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CHAPTER TEN

*The Reconstruction of Hominid
Behavioral Evolution Through
Strategic Modeling*

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INTRODUCTION¹

The reconstruction of hominid evolutionary history is a scientific problem of exceptional difficulty. Direct observation is impossible; fossil and archaeological evidence are scarce. It is also a pivotal problem, not only because of the scope and crucial character of the issues it addresses about modern human nature, but also because of the challenge it presents to evolutionary biologists. Humans are so singular a species, with such zoologically unprecedented capacities, that it is a major biological mystery how evolutionary processes could have produced us out of our primate ancestors. Yet unique cases are far from unsolvable in science, and many of them, such as Hamilton's (1964) and Williams & Williams' (1957) investigation of the enigma of sterile castes in eusocial insects, prove to be the stimulus for fundamental advances in the encompassing theories that seek to assimilate them. Hominid behavioral evolution can only be reconstructed through the use of powerful analytic models, and this article addresses the prospects for creating a model of hominid evolution that can, in fact, clarify how so unusual species was produced out of our primate ancestors.

Models are inherent to any scientific endeavor. Not only do they play a major role in the discovery and exploration of a subject, but a validated model is the final product of a successful scientific inquiry. The goal of research is to produce a validated model that both organizes and best interprets an expanding body of data. A model relates what was previously unrelated, allowing new inferences to

be drawn: a model gives data meaning. Newton's theory of gravitation united Kepler's laws of planetary motion with the previously unconnected dynamics of terrestrial falling bodies. Einstein's theory of general relativity was validated by looking for a minor deviation in the apparent location of a star during a solar eclipse—a previously unlooked for and otherwise minor phenomenon. And Darwin's theory of natural selection elucidated the previously ungrasped connection between, for example, the breeding of pigeons and the descent of man. Models do not simply account for data already observed—on the contrary, as Einstein remarked, "it is the theory which decides what we can observe" (Heisenberg, 1971:63). Models (or theories) function as organs of perception: they allow new kinds of evidence and new relationships to be perceived (Popper, 1972).

Because unique zoological features are involved and direct evidence is difficult to obtain, models are essential for the reconstruction of hominid behavioral evolution. Innovative models provide the potential for supplementing the existing paleontological and archaeological record with new kinds of data and inferences. For example, the theory of neutralism allowed the use of biochemical data to create molecular clocks; these resulted in alternative datings and more informative phylogenies (Sarich, 1980). Marks (this volume) connected primate cytogenetics to primate social structure. In short, models offer the eventual prospect of alleviating the shortage of information about hominid evolution.

It is the hallmark of a good model that, as it allows more and more indirect evidence to be focussed on a problem, it also allows a continual expansion in the body of sound inference. While paleontologists have become understandably impatient with the flood of speculations about human origins, they need to temper their desire to ground their field in solid fact with the realization that empiricism and modeling are natural—in fact, inalienable—allies. Reconstruction using data alone, in the absence of models, is not a logical possibility (Popper, 1959, 1972). The question is not whether to use models, but rather *what kinds of models are useful? how should they be used? and what are the criteria for good models?*

REFERENTIAL AND CONCEPTUAL MODELS

There is continuing confusion over what kind of models will prove most useful in reconstructing the history of hominid evolution. Although many different types of models are used in science, we offer a simple distinction between *referential models* and *conceptual models*.

In a referential model, one real phenomenon is used as a model for its referent, another real phenomenon that is less amenable to

direct study. An example is the use of animal models for humans in drug research, where ethics prevents the direct study of the effects of new drugs on humans.

For years, paleontologists have used referential models to reconstruct extinct species by comparing homologous features of the extinct form with a living one. Sometimes the fossil sample is disappointingly small; a single tooth, a piece of palate, the incomplete articular surface of a limb bone. Inferences from these fossil scraps to their analogous or homologous counterparts in living species are (or should be) rather modest.

The referential approach has been widely applied to behavioral evolution. As only bones, and not behavior, are preserved, attempts at behavioral reconstruction suffer from a one-stage-removed effect: the pieces of preserved skeletal material are first used to reconstruct a whole animal (technically, its skeleton), and this reconstructed specimen is then compared, by reference, to its nearest living counterpart. Such is the fascination with understanding behavioral evolution, however, that there has been no hesitation in proposing various living species as "models" for the behavior of our hominid ancestors. Typically, one or a cluster of prominent behavioral traits (such as "dominance" or "gathering") are advocated as the most illuminating approach to understanding hominid adaptation, and, at various times, different referential models have tended to dominate discussion: researchers have proposed common chimpanzees (e.g., Tanner, this vol.), baboons (see Strum and Mitchell, this vol., for review), living hunter-gatherers, various social carnivores (for review, see Teleki, 1981), and, recently, pygmy chimpanzees or bonobos (Zihlman et al., 1978).

Conceptual models, on the other hand, are not real phenomena. Instead, they are theories: sets of concepts or variables that are defined, and whose interrelationships are analytically specified. At its best, a conceptual model has elements that are well-defined and easily operationalized; the relationships between its variables are sharply constrained; and the assumptions on which it is based are validated (or at least realistic and clearly stated); the implications for specific applications of a conceptual model can be unambiguously deduced from these analytically interdefined variables (that is, it makes potentially falsifiable predictions); the same few elements economically explain a large range of phenomena, relating previously unconnected phenomena into new meaningful systems; these new systems of interpretation allow new kinds of inferences to be made from new data sets made relevant by the model; finally, new elements, when they are found necessary, can be defined and integrated into the model so that the model can be expanded to cover new domains

and new phenomena. At its worst, a conceptual model is highly artificial and obscure; it rests on unstated, unrealistic, or shifting assumptions; it leaves unintegrated, or absent, factors known to be important; it yields conclusions that are trivial, obvious, or absurd. Paradigmatic examples of good conceptual models are Newton's mechanics, Euclid's geometry, Dalton's chemistry, and Darwin's theory of natural selection (especially when combined with genetics in the Modern Synthesis). In each case, an enormous array of phenomena can be deduced from a few tightly interdefined central concepts.

Although referential models can be very useful where appropriate, as in medical research, their use in "behavioral paleontology" presents serious difficulties and should be carefully circumscribed. We will argue that the reconstruction of hominid evolution requires conceptual models. Although we are still far from achieving conceptual models that are both powerful and validated, efforts to create such models will surely be more fruitful than attempts to view one or another living species as a reflection of our distant past.

THE LIMITATIONS OF REFERENTIAL MODELS

How does one choose a living species as a referential model for extinct hominids, and once chosen, how does one know along what dimensions the model species resembles the unobservable referent? All real phenomena—baboons, chimpanzees, modern hunter-gatherers—have an infinite number of arbitrarily defined characteristics, some of which they will no doubt have in common with the referent (extinct hominids), and some of which will differ. A conceptual model is needed to substantiate the claim that a living species is a good parallel to an extinct one, and it is just this conceptual model that is lacking.

Because there is no validated principle to govern the selection of an appropriate living species as a referential model, the use of such models is arbitrary. Moreover, the question of which parts of the model are relevant (that is, display patterns of covariance) is usually not well specified, but left implicit, vague or intuitive. Consequently, there is no standard by which one can evaluate the large literature that discusses various species, and, at the preference of the author, asserts that hominids "probably" were like baboons, bonobos, or whatever, because they share some trait or other. In the absence of a sound conceptual model, there seems to be no way of improving the standards of the argument, assessing the probability of any assertion, or for that matter of extracting any substantive contribution to the progressive reconstruction of hominid behavioral evolution.

Moreover, without a well-specified conceptual model, there are no grounds for inferring how observed differences between hominids

and a model living species can be expected to modify hypothesized parallels. Baboons are quadrupedal and hominids are bipedal: Will this make any difference in whether dominance relations in baboons parallel dominance relations in hominids? Will it affect foraging patterns? If hominid males were more predatory than baboon males, how will that affect male-female relations? Without a conceptual model, there is no way to know.

The absence of any legitimate method for handling known differences between hominids and proposed referential model species has several unfortunate effects on those who rely heavily on referential research. First, referential models often lead to a disproportionate focus on the evolutionary period when differences between the model species and hominids is hypothesized to be at a minimum, that is, on the earlier more ape-like phases of our evolution. Unfortunately, this focus sheds little light on the forces that so significantly transformed the hominid lineage. Even if one were to learn everything about the hominid-pongid common ancestor, many of the most crucial questions about distinctively hominid evolution would remain unanswered: why we are humans and not chimpanzees, bonobos, or gorillas?

Second, and more important, because a referential perspective has no rigorous way to handle differences, similarities are emphasized at the expense of differences. The significance of the zoologically novel features of hominid evolution (such as high intelligence, language, sophisticated tool use, and an immense expansion in cultural traditions and learning) is de-emphasized or neglected. Discontinuities between hominids and catarrhines, such as bipedalism, (possibly) high degrees of carnivory, male parental investment, and male coalitional intergroup hostility, are similarly underemphasized. But organisms are systems of coevolved adaptations; a change in one feature resonates through the system, changing other features in the adaptive constellation. Hence, novel features will frequently alter the function and meaning even of identified similarities. Only uniquenesses can explain uniquenesses; one cannot invoke the features species have in common to explain their differences. By their nature, referential models tend to ignore or obscure the most important question in human evolution: where did our most crucial and novel adaptations come from?

Usually a referential model is conflated with, or presented as if it were the same as, a conceptual model about the referential species. So it was not simply savannah baboons that were proposed as a model for hominids, but a certain conception of male dominance relations in baboons (Washburn and DeVore, 1961b). When male dominance became less popular as a research perspective, the pu-

tatively more peaceful chimpanzee became a popular referential species (Tanner, 1981). As the aspects emphasized by the conceptual models implicit in these theories rotated in and out of fashion, the preferred referential model species changed—from baboons, to various social carnivores, to chimpanzees, to bonobos.

The perils and shortcomings of referential reasoning can be clearly seen if we take an example from another field entirely. Newton's theory of gravitation as applied to the orbital motion of the planets precisely tied together a number of different physical features into a single conceptual model (e.g., mass, the force of gravity, the year length of a planet, its orbital velocity, its distance from the sun). For the sake of analogy, assume that we know these physical features for all of the other planets in the solar system, but know only a few of them for the Earth. How, then, could we find out what Earth was like? We could use referential modeling, in which case we would propose that the Earth resembled Mars, or Jupiter, or Neptune, etc., and argue the relative merits of each case. This is clearly not a successful procedure, even if we found the "best" parallel planet by some criterion. At the very best, we are limited in the accuracy of our analysis by what parallels happen to exist.

The better strategy is to develop an appropriate conceptual model (in this case Newton's theory of universal gravitation), by finding the set of invariant relationships that exists between the variables known for the other planets. We could then take the few things that are known about the Earth, plug these parameters into our conceptual model, then precisely determine many (or all) of its unknown features. Newton used the other planets as data, not as models, and he used this set of data to derive and test the general principles that comprise the valid conceptual model of universal gravitation. By this method, the unique features of an unknown planet (in this analogy, the Earth), can be worked out. By the referential method, the Earth's uniquenesses would remain unknowable.

In short, the use of the referential approach should be discarded, and its literature assimilated into vertebrate behavioral ecology. Not only will this allow a better understanding of various primate species themselves, but it will allow the resulting conceptual models to address central questions of hominid evolution directly, including questions about the emergence of the many novel features of humans for which there are no tight parallels elsewhere in the primate world.

STRATEGIC MODELING AND HUMAN BEHAVIORAL EVOLUTION

Can a conceptual model be created that is powerful enough to allow the reconstruction of hominid behavioral evolution from avail-

able data? In other areas of science, the most successful conceptual models have been based on a strong deductive framework (e.g., the physical models of Maxwell, Newton, or Einstein). Fortunately, there exists in biology a set of principles with the requisite deductive power: evolutionary theory. By combining evolutionary theory (and its subdisciplines, such as behavioral ecology) with what is already known about primates and hominids, one can begin to construct and validate a specifically elaborated set of principles that together will comprise the desired conceptual model.

A central achievement of modern evolutionary biology has been the recognition that selection acts at the level of the gene (Hamilton, 1964; Maynard Smith, 1964; Williams, 1966; Cosmides and Tooby, 1981; Dawkins, 1982). The genes present in any given generation are disproportionately those that had, in preceding environments, effective "strategies" for their own propagation. The traits individuals express are present because the genes that govern their development have successful strategies of self-propagation. In other words, genes work through the individual in which they occur, and the individual's morphology and behavior embody the strategies of the genes it contains. Characteristics of groups or species are not selected or shaped *per se*; they are the result of the interactions among individuals whose behavior is controlled by proximate mechanisms whose properties correlate with genic fitness.

The genic strategies that have been identified, together with our understanding of how they interact, will be major ingredients in the conceptual model that must be constructed. Researchers now speak of organisms as "strategists," meaning that individual organisms are selected to manifest any property, behavioral or morphological, that correlates with strategies of genic reproduction—it is a convenient linguistic shorthand that bridges the gap between the level of the individual and the level of the gene. Thus, if one neglects the complications of intragenomic conflict (Cosmides and Tooby, 1981), animals will be selected to behave as if they were following strategies to promote their inclusive fitness (Hamilton, 1964).

We propose the term "strategic modeling" to cover the construction of conceptual models of primate and hominid behavior based on our understanding of 1) the genes as the unit of selection, and 2) animals as shaped to behave as strategists promoting their inclusive fitness. The premise involved is that species in the past were subject to the same fundamental evolutionary laws and ecological forces as species today, so that principles derived today are applicable throughout evolutionary history. Hence, each species is a unique expression of the same underlying principles: although no present species will correspond precisely to any past species, the principles that produced

the characteristics of living species will correspond exactly to the principles that produced the characteristics of past species. By studying the present, we can discover the principles that shaped the past. The principles that shape species do not vary, only the specific parameters that govern how these principles will interact in each case.

We can estimate the parameters believed to be true of hominids at various points in their evolutionary history, from the following data:

- 1) our knowledge of the patterns of primate homology (investigated through behavioral, morphological, and biochemical means),
- 2) the characteristics present in modern humans,
- 3) the paleontological record,
- 4) the archaeological record,
- 5) our knowledge of ancient habitats.

The hope is that the application of evolutionary principles will constrain the range of possible hominid traits such that future discoveries about hominids will uniquely determine the answers to many of our questions about our evolutionary history.

THE PRINCIPLES OF STRATEGIC MODELING

A powerful conceptual model for reconstructing hominid evolution does not yet exist in any well-developed form. Many components of it already exist, however, and we can make some headway towards a preliminary assembly of its elements. Behavioral ecology, socio-biology, and evolutionary theory comprise the primary analytic sources for strategic modeling. Salient component theories are kin selection (Hamilton, 1964), reciprocal altruism (Trivers, 1971; Axelrod and Hamilton, 1981), parental investment, sexual selection, and mating systems (Trivers, 1972; Emlen and Oring, 1977), aggression and social dominance (Parker, 1974; Popp and DeVore, 1979), foraging theory (Charnov, 1976), defense against predation (Curio, 1976), the ecology of disease and inbreeding avoidance (Tooby, 1982), and the theory of evolutionarily stable strategies (Maynard Smith and Price, 1973; Maynard Smith, 1982).

Analytic tools for applying and combining these component theories exist in a tentative form. No good review of them exists. Therefore, a preliminary, and by no means exhaustive, list of the principles of strategic modeling may prove useful. At this stage, of course, these are nothing more than heuristic guidelines for inference (a more

detailed discussion of strategic modeling in hominid evolution is planned for publication).

- 1) Individuals are selected to approximate inclusive fitness maximizers.
- 2) Interactions between individuals are to be analyzed in terms of their inclusive fitness impact on the actor.
- 3) Any heritable trait that increases the correlation between behavior and strategies for promoting inclusive fitness will be selected for. This correlation is all that is necessary (not any conscious pursuit or knowledge of the strategy). How strategies are incarnated differs widely, and includes morphological traits, reflexes, food and flavor preferences, complex but nonconscious learning mechanisms, and very sophisticated cognitive mechanisms. However, conscious awareness of proximate goals may have contributed to the correlation between fitness and behavior in some species; indeed, for some strategies it may have played an increasing role during hominid evolution.

4) There is no one-to-one correspondence between traits and selection pressures, and there is no fundamental distinction between behavioral and morphological traits. Selection for a trait will depend on all of the fitness components that trait impacts. To take an extreme example, a morphological change that makes locomotion extremely costly will also increase the cost of avoiding inbreeding (for example, winglessness in insects). Lowering the cost of locomotion makes it cheaper to search for less related mates, and therefore is, in part, an adaptation to inbreeding avoidance. A trait is an adaptive compromise to all of its positive and negative fitness consequences.

5) Individuals are selected to be adapted to their individual situation, not simply to their local habitat. This means that they may be facultative strategists (where appropriate) rather than inflexibly committed to the same behavior or morphology.

6) The situational specificity of adaptation depends on the selective history of similar situations. The degree of situational adaptation manifested by individuals will be a matter of a) how common in the species' evolutionary history that situation has been, b) how long (in phylogenetic terms) it has been recurring, and c) how large its fitness consequences are. Organisms will be well adapted to common, important situations, reasonably adapted to common less important conditions and uncommon highly important conditions, but not adapted to uncommon, unimportant situations.

7) To the extent made reasonable by the considerations above, behavioral variation observed within groups, and between groups of the same species initially should be presumed to be adaptive responses

to differences in individuals and local conditions, until accumulated evidence indicates otherwise.

8) Consequently, the tendency to generalize typologically to entire species from individual studies should be dispensed with in primate and hominid behavioral biology. Looking at behavior observed in individual studies as strategic adaptive responses to local conditions frees investigators from the perpetual confusion that arises from the discovery that primate behavior changes markedly at the same site when it is observed over many seasons, or from study site to study site.

9) Selection acts on all categories of individuals, and at each stage of the life cycle. No sex or age group is more "important" others; strategic modeling applies to all categories. The amount of kin and parental investment received, the age of the individual, the amount of prospective direct reproduction left to an individual, and the amount of prospective kin-directed altruism left to an individual, will all influence the intensity of selection on particular age-sex categories (Williams, 1966). However, no age-sex category whose behavior can still have consequences on kin is immune from selection. Therefore, to be complete and accurate, an account of hominid evolution must describe the special adaptations of each age-sex class, and the relation of each to the others. Any account of hominid evolution that concentrates only on males, or only on females, or suggests that any specific age-sex class is responsible for hominid evolution, is defective; both "Man the Hunter" and "Woman the Gatherer" analyses frequently suffer from this problem.

10) For certain social and reproductive behaviors, the favored strategy will depend on the distribution of other behaviors in the population. The prevailing analytic tool for dealing with this is game theory and evolutionarily stable strategies (ESS) (Maynard Smith and Price, 1973). Its application to sex ratio theory is well known (Hamilton, 1967). In hominid evolution such an analysis may be relevant to such issues as how much to hunt versus how much to gather, whether to pursue a high male investment strategy, how much intergroup male coalitional conflict there is, and so on. Hominid groups may not have had one best universally shared behavior pattern, but may have contained multiple alternative strategies over many generations. In fact, multiple strategies, such as complementary male and female foraging patterns, or dominance-subordination behaviors, may depend on each other and evolve together.

11) Despite recent attacks on the adaptationist program (Lewontin, 1979), there are many diagnostic means that can be used to identify likely adaptations. Notwithstanding naive claims to the contrary, all science uses and proceeds by "just so stories," that is, by attempting

to incorporate past events into the framework of established principle. What differs is the rigor with which this is done, how tightly constrained the predictions are, and to what extent their implications are susceptible to falsifying empirical tests. Evolutionary "just so" stories (reconstructions of adaptive patterns) can be extremely rigorous, if they are embedded in a deductive framework from which implications are deduced and tested. Predictions need not be about future events, only about data not yet gathered or analyzed. Predictions about patterns yet to be found in data relevant to hominid evolution can be a primary method of validating various hominid scenarios.

12) Moreover, the aim of reconstruction is not to test the theory of natural selection, but rather to discover past events and species characteristics using the theory of natural selection as an inferential tool. Natural selection is a well-validated theory, and does not require verification in every instance in which it is invoked. In no science is every principle tested every time it is applied. The point of potassium-argon dating is not to test theories of nuclear fission, but to date geological strata assuming the truth of the theory of radioactive decay.

13) Given that natural selection is the major constructive and ordering force in evolution, the initial presumption about a trait is that it is adaptive (i.e., promotes fitness). Some additional diagnostic indicators of adaptation include:

i) the greater the number of genes that contribute to a trait, the more likely it is to have been adaptively patterned since it is unlikely that they could all have become fixed through drift.

ii) the more uniquely derived a trait is, the more likely it is to have been created by natural selection. Such a trait is an indication that genes now present were not present ancestrally. As drift has stochastic properties that probabilistically limit the distance of departure from the ancestral genotype over time, the further away from the common ancestor the traits involved are, the stronger the evidence that the difference was driven by active selective forces.

iii) the more ordered traits are, the more likely they are to have been shaped by natural selection. Stochastic processes will tend to produce random results, not ordered ones. The cumulative probability that a large number of genes that just happen to fit together in an ordered relationship with various environmental variables all attained fixation through drift is extremely slight. Adaptation is also indicated when traits are highly interwoven or interdependent.

iv) the larger a trait's potential impact on fitness-related variables, the more likely it is to have been shaped by selective forces. It can

have an effect either because it is costly, or because its consequences are large. The intensity of selection will be a function of the magnitude of a trait's consequences on the various components of fitness, and the size of its cost.

v) variation in heritable traits (or more properly, that subset of heritable variation not explained by frequency dependent selection) is evidence that selection has not been acting on those traits very intensely or for very long.

vi) convergent evolution in parallel conditions is evidence for adaptation.

Therefore, any costly and complex behavior that individuals regularly direct towards others must benefit the actor by enhancing its eventual reproduction, or the eventual reproduction of its relatives. This is particularly true of any complexly patterned, nonhomologous behavior. *The hominid lineage is notable for its large number of ordered, complex, costly, and nonhomologous traits, and the complexity of the genetic basis of these traits.*

14) Systematic deviations from inclusive fitness promotion are the result of phylogenetic lag, phylogenetically rare individual circumstances, competition with coevolving antagonistic organisms, ontogenetic constraint, or intragenomic conflict (Dawkins and Krebs, 1979; Cosmides and Tooby, 1981). Each of these possible explanations, however, has implications that are potentially falsifiable.

15) To be selected for, a trait need not be advantageous under every conceivable potential circumstance. It need only be of benefit *on balance*. This means it must be advantageous more often than not, or that the frequency with which it is advantageous, times the magnitude of the advantage, outweighs the frequency of disadvantage times the cost. Thus, selection for a trait is always against a background probability distribution of ancestral environmental conditions, and cannot be understood when abstracted from this background.

16) For the above reasons, one begins with the methodological presumption that the great majority of significant traits are or were adaptive. Using these traits one tries to construct a coherent description of the organism's system of adaptation. The investigator should attempt to trace the adaptive consequences of a feature. If a sufficient explanation for the feature is not found (and validated), and all of the significant components of adaptation are ruled out, the nonadaptive nature of the feature will become evident. In such a case, the next step is to see how the feature fits in to the larger developmental, phylogenetic, and adaptive patterns of the organism. If a behavior appears to cost the organism, but confer no benefit, the

researcher then looks for a more encompassing system of adaptation of which the feature is an inevitable concomitant. If the feature or behavior under observation appears maladaptive, one investigates to see if, under other more common conditions, the feature might be adaptive, or if under other, rarer conditions, it might be compensatorily highly adaptive. Alternatively, one can investigate for evidence of other conditions that were more prevalent in the past. Finally, one investigates to see if the feature is the product of some sort of ontogenetic or physical constraint on adaptation. Adaptive or not, any feature requires explanation. However, explanations of features through an appeal to nonadaptive aspects of the evolutionary process remain the *weakest and least testable* kinds of explanations. The alternative stochastic processes such as drift and hitch-hiking that are frequently invoked (Lewontin, 1979) are almost unfalsifiable. In any case, despite criticisms of the adaptationist program, characterizations of traits as nonadaptive cannot be supported without the application of the adaptationist program.

17) There is a strong and underemphasized relationship between the psychological (and physiological) capacities of organisms and the adaptive strategies they pursue. There is an enormous gap between knowing what habitat a species occupies, and predicting its social structure and other behaviors. Thus, species that differ in intelligence and communicative ability may also differ in how they respond to the same ecological pressure. The reason why male coalitions for intragroup conflicts are frequent in savanna baboons but absent in Hanuman langurs may be partly due to different levels of and constraints on social cognition in the two groups. Similarly, the emergence of strong male coalitions for intergroup conflict in common chimpanzees may be due in part to their expanded capacity for social cognition.

18) Therefore, as capacities increase or diminish, the fitness and availability of various strategies will change accordingly.

During hominid evolution, intelligence and the ability to communicate expanded enormously, and therefore strategies made possible by intelligence and communication would have appeared or expanded accordingly (cf. Kurland and Beckerman, 1985). This must have had a major impact on almost every dimension of social strategy. For example, if a male can only aggressively punish behavior that takes place in his presence, this will influence where he can travel and what he can prevent. If, by communication, he can discover what has happened in his absence, that behavior can become a point of negotiation. He can deliver threats about what will happen when he is away; he can punish behavior that occurred during his absence. For example, for the first time, paternity certainty can be indicated

in his absence, making it possible for males to combine high investment strategies with periods of absence. A male's kin can keep watch for him, and even if they cannot prevent infidelity, the fact that they can report it may deter it. Similarly, large, regulated, and stable coalitions can be formed for intergroup aggression. Sharing in the fruits of cooperative effort can be mediated by communication. Reciprocity can be elaborated over longer periods of time, involve more individuals, and be made to apply to behaviors that take place during an individual's absence.

These new capacities allow the evolutionary elaboration of adaptively patterned behaviors to new levels of sophistication not found in other species. Although some of these behaviors are found only among hominids, they are still susceptible to evolutionary analysis. However, such an analysis will require the development of new theories of social psychology, based on the wedding of game theory to evolutionary principles (Axelrod and Hamilton, 1981; Cosmides, 1985; Tooby, 1985).

19) The interests of different individuals often will be in conflict. Therefore, larger patterns of social behavior are not necessarily optimal for any individual or group of individuals, but rather may be the emergent result of the conflicting interests of interacting individuals. Frequently, therefore, the behavior of an individual cannot be understood in isolation; its behavior will be the mutual result of its interests and the counter-strategies of those with whom the individual is associated.

20) Group processes and characteristics are not selected for in themselves (for example, by group selection), but are the emergent product of dynamic processes taking place at the individual strategic level, and must be analyzed at that level. Thus, intergroup conflict cannot be understood in terms of "benefit to the group", whatever that might mean. Instead, the costs and benefits to the individual actors must be analyzed. Thus, "intergroup hostility" may instead be hostility between different male coalitions (as in chimpanzees), or simply hostility between the dominant male of a group and outside males (as is usual in langurs). "Group" protection from predators in baboons is the defense of some individuals or sets of individuals by others (Strum, 1982). Similarly, infanticide in langurs is carried out by some individuals, in specific circumstances at the expense of others; hypotheses of "social pathology" posed at the group level have not been productive (Hrdy, 1977). It is necessary to analyze who is acting, who is experiencing the consequences, and the relationship between the two.

21) However, although group level characteristics and processes are the consequences of strategies at the individual level, they can

also operate in feedback as general conditions individuals must adapt to. Thus, male-male hostility and competition among male gorillas has a determinative impact on female strategies, and female foraging patterns and dispersion patterns in space and time are the primary determinants of male strategies in chimpanzees and orangutans (Wrangham, 1979a, 1980). The earlier patterns of individual choices add up to a set of circumstances within which those and other individuals make subsequent choices. Consequently, a hypothesized hominid scenario must not only describe strategies for all of the age-sex classes, but must make certain that *all of the hypothesized strategies are consistent with each other*. As we will discuss, it is not clear whether they are in Lovejoy's model (1981) or the "Woman the Gatherer" models (Tanner, this volume).

22) Adaptation is not an absolute standard, but a relative one. A proposed adaptation or system of adaptations must not only work, but must work better than all identified possible alternative strategies. This is a very useful inferential tool. For example, in modern hunting-gathering peoples, there tends to be a sexual division of labor, where men hunt and women gather. Proponents of the "Woman the Gatherer" hypothesis have claimed that gathering is the major hominid adaptation, and that it is and always has been primarily the activity of women. Hunting is considered to be a minor, supplemental, and late-appearing marginal activity, rather than a major and evolutionarily significant subsistence activity. However, because women gather, we know that men have had, as an available alternative strategy, the possibility of gathering just as intensively. If gathering was the superior subsistence strategy practiced by itself, why didn't men give up the inferior practice of hunting and exclusively gather instead? The fact that they did not strongly implies that for men, hunting was a superior strategy relative to gathering. The converse also applies: if hunting is globally superior, why don't females abandon gathering and hunt instead? Any hominid scenario that posits such a sexual division of labor must explain why gathering is the best strategy for females, and hunting is the best for males. It cannot simply assert that one subsistence pattern or the other is "better", irrelevant of gender and condition. From this principle, one can strongly infer that the gathering hypothesis, for example, is defectively incomplete. In general, any proposed hominid behavioral pattern must be examined with the question *could they be doing something else that is more adaptive?*

23) This form of analysis may be termed *evolutionary psychology* (Tooby, 1985). The psychology of an organism consists of the total set of proximate mechanisms that control behavior. Natural selection, acting over evolutionary time, shapes these mechanisms so that the

behavior of the organism correlates to some degree with its fitness. However, in the lifetime of any particular animal, it is the proximate mechanisms that actually control behavior. If these can be understood, behavior can be predicted exactly; understanding fitness-promoting strategies allows only approximate prediction. Behavior correlates exactly with these proximate mechanisms, but only approximately with the fitness promoting strategies that shaped them. Evolutionary psychology relates explanations in terms of adaptive strategy to explanations in terms of proximate mechanisms. Correct characterization of adaptive strategies gives precise meaning to the concept of function for proximate mechanisms. Reciprocally, a detailed analysis of the proximate mechanisms of a species gives rich insight into the present and past selective pressures that have acted on it.

The traits of modern humans, including their innate psychology, give powerful evidence of the nature of the past. Important clues can be found in such psychological phenomena as: the conditions that foster strong male-female bonds, the potential strength of father-offspring bonds, the pattern and timing of male and female aggression, the psychology of male coalitions and group aggression.

24) The comparative method is a crucial element in strategic modeling. Living species are used as the data base to derive, test, refine, and scale the evolutionary principles that comprise the conceptual model. Although this data base allows the confirmation of deductive principles, such as kin selection, it is also the primary source for empirical principles, which are equally important in inferential research. Certain processes are so complicated that they cannot be conceptually modeled and must be measured directly. These processes involve so many interacting factors, which singly or together are so little understood, that direct observation is still the primary or only method of investigation. For example, the correlates of sexual dimorphism must be studied in this fashion. The ecological factors influencing strategies of foraging, the differential impact of mate competition, the biomechanics of bones, the energetics of locomotion, the nutritional drain of pregnancy and lactation, the possible existence of limiting nutrients, the biochemistry of the detoxification of secondary compounds, the differential impact of predation, and many other factors may all feed into the cross-specific patterns of sexual dimorphism that are observed. Clearly, present knowledge is so inadequate that these patterns are not directly derivable from any existing deductive framework, and the comparative approach is the only method for their investigation.

By following patterns of convergence and divergence among homologous and uniquely derived features, and analogous and non-analogous adaptations, the comparative approach allows some in-

ferences to be made about functional and ontogenetic interdependence (see Wrangham, this volume). By tracing out the patterns of covariance among traits in related and unrelated species, one can tell which traits tend to form adaptive constellations, which traits are functionally incompatible and hence mutually exclusive, which traits may be developmentally linked, and which have little impact on each other. Minimally, if a series of adaptations are all present in the same species, they must be mutually compatible. Moreover, these kinds of data can occasionally allow one to scale relationships mathematically so that quantitative inferences can be made from known species to partially known (e.g., hominid) species. In addition, such studies reveal which kinds of traits are conservative, and which change more rapidly and hence track selective shifts more closely.

Although empirical principles derived from comparative data are useful, they are far from infallible. Empirically derived comparative principles are, first of all, probabilistic. They can be wrong in any specific case, because specific cases may have unique or unusual elements that can alter how functional variables operate on a specific species, making the general relationship inapplicable or misleading.

For example, some have argued (e.g., Zihlman, 1981) that the reduction in canines and canine dimorphism in the hominid line is evidence for a waning of male-male competition, because of the correlation between these two variables among cercopithecines. However, as Darwin first suggested, the functional uses of canines (attack, threat and defense) may have been supplanted by tools (Darwin, 1871). Alternatively, the shift to bipedal posture may have removed the head and mouth from close combat, with the greater striking distance of arms and hands replacing canines as weaponry. As both tool use and bipedalism are drastically increased in hominids, their functional appearance may render generalizations based on other primates inapplicable. This is an example of why, ultimately, empirically derived comparative relationships must be supplemented by (and ultimately subsumed into) functional relationships. With a functional model, the appearance of a unique element can be factored in deterministically.

25) One cannot explain hominid evolution by an appeal to factors that would have equally impinged on other species, especially if the other species had the same pre-adaptations: a theory must explain why we are not our close relatives, the chimpanzees, gorillas, or bonobos. Unique adaptations must be explained by unique factors in an evolutionary lineage. Prospective reconstructions of hominid adaptation must not only be internally coherent, but they must explain what was special about the events that produced the various unique features of hominids: bipedalism, high social and causal intelligence,

language, culture, and expanded sociality. Again, it is not clear whether Lovejoy's hypothesis (1981) or certain versions of the "woman the gatherer" approach have met this requirement.

PRIME DETERMINANTS, INFERENCE AND THE HOMINID TRAJECTORY

The real power of strategic modeling arises from the fact that species embody *systems of adaptation*. Because the traits of an organism co-evolved and are co-adapted, they constitute an articulated system of features that fit together in an interlocking and constrained fashion; the constrained nature of co-adaptation can provide a sound basis for inference. If some traits are known through paleontological observation, potentially some or all of the others can be worked out as the necessary concomitants of these observed traits, provided the applicable theory of co-adaptation is solidly developed.

Indeed, hominid reconstruction should be treated as a logical puzzle: One starts from what is known, then systematically applies the body of evolutionary knowledge and rules of inference to reconstruct the system of adaptations that characterize a particular hominid species at a certain point in its evolutionary trajectory. This process produces an integrated framework of specific knowledge about hominid evolution within which hypotheses about specific traits can be evaluated. Each hypothesis about a specific trait (hunting, tool use, mating patterns, child care, etc.) is a fragmentary element which, if true, would help comprise the entire scenario of hominid evolution. But such individual elements are impossible to evaluate in isolation; by gathering them together into a larger inferential web, they can be considered together, as part of the system of adaptations. By using behavioral ecology to structure relations among different features, one can investigate the combinatorial patterns that emerge among the hypothesized adaptations, and discern which proposed adaptations fit together and which do not. This process is similar to solving sets of equations (Gaussian elimination). By the simultaneous consideration of the known facts and principles, there may emerge just a single solution, or a limited number of possible alternatives. The more discoveries that are made, and the more vigorously these are milked for constraints and implications, the more unknowns will be filled in, and the range of possibilities will be narrowed.

To understand the sequence of human evolution, we need to characterize each hominid species at a given point in time by its distinctive system of adaptations, expressed in terms of the variables that vertebrate ecology suggests will be evolutionarily significant.

The set of variables necessary to characterize a hominid species is far more extensive than is commonly appreciated. The usual sketch of a few major adaptations (e.g., gathering, hunting, tool-use) is fatally incomplete.

Factors involved in a description of a species' distinctive system of adaptation include diet, foraging strategies, distribution of patch sizes, patterns of secondary compound distribution in dietary items, predation pressure, disease pressure, genetic diversity in disease resistance, locomotion system, costs of locomotion, habitat type, degree of seasonal variation in environmental determinants, weather, body size, nature and magnitude of sexual dimorphism, demographic and life history variables (e.g., age-sex class specific mortality rates, life-span, interbirth interval, gestation time, dependency period), ranging patterns, female advertisement of fertility, forms of male investment (carrying, predator protection, feeding toleration, provisioning, protection from infanticidal males and females), forms of female investment, kinship structure, mating structure, negotiation patterns, intergroup conflict, group size, group fissioning, coalitions, communication capacities, patterns of food sharing (kin based, dominance-based, extortive, reciprocal, mate-directed), nature of the species-specific social psychology, whether groups are male or female bonded, whether social groups are closed, whether there is cooperative labor in foraging or information, reliability of paternity identification, and how all these factors differ depending on age-sex class.

Major questions that structure the assembly of these factors into a coherent system of adaptation are: In what ways can an individual, in each age-sex class, help or harm other individuals, both kin and non-kin? What age-sex classes are exposed to each other, and under what conditions? What are the nonsocial limiting resources to reproduction (e.g., food, water, sleeping sites) and how do they vary from habitat to habitat and from species to species? What are the exogenous factors (e.g., distribution of food and patch size, predator pressure, disease pressure) that influence fitness, and how does their magnitude vary for each age-sex class? What are the pay-offs for cooperative and coalitional behavior between members of each age-sex class, in relation to these exogenous and social selection pressures? What are the pay-offs for reciprocal exchange among and between members of each age-sex class?

Depending on such factors as diet, resource distribution, locomotion, season, habitat, predation pressure, and phylogenetic constraint, strategically motivated patterns of association and avoidance will produce a local population's distribution of social systems. The goal is to describe a social system in terms of the strategies of the individuals that comprise it, and not just in terms of the physical

distribution of age-sex classes. A description based on strategic modeling would provide a foundation for interpreting how a species' system of adaptations can evolve from one structure into another over time and across habitats.

Such factors as those enumerated above (by no means an exhaustive list) all deserve to be considered in characterizing a primate species. Because of the interlocking nature of systems of adaptations, it is to be hoped that such factors can be weighted or separated into those that are prime determinants of a species' system of adaptations, and those that are secondarily determined by these systems. In the interpretation of the fossil record, the function of understanding the relationships of prime determinants to secondary determinants is to be able to infer those prime determinants that cannot be directly assessed from the fossil record on the basis of the measurable secondary factors that may be preserved, and which are tightly regulated by the prime determinants.

THE STAGES OF HOMINID EVOLUTION

Before the advent of reliable radiometric dating in the 1960s, it was widely believed that human evolution took place in a brief million year span, rather than in the six to ten million year period currently estimated. Although the vast expanse of time involved in human evolution is now recognized, certain habits of thought shaped by that narrow time frame still survive implicitly in much present day discourse about hominid evolution. Many researchers still compress hominization into a single process, rather than exploring the possibility that it consisted of a large number of discrete stages characterized by sharply differentiated selective forces and adaptive complexes. Hominid models have not yet expanded to fill the time available for human evolution. Although no one seriously argues for the existence of a single "missing link", this phantom makes its covert presence felt in the structure of many other arguments. For example, arguments that attempt to minimize the importance of a factor at one stage (e.g., hunting by australopithecines) have tended to be interpreted as generalized rejections of the importance of that factor at *all* stages of hominid evolutionary history. Similarly, reconstructions of hominid evolution often draw their inspiration from one stage (e.g., Tanner's [1981] description of australopithecine life), yet are treated as generalized accounts of human evolution and modes of life, often including even modern hunter-gatherers. If one recognizes that one is actually involved in a series of reconstructions of *different animal species*, it is easy to see that such generalizations are ill-founded. A feature, such as hunting, that seems to be an

inappropriate major adaptation for one chronospecies may be fully appropriate for others.

Both socioecology and the increasingly complete stratified fossil record require that hominid evolution be regarded as a discrete series of branches and stages. In the first place, the discovery that hominids were fully bipedal at 4 million years (Johanson, White, and Coppens, 1978), long before the appearance of the first detectable stone tools, has decoupled Darwin's compelling trinity of bipedalism, tool use, and brain expansion, at least in any simple form, and thereby made bipedalism the original trait requiring independent explanation. Second, the simultaneous and possibly sympatric existence of several hominid species in the 2 million year range is a fact which, by itself, destroys the linear model of human evolution. Morphologically distinguishable coexisting species must have differed in adaptive configuration, as must morphologically different species at different times. Distinct fossil forms are now known to represent species whose constellations of traits diverged sharply from each other and from those of any living animal. The huge cheek teeth, limited cranial capacity, and bipedality of australopithecines is evidence for a family of adaptive modes that are not human and not yet understood.

In response to these discoveries, many researchers view human evolution as a long corridor, where chimpanzees enter at one end and modern hunter-gatherers exit at the other. Modern hunter-gatherer traits, such as language, food-sharing and pair-bonding, are projected backwards towards the ape-hominid common ancestor, who is depicted as a slightly brainy, tool-using chimpanzee. Using these *referential* methods, ancestors are reconstructed with a combination of living ape and human traits—a "Piltdown approach" to behavioral ecology. Forms are often considered to be an intergraded series with australopithecines as a midpoint, half chimpanzee, half hunter-gatherer (e.g., Tanner, 1981). *Homo erectus* and subsequent forms are often depicted as inept or simplified versions of the !Kung San, Hadza, or Mbuti.

Strategic modeling requires a radically different approach to these issues. The landscape of hominid evolution is far richer than the linear, referential view can accommodate; interpolating between the two ends of a "corridor" is seriously misleading. The adaptations and traits of different species do not simply grade into each other, forming a smooth continuum, in which any feature is equally compatible with any other. Because a species' adaptations form a co-evolved and coadapted *system*, only some clusters of traits are mutually consistent with each other and are therefore acceptable as models of or hypotheses about a particular extinct hominid or hominoid form. Thus, each extinct form corresponds to a distinct con-

figuration of adaptations, and neither traits nor selection pressures necessarily follow a smooth trend line between earlier and later forms. Extinct hominids, both *Australopithecus* and early *Homo*, display combinations of traits that are not parallel to any living primate, including modern hunter-gatherers; these forms are not usefully analogous to any living animal. An extinct species should not be viewed as a crude, imperfect version of a living form, but as interesting in its own right, just as adapted to its own archaic present as any living animal. Each morphologically distinguishable fossil species needs to be characterized in terms of its distinctive interlocking system of adaptations. Other proposals can be winnowed out as "Piltown" mosaics of incongruous traits.

Therefore, the task of understanding human evolution becomes the understanding of each of a number of ancestral chronospecies in terms of its habitat and its distinctive system of adaptations. It is not the reconstruction of a single pre-modern mode of life. Each chronospecies corresponds to a stage, and requires the inferential reconstruction of its unique and interlocking constellation of selection pressures, strategies, and morphological traits. Each stage represents different clusters of mutually consistent adaptations, and these in turn correspond (at least) to each morphologically distinguishable chronospecies. Moreover, there may be forms not yet discovered in the fossil record.

A list of the stages requiring characterization includes (at least):

- 1) the pongid-hominid common ancestor,
- 2) the hominid common ancestor, putatively an early australopithecine, possibly *Australopithecus afarensis*,
- 3) the late ancestral australopithecine,
- 4) the transitional form to *Homo erectus*, possibly *habilis*, or *ergaster*,
- 5) *Homo erectus*, (possibly divisible into early and late),
- 6) archaic *sapiens*, if different from late *erectus*,
- 7) the Neanderthal period ancestral form, and
- 8) anatomically modern *Homo sapiens*.

To these should be added, secondarily, the non-ancestral branching species: the robust and late gracile australopithecines, European Neanderthals, and any others that can be identified. Knowledge of these species should shed light on ecological competition, phylogenetic constraints, and a host of other factors that would assist the elucidation of the hominid lineage which produced modern

humans. Of course, it is important to bear in mind that there are undoubtedly ancestral and branching forms that are yet to be uncovered in the fossil record and will need to be integrated as soon as they are discovered. The gap in the fossil record from 4 to 8 million years ago may uncover several such discrete ancestral chronospecies, which may throw light on the transition to bipedality and the causes of the hominid-pongid split. A similar mystery involves the location and characteristics of the direct precursor to modern *Homo sapiens*.

The estimate of 4 to 5 million years for the hominid-pongid common ancestor (Sarich, 1980) is discrepant with the discovery of fully developed bipedality 4 million years ago, indicating that the molecular clock may need some recalibration. In particular, the probability that a large fraction of protein polymorphism and recombination is driven by parasite pressure implies that substitution rates will differ somewhat depending on the variations in the ecological correlates of parasite load (Tooby, 1982). If this reasoning is correct, the hominid colonization of the savannah habitat and subsequent occupation of temperate areas—habitats freer of disease than forests—would have slowed substitution rates, giving a spuriously late date for the hominid-pongid divergence. Depending on the magnitude of this correction factor (perhaps back to 10 million years), there may well be additional room in the hominid ancestral line for additional chronospecies. Aside from uncertainties in dating the hominid-pongid split, confusion remains about how the split should be treated. The premise that the split was driven by some major new selection pressure is not necessary. The most common kind of speciation is created simply by geographical isolation (Mayr, 1963), and the early phases of hominid evolution may not have been fundamentally different from the early hominoid branches.

The explicit recognition of the existence of numerous stages of hominid evolution opens inquiry into a number of possibilities not usually addressed. In the first place, there may have been many abrupt reversals in adaptive patterns along the hominid lineage. The tacit assumption of continuity between different stages, especially those distantly separated in time, becomes suspect. To look at a chimpanzee diet (as an analog for the hominid-pongid common ancestor) and compare it to a San diet also rich in plant foods, and to infer continuity in dietary constituents in hominid diet is completely unwarranted. Hominid diet may have been initially rich in plant foods, then switched to long periods of intense meat consumption, and then returned to increased plant exploitation, as changing variables shifted the relative value of doing so. Any substantial change in a major socioecological variable may reorganize the relationship

of many of the others, causing the pay-offs of other activities to change markedly, and the labile components of adaptive configurations to alter abruptly. For trends to continue, the underlying forces that drive them must also continue. This is not just a logical possibility. In the case of the relative pay-offs of plant foods versus meat, there are a number of changes in underlying determinative variables that are known to have occurred, and are surely relevant. Cooking denatures plant secondary compounds (Rhoades and Cates, 1976), making them more digestible, and so the systematic use of fire (starting at least 500 thousand years ago) would have substantially altered the pay-offs of alternative dietary constituents and foraging efforts, opening up a far broader variety of plant foods to human exploitation. The disappearance of the Pleistocene megafauna would also have changed hunting pay-offs, again possibly dramatically altering diets.

Many such variables have changed over the course of hominid evolution, so that it is to be expected that hominids at various stages would be very different animals, sharply differentiated in at least some of their adaptations even from their direct precursors and successors. Sewall Wright's idea of separate peaks on an adaptive topography (Wright, 1951) helps one conceptualize the trajectory of hominid evolution: a single change in pay-offs or in other variables can make two previously compatible elements incompatible, pushing the whole matrix of adaptations rapidly into a different configuration or adaptive peak, potentially reversing earlier trends, perhaps several times in succession. For this reason (considering the large number of variables regulating adaptation that are known to be different), it is unlikely that *Homo erectus* and even archaic *sapiens* were merely simplified versions of modern hunter-gatherers. For example, the vast expansion in learning and culture changed pay-offs of a whole range of activities and behaviors, and it is surely unlikely that diet and social organization remained uninfluenced by these changes.

The value of adaptations is always specific to their context, and the context of each stage in the hominid lineage, on the basis of known differences in behavioral-ecological variables, is different enough that specific adaptive hypotheses concerning the importance of a given factor in hominization must be evaluated separately for each specific stage. Hypotheses must be linked to discrete stages. Consequently, given this expanded trajectory of hominid evolution, hypotheses (e.g., hunting, gathering) that are often treated as logical alternatives may, in fact, both be correct, but simply apply at different time periods.

All traits present in modern humans must have appeared during some specific ancestral stage, and each trait must be correctly assigned

to a stage. We thus know something very powerful about ancestral hominids which the fossil record alone cannot tell us: all innate traits characterizing modern humans evolved sometime in the past, in association with the morphological traits that we can directly observe. One profitable inferential exercise would be to take a trait known to characterize modern humans, hypothetically assign it to a particular ancestral stage, and then reason what consequences that introduced trait would have on the system of adaptations of that ancestral stage.

ANALYZING ZOOLOGICALLY UNUSUAL FEATURES OF HOMINID ADAPTATION

The zoologically unprecedented characteristics of humans require explanation consistent with modern evolutionary biology. These unique features of human life are not minor and incidental, but lie at the heart of our adaptive system. Consequently, the most telling test of hypotheses about hominid evolution is whether they provide an explanation for these divergent properties. Explaining how hominid systems of adaptation propelled the emergence of evolutionary novelty rests on interrelating the prime determinants of primate behavioral ecology to our unusual traits. To deal with human uniqueness in a principled way, these elements must be fitted together into novel but lawful patterns.

Such explanations should not be post hoc: novel features should emerge naturally as an inextricable part of the process of hominization rather than as forced adjuncts of a scenario. Powerful selection pressures were required to drive the hominid lineage along so differentiated an adaptive path: any analysis that makes us appear just like other animals is unlikely to have addressed the biological reality underlying our unusual trajectory. Close strategic analysis of these divergent features in terms of their socioecological meaning and consequences should transform the problem of human uniqueness from an imponderable mystery to a sophisticated but straightforward problem in evolutionary biology.

Zoologically unique hominid divergences include the following properties:

- 1) the ability to attain fitness goals through complexly organized, situationally-tailored, instrumental sequences of behavior;
- 2) unparalleled cognitive models of changing aspects of the world (high causal intelligence);
- 3) the ability to communicate these models of the world through language;

- 4) unmatched learning abilities, including skill acquisition;
- 5) an unparalleled degree of tool manufacture, variety, and use;
- 6) a vast expansion in cultural transmission and interindividual involvement in the creation and maintenance of information;
- 7) unprecedented development in the frequency and degree of reciprocity and the variety of its manifestations;
- 8) unparalleled degree of negotiation, intercontingent behavior, and social exchange;
- 9) quantitatively and qualitatively divergent patterns of food manipulation, including collection and transport, extensive processing and preparation, storage and sharing;
- 10) an increased division of labor between sexes;
- 11) far larger and more structured coalitions, including bisexual, female, and especially male coalitions;
- 12) a high degree of male coalitional intergroup aggression (war);
- 13) the controlled use of fire;
- 14) a set of psychological mechanisms regulating an expanded system of kin-directed behavior, manifesting situation-appropriate kinship systems:
- 15) mating negotiation and exchange, probably consisting of wife exchange among groups, or at least kin involvement in mate selection and the attendant intercontingent sequelae.

Hominid divergences from the apes include the following zoologically nonunique features:

- 1) bipedality;
- 2) situation-appropriate, intensive male parental investment and an increase in female parental investment;
- 3) a unparalleled degree of hunting and meat consumption;
- 4) a change in life history correlates: an extension of lifespan, an increase in the period of investment in offspring, a marked increase in the altriciality of human young;
- 5) an expansion of ecozones occupied, from tropical woodland and forest into savannah areas, but eventually including every other terrestrial ecozone;

- 6) concealed ovulation coupled with continuous sexual receptivity.

THE HUMAN PENETRATION OF THE COGNITIVE NICHE

The following section considers the hominid trajectory by exploring how these divergent features interact with the prime determinants of primate adaptation.

A significant fraction of any species' environment consists of constantly coevolving organisms; fitness gains by one species frequently occur at the expense of other species that are preyed upon, defended against, or parasitized (Van Valen, 1973). This is the Red Queen view of adaptation: species coevolve in antagonistic dynamic relationships. All food items (except such items as fruits whose seeds require dispersal) are parts of organisms whose fitness is antagonistically related to that of the forager. In order to survive, both plants and prey animals depend on an array of defenses to inhibit or prevent consumption. Because these defenses are genetically based, the rate at which they can change is relatively slow: within a lifetime, they are fixed defenses. Any balance that is maintained occurs because both attack and defense take place in evolutionary time; moreover, attacks are limited in innovation by the fact that every intervening increment must be advantageous to the attacker.

Humans have made a unique and major innovation in this co-evolutionary relationship—an innovation that is our most distinctive characteristic. The defenses of plant and animal prey species can be circumvented by "surprise" attacks, attacks that consist of many novel and discrete manipulations, evolutionarily unprecedented actions that prey defenses are not equipped to repel. Goal-oriented actions by humans, shaped to suit the particular situation, constitute surprise attacks. We accomplish this by conceptually abstracting from a situation a model of what manipulations are necessary to achieve proximate goals that correlate with fitness. These highly orchestrated and intricate situation-specific sequences of behavior are cognitively organized.

The core of our zoological distinctiveness is our entry into this *cognitive niche*. By entering it, humans have made available to themselves thousands of new plant and animal prey species. Burrowing animals, underground storage organs, nuts, seeds, bone marrow, birds, fish, mollusks, tool accessible nests, plant foods whose toxins or other inhibiting secondary compounds can be neutralized through processing or cooking, quick animals that must be ambushed, animals whose capture requires close cooperation, tools, or intelligent trickery—all are made accessible by the ability to perform appropriate

learned or invented manipulations. The rapidity with which cognitively guided manipulations can circumvent genetically fixed defenses in prey species accounts for the surge in extinctions that have accompanied the evolution and spread of humans into new habitats.

Not only are thousands of new items opened by cognitively guided manipulations, but expanded cognitive abilities also allow humans to adopt flexible solutions to a wide array of other adaptive problems. At the core of this lies a causal or instrumental intelligence: the ability to create and maintain cause-effect models of the world as guides for prejudging which courses of action will lead to which results. Because there are an infinitely large number of possible sequences of behavior (of which the overwhelming majority are maladaptive) "behavioral flexibility" is an insufficient characterization of our innovative adaptive pattern. Our cognitive system is knowledge or information driven, and its models filter potential responses so that newly generated behavioral sequences are appropriate to bring about the desired end. Of course, exploration, trial and error, and feedback are essential to the system, but, by themselves, they are inadequate to construct or maintain it.

Viewed this way, many other zoologically anomalous features reveal themselves to be aspects of the cognitive niche. Tool use is manipulation of objects instrumentally; skill acquisition is the perfecting of the cognitive tools necessary to bring about successful, situation-specific manipulations. It is no accident that language coevolved with or followed upon these cognitive innovations; language is different from other animal communication systems in that it allows the exchange of model-based information referring to cause-and-effect categories. This vastly increases the efficiency of occupying the cognitive niche, by drastically reducing the costs of information. The individual is no longer limited by the models he can construct himself, or the information he directly observes. This also means that a social animal occupying the cognitive niche is greatly favored: a useful piece of knowledge or a model innovation can benefit not just the individual, but all of its kin and descendants for generations, adding a huge pay-off to counterbalance the risks and costs of exploration. This social dimension to the cognitive niche constitutes the basis for culture, which is the transmission between individuals and generations of the information necessary to pursue fitness in a particular social and ecological habitat. Finally, the radiation of humans into all terrestrial habitats is also a product of entering the cognitive niche. The liberation of fitness goals from environment-specific, behavior-controlling cues means that novel manipulations can be manufactured to promote fitness in new and differing habitats. Human evolution involved the selection of psychological mechanisms that turned out

to be general solutions to local adaptive problems, allowing us to spread beyond our habitat of origin.

Since such abilities would be favored for many kinds of organisms, why did hominids evolve them and not others? First, an animal must not only know what manipulations to make, it must also be able to make them. The existence of hands that are dexterous in their manipulation of objects is a necessary precondition, limiting the possibilities to certain primates, especially the great apes. Numerous other factors, such as binocular color vision and a certain minimum body size are also probably important. Certain neural preadaptations are necessary, no doubt, but at the present state of neuroscience, such assertions remain vague and unhelpful.

Since the great apes have all of these preadaptations, why did they not develop along hominid lines? Chimpanzees, and probably all of the great apes, have significant cause-and-effect-oriented cognitive abilities that parallel in embryonic form those that developed in the hominid lineage. One possible answer is bipedalism; more sophisticated manipulations are possible if the animal can assemble in one place materials from different locations. Moreover, the results of such manipulations are more useful if they can be removed from the site of manipulation (for many reasons: safety, sharing, access to other nonmoveable things such as water, further processing, etc.). If bipedality evolved in the hominid line for some independent purpose (such as monitoring predators on the open savannah), then it would provide a factor that differentiated us from the apes.

Life in a social group greatly enhances the pay-offs and reduces the cost of information seeking. This could explain why gibbons, siamangs, and orangutans—solitary primates—did not more fully enter the cognitive niche. A third possibility involves the ratio of the costs of added cognitive abilities versus the increased pay-offs. The brain is a nutritionally and metabolically costly organ (Martin, 1983). To justify the marginal cost of increasing its size, the marginal benefit must be correspondingly high. It may be that for brain expansion to pay off, it must increase access to very nutritionally rich sources of food, such as meat. Open habitats are far more meat productive than tropical forests, and it may be that occupation of the meat-rich savannah is what differentiated hominids from the forest-bound apes. The role of meat may go beyond its production of calories: the constituents of the brain require essential fatty acids, which may prove to be the real limiting factor made available by meat.

Entering the cognitive niche is a matter of degree: reaching our present level of cognitive abilities and flexibility of behavior required several million years. As cognitive abilities grow, broadening the

range of possible food sources and habitats, radiation into the range of newly opened niches is to be expected. Modification and perhaps specialization of the digestive tract and dentition to take advantage of these new food sources provides an explanation for the hominid radiation that took place two to three million years ago separating hominids into several different "specialists" (e.g., meat specialists, underground storage organ specialists, or perhaps "habitat specialists"). This intermediate hominid radiation would have been ended when one diverging branch advanced far enough into the cognitive niche that its general solution to local adaptive problems proved superior to the specialists.

PRIMATE MODELS FOR HOMINID EVOLUTION: THE STATE OF THE ART

The articles in this volume provide an excellent cross-section of the state of hominid modeling. It appears that most (though not all) of the ingredients required to reconstruct hominid behavioral evolution are at hand, and that cooperative efforts towards their integration would bring substantial results. In what follows, we will attempt to show how the injection of even a few considerations drawn from strategic modeling can assist evaluation of the contributions in this volume, as well as of several prominent scenarios of hominid evolution drawn from other sources.

The State of Hominid scenarios

Woman the Gatherer. The advocacy of the "woman the gatherer" model by Tanner, Zihlman, and others (Tanner and Zihlman, 1976a; Tanner, 1981; Zihlman, 1981; Tanner, this volume) has offered a healthy corrective on key issues in hominid evolution. The model proposes that the key element in the pongid-hominid split, and the prime mover in the process of hominization, was the gathering of plant foods with tools—then as now, predominantly a female activity. Facts and beliefs that have lent weight to this hypothesis are:

- 1) the diet of our primate relatives (and hence presumably that of our pre-hominid ancestors) consists very largely of foraged plant foods;
- 2) early quantitative reports on the San and several other relict tropical hunter-gatherer groups indicate that 50–70% of the diet comes from gathered plant foods (Lee and DeVore, 1968);
- 3) hominid bipedality significantly antedates the first identifiable stone tools;

4) in evolutionary terms, all members of the population are important, and that in terms of their "contributions" or participation in the evolutionary process, females are as important as males; and finally;

5) the model is congruent with the social and intellectual climate engendered by feminism, with its vigorous advocacy of the importance of women in all areas, and its emphasis on the ubiquity of male biases and pretensions.

The emergence of this viewpoint has had widespread effects on paleoanthropology. It has not only contributed to the growing trend towards the balanced investigation of both sexes, which is essential to the creation of an accurate picture of hominid adaptation, it has also added impetus to the movement toward quantitative analysis of hunter-gatherer foraging and the role of gathered foods, as well as increased scrutiny of diet as a prime determinant in hominid evolution (see also Sussman, this volume).

Despite these valuable contributions, strategic modeling of the primary elements involved indicates serious problems with the gathering hypothesis, at least as articulated. Its premises and implications do not cleanly mesh with the principles of behavioral ecology. First, it fails genuinely to confront optimal foraging theory with the reality that males do, in fact, hunt. Given that members of each sex would pursue strategies that are the most productive, and if gathering is the most productive activity, why don't males gather (more than they do)? There is no constraint whatsoever on their doing so. On the other hand, the reciprocal question, *why don't females hunt* (more than they do), has a ready answer. Throughout most adult hunter-gatherer females' lifetimes, they are pregnant, lactating, and/or burdened with dependent offspring. Although there are situations in which they could (and do) hunt (Estioko-Griffin and Griffin, 1981), their ability to engage in the behavior, and profit from learning and maintaining the necessary skills is far less. Also, because of male-male competition, males are larger and stronger than females, and more experienced in aggression and weapon use. Other things being equal, many aspects of hunting are less costly for males to engage in than females. Conversely, it should be more advantageous for frequently burdened females to acquire the skills to allow them to exploit sessile and harmless food resources. Such division of labor exploits both dimensions of the same terrain, allows for complementarity of nutrition between plant and animal sources, and smooths out the risk that complete dependence on irregularly captured game animals, or seasonal plant foods produces (Lee, 1979). Regardless,

to be coherent, a theory of hunter-gatherers must account for why it is optimal for males to hunt and females to gather.

There are numerous other major zoological features of the human system of adaptations that "woman the gatherer" models do not predict or account for. Because plant collecting by females is so continuous with great ape behavior, there is little in such a model to explain differences between humans and the great apes. Among the great apes (and other primates), females forage for plant foods with their dependent offspring. Although tools and carrying devices make foraging easier, this improvement seems insufficient to be the major cause of changes in the hominid lineage (or, indeed, explain why the great apes did not follow the hominid trajectory). There is no explanation for increased male parental investment (MPI), for human altriciality, for the readiness with which males form male coalitions, for the frequency of agnatic kin-based coalitions, or for the ease with which humans penetrate habitats without substantial exploitable plant resources. Such models provide no persuasive selective advantage for why females would bring plant foods back to feed parasitic males. There is little to explain the hypertrophy of reciprocity and sharing. Other primates rarely share plant foods, because: 1) it is unlikely that many plant foods aside from nuts could, before the advent of cooking, repay the bioenergetic costs of collecting and carrying; 2) the realities of differing aggressiveness and formidability lead to the frequent expropriation of laboriously acquired foods (such as tubers), causing labor inputs to be limited to what can be readily consumed by the laborer; 3) extra high quality plant foods rarely occur in quantities that are substantially greater than can be consumed by the foraging group—when they do, it is more efficient (and less burdensome) to carry information about the location back to others.

Woman the gatherer models have offered no cogent treatment of male competition for mates. In systems where males associate with females in groups, and where males invest little in offspring, selection pressures act to create intense male-male competition and sizeable sexual dimorphism. The reduction in sexual dimorphism observed across the hominid lineage undermines the assumption that MPI is low. The assumption of low MPI contradicts the conclusion that social relations are gentle and egalitarian within and between sexes. Taking the two cases of common chimpanzees and gorillas, where male investment (except perhaps in the form of protection from other males) is minimal, one finds them anything but peaceful or egalitarian (Wrangham, 1979a, this volume). Chimpanzees sexually compete through aggressive male coalitions, and in gorillas, infanticide and protection from it are pervasive features of the social system. Sug-

gestions of male kin remaining with female kin (e.g., Tanner, this volume) contradict knowledge that inbreeding avoidance reduces intersexual kinship associations through forcing transfer, especially among long-lived animals (Tooby, 1982). There is no recognition of the nature and impact of intersexual negotiation (except female choice): of the threat of infanticide (as in gorillas or bonobos, [Wrangham, this volume]), of the possibility of meat provisioning, of the possibility of special relationships (as in baboons, [Smuts, 1983; Strum and Mitchell, this volume]), or even of the effects on females of intergroup male aggression (as in chimpanzees). In short, although females (and males) undoubtedly have gathered plant foods from the earliest times, this single component of hominid behavior seems wholly insufficient to account for the major features of hominid evolution, certainly in its later phases. Many of its proposed correlates do not make sense in terms of the basic elements of behavioral ecology.

If the "gathering hypothesis" characterization of the social life of hominids is modified to be brought in line with ecological principles, the great sexual dimorphism of the australopithecines is consistent with some of its major tenets. It is possible that *A. robustus* is an exemplar of "woman the gatherer" (but if so, its social system would more likely resemble that of gorillas). It is unlikely that *H. erectus* or any known variant of *H. sapiens* is such an exemplar.

Pair-bonding and the Lovejoy hypothesis. Lovejoy (1981; Johanson and Edey, 1981) has recently advanced a scenario for hominid-pongid divergence that invokes pair-bonding and male provisioning as the prime movers. He argues that the key hominid innovation was a discontinuous increase in MPI in the form of males provisioning their mates and young with collected plant foods. The associated mating system was monogamous, and carrying and provisioning behavior brought about the transition to bipedality. Lovejoy's effort is valuable for two reasons: 1) its attempt to introduce principles from evolutionary ecology to organize our understanding of hominid evolution, and 2) its focus on behavioral innovation (in this case) MPI as an important factor in human social life. Unfortunately, Lovejoy's analysis is inconsistent with several branches of modern behavioral ecology including life history theory, mating theory and the modern understanding of levels of selection (he implicitly invokes group selection). Although he has borrowed some key concepts from ecology (most notably the concepts of *r* and *K* selection (MacArthur and Wilson, 1967; Pianka, 1970), his application of them is seriously at variance with their valid use and meaning. He argues that the apes are somehow caught in an orthogenetically driven *K*-strategist cul-de-sac, from which hominids escaped by their innovation of mon-

ogamous MPI through bipedal carrying of collected plant foods. Supposedly, this increased "reproductive rates".

Fundamentally, Lovejoy appears to confuse issues at the heart of the r and K strategy distinction: net reproductive rate versus maximal intrinsic rate of increase in a competitive vacuum. The very long term net reproductive rate of any persisting species, r-strategist or K-strategist, must be very close to 1 (otherwise it will either become extinct or fill the universe), so a position on the r-K spectrum does not refer to how successful a population is at expanding its numbers, except locally. Instead, the r-K spectrum refers to how much evolutionary time a population spends either far below or near K, the carrying capacity of the environment. In r-selected species, the population fluctuates sharply, whereas in K-selected species the population is relatively stable. As concepts, r and K selection are used to make sense of certain types of correlated life history variables: r-selected species are species that are subjected to repeated and intense pulses of density independent mortality, and so are often well below the carrying capacity of the environment. The correlates of r strategy are lax or reduced intraspecific competition, rapid development, early reproduction, high rate of increase, small body size, and short lifespan. K-selected species tend to hover near carrying capacity, and mortality is accordingly mostly density dependent. As a result, the major selection pressures tend to be the results of intraspecific competition, resulting in slower development, delayed reproduction, larger body size, repeated reproductions, and greater parental care (Pianka, 1970). Such distinctions are more meaningful when applied to species that are more sharply differentiated in terms of life history variables than are apes and humans. Lovejoy presents no basis for believing that density independent mortality struck hominids more frequently than other hominoids, and judging by the correlated attributes listed above, humans and hominoids appear very similar, with humans being, if anything, the greater K-strategists. Finally, once all exogenous limiting factors are removed, there is little evidence on whether apes and humans do have different maximum intrinsic rates of increase. Many of Lovejoy's other assertions about life history are also inconsistent with current life history theory (Stearns, 1976).

Leaving such issues aside, however, the major inadequacy of Lovejoy's formulation involves his treatment of mating systems. He correctly relates monogamy and MPI, and the existence of extensive MPI among modern humans does argue for its emergence at some stage in hominid evolution. However, mating systems are best treated as dependent variables, driven by other ecological factors, rather than as independent determinants themselves. The onset of substantial MPI would require some combination of the following: 1) a reduction

in the relative profitability of investing energy in competition for additional females (which argues for the absence of a female-based social group); 2) certainty of paternity (which argues for males and females foraging together); and 3) an increase in the efficacy of MPI (which argues for some new and concentrated food source, not utilized previously, with which males can efficiently provision the mother or feed the offspring). Lovejoy's model does not deal convincingly with any of these issues. He explicitly rejects provisioning with meat, the only type of food that mammals regularly use to provision young. Carnivore provisioning of females and/or young is widespread, and meat is one of the few foods primates share (Strum, this volume). Although other forms of food investment are logically possible, they must fit the requirement that they be energetically efficient, as compared to the costs and benefits of competing for females. It is unclear what vegetable foods meet these criteria, although very large underground storage organs are a possibility. However, even among modern hunter-gatherers, small quantities of favored food items are usually consumed on the spot; only large quantities of food (meat or items such as mongongo nuts among the !Kung in season) are brought back to be shared. It seems likely from these considerations that intense male parental investment through provisioning awaited the onset of more intensive hunting practices.

Finally, Lovejoy's assignment of monogamy to the earliest phases of hominid evolution is inconsistent with the realities of australopithecine sexual dimorphism (see also Crockett, this volume). Gibbons and other monogamous species exhibit the least sexual dimorphism (there are also primates, such as *Brachyteles*, that are monomorphic but not monogamous [Milton, 1985]). Moreover, although not impossible, the existence of social groups within which there are stable monogamous pairs is very rare in the primate world (Kinzey, this volume). When females gather into social groups, selection pressures for intense male-male competition become great. Gibbons are monogamous, but manage this sexual exclusivity through the absence of a larger social group. However, even solitary females are no guarantee of male investment, as the case of orangutans demonstrates.

Home bases, food sharing, and scavenging. Isaac (1978a, b) has been the most eloquent advocate of what might be called the dual foraging and exchange model of hominid evolution. He and others originally interpreted finds from the rich East African fossil and archaeological sites of Plio-Pleistocene hominid activities as evidence for 1) food sharing; 2) home bases as centers for food exchange and processing; 3) tool use; 4) meat consumption based on some combination of hunting and scavenging; and 5) bipedal transport. Females

were assumed to have gathered plant and other collectable foods, males to have acquired meat; individuals met at home bases for the exchange of food items in a sex-based division of labor and reciprocal exchange that is similar to the practices of modern hunter-gatherers. The lack of evidence for plant foods and plant collecting tools is, as is customary, attributed to preservational bias in the fossil record.

More recently Isaac and others have begun to entertain a wide range of alternative hypotheses about the accumulations of tools and bones in these early sites; some of these alternate scenarios bear little resemblance to the campsites of living hunter-gatherers (e.g., Isaac 1983a, 1983b, 1984; Potts, this volume). Indeed, one of the problems with the earlier formulations was that they hypothesized behavior so similar to that of contemporary hunter-gatherers that it left unexplained the rise of many distinctively human traits, traits which (in this view) took place during stages that preceded the period the model depicts. Additional models of earlier stages must be added. Also, this approach is more a description of behavior than an analysis of the selection pressures that shaped it. These pressures require more precise characterization.

Food collection and sharing is not, *per se*, advantageous. In fact, it is rarely practiced in the animal world. Food sharing requires explanation because the forager is laboring to collect and transport food he or she will not consume: for this to be advantageous, the return must exceed the cost. Either other food or equal value must be returned at the time (exchange) or later (reciprocity), something else of equal or greater value must be provided (e.g., protection or sexual access), or sharing must sufficiently benefit offspring (provisioning) or kin.

Why share food? Each type of answer imposes certain assumptions about the nature of the social system, which should be spelled out. In a richly negotiative social life, collected and transported food represents one kind of good that can be used in a large variety of ways. Provisioning of young is not exactly food sharing, and does not bring adults together (except mates or kin). If the force involved is kin selection, cross-sex food sharing will be more limited, since adult members of different sexes are pulled apart by inbreeding avoidance and transfer. Adults will most often maintain relations with kin of the same sex, and if the sex ratio of transfer is heavily biased, one sex may be frequently separated from most of the close kin of both sexes. As a result, one would expect one sex to be more cooperative than the other. Food provisioning based on males bargaining for mating opportunities from females is possible, but does not explain female food sharing with males (if any). Within and between sex reciprocation constitutes another kind of force: in this

case, exchange is based on shifting marginal values of different kinds of food to different individuals at different times. However, in this case, one must explain why other primates do not engage in such exchanges. Perhaps a diet based on both animal and plant foods is superior to a diet based on either alone. Additional reasons for "sharing" involve the avoidance of aggression, and extortion (Moore, 1984). However, such expropriation, if widespread, selects against foraging for more than the forager can consume himself. In short, although the elements proposed are plausible, they need to be assembled into a strategic model of an entire social structure, and questions about what forces shaped food sharing and exchange need to be more fully addressed: how do males compete for mates? do they invest? how would females gain sufficient resources for reproduction? why would they gather more than they needed? An account of how hominids evolved to such a stage must also be provided.

We entirely agree with Potts' (this volume) lucid and cautionary arguments about the possible misuse of analogies between individual modern primate species or modern hunter-gatherers and extinct hominid species. He argues that there is evidence indicating that extinct forms were morphologically unlike any living primate, therefore many adaptations of archaic hominids were also undoubtedly unique. He also points out that many widely accepted parallels between modern hunter-gatherers and archaic hominids may fail to capture the unique adaptive systems of those extinct animals. In support of this contention, he advances an imaginative alternative interpretation of the Plio-Pleistocene archeological sites that for the main evidential base for the home base and food sharing scenario. Potts (1984b, this volume) proposes that instead of home bases, the early Olduvai sites functioned as "stone caches", that is, storage locations where stone tools and tool making materials too heavy for regular transport were deposited, brought from more distant sources of raw materials. Parts of animal carcasses, either scavenged or from hunts, were transported to these stone caches, where they were slaughtered or otherwise processed. According to this view, an individual hominid or hominid group established many such caches within its range, so that when they opportunistically acquired animal tissues, they could bring them to the tools for processing. Therefore, "home base" is not a necessary conclusion based on the presently available evidence. Moreover, the evidence for frequent carnivore exploitation of these faunal remains makes it unlikely that the more vulnerable members of hominid groups (i.e., children, females, the sick and old) occupied these locations as home bases.

The most valuable aspect of Potts' discussion is his recognition that if Plio-Pleistocene hominids were hunting and/or scavenging,

they would be engaged in intensive direct and indirect competition with carnivores, and that if the processing sites were also home bases they would be very unsafe ones, particularly for dependent young. The evidence for repeated attraction of carnivores to these sites argues that they are not home bases. However, this does not mean that there were no home bases, that is, occupation sites where a social group can rejoin and exchange provisions. In fact, the threat that attraction of large predators creates provides a rationale for separate processing sites. As Potts points out, these sites would serve as processing centers where stone tools and associated materials too heavy to be continually carried could be cached. When animal tissues are acquired, they can be transported to the tools required for their processing. These sites would also function as garbage dumps, where the residue that attracts carnivores can be abandoned. The home base or core social group would be located some safe distance away (upwind). As Potts points out, modern hunter-gatherers, defended by fire and better weapons, have the leisure for more efficient and more complete processing of large kills. Earlier less formidable hominids may have been forced to more hit and run hunting and slaughtering tactics. If carnivores provided a significant threat to such hominids, group size might have been at a premium, not only for social hunting but also for social defense of successful kills and social transport of larger kills to rapidly vacated processing sites. Finally, Potts' hypothesis needs to be considered in the light of a completed social structure: in this case, that of intergroup relations. If stone tools and materials are scarce and valued resources, how can this be reconciled with the possibility of intergroup conflict, or even of overlapping ranges? The question of how members of such a social group would protect their labor and effort needs to be addressed.

The discovery of these sites has raised an important issue: What proportion of hunting versus scavenging did Plio-Pleistocene hominids engage in? Perhaps spurred by the increasing popularity of the gathering hypothesis, some researchers are skeptical that the Plio-Pleistocene archaeological and faunal assemblages do, in fact, indicate hunting. They propose scavenging as the major source of whatever animal tissues were in the early hominid diet (e.g., Shipman, 1985).

This hypothesis can be evaluated by subjecting it to ecological principle. The ecology of predation and scavenging makes it unlikely that "scavenging" is an adequate characterization of our ancestors' major subsistence patterns. In the first place, due to their position on the food chain, large ranges are required to support predators, and consequently, in any specific area kills by large predators are rare. Scavenging as a form of subsistence is dependent on what is left over (often, very little) from such rare kills after the predator

has finished. Add to this intense competition with micro-organisms, insects, avians, and mammalian carnivores and scavengers (not to mention the returning predator or its kin). The ability of avian scavengers to scan large areas from a great height, and to escape readily when threatened, make scavenging a feasible mode of subsistence for them. Micro-organisms have their own defenses (Janzen 1979), which rapidly render carcasses toxic, disease-ridden, or otherwise dangerous to vertebrate competitors. Specialized vertebrate scavengers have dietary adaptations which, to some extent, counteract these dangerous aspects of rotting meat. Moreover, hominid competition for such remains would be actively dangerous: most mammalian scavengers are themselves predators. Active scavenging would continuously lead hominids to converge on the same resources as those dangerous animals. To compete for meat against the formidable predators who killed it, and the large and/or social scavengers who otherwise exploit such resources indicates a substantial measure of aggressive formidability not well captured by the phrase "timid". Even if scavenging opportunities are imagined to be limited to the even rarer occasions when kills have been abandoned by the predator(s) and have not yet been discovered by other scavengers, such behavior continually courts danger. The older the meat, the more dangerous and unwelcome it would be to the less well defended members of hominid groups. Given the possible costs, avoidance rather than exploitation might be the expected behavior.

Scavenging as a niche is a specialized and competitive one. Observed primate behavior testifies to this: many kinds of primates have been exposed to abandoned kills throughout their evolutionary history as an occasional opportunity, but they very rarely avail themselves of dead carcasses (DeVore and Hall, 1965; Strum, 1981). Instead, they tend to limit their meat consumption, with few exceptions, to animals that they themselves have killed. Even modern humans do not seem to scavenge much, despite the fact that the dangers posed by parasites and toxins can be neutralized by cooking. Modern hunter-gatherer practices would seem to set an upper boundary on scavenging as a hominid activity.

In short, those who propose that hominids acquired most of their meat through scavenging are confronted with a number of problems and a major contradiction: if hominids were formidable enough to scavenge, hunting itself was open to them as an option. Why not also hunt, or solely hunt? Hunting only opposes the hunter to game animals, which are intrinsically far less dangerous than predators. The fact that mammals that scavenge also tend to hunt indicates that scavenging without hunting is not a realistic mode of subsistence. Cooperative and manual or tool-based hunting seems far less dan-

gerous, given the possibilities of game driving, ambush, and weaponry. Moreover, slaughtering the freshly killed animal and carrying off the richest and most rapidly consumable parts is far less conspicuous to scavengers who search by scent, and would be less likely to draw them to vulnerable hominids at their home bases. Instead of the opposed concepts of the timid scavenger and the fearless hunter, a fairer characterization would be the timid hunter and the fearless scavenger.

Finally, the archeological finds indicate that meat and bone handling were major activities. For hominids to develop the practice of stone tool manufacture, stone transport over large distances from the sources of raw materials, and localization of recurrent animal processing sites—and that evidence of these activities and the attendant heavy bone accumulation is rich enough to have survived across 2 million years—indicates that these activities were neither marginal nor occasional. Opportunistic scavenging alone with its rarity and risks would not justify the expenditure of the efforts the archaeological record indicates. The skills this requires would have also opened the far richer (and less dangerous) food source of direct hunting.

From the evidence of cut marks on large bones (from animals that were presumably too large to have been killed by early hominids), most observers would agree that some opportunistic scavenging of meat occurred. (It is equally true that the remains of smaller, hunted game will have been lost from the fossil record). From the evidence of large, broken bones in association with battering stones, it seems equally clear that scavenged bones were exploited for their marrow content (Isaac 1983b; Binford 1983, 1984). What remains at issue is the frequency and importance of scavenging behavior at the various stages of hominid evolution.

The hunting hypothesis. Numerous authors, beginning with Darwin, have argued for the primacy of hunting in human evolution (Darwin, 1871). The hunting hypothesis was advanced in both sophisticated (Washburn, 1958; Washburn and Lancaster, 1968) and sensational forms (Ardrey, 1961, 1976; Dart, 1953), but has since fallen from favor for cultural reasons (feminist revisionism) and because quantitative analysis of certain modern hunter-gatherer diets indicates that plant foods provide the majority of the calories. The refutation of the hunting hypothesis in its extreme and unsophisticated forms has been regarded by many (Lovejoy, 1981; Zihlman, 1981; Shipman, 1985; Tanner, this volume) as definitive, and with only a few notable exceptions (see especially Hill, 1982), the role of hunting has been discarded or downplayed in recent discussions of human origins. However, the application of strategic modeling to the issue

of the role of hunting indicates that, when considered in the context of an integrated social structure, hunting offers certain compelling features that make a reassessment of its role necessary.

Although only a cursory analysis is possible here, the major conclusions are clear: if hunting were a major part of hominid foraging, it would elegantly and economically explain a large number of the unusual aspects of hominid evolution:

Male parental investment: Meat is a richly concentrated food source, well worth transporting and effective for provisioning. The major cost of acquisition and transport can be accomplished by males, making MPI an attractive alternative to additional competition for females. Hunting provides a ready explanation for MPI, which gathering vegetable foods cannot plausibly match; it is not efficient to carry low calorie foods large distances. High MPI through food provisioning among mammals is very rare in the absence of carnivory. If MPI is considered to be a major feature of human adaptation, hunting is the most likely explanation for it.

Sexual dimorphism: The reduction in sexual dimorphism across the hominid lineage may be explained through increased male parental investment. As noted, the most bioenergetically plausible form of investment is the provisioning of females and young through the capture and transport of animals.

Male coalitions: As Eisenberg (1981) and others have pointed out, the availability of large game animals has selected, among the carnivores, for social hunting. The degree of human coalitional behavior and capacity for extended cooperation represents a phenomenon requiring explanation, and social hunting provides one major plausible explanation. Any explanation of the elaboration of the cognitive and motivational substrate for cooperation and coalitions must posit recurring situations with major economies of scale and returns to cooperation of additional individuals. The only alternative (but not mutually exclusive) explanation is intergroup aggression and defense, as in chimpanzees.

Reciprocity, sharing, and social exchange: There is little limiting nonhuman primates from engaging in extensive reciprocal relations except the relative rarity of items and actions for exchange. Reciprocal altruism is far greater in humans than in any other animal. Meat, unlike vegetable foods; comes in discrete quantities: an entire animal is either captured or lost. Moreover, the size of the animal pursued depends more on what opportunities present themselves than on the degree of hunger of the hunters. Vegetable foods, on the other hand, come in more continuously graded quantities, and the quantity gathered is more directly related to the energy expended and the amount needed. As is well recognized, the variability in hunting success, and

the fact that meat comes in chunked quantities often in excess of what the capturers can readily consume, provides a ready explanation for food sharing, food exchange and risk sharing through deferred reciprocation among the larger social group. It is difficult to find in plant foods plausible attendant selection pressures that could explain these unique hominid psychological capacities. Strum and Mitchell (this volume) report that extensive hunting among baboons in their study has led to occasional meat sharing, a behavior notably unlike the usual reluctance of baboons to share food.

Sexual division of labor: Among primates, males differentially engage in hunting, no doubt because of their greater size and because females are so often encumbered with dependent offspring. As noted, successful hunts frequently leave the hunters with more meat than they can readily consume, and this provides an explanation for food sharing and reciprocation between the sexes. Extreme differentiation of foraging is not feasible without food exchange between males and females. If males changed from occasional to intensive hunting, one consequence would be the extreme sexual division of labor found among humans, with females exploiting the more sessile food sources. Male parental investment through provisioning, exchange of hunted for collected food, and exchange of meat for sexual access all provide possible and mutually compatible avenues for the extreme development of the sexual division of labor characteristic of modern humans. The evolution of this behavior requires no qualitative leaps from other primates: in chimpanzees (Teleki, 1973) and baboons (Strum, 1981; Strum and Mitchell, this volume) estrous females receive disproportionate shares of meat from hunts made by males.

Home bases: For food exchange and meat provisioning to take place between independently foraging subgroups, there must be a home base. Such a meeting area to exchange food makes sense if the supply is irregular: either more (in the case of success) or less (in the case of failure) than the hunters would need for themselves. It is harder to create a plausible model of selective forces that would make this novel behavior pattern adaptive if the only food exchanged is collected plant foods. Other primates, foraging on vegetable foods, have never engaged in extensive (non-meat) sharing, or met regularly at any location to share foods. In contrast, male *anubis* baboons do return to the social group with kills (Strum and Mitchell, this volume).

Stone tool use: The major function of stone tool use appears to be for the slaughter of game animals. The earliest hominid archaeological evidence, dating from over 2 mya, is of slaughter sites and game butchery. Unambiguous evidence of plant processing does not appear until far later, though preservational bias could wholly explain this difference (Isaac 1978a, b).

Brain size: The human brain is an extremely metabolically costly organ (Martin, 1983). It may well be that this cost can only be justified if this expanding hominid brain, in turn, also makes rich new sources of food possible. We know that all carnivores have significantly higher encephalization quotients than do non-predators (Jerison, 1973), that some nutrients found in meat are particularly important to brain tissues, and that these are hard to obtain and metabolically process from plant foods (Crawford and Crawford, 1972).

Pongid-hominid divergence: Many scenarios invoke selection pressures that would have impinged equally on other hominoids, and hence fail to explain the pongid-hominid split. However, open country habitats support far more game animals, so that the opportunities and payoffs of shifting to increased predation are highest on the savannah. The forest dwelling pongids, on the other hand, would have had more fruit and much less game available. Hominids penetrating the savannah would have had increased opportunities and payoffs for hunting, and the requisite size and strength to exploit them. It is notable that the largest open country primates, savannah baboons, have been reported to have the highest rates of hunting for any nonhuman primate (Strum, 1981; Strum and Mitchell, this volume).

Geographical distribution: Human predation as a major component of a flexible subsistence strategy explains in part the ease with which humans have been able to penetrate temperate and even periglacial habitats where plant foods would be scarce during the winter.

The observation that modern tropical hunter-gatherer groups derive only about 40% of their calories from meat has been considered to undermine severely the hunting hypothesis. However, this is a *non sequitur*, unless one implicitly employs typological thinking (humans as either "hunters" or "gatherers") rather than quantitative analysis. Such findings only undermine the naive early view that humans were nearly exclusive hunters. Recent discussions of primates as general "omnivores" have similarly obscured vital distinctions in diet among different primate species (Harding and Teleki, 1981). Even if it were true that throughout human evolutionary history (and not just among modern relict populations living in unproductive habitats) humans derived no more than 40% of their calories from meat, hunting would still have played a crucial role in hominid differentiation. Such a major fraction of the diet is far from selectively insignificant, and such a proportion is far greater than that of any other primate (Harding and Teleki, 1981; Hill, 1982).

The issue is not whether humans eat nothing but meat, or even whether they derive more from vegetable foods than from meat (if

this is true), but rather, how much more meat humans eat than does any other primate. In the search for divergent selection pressures on hominids, proportions relative to other primates are what are important. Even fire-using modern human hunter-gatherers eat a large amount of meat. The lowest estimates are far higher than that of any other primate, and most temperate and high latitude human groups live almost exclusively on animal products for most or all of the year. Moreover, total caloric content is far from the sole measure of nutritional importance: the metabolic costs of synthesis and the existence of rate limiting nutrients may make calories the least important factor in optimal health or successful reproduction. To gauge accurately the relative importance of animal foods in the hominid diet, vitamins, trace minerals, essential fatty acids, calcium, and the necessity to balance amino acid proportions all need to be examined by contrasting plant foods with animal foods. Nutritional analysis needs to extend beyond muscle tissues to include the nutritional value of internal organs and blood. At the grossest level, it is impossible for modern humans to live exclusively on uncooked plant foods (e.g., cyanocobalamin deficiency).

The view that plant foods were predominant in tropical hunter-gatherer diet was based largely on the work of Lee and Tanaka (Lee, 1969, 1979, 1984; Tanaka, 1980). Although this view has gained nearly universal acceptance, it must now be revised in the light of new data. Draper's (in press.) report on the !Kung at /Du/da, who do not have access to the copious supplies of mongongo nuts available to the !Kung at Dobe (studied by Lee) indicates that the men at /Du/da invest far more time and effort in hunting, and have far more success. Similarly, Silberbauer's (1981) study of the G/wi, undertaken just prior to Tanaka's study of the same population, reports a much higher rate of hunting success and a far greater dependence on meat. The reports by Draper and Silberbauer are much nearer the qualitative estimates of hunting and meat eating made by the Marshalls among !Kung at Nyae Nyae in the 1950's (Marshall, 1976).

By considering the strategic ramifications of hunting on hominid adaptations in systematic combination, its explanatory power becomes clear. Although there has only been space to sketch in a few major relationships here, even such cursory examination shows that hunting has features that are not only fully compatible with the known outlines of human evolution, but the distinctive properties of hunting predict or account for many (though not all) of the unique features of hominid sociality.

The state of primate-derived models

Although the use of particular primate species as direct analogies for extinct hominids is fraught with problems, primates remain the

major source of data from which to derive and test evolutionary principles, explore comparative relationships, and discover the patterns of homology and phylogenetic constraint relevant to human evolution. Moreover, they provide important heuristic examples for the partial exploration of certain issues which cannot be confidently assessed on theoretical grounds alone.

Shared features of African apes. Wrangham (this volume) uses phylogenetic comparison to identify possible conservative features in social organization in an attempt to characterize the hominid-pongid common ancestor. According to this approach, shared features of social organization among humans, gorillas, chimpanzees, and bonobos are likely to have been present in the common ancestor, and can be viewed as part of an "ancestral suite" of behaviors likely to have characterized hominids (and pongids) at any point in their evolutionary history. After reviewing the available data, he concludes that the hominid-pongid common ancestor probably had closed social networks, male-dominated intergroup aggression, female transfer, a lack of alliances among females, and males mating with more than one female.

Wrangham's study constitutes an innovative contribution, and can provide important supplementary evidence to guide hominid behavioral reconstruction. However, as Wrangham himself notes, this approach as applied to these hominoids is in its infancy and adequate data are presently lacking, especially on lowland gorillas, open country chimpanzees, and bonobos. Also, there are a number of pitfalls that must be kept in mind. The first is simply statistical or probabilistic. A clear model of the number of alternatives for a given behavioral category needs to be developed, and the relative independent probabilities of each estimated. Since the number of "independent" taxa compared is small, (four), and the number of possible features that might be held in common are large, the process of exhaustively searching for common features will inevitably produce commonalities, even if features vary rapidly along lineages, and commonalities are produced entirely by chance rather than common ancestry. In Wrangham's list of fourteen characteristics, eight were considered to be similar, whereas six varied. If one simply searched for all possible similarities among, say olive baboons, Japanese macaques, howlers, and humans, one might also generate a list of identified behavioral "homologies", especially if the search list was extensive. Because these probabilities are difficult to quantify, one type of control might be to select several sets of well-studied primate species randomly, and see how many features from the same master list are held in common among each set. Although it is likely that many of the common features Wrangham identified are genuinely produced by

phylogenetic factors, and there are independent reasons to believe they constitute accurate characterizations, the cladistic method of demonstrating behavioral homologies would appear more powerful if some kind of control were incorporated.

A second dimension that needs to be closely scrutinized is the method of behavioral categorization. Behavioral categories in primatology have been fluid and often unreliable, and one wants to be certain that behaviors categorized as similar are genuinely unitary phenomena, rather than simply superficially similar. For example, common chimpanzees engage in male coalitional intergroup aggression (Wrangham, 1979a, 1980), whereas intermale aggression among gorillas, usually not coalitional, tends to occur between single males living in single male groups (with rarely more than two breeding males). It is not clear whether gorillas and chimpanzees are equally well categorized as engaging in "intergroup" aggression. To decide such questions, arguments about the appropriate categories for behavioral homology must ultimately be grounded in their functional explanation and evolutionary source: Are they adaptively the same behaviors, shaped by the same selection pressures? Alternatively, are they the consequence of the same ancestrally derived psychological or physiological mechanisms? As powerful a tool as phylogenetic inference is, it must be complemented by a comprehensive strategic model: even the successful reconstruction of the hominid-pongid common ancestor, useful as it is, will leave unanswered one of the most crucial questions of human evolution, *why are we so different from our near relatives?*

The pygmy chimpanzee. Susman's review (this volume) of the behavior and ecology of the pygmy chimpanzee or bonobo (*Pan paniscus*) contains several features relevant to the formulation of a strategic model. Compared to common chimpanzees, bonobos appear to manifest increased arboreal feeding, smaller day ranges, less time spent feeding, lower levels of aggression, less sexual dimorphism, and higher male-female and female-female affinities. Susman interprets many of the differences between common chimpanzees and bonobos as consequences of differential occupation of open country vs. forest habitats. Morphological differences are attributed to the increased adaptation of bonobos to arboreal feeding, involving modifications for climbing and suspensory activities. Such adaptations may, in fact, preadapt hominoid morphology more closely for the transition to bipedalism. As Susman points out, research on bonobos may help us judge the probability that the earliest hominids were more forest than open country dwelling.

Bonobos are the least well known of any ape, and data from bonobo studies are only beginning to be organized into a picture of

bonobo social life. Some morphological and behavioral features have prompted the proposal that they are yet another "best" model of early hominids (Zihlman et al., 1978). Regardless of their use as a single species model, however, bonobos do have features that may prove pivotal in discovering the principles governing male-female relations among hominoids, by providing yet another distinctive configuration of evolutionary variables. These features include nearly continuous sexual receptivity, the resumption of cycling within 1 year of giving birth, semipermanent male-female associations, food sharing, differential male hunting, meat sharing contingent on copulation, and cohesive mixed sex groups. Bonobos provide another case of extended male-female associations developing within the context of a larger social community. From the point of view of modern human sociality, these features are especially striking, and a principled understanding of what forces shaped them in bonobos would go a long way towards explaining many related features in humans. Close comparison between bonobos and common chimpanzees with respect to social organization may prove to be especially illuminating (see Wrangham, 1985), especially with respect to the strategic structuring of male coalitions, intercommunity relations, and male-female associations.

Baboons. Strum and Mitchell (this volume) have made an outstanding contribution both in their general remarks about the limitations of direct analogies between hominids and living primates, and more especially concerning the use of their baboon studies (*Papio anubis*) to explore a number of crucial issues in hominid behavior. First, reports on hunting by baboons under study, and leading to the highest predation rate recorded for any nonhuman primate. The relative absence of carnivores has two types of consequences: 1) the opportunities for predation among open-country forms are substantial, so that hominid penetration of the savannah markedly changed the possibilities for predation; 2) as far as hunting is concerned, phylogenetic constraint is not an insurmountable pressure: the baboons responded to the direct effects of changed ecological conditions within the short time span of the study by major alterations in the frequency and kinds of hunting practiced; 3) when carnivores are present, the risk to the baboons is significant enough to deter temporary departures from the social group; therefore, anything that reduces the risk of being preyed upon (increased body size, effective coalition formation, improvements in morphological or tool-based weaponry) increases the advantages of hunting; 4) the upper boundary on prey sizes is determined, before the advent of weapons, by the body size of the primate predator; and 5) male-female relations are indeed influenced

by hunting: males differentially do the hunting, and they share the kills differentially with estrous females, and/or with females with whom they have special long term relationships.

Strum and Mitchell's chapter also documents their careful construction of a more sophisticated picture of baboon social life, involving the increasing recognition that baboons are sophisticated social strategists, and that aggression is only one dimension of the intricate social negotiation that goes on. Additional dimensions include "friendships" between individual females and males, female buffering of male aggression, meat sharing between males and females, and the importance of social knowledge, social skills, the length of residency, cooperation, and manipulation in the web of intercontingent negotiation that dominates baboon social life. Their valuable observations and interpretations provoke a flood of questions, indicating the need for a surer analytic understanding of social interaction. For example, if prospectively delivered assistance from males towards females is "paid" for by copulations or female consortship, what protects the male from a female cheater? How are such exchanges structured? How can male investment antedate direct female reciprocity by months or years? The answers to such questions will prove vital to hominid behavioral reconstruction, because the true evolutionary parallel for hominid "monogamy" might be found in incipient form in such male-female friendships existing in a larger social context, rather than in the sexually exclusive relationships found among more solitary primates such as gibbons.

Monogamous primates. There is no issue more central to the reconstruction of hominid social systems than that of the role of monogamy, and Kinzey (this volume) addresses an array of questions that throw light on this issue. Kinzey outlines the central features of monogamous mating and breeding systems, and stresses the social poverty (or simplicity) of nonhuman primate monogamy, possibly resulting from its evolution out of solitary ancestral conditions. This naturally raises the question: Did hominid monogamy precipitate out of a larger social group and social system (like long term associations and consortships among baboons or bonobos), or did, as Kinzey asks, "a monogamous primate augment its social system to include other members into the social group?" If hominid monogamy originated inside a larger social group, the dynamics structuring male-female relationships would have been considerably different from those governing mating among initially solitary primates that became monogamous through the recruitment of the male to the mother-infant dyad, and whose social group grew in size through retaining "helpers at the nest".

There are a number of dimensions relevant to human and non-human male-female relations and the question of monogamy. They can be inventoried with the following series of questions:

- does a specific female mate exclusively with a single male?
- does a specific male mate exclusively with a single female?
- do males invest in their offspring or assist their mates or both?
- how successfully can unassisted females raise offspring?
- is there only one breeding female in the social group?
- is there only one breeding male in the social group?
- if the two mates practice sexual exclusivity, what is the duration of their relationship?
- are members of the species facultative in their selection of mating strategy?

Among primates, humans are unique in simultaneously practicing (on a facultative basis): high MPI, multiple breeding males and females in the same social group, and sexual exclusivity (of at least limited duration) of individual females for males and males for females, frequently simultaneous and reciprocal. The features of this unique mating system are not directly paralleled by any other primate, and are not well captured by the term "monogamy", especially given the statistical distribution of deviations on most of these practices. To construct an image of the selection pressures constituting these unusual behaviors, one must look to many different primate mating systems to find the component parallels, and it requires behavioral ecological principles to analyze how they all work in combination. Common chimpanzees, bonobos and savannah baboons manifest extended relationships between individual males and females among larger social groups. Gibbons and a few New World primates practice monogamous sexual exclusivity. Hamadryas baboons and gorillas have females exclusively attached to a single male, while certain tamarins and marmosets, formerly thought to be monogamous, now appear polyandrously to have several males attached to and mating with a single female (Sussman and Kinzey, 1984; Kinzey, this volume). Although many aspects of mating systems and their consequences are beginning to be understood (e.g., the reduction of sexual dimorphism in monogamous species, the relationship between paternity certainty and MPI), many still need to be sorted out. These puzzles include the determinants of female-female tolerance and intolerance (an important factor in neotropical monogamous and polyandrous species), female dominance and the inhibition of ovulation, and the determinants that lead to low female reproductive success in the absence of male assistance. However, perhaps the single major question facing hominid social theory is the reconciliation of group life with high MPI and sexual exclusivity. What role intergroup conflict

(as in lions and chimpanzees) may have played in this process is another crucial question.

Howler Monkeys. Beginning with Carpenter's pioneering work in 1934, howler monkeys have been the object of systematic study longer than any other primate. Because many of these studies have been based on Barro Colorado Island, there are now more long-term data on the BCI population than for any other monkey or ape. Howlers have also been studied in a greater variety of habitats than other primate genera, and provide a New World counterpart to the numerous studies of macaques and baboons.

By virtue of their phylogenetic distance from the Old World primates, no one, including Crockett (this volume) has yet been tempted to propose a "howler model" of hominid evolution. Instead, Crockett's approach is very much in the spirit of the strategy urged in this essay, namely, the development of principles of behavioral ecology that apply across taxonomic groups, and hence can be used to reconstruct aspects of hominid behavior. As she points out, the observation of sexually selected infanticide among red and mantled howlers provides additional confirmation of at least one evolutionary principle that applies systematically across highly diverse taxa, raising the question of what role, if any, sexually selected infanticide played in human evolution. Her documentation of female emigration, a rare occurrence in mammals (but present in the African apes and humans), is a welcome addition to our principled understanding of this feature of primate social organization.

Because her report includes behavioral ecological comparisons of six howler species occupying a broad range of habitats, it is now clear that the feeding strategy in this folivore-frugivore is anything but simple. While howlers can be said to occupy a "single" feeding niche, it is obvious that their foraging and activity patterns are enormously affected by environmental variation, both in habitat and in seasonal differences. Such observations suggest the perils of relying on the purported implications of a "single" feeding strategy, whenever this is advanced for a particular stage of hominid evolution. Finally, her discussion of sexual dichromatism is a healthy reminder that many features of sexual dimorphism (including important secondary sexual characteristics of humans) will not be preserved in the fossil record, and that natural selection may operate very differently on the two sexes.

The state of paleoecological methods

Paleoecological reconstruction depends on the mutual development of evolutionary principles and the methods that supply the data

necessary for inferential reconstruction. Evidence is only interpretable or made meaningful by validated theory; without coherent theory, one is unable to recognize evidence, categorize it, relate it, or make valid inferences from it. Precisely because hominids are so remote from direct observation, methods (and the models that make them possible) play a central role in hominid reconstruction. Both Marks (this volume) and Sussman (this volume) suggest what may become important new methods for paleoecology, methods that use the features of living animals comparatively to assess ancestral conditions.

Cytogenetic Methods. Marks proposes an ingenious new approach to the determination of ancestral hominid and pongid social structure. By searching for the social and ecological correlates of recognizable cytogenetic patterns, and examining humans and pongids for these patterns, Marks suggests that the long term average mating structure along lineages can be inferred. According to this method, the rate of karyotypic changes indicates the degree to which a lineage's mean mating system favors genetic drift and lineage fixation of neutral chromosomal variants. Small group size, monogamy, arboreality and small range size are factors that may inhibit gene flow, whereas polygyny, high rates of transfer and large social groups are the sorts of factors that retard the establishment of chromosomal variations among populations. Because Marks estimates that the number of chromosomal variations along the human lineage is approximately comparable to those among chimpanzees and gorillas, he infers that in terms of social structure, humans more closely resembled chimpanzees and gorillas than they did the social structure of either gibbons or baboons. He is properly cautious about the reliability of the results, and fully cognizant of the work that remains to be done to establish the validity of the method.

The prospect of assessing, even approximately, average parameters of a lineage's social structure is very intriguing. Certainly the direction taken needs to be developed as fully as possible. Relating observed cytogenetic patterns to observed social systems is the first step, but further elucidation of the causes of the relationships will allow the interpretation to become more detailed and reliable. There is good reason to believe that many aspects of the genome are shaped by the interaction between parasite pressures, ecological factors, and social organization (Tooby, 1982), including the degree of polymorphism, the rate of protein evolution, and chromosome number and conformation. Some of the relationships between social organization and chromosomal evolution may not be due simply to their effects on fixation of neutral variants, but might be driven by parasite pressure instead. If so, the estimates drawn from the observed rate

of changes may need to be somewhat recalibrated to take into account differing degrees of parasite pressure. However, this in itself may provide interesting data about ancestral habitat.

Morpho-behavioral Analysis of Primate Diets. Sussman (this volume) proposes that ancestral diet can be inferred on the basis of conservative features of the digestive tract. On the basis of a preliminary, allometrically corrected, comparative analysis of the proportionate potential areas of absorption in gastrointestinal compartments, Sussman found that his sample of modern humans clustered with other faunivorous mammals. This is consistent with the results of Martin *et al* (1985). However, Sussman cautions that the factors he has chosen to study may unfortunately be environmentally malleable, and so may not after all tell us about ancestral diets.

Regardless of the specific merits of Sussman's method, the general direction of study has much to commend it. Diet is the primary factor allowing or constraining the rest of a species' system of adaptations. If it could be ascertained what a given ancestor's diet was, (i.e., 40% meat, or 90% fruit, etc., many of the constraints necessary for the inference of its system of adaptations would be present. The inference of ancestral diets from modern humans is an effort that has scarcely begun, and the scrutiny of conservative aspects of our dietary physiology and biochemistry may ultimately reveal a great deal. Species-specific nutritional requirements provide an entry point: the patterns involved in what must be supplied in the diet, what can be synthesized, and what must be present to effect cross-synthesis all constitute an unmined vein of information on ancestral diets. An animal can afford to lose the ability to synthesize a nutrient if it is reliably present in the diet. An animal must be able to synthesize out of available dietary substrates what is essential but always lacking in the diet. The hierarchy of absorption and cross-synthesis can potentially reveal considerable information on the relative abundances of different nutrients in the diet. Vitamins, essential fatty acids and structural fats, minerals (especially calcium), and amino acids all provide a starting point. The biochemistry of digestion, absorption, and detoxification may also prove to be highly revealing: special function digestive enzymes all provide compelling evidence that a specific protein, sugar, or toxin was abundant in the diet. Various amino acids are differentially absorbed, and can displace each other in a hierarchy. Presumably, the scarcer and more important the amino acid is, the more the digestive system is selected to absorb it efficiently. The profile of amino acids in ancestral diets might be inferred from such a hierarchy. Examining the physiology and biochemistry of human digestion and matching it against the nutritional

profiles of various foods (cooked and uncooked fruits, tubers, nuts, shoots, leaves, bulbs, seeds, meat, liver, heart, brain, blood, marrow, etc.) can settle debates about recent hominid diet.

DISCUSSION AND CONCLUSIONS

Strategic modeling has the potential for resolving a number of the thorniest issues concerning human evolution. For example, many social scientists (e.g., Geertz, 1973; Sahlins, 1976; Harris, 1979) have defended the notion that, due to intelligence and the capacity for culture, human behavior has become independent of evolutionary forces. They argue that in the transition from simpler primate behavioral mechanisms to the more elaborated and powerful ones present in modern humans, a crucial boundary was crossed. Many regard this, almost mystically, as a watershed transition that places human phenomena in another category entirely, beyond the capacity of evolutionary and ethological methods to study, model or understand. They take the uniqueness of humanity to mean that human behavior is incomprehensible in evolutionary terms.

The immense difference in the complexity and variation of behavior among primates, protohumans and humans is tractable to strategic modeling. Essential to strategic modeling is the distinction between proximate means and evolutionary ends. Proximate mechanisms are selected ("designed") to accomplish the promotion of inclusive fitness. This end is fixed; it is intrinsic to the evolutionary process. However, the proximate mechanisms by which fitness is promoted change over evolutionary time, depending on factors such as the previous adaptive constellation of the species, what mutations have occurred, ontogenetic constraints, and the existence of preadaptations (exaptations [Gould and Vrba, 1982]). The elaboration of mechanisms from the simple into the complex changes only the proximate means, not the evolutionary ends. In fact, such changes will occur only when they increase inclusive fitness—only when they better promote the same evolutionary ends.

Humans are characterized by a remarkable expansion in intelligence, consciousness (however defined), complex learning, and culture transmission mechanisms—all interpenetrated by a sophisticated coevolved motivational system. Strategic modeling is uniquely suited to the analysis of these mechanisms, precisely because it analyzes mechanisms in terms of evolutionary ends, which do not change. As intelligence, learning, consciousness and motivational systems progressively become more sophisticated, they still serve the same strategic ends according to the same evolutionary principles. To methods of analysis that focus only on proximate mechanisms, unprecedented

capacities are discontinuities, difficult to investigate. But to strategic modeling, they are not discontinuities at all; they are new (and gradually complexifying) expressions of the same adaptive processes. For rapidly changing proximate mechanisms, invariances exist only at the strategic level. Hence, strategic modeling is the method most suited to the investigation of hominid evolution and human behavior—it is the method least thwarted or confused by hominid singularity.

In fact, instead of being divergent from evolutionary principles, sophisticated hominid mechanisms may more purely incarnate adaptive strategies. Hominids' more intelligent, flexible and conscious systems are less limited by mechanistic and informational constraints; they can more sensitively track special environmental, historical, and situational factors and modify their behavior in adaptively appropriate ways. Evolutionary processes select for any behavioral mechanism, no matter how flexible or automatic, that increases fitness. Although the invocation of strategies does not imply that the actor is conscious of what he is doing or why, it may in fact be true that humans are more aware of their strategies for pursuing proximate motivational goals (goals that correlate with fitness).

Those who continue to assert that humans became immune to the evolutionary process must somehow reason their way past the following fatal objection to their position: the innate characteristics that have become incorporated into the human genome were incorporated because they increased inclusive fitness, and therefore they are adaptively patterned. To assert anything else is to maintain that somehow a large number of less fit innate characteristics (ones that did not correlate with fitness) displaced those that were more fit. In other words, advocates of this position must explain how evolutionary processes systematically produced maladaptive traits.

Twenty years ago, evolutionary theory and behavioral ecology did not have sufficient definition to be very helpful in research on human origins, but their present maturity and accelerating progress mean that they have the potential to become an essential tool in paleoanthropology. Even in its present form, behavioral ecology is largely neglected as a resource for paleontological interpretation. However, it is no longer possible to treat a proposed scenario as if one hypothesis is as good as another. We know that certain hypotheses, such as Lovejoy's (1981) and Zihlman and Tanner's (1978), cannot be true, because they violate validated principles of evolutionary biology. To construct hypotheses about extinct hominids seriously, a researcher must now be cognizant of an entire armamentarium of principles and analytic tools. To progress, paleoanthropologists must be prepared to discard prime mover and single-primate-species models of human

evolution, and recognize that evolutionary biology can provide the conceptual model that will organize our understanding of hominids. The central labor in paleoanthropology is the development of this set of inferential procedures (the principles of strategic modeling), deduced from evolutionary theory, refined with empirically validated evolutionary biology, phylogenetically honed by primate studies, and fitted with specific evidence about hominids deduced from traces left in their living descendants, their fossils, the archeological record, and the reconstruction of paleoenvironments. The trajectory of hominid evolution can eventually be deduced by applying these inferential procedures to the available data. This set of tools is far from complete, but at least we now can begin to outline what, at minimum, a serious effort at hominid behavioral reconstruction should encompass. We can now target the specific knowledge we will need to recover about hominids to discover how these evolutionary principles uniquely express themselves in the hominid lineage. By this process the enterprise of understanding hominids will eventually be transformed from a historical and descriptive enterprise into a fully scientific one: of theory, hypothesis testing, reduction of uncertainty, and the explanation of many facts by a few central features.

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