male groups of humans it appears to be extraordinarily influential. If women could have retained perfect (and peaceful) identification and control of ovulation, while evolving its complete concealment from males, they surely would have come even closer to ruling the world of human sociality. Except in isolated, cooperatively territorial, monogamous pairs (e.g., gibbons), mate-guarding alone cannot replace concealment of ovulation. In group-living species, males that evolve the ability to displace males guarding females that are advertising ovulation will tend to win, and the direction of change will favor promiscuity and polygyny (e.g., chimpanzees, bonobos), or else one-male bands and extreme sexual dimorphism (e.g., gorillas and orangutans).

Inter-Group Competition

Another set of unique and incredibly influential human traits must be considered to understand the forces that have given rise to modern human behavior and society: within-species, inter-group competition, which has all too often contributed to not only hyper-patriotism, extremes of amity and enmity, we-they confrontations, aggression, and war (traits 19-22), but as well to virtually all other traits described on the handout. Today, the makeup of the world is affected prominently and continually by the competitive interactions of nations (see the last three paragraphs of the abstract). Without the effect of this unique feature of human life we would be hard-pressed to find a reason for the seemingly inexorable pressure generating and continuing elaboration of the unusual and sometimes unique aspects of virtually all of the traits described on the handout. Inter-group competition, combined with means of establishing differing degrees of kinship (i.e., concealment of ovulation and the honoring of spousal bonds), may appropriately be termed the major enablers of human distinctiveness.

Once the major source of deaths and defeats becomes a within-species, inter-group phenomenon, the principal way to win, or to maintain a competitive position, is to increase the size and strength – and as a necessary result, the social and organizational complexity -- of the competitive unit. Extended families can be socially complex, but larger coalitions of multiple and extended families (the “segmentation” of social anthropologists) complicate increasingly the questions of cooperation and leadership [as well as kinship and all of its correlates]. Trends toward larger groups are probably the most effective way of competing with other similar groups. For this reason trends toward larger sizes of groups and more complex social systems have surely been a main force continuously driving the evolution of the extreme and calorically expensive human mental apparatus and all of its unusual and unique functions. In the trend toward large sizes of tightly knit, patriotic, within-species competitive groups, inferior or “losing” groups will tend never to be far behind winning groups; otherwise, because of their conspecificity, they will be absorbed by interbreeding and lose their identities. The upper limits of group size, strength, and force will depend on advances in cooperative social behavior and organizational superiority. There will necessarily be an accompanying race of strong selection on all traits that keep larger, more complex

groups organized and effective (such as concealment of ovulation and all of the correlated traits and tendencies that enable kinship to be organized and complex in multi-male groups).

A mountain of information exists on the topic of warfare and all its relatives. I began speaking and writing about inter-group competition as unique in extent and form in humans more than 41 years ago. In 1990, I referred to the turmoil of within-species inter-group competition and aggression as a balance-of-power race. More recently, Richard Wrangham has several times referred to apparently the same situation as an imbalance-of-power race. Both terms are understandable and appropriate. I was emphasizing what I think must have been the most continual and desperate kind of striving -- the effort to ensure that one's group remains strong enough, and sufficiently prepared, to avoid being subjected to relentless attacks or virtual slavery by larger groups. It is surely always unusually costly, and also risky, to maintain a tightly knit group larger and more demanding in organizational cooperation and complexity than would be needed merely to maintain a balance of power with neighboring groups. As has been amply demonstrated, since at least 1776, clever, determined, relatively inexpensive wars of attrition can bring down the mightiest, especially when fought on home ground against a distantly based foe. Nevertheless, increases in group size and strength through increasing mental as well as physical skills, and including skilled crafting and use of tools and weapons, have surely been the principal changes available to warring groups that account for the unique rise of human intelligence, sociality, and culture. The cumulative learning of cultural skills continually multiplies tools, weapons, and skills, and adds to the resourcefulness of groups whose chief competitors and enemies are members of their own species. Evolutionary effects of increasingly complicated social and cultural interactions can result in enhancement of all mental performances potentially related to adaptiveness.

Possible Trait Combinations in Ancestors of Humans

If the above arguments are roughly correct, we should be able to consider the combinations of traits making up humans and the apes as if they parallel playing cards (as in decks of "playing cards") that can make up "hands" (combinations of dealt cards -- or, for organisms, combinations of traits) characteristic of the individuals of each species. In efforts to discover the kinds of "hands" "dealt to" or characterizing both groups and individual members, we should be able to shuffle traits that can be understood functionally in the manner of cards in a deck -- not only traits of all of the extant species of Hominidae, but some of the several postulated species or stages comprising the progressions of fossil species ancestral to humans. If traits can be interpreted accurately with respect to function, we should be able to arrange traits in individuals and species that can function as combinations that we have otherwise had no opportunity to either witness or reconstruct. We should be able to eliminate combinations that we have learned cannot occur together. We should be able to discover sequences by which traits have changed and combinations of traits have been realized in our own ancestors.

Females in one-male groups, such as gorillas, and in a slightly different fashion orangutans (which are more dispersed), advertise ovulation less extensively and less obviously than do chimps and bonobos. Paternity confidence exists because a single resident male is typically able to mate with females in the band. But gorillas and orangutans probably show none of the special human traits described on the handout.

Gibbons live mostly as separated monogamous pairs, and as with gorillas they do not advertise ovulation widely. They too may show none of the human traits on the handout.

Obviously, some imaginable trait combinations would be incompatible in an organism or a social group. We can see this by comparing our relatives among the apes. Thus, chimpanzees and bonobos live in multi-male groups and their females advertise estrus almost “with abandon.” From this we could have predicted that these species do not distinguish kin extensively because ovulation is not concealed in the manner that would allow distinguishing kin of both mother and father. Adaptive menopause, then, and the lengthening of adult lifetimes, also appear not to be possible. Nor, as we have seen, are virtually any of the human traits listed in the handout. Although groups of adult male chimps go on cooperative “raids” searching out individual males from other groups, which they brutalize or kill, their aggression is minor in nature compared to our own, and it is at least typically a group against an individual. Chimps and bonobos show trait 17 on the handout, and chimps as well a rudimentary form of inter-group aggression (traits 18, 19, 22). Otherwise our closest relatives exhibit virtually none of the remaining traits of humans listed in the handout. This is the reason for my 1990 labeling the human species as an “N of one,” requiring a special analytical approach, comparable to that used by theoretical physicists engaged in enumerating and assessing the functions of the single physical universe available to them. I referred to this method as a “Jigsaw Puzzle” method – the identification, assembling, and coordinating of the evolved functions of discernible human traits.

What are the possible and likely successions of changes in trait combinations in the extinct ancestors of humans? Here are some meager suggestions for possible models:

1. Either monogamous pairs or mobile one-male groups would likely mean there would be little sexual dimorphism (as in humans) and no extravagant features in estrus (as in humans). From some such beginnings there could eventually be starts toward consortships and pair bonds, and, also eventually, males beginning to honor the pair bonds of other males (perhaps originally brothers or other close relatives). Manipulation of estrus toward the essential trait of concealment of ovulation may begin in such an ancestral situation. We can take into account recent studies showing that gibbons sometimes engage in both polyandry and polygyny. Apes resembling gibbons in these regards, but phylogenetically nearer to humans, could become groups larger than a single family, and multi-male, perhaps by sons joining father or brothers joining one another, and because of that kind of beginning pass rather directly to a closely knit kin group and move toward groups intermediate between ancestral apes, and socially resembling gibbons, yet groups that are similar to a possible human ancestor. In this scenario, however, attaining of large competing groups might be more difficult. But group-living can be initiated as a response to predation, and further developed by hunting in groups, whether or not it is followed by within-species inter-group competition and conflict.

2. Predators were probably reduced in seriousness in early stages of human evolution, perhaps partly through group-hunting by ancestral humans, and also habitat change; such reduction of predation would have allowed more effort to be devoted to increased competitive interactions between groups. In 1990, I referred to this change as a kind of ecological dominance by evolving humans. Ecological dominance may at first seem a too-broad term (although it applies with enormous and destructive force today), but it has always had a similar connotation in the field of

ecology. I used this term, first, because humans, as with other organisms, are of course subjected to the entire broad ecological sweep of what Darwin called the Hostile Forces of Nature: predators, parasites, diseases, food shortages, climate, weather – and, of course, sexual and social selection. Second, I used the term because organisms are described as ecologically dominant whenever they begin to displace competitors and outpace their enemies. It is indisputable that humans generated the ability to reduce the significance of large predators, probably early in human evolution, and just as indisputable that anthropologists were right when they described the human species as – to a greater extent than other species – seeming to create its own environments rather than passively occupying an existing environmental situation. Changes that allow a higher proportion of calories to be associated with within-group competition, and lead to more trait changes and more profitable risk-taking in that context, are appropriately described as changes toward the familiar concept of ecological dominance.

3. Competition and aggression must have become increasingly severe and frequent as, across pre-history and recent history, human groups became larger and stronger. Within-group amity (kinship, patriotism) correspondingly would have become more intense and unifying. Modern humans are able to shift rapidly between (1) a continuing compatible flow of within-group competitiveness and cooperativeness, the latter effective because of (a) kinship and social reciprocity, and (b) acceptance of authoritatively imposed rules of ethical or moral conduct (usually mediated by some form of religion, and often varying in ways that, unfortunately, stimulate or aggravate potential conflicts with competing groups), and (2) a correlated and coordinated ability to initiate and maintain intense patriotic fervor in the face of threats from other groups.

It will not be easy to convert mere understanding of such facts and issues into the kinds and degrees of cooperativeness that -- because of our increasing population sizes and densities, our continually evolving weaponry, and the growing effects of our activities on climate and pollution -- will be necessary to diminish significantly the novel and looming likelihood of otherwise inescapable global disasters.

3. Lecture Handout

A brief recounting of recent evolutionary findings

Note: This document is a brief recounting of major findings during the past 50 years, regarding, in particular, how the *process* of evolution works. The references are mostly restricted to authors and dates because the handout was designed to be a single page for use before audiences familiar with most of the authors and publications mentioned. Most of the references can be found in their entirety in the articles and chapters listed below.

- (1) *How Did Humans Evolve? Reflections on the Uniquely Unique Species*. U-M Museum of Zoology Special Publication 1 (1990): iii + 38 pp.
- (2) Evolution of the Human Psyche. In: C. Stringer and P. Mellars (eds). *The Human Revolution*. Univ. Edinburgh Press (1989), pp. 455-513. <http://insects.ummz.lsa.umich.edu/pdfs/RDAHHumanPsyche.pdf>.
- (3) Evolutionary Selection and the Nature of Humanity. In: V. Hosle and C. Illies (eds). *Darwinism and Philosophy*. U. Notre Dame Press (2005), pp. 424-495.
- (4) The Challenge of Human Social Behavior. Invited review of: Hammerstein, Peter (ed) 2003. *Genetic and Cultural Evolution of Cooperation*. MIT Press, Cambridge, Massachusetts, and London, England. (2006). *Evol. Psych.* 4(2):1-28.

A. The study of evolution has involved five main undertakings: (1) discovering from fossils and living forms that change occurs with time, (2) discovering how the actual process of evolution works, (3) discovering how evolution can lead to irreversibly separated populations called species (speciation, species multiplication), (4) working out genealogies (phylogenies) of species and their traits, and (5) using all we know about the long-term, cumulative effects of the process of evolution (the nature and causes of evolutionary adaptation) to improve our understanding of extant (modern) organisms. Most important is (5) because it summarizes or focuses the ultimate use of evolution in the effort to understand every aspect (heredity, development, morphology, physiology, behavior, the life sequence) of every form of life, including ourselves. But (5) is also controversial because it invariably becomes extremely difficult and is easy to over-simplify, because people don't like all it suggests about them, and because people fear that by acknowledging that humans have evolved to do things no one wants (other) humans to do we might be sanctioning unpleasant or immoral actions.

B. A concentration of contributions to knowledge of the evolutionary process: 11 major subtheories in 23 years.

1. George C. Williams (1957) developed the Pleiotropic Theory of Senescence -- suggested by Peter Medawar 1955 -- beginning an accounting for the general patterning of lifetimes in organisms with disposable somas.
2. G. C. & D. C. Williams (1957) elaborated on Darwin's (1859) explanation for the sterile castes of eusocial forms: if the trait of sterility can be carried without being expressed, then if those who express it help sufficiently those who carry it without expressing it, the trait itself can be advanced by natural selection (this wonderful bit of Darwinian reasoning resolved a major challenge to evolutionary selection as differential reproduction).
3. W. D. Hamilton (1964) developed the theory, suggested by R.A. Fisher (1930), that organisms evolve to treat kin according to their overlap in genes identical by immediate descent (humans are the prime example).
4. George C. Williams (1966) argued -- as suggested by Fisher 1958 -- that when directions of selection conflict at different levels in the hierarchy of organization of life, it is parsimonious to assume that selection is most effective at the lowest level (genes have evolved to persist, individuals

and social groups to facilitate that persistence; differential reproduction is less effective at most or all higher levels excepting genetically isolated species populations). This argument by Williams enabled evolutionists to proceed with (A5) above.

5. William D. Hamilton (1967) expanded on the sex ratio theory of Fisher (1930) (see also Dusing 1883 via Edwards 1998. *Am. Nat.*) by accounting for inbreeding situations in which extraordinary sex ratios evolve.
6. Robert L. Trivers (1971) developed the first evolutionary theory of reciprocal altruism (social investment).
7. Robert L. Trivers (1972) elaborated on Bateman's 1949 theory about how and why selection works differently on the reproduction of males and females, and the consequences.
8. Robert L. Trivers and D. E. Willard (1973) developed a theory predicting sex ratios of offspring under special conditions, and predicting different patterns of parental care to different sexes in polygynous species.
9. Robert L. Trivers (1974) developed a theory of parent-offspring conflict with respect to parental care.
10. Nicholas K. Humphrey (1976) suggested that the human intellect evolved as a social tool.
11. William D. Hamilton (1980-82) developed Jaenike's 1978 hypothesis that random scrambling of genotypes during sexual reproduction functions in out-racing rapidly-evolving parasites and diseases.

C. Developing an overall picture of the human species as a result of the evolutionary process: A "Jigsaw Puzzle Method" of analyzing an N of one. Humans are so distinctive that many traits are difficult to understand by comparing them with traits of close relatives; but traits can be related functionally to explain the whole organism because the organism is evolved with the singular function of persistence of its genetic materials.

1. Generating and testing hypotheses explaining evolved functions of unusual or unique traits of humans.
2. Combining the hypothesized functionality of both ordinary and unusual or unique traits to generate a coherent functional picture of the whole organism – i.e., comparing functionality between traits within the same species as well as between species, the latter being the more usual approach in comparative study (Theoretical physicists use a version of this method in analyzing the single universe available to them.)

D. Some unusual and unique human traits and their likely functions, as a route toward understanding the traits (especially behavior) of the human organism as a whole -- arguably the most important human task.

1. Menopause (unique?) (the human female ovulates only to midway through the maximum average lifetime and converts to reproducing via helping grandchildren, diverse kin, and sometimes the entire circle of kin).
2. Concealment of ovulation (unique?) (disenfranchises fickle males; promotes biparental care via bonding, and kinship systems via social learning of differential kinship bilaterally)
3. Sexual activity not limited to times near ovulation (unique except for bonobos?) promotes parental (spousal) bonds.
4. Rates and timing of spousal sexual activity apparently (often?) unrelated to production of offspring, which may have become incidental to sex that generates, elaborates, and maintains the parental bond (unique?).
5. Multi-male groups with extensive paternal care (sometimes!) (unique among mammals?).

6. Highly altricial («helpless») infant (unique among primates): frees juvenile to grow, develop, and learn rapidly by transferring protective functions to its parents.
7. Lengthened juvenile life (unique among primates, possibly among all vertebrates with altricial juveniles).
8. Rapid, cumulative, complex, and retained learning and other brain functions (unique in extent).
9. Head (brain) is the most frequently limiting birthing problem (unique among mammals?).
10. Brain of juvenile grows extremely fast (unique in degree among primates).
11. Brain may have accelerated in evolutionary size increase *after* becoming uniquely large among primates.
12. Human brain is largest, most complex, and calorically most expensive brain among primates.
13. Human brain seems to have evolved as a social tool (interpreting the motives and intentions of others)

14. Human groups involve extended kin groups, with multiple degrees of relatedness recognized (unique?).
15. Extensive kinship systems and extensive differential nepotism are universal -- or were (unique).
16. Complex social reciprocity of a high-risk kind, both direct and indirect, is universal(?) (unique)

17. Outbreeding commonly occurs via exchanges of females, not males, between social (kin) groups (unusual?)

18. Sufficient relief from Darwin's Hostile Forces that effort can be exerted successfully in intergroup conflict.
19. Conspecific intergroup conflict becomes intense and frequent, a main source of differential reproduction.
20. Incredibly strong amity-enmity axes – i.e., tendencies to divide other humans into we's and they's.
21. Group-against-group competition in play (unique, lifelong practice affecting severe intergroup rivalries)
22. Rapid and dramatic alternations between extreme patriotism and intra-group cooperativeness, and intense intragroup competition (Is this the selective engine driving evolution of the social brain?) (unique?).

23. Cumulative learning of learned behavior (i.e., culture), purposeful generation of (evolutionarily) novel environments (tending to be appropriate, or at least desired) that in turn guide environmental change, including technology and the phenotypic (e.g., learned and cumulatively learned) changes themselves; both automatically become aspects of the human environment, therefore alter evolutionary selection. Completion of the need-novelty feedback loop that never was accomplished by genetic change *per se* during evolution.
24. Language (unique in degree of complexity, and in many features – e.g., displacement)
25. Extensive consciousness (ability to predict and plan, to know that we do, and to tell others about it).
26. Large-scale and virtually continual scenario-building of (especially?) the *social* future (unique?)
27. Generation of multiple alternative scenarios (projected choices) (hence the concept of free will? (unique?).
28. The arts elaborate and extend reality via communication of novel scenarios to others (unique?)
29. Complex music, arising perhaps from judgments (initially of mates and social partners?) via indicators of quality, including physical and mental well-being (initially in rhythmicity and melodiousness of speech?)

30. Social-intellectual play, including the reality-mocking of humor, as lifetime social strategizing (unique?).

31. Moral concepts (and laws) arise as selfishness-restraint systems for dealing with «built-in» conflicts of interests when closely-knit cooperative groups are obligate (generation of conscience?) (unique?)

32. Concepts of supernaturalism, everlasting life, and benevolent gods, promoting group stability and success in inter-group competition and conflict (unique?). Did these concepts generate as social instruments restricted to the world of humans – including their use as extensions to cause-effect explanations of the physical world and the non-human living world; and is God sometimes a metaphor for serving the «entire» kin group – and later, larger social groups functional in inter-group competition – i.e., via patriotism?

33-34. Patterned hairlessness and bipedalism (long discussed but actual functions not yet well understood?).

The following explanatory footnotes were not included in the published essay. I include them as explanations to readers with little background in the theories and conclusions underlying some of the things I discussed in the preceding materials.

1. I say this, but I don't think it. There is some hilarity behind it all! [This one fits on p. 1 where I say my failure to complete my talk was all my fault.]

2. The overlaps between this essay and the autobiography [included in the packs of essays I sent my fellow alumni] are either because I am moving toward a «mighty synthesis» or else I am just continuing to run out of ideas! [One of my former doctoral students offered a third uplifting suggestion: that I'm probably just losing my memory.] There is also a third overlapping paper, but it's too long to ask anyone not in this field to read. For reference, it is Alexander «ms 1» among the citations at the end of the autobiographical essay

3. Re the complexity of ontogeny: Because of the incredible parade of both extrinsic and intrinsic environmental changes, an individual gene that makes only a single product can yield hundreds (more likely, thousands) of trait expressions -- because it makes or does not make its product in thousands of different situations. Despite Dobzhansky's 1961 statement (presented at the end of the Kyoto paper abstract), this apparent fact has only begun to be accepted among geneticists and developmental biologists [who have too been impressed far too long and thoroughly with the possibilities of extreme reductionism, and by the fact that individual genes only make one product -- ignoring the point that they can do it in untold numbers of different environments -- and that merely turning on and off in one set of environments, when there are ca. 25,000 genes that can be turned on or off in all possible combinations starts us with the number 2 to the 25,000th as a "base" set of possible "actions." (David Marshall asked his computer how large was that number and it replied: INFINITY). Of course, a lifetime of 85-90 years, with billions of actions occurring in split seconds is -- well, the most complex thing anyone has yet imagined, I suspect, in the entire universe.]]

4. Re altriciality of the human infant: The altriciality (helplessness) of the human baby represents a transfer of its care and protection to the parents, leaving the young juvenile to use nearly all its calories to be used getting a «head-start» (bad pun!) in growth and maturation of the brain (in particular), and in generating, storing, and using social learning (Alexander 1990b in autobiographical essay).

5. Re kinship systems: Extensive and complex kinship systems have been found in every pre-technological human society studied by anthropologists -- and not in any other species.

6. Re concealment of ovulation: My hypothesis is that the so-called continuous sexual receptivity of human females, and sex that occurred without knowledge of the timing of ovulation in pre-industrial (or pre-technological) societies, evolved as a generator, elaborator, and maintainer of the parental bond (spousal bond). This condition could be favored because concealment of ovulation protected the female from rapists and love-em-

and-leave-em males (thereby increasing the likelihood of male parental care), and because frequent sex in the context of parental bond integrity would automatically produce children, even if incidentally in terms of sexual behavior.

7. Re sexual reproduction: Sexual reproduction is extremely expensive: a female tending offspring produced by mating with a male is using her reproductive effort to tend an offspring only half like her genetically. Evolutionary biologists have worked across decades to discover why selection has favored sexual reproduction in the vast majority of species, rather than parthenogenesis or other inexpensive asexual forms of reproduction. The current consensus is that the adaptive significance of sexual reproduction lies in the outracing of fast-evolving parasites and diseases. Sexual reproduction - especially when outbreeding prevails -- involves rapid and not easily tracked changes in the genetic makeup of individuals. Incidentally, on that topic, think about not only the numbers of micro- and macro- and intrinsic and extrinsic environments across the human lifetime, but about the consequences for variation – and compatibility -- among genomes in sexual species that will virtually always be moving among a myriad of different environments – including not just differences in mutations in different regions of the species.

8. Re the social consequences of sex ratio selection: Sex ratio selection produces approximately equal numbers of males and females, regardless of the breeding, mating, or marriage system. As Sir Ronald A. Fisher pointed out 78 years ago, this happens because half of the genes of a population occur in males, and half in females, causing male genes and female genes to be equally valuable. If sex ratio gets skewed one way or the other, selection favors parents who produce more of the less prevalent (and more valuable) sex. In societies in which males practice polygyny, females are devalued, sometimes horrifically. People with agricultural backgrounds will perhaps recall that the agricultural extension agents used to counsel a farmer that «Your bull is half the herd.» In other words, half the genes of a polygynous bovine population reside in the (usually) single bull, the other half in all the females collectively, because each offspring will get half its genes from each parent. Young human males in societies that allow polygyny are disenfranchised in such a population, either by failing to get mates, or by being able to acquire mates only at later ages. Young males thus have considerable interest in successful polygynous older males (sometimes defined as “toadying”) because such older males have daughters to «give» -- or sell -- to young males of whom they approve. This situation also sometimes causes young females to be wed (or promised) when they are quite young, as at puberty or even before. Young males are also encouraged to do heroic things for their families as ways of making themselves desirable mates for young women. There is surely a relationship between all these circumstances and the phenomenon of suicide bombers in times of inter-group conflict, a high proportion of which qualify as «young men» still lacking families. Because of these conditions -- especially the differential statuses of different classes of individuals -- I would speculate that, among other things, it will be exceedingly difficult to generate circumstances leading easily and directly to democracies in societies in which polygynous marriage systems are permitted.

9. Group-against-group competition in play evidently occurs only in humans (Alexander 1979, 1987). When I realized this, I said it in print and held my breath wondering if

anyone would find an exception. The first comment in print was from Donald Symons, an anthropologist at Santa Barbara, who had done his doctoral thesis on play in rhesus monkey. He said he had considered it carefully and that "Alexander is right." If play is interpreted as practice in low-cost situations -- and ways -- for full-cost situations in actual, "real-life" competitions, this "discovery" becomes a huge support for the notion that inter-group, within-species competition is the main adaptation of the human species.

10. Re language features: In language, displacement means ability to converse about events or people that are not present.

11. Re music: I suggested that music began as rhythmic, melodious speech, which indicated good physical and mental health, and constituted more effective communication. I speculated that the elements of music as we know it now were emphasized as a result of sexual and social selection elaborating the early elements of musical speech, and perhaps generating new functions and somewhat different directions of selection. More recently it has occurred to me, in regard to the arts, that -- for example -- rhythm, rhyme, melody, repetition, inspiration, novelty, and other components of the arts (previously in the absence of written language) can be viewed as proximate devices that cause attentiveness and stimulate novelty and entrepreneurship in social matters. It seems possible that a general theory of the arts can be constructed from this observation. The situation may be unusually difficult because the multifarious uses of language have caused a burst of social possibilities that have been so complex and diverse as to conceal the adaptations of the arts that evolutionists have been seeking. Unlike investigations of most evolved traits, in which the proximate mechanisms, rather than the ultimate adaptations, may be difficult to unravel. Biologists trying to comprehend the adaptiveness of the arts may have consistently bogged down in the mire of adaptive changes in proximate mechanisms, without ever comprehending the ultimate adaptations because of their immensity -- the massive cloud of sociality. Humans are the future-seeking animal, and perhaps the adaptation in question is really all of the components of future-seeking: hypothesizing, planning, testing, scenario-building, and all the rest of the human social microcosm -- creating and holding alternatives for the most effective use -- betting on the future. We are all doing it all the time, whether we are scientists or artists.

12. Re moral systems: I have hypothesized that the authoritatively-derived moral systems that tend toward absolutism thrive because they minimize within-group conflicts of interest, thereby maximizing within-group harmony. This outcome maximizes patriotism and cooperativeness, thereby strengthening the group in connection with inter-group conflict. If so, harmony and cooperativeness within functional groups, not justice per se, are the goal of morality. As an old man in Detroit said not long ago, «It ain't JUSTICE; it's JUST-US!» As we all know from recent political competitions, the information-seeking methods of science, although much more similar to the arts than is commonly recognized, are somewhere near the opposite end of the spectrum that begins with authoritatively-derived moral systems that tend toward absolutism. And that has come to be involved in politics, in ways that seem to me most often to be unfortunate.

13. Re how lifetimes came to be as they are: Williams's 1957 pleiotropic theory of senescence provided an answer to the question: Why do we senesce and die? Footnote 3, incidentally, developed from recent findings (or realizations) that, although presaged by Dobzhansky (1961), are today bolstering Williams's theory. Because of the myriads of internal and external environmental variations affecting the human body, and its reproductive success, we have recently come to realize that any individual gene, although generating only a single product, can have many different effects if it is turned on and off in enough of those different environments. If those of its effects that have a positive influence on the organism's (hence, the gene's own) reproduction contribute sufficiently, then the gene is likely to appear in subsequent generations. Gene effects different from those leading to reproductive success -- or incidental to such -- are called pleiotropic effects. Effects of genes that occur early in the organism's life will have undergone intense selection because they are more crucial to the gene and the rest of its genome being passed to subsequent generations. They are more crucial because the young organism has all or nearly all of its reproduction ahead of it. Pleiotropic effects that occur late in life tend to be less important to reproduction because reproductive possibilities for older organisms are less frequent and less effective. Accordingly, natural selection cannot easily remove late-acting pleiotropic effects even if they are deleterious -- because they are incidental effects of genes being selected favorably. Such late-acting pleiotropic effects thus remain as difficult-to-erase effects of genes that are saved because of their (the genes') early positive effects on reproduction. Because selection on late-acting deleterious pleiotropic effects is so weak, they accumulate, and those accumulations are expressed as the features we all recognize as the growing effects of ageing.

How, then, can lifetimes evolve to be longer, as has the human lifetime? If, for whatever reason, an organism begins to sustain or increase its reproductive output as life continues (e.g., if new opportunities to reproduce generate), then natural selection will operate more similarly to its operation earlier in life. Among other things (such as new genes being saved because of positive effects later in life), deleterious pleiotropic effects that were of little importance before become reproductively more important in the newly lengthened life, and selection can become important enough to damp their effects. In the essay I give examples of several species that have evolved extraordinarily long lives, and the reasons. I have suggested that human lives doubled compared to our closest relatives, the apes, because we alone evolved in multi-male groups with extreme parental care (infant altriciality, longer juvenile lives, concealment of ovulation yielding confidence of paternity as well as maternity) and enabling of the extensive, complexly organized kinship systems that became sources of increased reproduction late in life by tending relatives according to their degrees of genetic overlap with us. No other species has such elaborate kinship systems, or even comes close to having the brain power necessary to generate them and function within them. In a recent four-part NPR program on how humans evolved, not a thing was said about group sizes in the various primate forms said by the scientists to be primitive humans; not a thing was said about group sizes, the possibility of multi-male groups, or massive increases in life lengths. It would seem that there is a general reluctance to utilize the actual evolutionary process to discover what happened to produce the modern human.

GIBBONS	ORANGS	GORILLAS	CHIMPS	BONOBOS	HUMANS	
territorial pair, one male, monogamous	one-male, dispersed females	one-male harem group	multiple males and females in groups, much promiscuity		multiple males and females in large kin groups, monogamy and harem polygyny	
_____	_____	_____	_____	_____	menopause	(1)
_____	_____	_____	_____	_____	ovulation concealed	(2)
pair bonding	_____	_____	_____	_____	pair bonding	(3)
least sexually dimorphic	most sexually dimorphic	dimorphic	less sexually dimorphic		least sexually dimorphic	(4)
biparental care	_____	_____	_____	_____	biparental care	(5)
_____	_____	_____	_____	_____	bilateral kin groups	(6)
40-45	40-45	40-45	40-45	40-45	80-90 year lifetime	(7)
_____	_____	_____	_____	_____	altricial offspring	(8)
_____	_____	_____	_____	_____	long juvenile life	(9)
_____	_____	_____	brains larger than the other three apes		huge complex brain	(10)
_____	_____	_____	_____	_____	extensive language	(11)
_____	_____	_____	_____	_____	extensive imagination	(12)
_____	yes?	yes	yes	yes?	self-recognition	(13)
_____	_____	_____	_____	_____	partial nudity	(14)
_____	_____	_____	_____ sometimes		bipedalism	(15)