20 • Savanna chimpanzees, referential models and the last common ancestor

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INTRODUCTION

Many a great ape grant proposal has waxed on about insights that the proposed research would provide into the behavioral ecology of our early ancestors (see Zihlman, Chapter 21), and the term 'model' is ubiquitous in the resulting literature (e.g. Jolly, 1970; Kinzey, 1987). What is a model in this context? It is important to know, because (justified or not) people often draw inferences about modern humans from such models. Skybreak (1984) describes the referential (i.e. analogical with an existing species) baboon model:

> Implicitly or explicitly, savanna baboons have been repeatedly proposed as models for our own earliest origins or as a basis for understanding human aggression, xenophobia, class structure, and the domination of women, all seen as rooted in biological evolution (and by implication, thus very resistant to change).
>
> *Skybreak, 1984, p.84*

One might think that she would reject all such referential models, with their putative biological determinism, but instead she supports Tanner's (1981) chimpanzee model. One of the many meanings of the word 'model' is 'something held up before one for imitation or guidance' (*Webster's New Collegiate Dictionary*, 1951), and one wonders whether there might be some cognitive spillover among usages. It would be understandable; the word is remarkably protean, as illustrated by this imaginary dialogue (italicized words have been used as approximate synonyms of 'model' in the literature):

'Your so-called *hypothesis* is nothing but an untestable *scenario* based loosely on some vague *metaphor*. It has no *theory* supporting it, leaving it no more than a crude *sketch*, an *overview* without substance.'

'On the contrary! It is a detailed *reconstruction* based on the best available *analogy* for the phenomenon, suggesting a reasonable *prototype* for consideration as a *precursor* to hominids.'

In addition to argument over the best referential model (i.e. species) to use, there seems to be much uncertainty about what a model *is* and what *type* of model (if any) is useful in scientific inquiry. I begin by addressing these two issues, and then discuss the potential for use of savanna-dwelling chimpanzees in modeling early hominids and the last common ancestor (LCA) of humans and the African apes. My goal is not to construct a particular scenario, but to pose a series of specific questions that we might ask of a chimpanzee model. By doing so I hope to suggest directions for paleoanthropologically relevant research on modern chimpanzees, and to stimulate discussion regarding the utility of such referential models in research on hominid behavioral ecology.

WHAT IS A MODEL?

A model can be a world view ('the scientific model'), a body of theory (saltational models of evolution), a strict set of formal instructions (a mathematical model), a set of ideas related to a central conceptual focus ('the hunting model'), or a direct referential analogy ('the chimpanzee model'). At first these usages seem divisible into two classes that are sets of linked ideas and concrete physical analogies, but the line is blurred, e.g. the 'social carnivore model.' Table 20.1 presents an attempt to sort out the relevant terminology. It is offered not in any naive hope that the discipline will adopt these distinctions, but to encourage others at least to be explicit about how they use the terms.

Table 20.1. *An idiosyncratic thesaurus for hominid modelers*

Analogy. A relation based on similarity between specific attributes of two things, a model and its referent. The similar properties can be thought of as the positive analogy of the model and dissimilar properties the negative analogy; finally, properties of the model which may or may not be similar to the referent are the neutral analogy – and it is these properties that are of interest (Hesse, 1966, pp. 8–10). Formally, analogy refers to similarity due to convergence rather than common descent (i.e., homology); in the present context the two seem almost inextricably interwoven.

Hypothesis. A specific tentative idea that is in principle amenable to qualitative or quantitative testing; distinguished from scenario in being more narrowly circumscribed.

'Just-so' story. Someone else's model (*sensu lato*), with which one disagrees.

Metaphor. A figure of speech intended to invoke a feeling of similarity without providing a formal hook upon which to hang it; useful rhetorically but not analytically.

Model. (noun) The known member of an analogous pair. (verb) The process of constructing a scenario of or about the unknown member of an analogous pair (the referent).

Overview. Similar to 'sketch,' with little power to mislead.

Precursor. Outside of science fiction, we cannot make a literal precursor of an extinct species; the very concept of an evolutionary 'precursor' is uncomfortably teleological. To be avoided.

Prototype. As with 'precursor,' only more so; carries the additional danger of invoking the image of a Platonic 'ideal type' and so implicitly downplaying variation (ecological, genetic, sexual) among both model and target populations.

Reconstruction. This is not literally possible (except as applied to fossils); as commonly used, it is synonymous with 'scenario' but sounds more precise. Precisely for that reason, the noun should be avoided. As a verb it is more useful; one can use an analogy to help reconstruct (model) a facet of the past for use *in* a scenario.

Scenario. A broad, internally consistent 'story' about the behavior and ecology of a specific extinct taxon, e.g. 'the hunting scenario for *Homo habilis*' (which generates a number of specific hypotheses, e.g. 'if hunting was important, butchery marks on bones should be distributed in X fashion').

Sketch. Deliberately self-effacing, the term cannot do much damage however it is used.

Theory. Too often used as a formal-sounding synonym for 'idea' or 'suggestion,' which is the sense in which it has overlapped with 'model' in the evolutionary literature.

In this paper I will argue for the utility of a chimpanzee analogical model in trying to construct testable scenarios describing the behavioral ecology of the LCA and earliest hominids. Before doing so, the danger of 'mental spillover' between theory and model must be emphasized. It is all too easy to see in the data what theory predicts, or begin incorporating into theory what is really only an aspect of the analogical model (Fedigan, 1992, 16–21). For example, a considerable amount of primatological 'theory' may owe its origins more to the 'terrestrial cercopithecine model' than anything else, given unavoidable biases against arboreal and New World monkeys (Moore, 1993; Strier, 1994). (Note: there is little difference between referentially using one species or a dozen; the plural of example is examples, not 'law', at least until such time as the sample is exhaustive.)

ARE ANALOGICAL OR REFERENTIAL MODELS USEFUL IN SCIENCE?

There are two axes to this question. First, are referential models anything more than heuristic devices; second, if we accept referential models as useful, what are the roles of analogy and homology in choosing a given model?

Models: mere heuristics, or essential components of understanding?

Hesse (1966) discusses analogies and models using the arguments of physicists Pierre Duhem and N. R. Campbell to characterize two major positions. To Duhem, analogical models may be useful heuristic devices in thinking about a problem, but ideally are supplanted by the final static logical or mathematical theory that fully specifies the solution. Campbell believes that theories are dynamic and depend for growth and predictive ability in new domains upon analogies with existing models; secondarily, to be successful a theory must be intellectually satisfying and this often depends upon being intelligible in terms of a model (Hesse, 1966, pp.1–5).

Tooby & DeVore (1987) open a similar debate in paleoanthropology. They argue that 'referential models' based on analogy are inherently inferior to 'conceptual/strategic models' derived from evolutionary theory. Without rules for determining which traits are shared by model and referent, choice of a model is arbitrary; furthermore, without some guiding theory there is no way to know which differences are important or what their effects will be. In the absence of such rules and theory, referential modelers are forced to emphasize similarities between model and referent – when the ultimate goal of paleoanthropologists is to understand what makes humans different. Therefore, Tooby & DeVore say, we should focus on developing conceptual rules and theories; individual taxa should be treated as sources of data points for comparative studies, not as models.

It is likely a mistake to try to opt absolutely in favor of either conceptual or referential modeling in paleoanthropology. It is more productive to see each as contributing to overall understanding through a cyclical process of refinement (see Rubinstein et al., 1984, pp. 131–9). The essential step is to attempt to use a combination of referential and conceptual modeling to generate hypotheses that are or may become testable using paleoanthropological or comparative data.

For example, in discussing possible sex differences in hominid food sharing, Tooby & DeVore (1987, p. 218) rely on the theoretically-based assumption that emigration is essential in order to avoid inbreeding depression. Theoretical debates notwithstanding (Moore,

1993), evidence is mounting that in some primates and delphinids, *neither* sex consistently emigrates from its natal social group (Moore, 1992c; Amos et al., 1993). Thus 'referential models' – here, Barbary macaques (*Macaca sylvanus*), pilot whales (*Globicephala melas*) and killer whales (*Orcinus orca*) – can demonstrate the inadequacy of existing theory for conceptual/strategic modeling of a particular unique species: when there are three exceptions to a pattern, there may be more. Clearly humans are not killer whales; these exceptions show that Tooby & DeVore were *premature* in their conclusion but they do not show that the conclusion was *wrong*. Only after discovering the underlying basis for the distribution of natal philopatry by both sexes can we hope to say that early hominid food sharing likely was or was not constrained by emigration patterns. It is the continuing cycle of incorporating insights derived from natural history and referential modeling into the theories used by strategic models that is important.

Analogical or metaphorical models can be important ways of representing phenomena. To explore this issue would lead into philosophy of science on the one hand and into cognitive science and linguistics on the other (see Merrell, 1991; D'Andrade, 1992; Wharton et al., 1994; Holyoak & Thagard, 1995, for starting points). To the extent that (some) people think metaphorically, models of one sort or another are simply unavoidable; as stories they are remarkably common in paleoanthropology (Landau, 1991).

Models: the proper use of homology and analogy

A referential model may be based on homology (similarity due to common descent, e.g. related chimpanzee), or analogy (similarity due to common adaptation; e.g., terrestrial baboon). The importance of distinguishing such bases is illustrated in the controversy over the 'pygmy chimpanzee model' of Zihlman et al. (1978). Responding to Johnson (1981) and to Latimer et al. (1981), Cronin (1983) writes:

> ... objections to our model center around the observation that *Australopithecus* sp. ... do not look like *P. paniscus*. This constitutes an absurd mastery of the obvious. ...
> We did not say that *P. paniscus* would be identical to the *Australopithecus* sp., but instead that the earliest hominids

would resemble *P. paniscus* more than the other living African hominoids.

Cronin, 1983, p.132.

That so many capable researchers end up arguing at such cross-purposes is more than a little worrying. I believe that there was confusion over the *purpose* of the model, which in principle may have been intended either to: (a) suggest a morphotype of the LCA based on homology, in order to facilitate recognition of relevant fossils; or (b) help illuminate the general characteristics of the LCA, in order to function as an analogy – in which case the key thing is *not* to resemble the target too closely, since the information sought may lie as much in the difference as in the similarity (Hesse, 1966; Hinde, 1976).

In reading the exchange, it seems that neither Zihlman *et al.* (1978) nor Latimer *et al.* (1981) have a very clear idea of which of these was intended. The former cite pygmy chimpanzee sexual and communicative behavior, irrelevant to an osteological morphotype; the latter dismiss the model because of lack of identity – which clearly misses the point, as Cronin (1983) shows. Explicit attention needs to be paid to the purpose as well as to the structure of referential models. Further discussion of analogy and homology can be found in von Cranach (1976), Cartmill (1990, 1994) and Gifford-Gonzalez (1991).

Are referential models useful in paleoanthropology?

A referential model potentially can prove useful in several ways (see Potts, 1987 and McGrew, 1992, for further discussion):

It can show what is possible, e.g. the hypothesis that significant rates of hominid hunting would have required weapons and conscious coordination of hunters is disproven by chimpanzees (Stanford, 1996).

As part of a narrow-focus comparative approach, it provides the only possible method of incorporating certain demographic parameters such as dispersal into our scenarios (cf. Wrangham, 1987).

It can suggest important new ideas, such as the realization that sex differences in chimpanzee

insectivory might illuminate origins of sexual division of labor in hominids (McGrew, 1979, 1992).

It can generate a detailed scenario from which testable predictions can be derived ('if the LCA was just like a baboon except for [insert fossil data], then we should see X in the paleontological record of the LCA'; see below). While this approach can be useful, it is the most dangerous because it is here that confusion of model and referent is most likely to occur (cf. Tooby & DeVore, 1987).

Referential models have a number of advantages as well as dangers. At the least they provide a heuristic framework for thinking about a problem, and at best can be used to set up middle-range tests of hypotheses (see below). Their greatest danger is that models are easily mistaken for that which they model; critically, by creating a mental prototype they can mask variation and so block use of the comparative method for testing hypotheses (Hinde, 1976; Strum & Mitchell, 1987; Wrangham, 1987; Potts, 1994). This danger is especially serious in hominid modeling; normally the information provided by an analogy lies entirely in the difference between model and target (Hesse, 1966; Hinde, 1976), but in paleoanthropology this is too strict – a living hominoid identical to the LCA would be extremely informative. This difference in the nature and utility of paleontological analogy versus analogies in physics or human biology may contribute to the confusion over appropriate use of models in the field. Every sort of model has its hazards.

CHIMPANZEES AND THE LCA: SIMILARITY AND DIFFERENCE

Before any living ape can serve as a referential model for early hominids and the LCA, it is important to be as clear as possible regarding similarities and differences between the model and the referent. My thesis is that:

1. The LCA was roughly similar to modern chimpanzees in size, encephalization, habitat, diet (but with important differences) and perhaps locomotion. This thesis is supported by two lines of evidence: the fossils themselves and

molecular evidence suggesting that the African ape lineage is morphologically conservative (see Appendix to this chapter and also Zihlman, Chapter 21). It simply is not true that chimpanzees and modern hunter–gatherers are equally useful (or useless) as models of the LCA (*pace* Cameron, 1993).

2. These similarities suggest that the LCA and early hominids would have been subject to selective forces similar to those affecting modern chimpanzees. Further, the transition from forest to savanna that occurred in the hominid lineage may therefore have involved ecological and social adaptations similar to those exhibited by a comparison of forest versus savanna chimpanzees (Collins & McGrew, 1988).

   However, the LCA and early australopithecines may have been very unlike modern chimpanzees in being highly sexually dimorphic (Kelley, 1993; Kimbel *et al.*, 1994). It is therefore necessary in effect to consider two chimpanzee models. The first is a direct analogy in which the LCA and early hominids are considered similar in dimorphism to modern chimpanzees (cf. Zihlman, 1985). In the second, they are considered highly dimorphic and the principles of strategic modeling (*sensu* Tooby & DeVore, 1987) are used to 'adjust' the analogy accordingly.

3. The initial hominid adaptations to a 'savanna'-type niche took place in savanna woodland, rather than in denser forest or open shortgrass plains (Suzuki, 1969; Moore, 1992a). For now, this is merely an assumption of the model to be tested against future paleo-environmental reconstructions. Recent analyses support a woodland habitat for Plio-Pleistocene hominids, so the assumption is not ungrounded (e.g. Sikes, 1994).

4. The utility of the analogy will depend on the ability to test elements of it against paleontological data; with increasing correspondence between discoverable elements will come increasing confidence in nonverifiable aspects of the analogy. Conversely, to the extent that elements of the analogy are untestable or

are disconfirmed by data, the usefulness of the general 'chimpanzee model' is questioned.

5. Even if the analogy seems to work well, it is important to remember the limits of analogy. The analogy between waves of sound and light was useful in the development of optical theory, but did result in the erroneous postulation of 'ether' (Hesse, 1966).

Together these assumptions constitute the basis for a referential model that can be used to generate specific hypotheses to be tested against either fossil or archaeological data (e.g. 'savanna chimpanzees prefer hillsides, so the distribution of early hominid sites should be biased toward hillsides') or modern forest versus savanna comparisons (e.g., 'early australopithecines showed a trend toward postcanine megadonty suggesting exploitation of rough or hard foods, so savanna chimpanzees should incorporate more such foods in their diets'). These two examples may seem hopeless or naive: how many *in situ* early sites of demonstrable topography can we hope to find? Why assume a connection between expanded diet breadth in modern apes and the highly specialized megadonty of australopithecines? Here I hope to push this chimpanzee model to its limit; if the result is uninformative, then skepticism toward chimpanzee models in general is supported.

THE SAVANNA CHIMPANZEE MODEL

What about humans would we like a model to help explain? Several authors have generated lists of 'human' attributes (Alexander & Noonan, 1979; Tooby & DeVore, 1987) (see Table 20.2). Human attributes we might expect to have existed in the LCA fall into two categories: those we are confident appeared near the time of the LCA (column 1) and those that might have appeared at virtually any time in our subsequent evolution (column 2). A number of these attributes leave no direct fossil or archeological evidence. Alternative approaches that have been used to build explanatory scenarios for their evolution include:

1. Direct referential models (e.g., McGrew, 1981; Tanner, 1981, 1987).
2. Cladistic analysis (Cameron, 1993; Foley, 1989; Wrangham, 1987).

Table 20.2 *Attributes of the LCA and hominids addressed by hominid modeling*

Likely characteristics of the LCA	Novel attributes of early australopithecines	Novel attributes arising sometime post-LCA	Novel attributes arising with *Homo*
Closed social network	?Increased terrestriality	Increased meat eating	Increased encephalization
Female dispersal	Bipedality	Hunting of prey larger than self	Fire
Not monogamous	?Postcanine megadonty	Increased infant helplessness	Language[a]
Hostile intergroup relations		Increased male parental investment	Extensive reliance on (stone) tools
Male stalk and attack strangers		Concealed ovulation	Loss of megadonty
Extreme sexual dimorphism[b]		Prolonged female sexual receptivity	Reduction in sexual dimorphism[b]
		Enlarged penis	Adolescent growth spurt [females only?][c]
		Hairlessness	Food transport and storage
		Increased sexual division of labor	Kin involvement in mate selection
		Large structured male coalitions	

Source: Based primarily on Alexander & Noonan (1979), Tooby & DeVore (1987) and Wrangham (1987).

[a]Timing speculative, but probably postdates the origin of *Homo*.

[b]Reality of the attributes depends on particular taxonomic decisions.

[c]It is unclear whether or not the adolescent growth spurt is unique to humans, when it appeared, and what relation (if any) it might have to changes in (especially female) stature with *H. erectus* (Leigh, 1992; McHenry, 1994).

3. Strategic modeling (Tooby & DeVore, 1987).

4. The use of intraspecific variability in a referent to model diachronic change in the hominid lineage (Susman, 1987); to focus on process and not stasis (Potts, 1987).

In this paper I use the fourth approach, focusing on comparison of savanna with forest populations of chimpanzees and building on the work of Suzuki (1969), McGrew *et al.* (1981); Kortlandt (1983, 1984) and Laporte & Zihlman (1983); see Moore (1992a) for a definition of 'savanna chimpanzees'. I begin by asking what, from a hominoid's point of view, is different about savanna woodland?

Climate

Relative to forests, savanna woodlands are drier and rainfall is more seasonal (McGrew *et al.*, 1981; Moore, 1992a; Fig. 20.1). Water may be seasonally hard to locate and thermoregulation may be demanding.

Food

Greater aridity should be most important via effects on the supply of food plants. Taxonomic differences in

vegetation are presumably not informative with regard to modeling the LCA, but the following general features of savanna plants may be:

1. *Types.* Many savanna plants have hard-shelled seeds or nuts, and many have underground storage organs (USOs) such as tubers; both food-types have been proposed as key resources for early hominids (Hatley & Kappelman, 1980; Peters, 1987).

2. *Seasonality.* The greater seasonality in rainfall experienced at savanna sites (Bourliére & Hadley, 1983) is likely to result in greater seasonal variation in relevant resources, though this needs to be confirmed empirically.

3. *Dispersion.* Without scale-independent measures of patchiness for savanna and forest sites it is difficult to know whether hominoid resources in savannas are more patchily distributed or simply more thinly distributed. Chimpanzees range more widely in savannas (Suzuki, 1969; Kano, 1972; Baldwin *et al.*, 1982), *ipso facto* evidence that important resources are more dispersed in such habitats. Assuming comparability of diets, a savanna hominoid must travel farther on at least a seasonal basis than a forest hominoid.
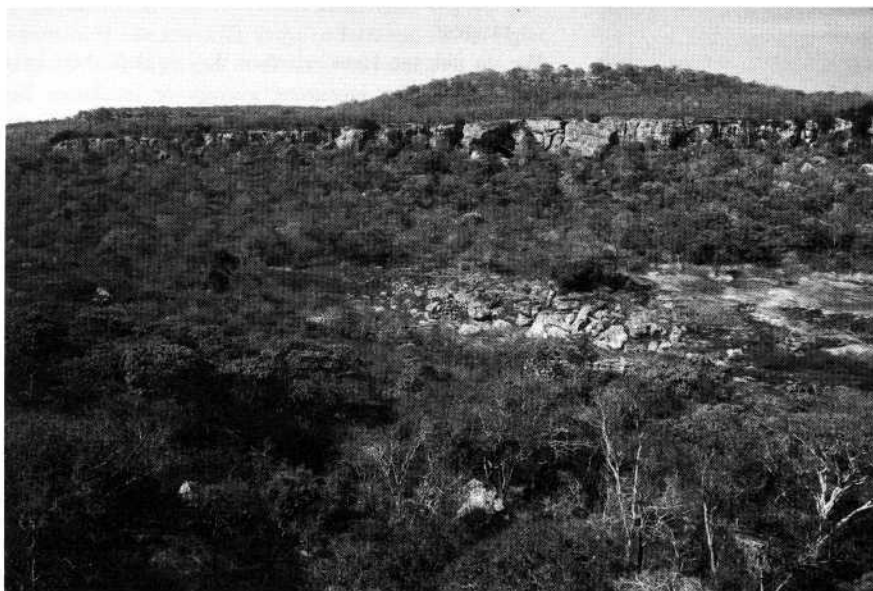
Fig. 20.1. Savanna habitat inhabited by chimpanzees in dry season at Ugalla. (Photo by J. Moore)

Predation

Relative to forest, savanna woodland has a greater variety of predators – lion (*Panthera leo*), hyena (*Crocuta crocuta*) and wild dog (*Lycaon pictus*) are more common, and leopard (*Panthera pardus*) appear comparably abundant. However, savanna woodland is importantly different from open shortgrass savanna in that relative safety in the trees is generally only a few meters away (Moore, 1992a). It is difficult to judge the actual risk of predation, since greater time spent on the ground (hence vulnerable) may be balanced by the greater visibility at ground level and hence reduced risk of ambush. At Ugalla near-ground visibility is usually > 20 m, while at Gombe and Mahale near-ground visibility is usually < 5 m (personal observations and unpublished data). Two caveats apply here: first, while chimpanzees at Ugalla utilize open woodland, they almost certainly bias their time toward denser vegetation. Second, the potential for ambush is still very real, as I realized when my assistant and I accidentally flushed a lion from behind a rock about 6 m away, where he was evidently stalking some warthogs (*Phacochoerus aethiopicus*) (see also Itani, 1979).

Competition

Relative to the forest, there are fewer species of primates and birds for chimpanzees to compete with. Whether competition is actually reduced or not is unknown, however, as elephants (*Loxodonta africana*), perhaps some browsing antelope (e.g. *Tragelaphus scriptus*), perhaps vervet monkeys (*Cercopithecus aethiops*) and especially baboons (*Papio* spp.) overlap with chimpanzees in diet (Peters & O'Brien, 1981; Collins & McGrew, 1988). McGrew *et al.* (1982) note that dietary overlap between Guinea baboons (*Papio papio*) and chimpanzees at the savanna site of Mt Assirik is about five times greater than the generic *Pan–Papio* overlap estimated by Peters & O'Brien, suggesting a possible increase in competition in arid habitats.

These differences between savanna woodland and more forested habitats may promote morphological, social or behavioral differentiation between savanna and forest chimpanzees (or facultative shifts in behavior among chimpanzees according to habitat at mosaic sites such as Gombe or Mahale). When such potential differentiation bears on traits considered important in human

evolution, understanding of the bases for the differences – or their absence – can shed light on our scenarios of hominid behavioral ecology. The following questions, grouped by topic, are intended to suggest an approach to the use of chimpanzee referential models in paleoanthropology. The list is not exhaustive, and the questions vary markedly in both potential ease of answering and in the degree to which, when answered, they disconfirm hypotheses about early hominids and the LCA.

Bipedalism

Hunt (1994) has recently evaluated leading hypotheses for the origin of hominid bipedalism, which include vertical climbing (Fleagle *et al.*, 1981; Prost, 1985; Doran, Chapter 16), a combination of vertical climbing and above-branch bipedal locomotion (Tuttle, 1981), the need to increase terrestrial travel in order to reach scattered arboreal resources (Rodman & McHenry, 1980), or thermoregulation in a dry, open habitat (Wheeler, 1994). Hunt argues that bipedal posture was initially favored in the context of feeding upon small fruits in closely-spaced, rapidly depleted patches; chimpanzees exploit such fruits by shuffling bipedally while harvesting with their hands.

Do savanna chimpanzees make greater use of large vertical trunks?

Hunt (1994) also points out that vertical climbing of large-trunked trees is rare at Gombe and Mahale, with apes preferring to enter trees via lianas or smaller-trunked neighbors (but at other forest sites vertical climbing may be common: Kortlandt, 1986; Doran, Chapter 16). At Ugalla, lianas are only locally abundant and many trees used for nesting appear to require vertical climbing. While large-stratum vertical climbing may not be the chimpanzee's primary adaptation (Hunt, 1994), greater forced reliance upon this niche in savanna chimpanzees would be consistent with Tuttle's (1981) and Prost's (1985) hypotheses regarding the LCA. While discovery of significantly more vertical climbing in woodlands could not disprove Hunt's shuffling-forager hypothesis, lesser amounts of vertical climbing in woodland seems inconsistent with the vertical-climber hypotheses.

Do savanna chimpanzees have larger day ranges?

We do not yet know whether they exploit their large home ranges by increasing average or maximum day ranges (cf. the Rodman & McHenry, 1980, hypothesis) or by steadily traveling through the annual range, with minimal backtracking, in increments similar to day ranges at more forested sites (e.g. Gombe: 3–5 km; Goodall, 1986). If the latter, it would demonstrate that increased locomotion is not a necessary consequence of lower resource density and greater home-range size, and so cannot be assumed for the LCA facing shrinking or mosaic forests.

Do savanna chimpanzees do more terrestrial shuffle-foraging?

In conjunction with development of paleoecological analogs (Sept, 1994), observations of notable reliance on shuffle-foraging at savanna sites would provide strong support for Hunt's hypothesis.

Are savanna chimpanzees constrained by thermoregulation and water balance?

Failure of savanna-living chimpanzees to exhibit signs of thermoregulatory constraint would be evidence against Wheeler's major hypothesis (Wheeler, 1994). While it has been suggested that chimpanzees at Mt Assirik are so constrained because they favor gallery forest in the hot season (McGrew *et al.*, 1981), data to distinguish effects of temperature from seasonal resource distribution have not yet been presented.

Home bases and the division of labor

Much effort has gone into trying to discover the function of hominid archeological sites and the possible implications of such sites for social organization and behavior (e.g. Isaac, 1989; Clark, 1993). It has been argued that regular use of specific sleeping or feeding places is a necessary and sufficient indication of a division of labor in which males (?) travel long distances hunting or scavenging for meat while females (?) gather plant foods; resources are then shared at the 'home base' (Isaac, 1978; reviewed in Potts, 1994). Sept (1992) pointed out that creation of 'sites' by chimpanzees would invalidate the

sufficient portion of the above argument. (Here, 'site' means to re-use a specific grove or location, on the order of a few tens of meters in diameter at most.)

Do savanna chimpanzees create 'sites' by repeated returns to the same location?

Data on nest distributions indicate that the answer is 'yes' (Sept, 1992; Moore, 1992b and personal observations), but the relative importance of such site fidelity remains to be established. Knowing the prevalence of such sites is important for comparison with the archeological record of site-concentrated versus background scatter of artifacts (the 'scatter between the patches') (Isaac, 1981).

Do savanna chimpanzees re-use sites more than do forest chimpanzees?

'Yes' would provide support for the idea that adaptation to drier habitats played a role in accentuating the importance of sites. 'No' suggests that the explanation for eventual adoption of home-base sites in hominids should be sought in some other aspect of hominid behavior and ecology.

What are the environmental correlates of chimpanzee sites?

Preliminary evidence shows that savanna chimpanzee nesting areas are non-randomly placed at least with respect to topography (Baldwin et al., 1982; Kortlandt, 1992; Moore, 1992b; Sept, 1992; Fruth & Hohmann, Chapter 17; see Fig. 20.2). If hominid sites were placed similarly, *ceteris paribus* we could conclude that they need not indicate anything other than chimpanzee-like social organization.

Even in the absence of specific 'sites', the increased patchiness of savanna habitats may promote return use of certain areas (e.g. riverine strip or valley, on the order of 1 km² or so) and thus facilitate reunions of parties through vocal contact; ease of reunion could promote increased sex differences in ranging patterns (cf. McGrew, 1981, p.60). Thus, adaptation to savanna might promote increased sexual differentiation of diet and behavior without the exchange or provisioning envisioned in home-base scenarios. The question then is, does savanna habitat promote increased ecological segre-
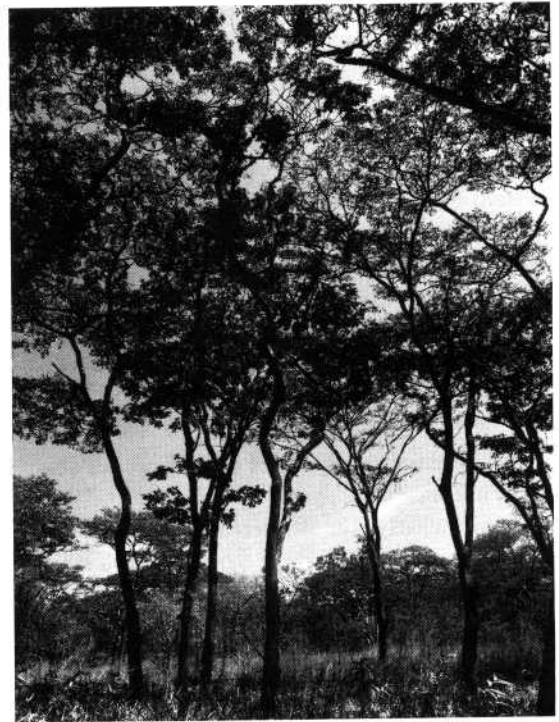

Fig. 20.2. Nest-site in savanna with herbaceous understory at Ugalla: two nests visible at top center. (Photo by J. Moore)

gation of the sexes in chimpanzees? Such differentiation, a stable adaptation in itself, would be an obvious preadaptation for later division of labor.

Are sex differences in diet greater for savanna chimpanzees?

Without detailed behavioral data on habituated apes, answering this question requires an indirect approach. Based on stable isotope ratios in hairs found in nests, Schoeninger (personal communication) has recently found indications of high within-group dietary variation among savanna chimpanzees; the range of $\delta^{15}N$ values in a small sample was twice that found in controlled diet studies (Fitzer et al., 1993). Further analysis and correlation with sex (determined cytogenetically from hair follicles, a procedure just moving from experimental to practical) should answer the question.

Increased sexual dimorphism in body size might correlate with increased sex differences in diet and ranging,

either because males and females have different optimal sizes due to different energetic or social requirements, or through intersexual character displacement driven by competition for similar resources (Slatkin, 1984). Alternatively, increased sexual dimorphism might be favored by sexual selection if parties become more stable in savanna habitats, shifting toward a hamadryas-like social pattern (K. Hunt, personal communication). Given the extreme sexual dimorphism reported for early australopithecines, any insights chimpanzees could offer to our understanding of the ecological basis of sexual dimorphism would be important (see also McGrew, 1992, Chapter 5).

Do savanna chimpanzees exhibit greater size dimorphism?

It seems unlikely that any savanna chimpanzee populations have been isolated long enough for such evolution to occur (Morin et al., 1994), but since Groves, Shea and others are already studying skeletal variation in *Pan* (e.g. Shea et al., 1993), asking this question may be justified by its low cost and high potential gain.

Are savanna chimpanzee parties more harem-like in stability and composition?

There is some evidence of greater mixed-party stability at Mt Assirik (Tutin et al., 1983). In principle, party stability and its relationship with paternity can be assessed using DNA from shed hairs (cf. Morin et al., 1994).

Diet and tool use

The scarcity of reported scavenging by chimpanzees and other primates has been cited as evidence that scavenging was unimportant to early hominids (McGrew, 1981; Tooby & DeVore, 1987; but see Hasegawa et al., 1983; Nishida, 1994). It is worth considering, however, that Gombe National Park has few large predators and that the combination of moister habitat and denser forest at Mahale may reduce the effective 'shelf-life' of predator kills while at the same time making them harder to locate. If savanna woodland is at an ecological extreme for chimpanzees, one would expect their diet breadth to broaden and thus scavenging might become more

important; the same logic predicts increased hunting as well. Another aspect of savanna diet expansion might be an increased reliance on tools for extracting or processing foods such as hard seeds or tubers (McGrew, 1981; but see Boesch-Achermann & Boesch, 1994; Nishida, 1973, regarding the significance of tool-use in the forest). Finally, increased reliance on nuts, tubers or grass seeds by savanna chimpanzees would provide support for various explanations of postcanine megadonty and enamel thickness in australopithecines (Moore, 1992a).

Are savanna chimpanzees more likely to hunt or to scavenge?

This is an obvious question, but one both difficult to answer (McGrew, 1992, p.150–3) and ambiguous in its implications since scavenging niches have changed drastically since the loss of Pliocene megafauna and their specialized sabertooth predators. The sabertooths probably could not chew close to the bone and so likely left both relatively and absolutely more scavengable material at their kills (Marean, 1989).

Do savanna chimpanzees have more robust mandibles?

Greater robusticity would be a sensitive indication that savanna diets place greater demands on the chewing apparatus. Such robusticity in savanna chimpanzees would likely be purely developmental rather than phylogenetic.

Do savanna chimpanzees use tools more often or in more ways?

There is no indication that they do, but since observations of tool use are correlated with length of observation and degree of habituation (McGrew, 1992), this is not surprising or meaningful. 'Yes' would provide support for the general 'out of the trees, onto the ground, pick up tools' scenario, but 'No' would not be informative, since this failure could be seen as the key point at which hominids and hominoids diverged.

Intergroup relations

Intercommunity relationships in chimpanzees appear to be generally hostile, and similarities with patterns of

human aggression have led Wrangham to suggest that the LCA would also have exhibited intercommunity hostility by males, with stalking and fatal attacks probable (Wrangham, 1987; Manson & Wrangham, 1991). At the same time, it seems plausible that lower population densities in savanna hominoids would militate against the fission-fusion system at the core of forest chimpanzees' intergroup relations (Moore, 1992a). Also, where resource patches are dispersed but non-depleting (e.g. dry-season waterholes) communities might be forced into periods of coexistence (McGrew, 1981) (or outright battle, as in the opening scene of the film *2001: A Space Odyssey*).

Do savanna chimpanzees exhibit intergroup hostility, with stalking attacks by males?

There is some evidence that they do (Goodall, 1986, p. 521). However, this incident involves reactions of wild individuals to tame ones, and the possibility remains that the attacks were stimulated by some aspect of the human presence or relationship with the rehabilitants. A negative answer to this question would support a 'U-shaped' trajectory for intergroup violence in human evolution, analogous to that proposed by Knauft (1991), in which forest chimpanzee-like hostility gave way to relatively more peaceful relationships in early, low-density hominids only to return later, with the emergence of *Homo* or of the state.

Is female-only dispersal the pattern for savanna chimpanzees?

If the fission–fusion social organization of forest chimpanzees breaks down at low densities, it may be that the female-only dispersal pattern may not apply to savanna-living populations (cf. Sugiyama *et al.*, 1993). If so, we might see the origin of the mixed dispersal patterns exhibited by human societies in the low densities and large ranges of savanna-dwelling early hominids.

Ecology and brains

Given their large home ranges, it seems reasonable to postulate that misremembering the location of a waterhole or the phenological cycle of a particular fig tree might be more costly to a savanna chimpanzee (McGrew,

1981, p.59). If savanna chimpanzees are living 'at the edge,' it may be necessary to adopt more complex or more secure resource acquisition tactics. Either or both of these possibilities suggests that savannas may be ecologically more challenging for chimpanzees than are forests. Might comparable complexity have played a role in the evolution of hominid encephalization?

CONCLUSION

The great apes are fascinating beings in their own rights, and richly deserving of long-term study for what we can learn about other ways of being intelligent, long-lived social animals; so are elephants, dolphins (Odontoceti) and perhaps others such as parrots (Psittidae). The apes' particular utility for illuminating the behavioral ecology of our extinct ancestors has, however, been questioned. Cladistic methods such as pioneered by Wrangham (1987) avoid the pitfalls of assuming that an extinct species could not have been uniquely different from any modern analog. Unfortunately such cladistic conclusions are limited to those traits that are shared by all the modern taxa used in the analysis; while we have some confidence in the picture of the LCA so created, it is missing precisely the bits that might explain differences between hominids and apes.

Strategic modeling relies upon our understanding of the principles of behavioral ecology. It is the only approach that can hope to address the significance of certain early hominid traits such as the extreme dimorphism of *Australopithecus afarensis*. However, as long as we continue to be surprised by the natural history of modern taxa, we need to keep in mind that our strategically-constructed scenarios concerning the past are based on a young, developing and still uncertain field (Wrangham, 1987).

In this paper I have advocated the use of a referential approach in which the model is not a single typological modern species *per se*, but the set of differences observed between populations of that highly variable species (in archeological terms, a *relational* as opposed to *formal* analogy; Gifford-Gonzalez, 1991). I believe such an approach has great potential, though it will be difficult and expensive to collect all the relevant data. I do not believe the method can stand on its own, though, any more than can the simple analogical, cladistic, or

strategic modeling approaches; and none of these approaches to behavioral scenarios will get far without careful attention to the fossil and archeological evidence. As Glynn Isaac (1980, p. 227) put it in a not-too-different context, 'the varied company of scientists inquiring into human origins must cast their net of investigation more widely.'

APPENDIX: FOSSIL AND MOLECULAR EVIDENCE FOR A CHIMPANZEE-LCA ANALOGY

Fossils

The fossil record provides little evidence regarding the LCA (Ciochon, 1983; Hill & Ward, 1988), and so physical reconstruction of the LCA must be based primarily on the earliest known hominids, *Australopithecus afarensis*, present as early as 3.4–3.9 mya (Kimbel *et al.*, 1994), the recently described *Australopithecus ramidus*, at *c.* 4.4 mya (White *et al.*, 1994), and on the Miocene hominoids (Pilbeam, 1985). Given an ape-hominid divergence of about 5 mya, *A. afarensis* is by far the temporally closest, reasonably well-characterized taxon. Everything currently known of *A. ramidus* suggests that it was considerably more chimpanzee-like than *A. afarensis* (White *et al.*, 1994), rendering the following comparisons conservative with respect to a chimpanzee or bonobo analogy.

Size

Australopithecus afarensis weighed about 30–45 kg, within the range of chimpanzees, but perhaps slightly on the small side (McHenry, 1994), though Hartwig-Scherer (1993) estimates up to *c.* 75 kg or more for some specimens. *A. afarensis* were built like chimpanzees in terms of weight-for-stature (Aiello, 1992). There is a general evolutionary trend for body-size to increase within lineages (Cope's Law; see Maurer *et al.*, 1992), so it would be unlikely for the LCA to have been larger than *A. afarensis* or modern chimpanzees; it may have been smaller, in the 15–25 kg range.

Encephalization

Relative and absolute brain sizes of the earliest australopithecines were no different from modern chimpanzees (Foley & Lee, 1991; Hartwig-Scherer, 1993). Much debate exists about the organization of their brains (Falk, 1987).

Habitat

Considering the range of habitats used by modern chimpanzees, only if the LCA was found in habitats at least as dry or open as bushland or *Acacia* woodland would they differ (terms from Pratt *et al.*, 1966). Several recent studies have concluded that habitats of the earliest hominids were well-wooded (Cerling, 1992; Kingston *et al.*, 1994), and arboreal adaptations of *Australopithecus afarensis* suggest significant time spent in trees (Susman, 1987). Based on remains from a single site, *Australopithecus ramidus* is thought to have lived in a 'wooded' habitat (WoldeGabriel *et al.*, 1994). Assuming that hominids in some sense moved out of the trees, the LCA would likely have lived in forest-woodland or wetter habitats (e.g. Bernor, 1983). The LCA may have preferred drier habitats than those in which chimpanzees are found (500–800 mm rain per year; Pickford, 1983) but the inferred habitat of *A. ramidus* makes this unlikely.

Diet

The resolution of dental morphology and microwear studies is not fine enough to determine *Australopithecus*

afarensis' diet with any precision. Research suggests broad dietary similarity with chimpanzees (Grine & Kay, 1988; Andrews & Martin, 1991), or gorillas, but with seasonal reliance on hard gritty foods (Ryan & Johanson, 1989). It is worth noting that Ryan & Johanson based their comparison on western lowland gorillas which appear to have diets highly overlapping with chimpanzees' (Tutin & Fernandez, 1993). Molars of many Miocene hominoids as well as of early australopithecines were much larger, and their enamel thicker, than those of the African apes (Andrews & Martin, 1991). This suggests that the LCA's diet differed in some important ways from modern chimpanzees: at least seasonally, the LCA and earliest hominids probably relied on gritty or hard foods (Peters, 1987; Ryan & Johanson, 1989). *Australopithecus ramidus* molar enamel is thin, comparable to chimpanzees' (White *et al.*, 1994). While strengthening a chimpanzee analogy with the LCA, this finding complicates the overall picture of enamel evolution in the hominoid and hominid lineages.

Locomotion

A knuckle-walking LCA is possible (Zihlman, Chapter 21; though the available *Australopithecus ramidus* material shows no signs of knuckle-walking adaptations). *Australopithecus afarensis* was at least capable of exploiting the arboreal environment (Susman *et al.*, 1985; Tuttle, 1981). Since the energetic efficiency of locomotion may have been important in the evolution of hominoid social structure (Rodman & McHenry, 1980; Wrangham, 1979), locomotor mode remains an important loose end in models of the LCA.

Molecular evidence

Chimpanzees and bonobos diverged about 2–3 mya (Cronin, 1983; Goodman *et al.*, 1994). At that time our ancestors (early *Homo* sp.) were very different from modern humans in size, dentition and brain size (Wood, 1992); by contrast, chimpanzees and bonobos are easily mistaken for each other by the casual observer and hybridization in captivity has been reported (Vervaecke & van Elsacker, 1992). More recently, on the basis of mtDNA divergence, Morin *et al.* (1994) have concluded that *Pan troglodytes verus* and the other two chimpanzee subspecies diverged about 1.6 mya, roughly contemporaneously with the origin of *Homo erectus*; *P. t. verus* cannot be distinguished reliably from *Pan troglodytes*

troglodytes or *Pan troglodytes schweinfurthii* on morphological grounds (Shea *et al.*, 1993). Mountain and lowland gorillas differ in mitochondrial COII sequences more than do chimpanzees and bonobos (Ruvolo *et al.*, 1994), suggesting a divergence date of almost 3 mya (Morell, 1994); again, morphological differences are slight. Finally, lowland gorillas and chimpanzees (molecular divergence date about 5.5–7 mya; Hasegawa, 1992; see discussion in Goodman *et al.*, 1994, and Zihlman, Chapter 21) are similar in shape and diet, and gorillas can be viewed as essentially allometrically scaled-up versions of chimpanzees (Shea, 1990; Doran, Chapter 16). All of these comparisons indirectly suggest much morphological conservatism in the African pongid lineage, and therefore support the notion that the LCA would have resembled a chimpanzee.

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NOTE ADDED IN PROOF

Australophithecus ramidus has been placed in its own genus, *Ardipithecus*, in recognition of the belief that it may be a sister taxon of the hominids (White *et al.*, 1995). In 1995, *Australopithecus anamensis* was described, based on specimens found in Kenya at two sites that probably were riverine gallery-open dry woodland/bushland mosaics; this species dates from about 3.9–4.2 mya. It appears to have been bipedal and to have had dental enamel similar in thickness to *Australopithecus afarensis* (and much thicker than that of *A. ramidus*), features that are consistent with its being ancestral to *afarensis* (Leakey *et al.*, 1995). If *ramidus* is a sister taxon to the hominids and *anamensis* is ancestral to *afarensis*, the picture of dental enamel evolution in the early hominids would be simplified somewhat and the chimpanzee analogy with the LCA weakened (cf. p. 287).

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