Finite Social Space, Evolutionary Pathways, and Reconstructing Hominid Behavior

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Changes in social behavior were a key aspect of human evolution, and yet it is notoriously difficult for paleobiologists to determine patterns of social evolution. By defining the limited number of distributional strategies available to members of each sex of any species and investigating the conditions under which they may occur and change, the social behavior of different hominid taxa may be reconstructed.

Paleoanthropologists have long speculated on the nature and role of social behavior in human evolution. Since many distinctive features of the human species relate to social behavior, an understanding of the patterns and processes of human evolution must include these characteristics. Social systems as diverse as monogamous pairs (*1*), food-sharing families (*2*), and chimpanzee-like fission and fusion societies (*3, 4*) have all been proposed for ancestral hominids (Table 1). If it is possible to reconstruct the social systems of extinct animals, then a high priority is to establish the criteria by which social evolution can be modeled (*5*).

Hominid Sociality: The Problem

Early hominid evolution occurred in sub-Saharan Africa during a period of increasing environmental instability, with contracting forests, expanding savanna habitats, and drier, seasonal climates (*6–8*). Furthermore, it is widely recognized that early hominids were not all simply chronospecies of modern humans, but part of an adaptive radiation. These include small early forms with only partial bipedalism (for example, *Australopithecus afarensis, A. africanus*) (*9*), larger bodied forms with adaptations for heavy mastication (*A. robustus, A. boisei, ?A. crassidens*, and *?A. aethiopicus*) (*10–12*), as well as larger brained species probably more closely related to ourselves (*Homo habilis, H.* sp., and *H. erectus*) (*13*). Later hominids may also represent a diversity of forms (*14*).

It follows that reconstructions of early hominid social behavior cannot all simply reflect stages leading to modern humans; species diversity and ecological variability must be incorporated.

Reconstructing Social Evolution: The Method

Social behavior, among mammals in general and primates in particular, is highly variable; consequently hominids may be placed into any number of different categories, depending on the criteria used. The main function of this model-building exercise is to provide criteria by which the range of possible outcomes can be narrowed and to specify the conditions for their occurrence. The basic options for social strategy are quite limited, and the potential range of social systems finite.

Sexual strategy and distribution states. Stable long-term relationships between individuals represent the core structure of permanent groups. These relationships can be categorized as cooperative, competitive, and reproductive (mating and parental). Two familiar assumptions about behavior in relation to reproductive success [succinctly stated by Wrangham (*15*)] form the basis for demonstrating the finite range of social sets within groups. For females of most mammalian species, offspring production is limited by energy; they thus tend to distribute themselves to maximize resource access. From the male's perspective, offspring production is limited by access to females, and males attempt to distribute themselves in relation to females. The options available for male and female distributions and associations (that is, groups) in response to these basic constraints are limited.

Each sex may be described in terms of its distribution state—the nature of associations between individuals of the same sex after they have reached maturity, often arising from patterns of residence in or dispersal from the parental unit. Three practical options are available to each sex. Males and females can either be solitary in relation to same-sex individuals in associations with kin, or in associations with nonkin. Other options, such as temporary or fluid aggregations, represent unstable combinations of the basic choices.

Given that larger and longer living animals can recognize and maintain relationships for long periods of time, with individuals who are only infrequently contacted, kin relations within groups can be extended to affect and structure relations (mating, cooperation, defense) between different groups. The term lineage as used here denotes those social states with kinship recognized between groups. Four distribution states in relation to other individuals of the same sex are thus possible within a stable group. These relationships can be further patterned by the nature of relationships between the sexes. In this model, male-female associations can either be transitory (primarily during brief mating periods) or stable, representing associations which occur for longer than mating opportunities (*16*). Combining these distributional strategies gives rise to a limited set of only 32 potential core social systems (Fig. 1).

These limited options represent the fundamental building blocks of a social system, on which variability in group size, patterns of stability (for example, fission and fusion), spatial variation, and intensity of relationships, are built. Alternative individual strategies can often be described, but these are embedded in the core social system.

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This model of social variability has two strengths. First, it describes the potential social system with principles of behavioral ecology, but independent of observations of specific species, and hence avoids the problem of using living species as direct models of extinct forms. Second, it defines a range of possibilities from which the more probable can be deduced. This latter step involves describing the constraints on the occurrence of each social set.

Constraints on evolutionary pathways. Evolutionary change may be described as the movement from one adaptive point to another (*17*), and the evolutionary history of a species may be treated as the pathway taken when making transitions between adaptive points (*18*). In practice the number of evolutionary pathways available to a species is constrained when movement to an adjacent evolutionary point involves a loss of Darwinian fitness for those individuals (*19*). A model of social evolution should therefore specify the pathways available, and the extent to which these are viable (that is, do not involve a loss of relative fitness). The absence of an evolutionary pathway would represent a historical or phylogenetic constraint on evolutionary change.

In this model, evolutionary pathways can be described by specifying which states are adjacent. The matrix of social sets (Fig. 1) showed 32 possible states, defined by three variables (female distribution state, male distribution state, and the stability of male-female associations). The first two variables have four potential states, the last, only two. The difference between any two social states, and hence evolutionary distance, can therefore be defined by the extent to which they share the same values for these variables. Social states differing in only one variable are considered closer to one another than those differing in two or all three.

A more sensitive measure of evolutionary distance can be obtained if, for male and female distribution states, values are ranked so that certain variable states are placed adjacent to each other, thus constraining free movement from one social state to any other. These may be treated as polarities in the sense used by cladistic analysis (*20*), with certain states considered either primitive or derived relative to others (*21*). The values (−1, 0, 1, and 2) in Fig. 1 indicate these polarities. They can represent the minimum unit of behavioral change and assume that certain state changes would be improbable without a lowering of individual fitness. For example, females or males can be constrained in moving from association with kin to association with nonkin in a single transition by assuming inbreeding and a loss of mating opportunities (*22*). Thus, for male and female distribution states, "with nonkin" and "with kin" are not evolutionarily adjacent. For example, among *Pan paniscus*, where females may cooperate to defend large food patches (*23*), this cooperation is achieved by intensifying female affiliation among nonkin rather than a shift to a female kin residence system (*24*). State changes do not necessarily map directly onto behavioral changes, since distribution states reflect relationships rather than single behavioral units.

A change from any one social state to another therefore involves a maximum of seven changes. A shift from male solitary–female solitary with transitory relations between the sexes (social state 14 in Fig. 1) to a male solitary–female nonkin system (social state 2) requires two state changes (stabilizing male and female relationships and females associating with nonkin). To produce stable male kin–female nonkin (social state 3) requires a further change to males associating with kin.

Table 1. Previous models for the evolution of hominid social behavior.

Author	Key behavioral features	Basis for inference	Key hominid taxon	Key paleobiological evidence	Social structure
DeVore and Washburn (*61*)	Male competition and dominance in large groups	Baboon ecology and behavior (environmental similarity)	Early *Australopithecus*	Not specified	Large multimale group
Isaac (*2*)	Food-sharing, division of labor and home bases	Behavior of modern hunter-gatherers	*Homo habilis*(?)	Animal bone or artifact concentration in East African Plio-Pleistocene	Family units (monogamous?)
Tanner (*3*)	Intensification of female foraging, female-offspring bonds, female mate choice	Chimpanzee behavior (phylogenetic relationships)	Protohominid or common ancestor with chimpanzee	Not specified	Groups of females and their offspring
Lovejoy (*1*)	Provisioning of females and young, pair bonds	Differences in reproductive rates between extant apes and humans	Protohominid or earliest hominid	Early presence of bipedalism	Monogamous family units
Hill (*62*)	Hunting and male provisioning	Differences in rates of meat consumption between nonhuman and human primates	Not specified	Early evidence of hunting	Most probably polygynous harems
McGrew (*4*)	Tool-use and manufacture	Similarities between humans and chimpanzees	Not specified	Archeological evidence for tool-making	Compare chimpanzee
Wrangham (*37*)	Closed social network, female exogamy, polygyny, hostile intergroup relationships	Comparative socioecology of African apes	Common ancestor of hominids and African apes	Not specified	Closed social networks of related males and exogamous females
Gighlieri (*32*)	Female exogamy and male alliances	Comparative socioecology of apes (phylogenetic relationships)	Earliest hominid	Not specified	Male kin territorial groups
Parker (*63*)	Female mate choice and sexual selection	Reproductive energetics of extant primates	A chronological sequence from the earliest hominid to modern humans	Archeological evidence for scavenging or hunting and rates of brain expansion	Pair bonds (monogamy)

A matrix of minimum evolutionary distance can be constructed from ranked distances between social states (Fig. 2). Those social systems separated by only one character change may be considered to be evolutionarily adjacent; a larger number of state changes implies a greater evolutionary distance. From this matrix evolutionary pathways can be mapped (*25*).

Figure 3 shows alternative pathways from the simplest evolutionary state (social state 14); each step represents one change of state. From this diagram, for example, the alternative evolutionary pathways producing a harem system with one male in stable associations with nonkin females (social state 2) can be identified. The adjacent states are 1, 3, 6, and 10. Each of these social states may in turn be reached by a variety of routes.

Ecological constraints. Even constrained in this way, a large number of alternative routes exist to any one social state. The ecological viability of these states can limit the pathways. In Wrangham's model (*15*), food patches large enough to be used by several females tend to promote grouping when scramble or contest competition limits individual access to food. Two females cooperating to defend a patch will be able to halt other females invading that patch. Such cooperation is often biased toward kin in accordance with principles of inclusive fitness (*26*). The patch size, its quality, and its renewal rate through time are important determinants of females' ability to monopolize or defend a patch, on their own or in a group with female kin. Under such resource conditions, females are most often solitary or in groups with female kin.

Male distribution must thus take into account female dispersal patterns in relation to resources as well as the nature and degree of competition between males. A single male can potentially monopolize (relative to other males) a single female and her resources, or a group of female kin. With competition between males for access to females, several males may end up associated with a single female (as in polyandry) or with related females. When resources do not initially promote female aggregations, groups composed of unrelated females attached to a specific male result. Males can associate with kin when the advantages of male coalitions are biased toward cooperation for controlling either females or their resources in the face of competition from other males.

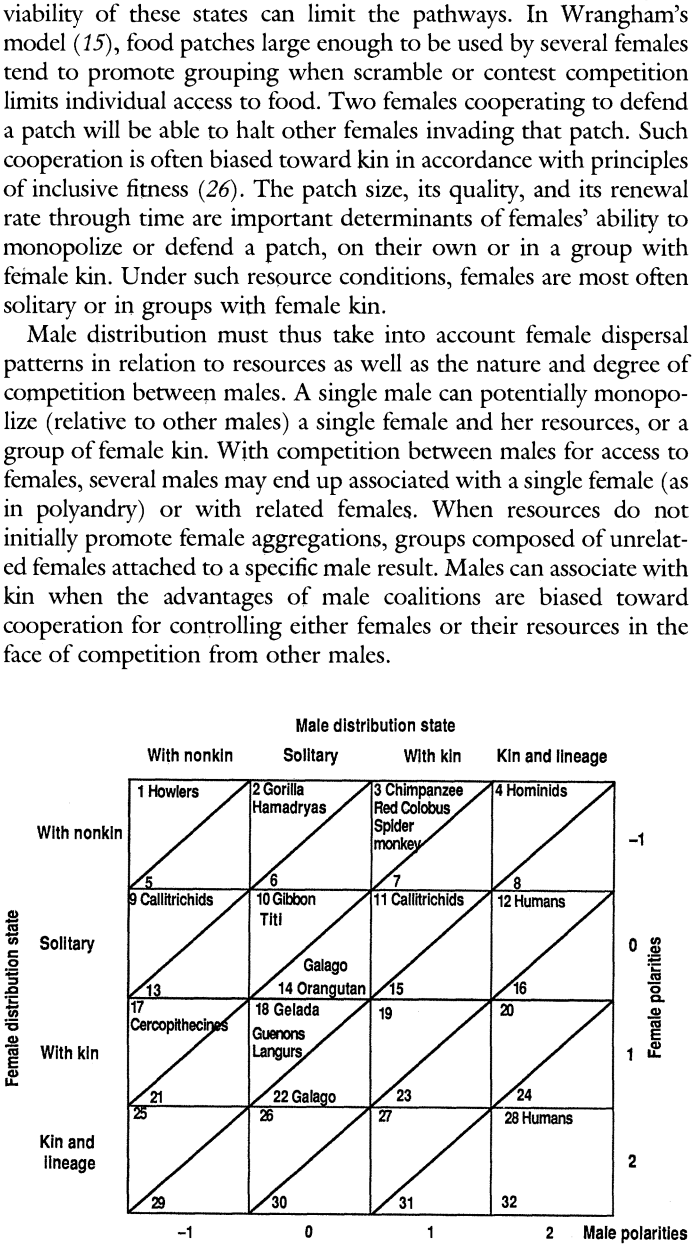

Fig. 1. Core social systems based on distribution states defined for males and females in relation to same-sex individuals. Associations between sexes are indicated by the angular divisions within each box: top left, stable; bottom right, transitory. The distribution states are ranked by polarities and numbered (1 to 32). All extant hominoids and at least one other representative primate species are presented for currently known states (*64*). Species can appear in more than one state.

A large number of other parameters may be added that further constrain evolutionary options, such as predation, birth rate, and other life history variables (longevity, growth, and developmental rates). The persistence and success of a potential social state will depend on ecological conditions.

The alternative pathways generated can be examined using the example shown in Fig. 3. Two of the immediately adjacent routes to social state 2 involve systems undescribed in extant primates (social states 1 and 6). Such systems may be relatively improbable for a primate, involving only transitory male-female relationships. A male who stabilized relationships with a female whenever ecological or demographic contexts allowed would be at an advantage over males who lost mating opportunities while searching for females. At a more distant level, several routes include a state of polyandry (social states 9 and 11); others (social states 3 and 4) consist of a shift from a more complex (or derived) state to one less derived. These situations should not be ruled out and indeed some may occur as a transitory phase under specific demographic [for example, the temporary establishment of female kin lineages among mountain gorillas with very long silverback tenure (*27*); multimale and harem groups of langurs (*28*)] or ecological [for example, the facultative alternation between polyandry, polygyny and monogamy of some callitrichids (*29*)] conditions. These transitory states provide a means for defining the circumstances where they might stabilize. Again, individual alternative strategies within a social system, such as followers among gelada (*30*) or brothers dispersing together among vervets (*31*), provide the potential for new states if these strategies come to predominate.

Application to the Hominids

To apply this methodology to the problem of hominid socioecological evolution requires establishing the ancestral social state from which hominids are derived, the potential pathways from this social state, including that of modern humans, and the constraints and selective pressures that determine the pathways followed.

The hominoid socioecological context. Hominids are hominoids, and more specifically African hominoids (*32, 33*); they may form a sister clade to the chimpanzee and gorilla together, or to the chimpanzee alone (*34, 35*). While diverse, social systems of living hominoids support the general principle of evolutionary pathways, for the observed social states are adjacent (Figs. 1 and 3). This suggests a limited number of possible social strategies for hominoids. Particularly striking is the absence of strategies based on relationships between nondispersing, related females, in marked contrast with the predominance of such systems among the cercopithecines (*36*). The evolutionary pathways found among the hominoids are relatively short, do not involve implausible steps, and are consistent with phylogeny. In particular, a trend toward more stable relationships between males and females and stronger associations of male kin can be observed (*36*), especially among the African apes.

As the Late Miocene forests in Africa became restricted in distribution, drier woodland regions became more widespread, and overall habitat diversity increased. The effects of this paleoenvironmental change would have depended upon the precise location of any population and its ecological requirements. For those located in areas where foods became more patchy and the patches smaller due to reduced rainfall and increased seasonality, females were unlikely to forage as a cooperative unit, and thus have few reasons to associate in kin groups. With the expansion of female foraging areas, male kin coalitions defending the range of several females would have been advantageous for the small-bodied early hominids. Both chimpanzees (*37, 38*) and these early hominids thus have been proposed to be relatively similar in social strategy (*36*).

The first hominids. The model of finite social sets shows the initial conditions of early hominid behavior, and the basis for considering subsequent evolutionary patterns. As part of an African hominoid radiation, the earliest hominids occupied more open, savanna-like habitats than is typical for the other African hominoids (*39, 40*). The earliest known hominids from Tabarin (*41*), Lothagam (*42*), Laetoli (*43*), and Hadar (*44*) have all been found in association with sedimentological or paleontological indicators of habitats with large patches of grassland and bushland.

Category of social state	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	0																															
2	1	0																														
3	2	1	0																													
4	3	2	1	0																												
5	1	2	3	4	0																											
6	2	1	2	3	1	0																										
7	3	2	1	2	2	1	0																									
8	4	3	2	1	3	2	1	0																								
9	1	2	3	3	2	3	4	6	0																							
10	2	1	2	3	3	2	3	5	1	0																						
11	3	2	1	2	4	3	2	3	2	1	0																					
12	4	3	2	1	5	4	3	2	3	2	1	0																				
13	2	3	4	5	1	2	3	4	1	2	3	4	0																			
14	2	3	2	4	2	1	2	4	2	1	2	3	1	0																		
15	4	3	2	3	3	2	1	2	3	2	1	2	2	1	0																	
16	5	4	3	2	4	3	2	1	4	2	2	1	3	2	1	0																
17	2	3	4	5	3	4	5	6	1	2	3	4	2	3	4	5	0															
18	3	2	3	4	4	3	4	5	2	1	2	3	3	2	3	4	1	0														
19	4	3	2	3	5	4	3	4	2	2	1	2	4	3	2	3	2	1	0													
20	5	4	3	2	6	5	4	3	4	3	2	1	5	4	3	2	3	2	1	0												
21	3	4	5	6	2	3	4	5	2	3	4	5	1	2	3	4	1	2	3	4	0											
22	4	3	4	5	3	3	3	4	3	2	3	4	2	1	2	3	2	1	2	3	1	0										
23	5	4	3	4	4	3	2	3	4	3	2	3	3	2	1	2	3	2	1	2	2	1	0									
24	6	5	4	3	5	4	3	2	5	4	3	2	4	3	2	1	4	3	2	1	3	2	1	0								
25	3	4	5	6	4	5	6	7	2	3	4	5	3	4	5	6	1	2	3	4	2	3	4	5	0							
26	4	3	4	5	5	4	5	6	3	2	3	4	4	3	4	5	2	1	2	4	3	2	3	4	1	0						
27	5	4	3	4	6	5	4	5	4	3	2	3	5	4	3	4	3	2	1	2	4	3	2	3	2	1	0					
28	6	5	4	3	7	6	5	4	5	4	3	2	6	5	4	3	4	3	2	1	5	4	3	2	3	2	1	0				
29	4	5	6	7	3	4	5	6	3	4	5	6	2	3	4	5	2	3	4	5	1	2	3	4	1	2	3	4	0			
30	5	4	5	6	4	3	4	5	4	3	4	5	3	2	3	4	2	2	3	4	2	1	2	3	2	1	2	1	1	0		
31	6	5	4	5	5	4	3	4	5	4	3	4	4	3	2	3	4	3	2	3	3	2	1	2	3	2	1	2	2	1	0	
32	7	6	5	4	6	5	4	3	6	5	4	3	5	4	3	2	5	4	3	2	4	3	2	1	4	3	2	1	3	2	1	0

Fig. 2. Matrix of evolutionary distance showing the minimum number of character changes necessary to move from a specific social state to all others. Numbers refer to states and are indicated on each axis. Values of 1 indicate adjacent states; evolutionary distance increases with the value shown.

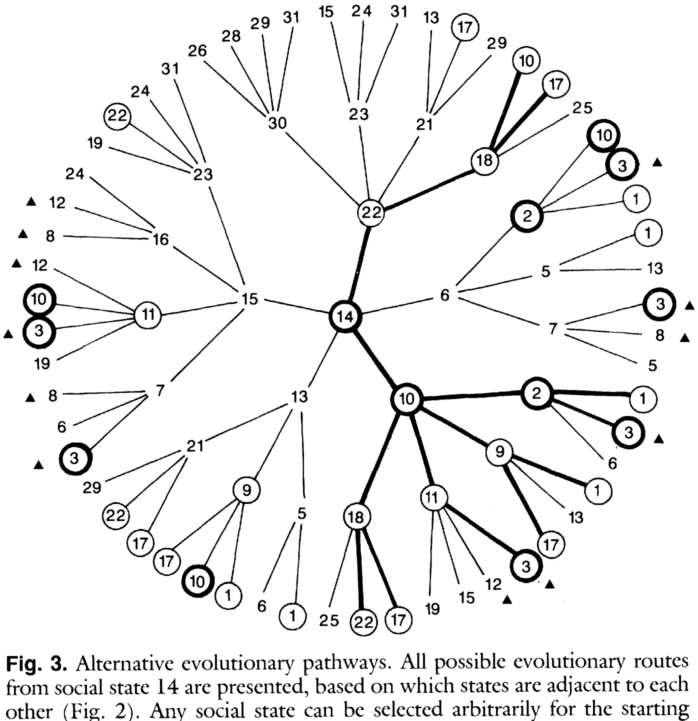

Fig. 3. Alternative evolutionary pathways. All possible evolutionary routes from social state 14 are presented, based on which states are adjacent to each other (Fig. 2). Any social state can be selected arbitrarily for the starting point and pathways can be traced in any direction, not just away from the center. The dark lines highlight routes through extant primates. Dark circles refer to hominoids and triangles show states that could lead on to the hominids (social state 4).

Such environments appear to promote, among other things, larger group size among primates (*6, 45*), partly as a response to the greater threat of predation (*46*), partly due to the effects of resources being more patchily distributed (*15*). The model described above, and the socioecological character of the African hominoid clade as a whole, would suggest that such larger groups would be built on male kin alliances rather than related females; to "switch" to the female-based patterns found among savanna-dwelling cercopithecines would involve more social changes during the transition, including a reduction in group size potentially placing small groups at a competitive disadvantage, a period of inbreeding, and a premium placed on male body size in competition over females, which would pose additional nutritional burdens for growth.

The most probable social organization for the early australopithecines consists of mixed sex groups, with males linked by a network of kinship. Females, forced to forage over larger areas to find dispersed and seasonally limited food and to aggregate in the face of some predation, would be expected to form more stable associations with either specific males within the alliance or with the entire alliance of males.

This reconstruction of earliest hominid social structure builds the selective pressures of open tropical environments onto the social state of the evolving African hominoids (social state 3). The critical change of social state is the elaboration of male alliances (social state 4).

Australopithecus afarensis, as the earliest recognized hominid species, is the best candidate for this ancestral pattern of hominid socioecology. Problems exist, however, in relating this proposal to characteristics inferred from the fossil evidence. One interpretation is that the entire hominid fossil assemblage from East Africa from the period 5 to 2 million years ago belongs to a single, highly dimorphic species (*47, 48*). Current estimates suggest a range of body weights of 70 kg for males and 31 for females—a level of sexual dimorphism of 226% (*49*). This could imply intense competition between males, and consequently a significant weakening of kin-based male alliances. Such a pattern might require a high density and low patchiness of high-quality food for mothers to sustain high growth rates among sons and for males to enhance their post-pubertal growth. Among living hominoids this level of sexual dimorphism is similar to that of the orangutan, with a solitary existence for both sexes viable in the absence of predators and relatively abundant high-quality foods which are dispersed in small packets (*50*). The high levels of sexual dimorphism among gorillas are associated with intense male-male competition and abundant low-quality foods (*27*). Either of these interpretations for the hominids is inconsistent with paleoenvironmental considerations. The alternative interpretation of this Pliocene material implies taxonomic differentiation (*51, 52*), suggesting the early hominids included both large and small body–sized species with relatively little sexual dimorphism, more in keeping with the model suggested above.

The "robust australopithecines." One trend among African hominids (2.5 to 1.0 million years ago) involves relatively little encephalization, enlargement of the posterior teeth, and the evolution of cranial and facial musculature and architecture associated with heavy mastication [informally referred to as the robust australopithecines, although some prefer the designation *Paranthropus* (*53*)]. Functional interpretation of this morphology suggests a greater degree of dependence on coarse, hard, plant food, most probably of low nutritional quality (*6, 54, 55*). When such savanna foods (underground plant storage organs, grasses, and seeds) occur in large, dispersed patches, larger group size can result, especially if grouping reduces the probability of predation in open environments (*46*). The expected effect on the ancestral hominid socioecology described above would have been to weaken male kin bonds within a less structured large or fluid group. In these large groups individuals with a relatively low degree of relatedness would be in close proximity, resulting in males investing more effort into the defense of a female or females—in other words, a harem structure within a larger group context that still has male kin throughout the group as a whole. Female kin within the harems would be unlikely (in contrast to gelada baboons), since with long male tenure (as in the gorillas), young females could suffer costs of continued inbreeding and reduced mating opportunities if they did not disperse away from their mothers. The resulting large group would consist of reproductive units with unrelated females in stable associations with a single male, but with both male and female kin present. Related males would be available for group defense against coalitions of conspecifics, while the advantages of kin coalitions for females, reproductive assistance, and enhanced feeding opportunities, would be less immediate since these female kin would not be in close associations and thus less available for supportive interactions.

Some evidence relating to life history characteristics may also be deployed to support this reconstruction. Calculations of growth rates from deciduous dental enamel (*56, 57*) indicate that this group of hominids matured rapidly relative to later hominids. A trend toward more rapid early growth is associated with increasing environmental uncertainty and high fertility (*58*), suggesting a competitive multimale environment in which an immature individual has low survivorship.

Early Homo. Other early Pleistocene African hominids lack the dental specializations of the later australopithecines, display a trend toward greater encephalization, and share a greater number of locomotor characteristics with modern humans. Tool-making on an increasing scale is associated with these species. Environmentally, archeological and fossil remains are associated with savanna mosaic habitats. This is the genus *Homo*, best known by *H. erectus*. These morphological and behavioral contrasts with the later australopithecines imply a different adaptive strategy, and hence another modification from the ancestral hominid socioecological system.

The central problem for hominids living in more arid grassland and woodland environments is maintaining a successful foraging strategy in the context of markedly seasonal conditions. For the robust australopithecines a shift to lower quality plant foods has been suggested as their survival strategy during dry season periods of food limitation (*6*). An alternative solution would be to increase the amount of animal tissue consumed. The benefits of meat-eating are high nutritional quality, large package size, transportability, and dry season abundance; the costs are a patchy and unpredictable distribution, and an increased risk of injury during capture or processing.

Despite considerable controversy surrounding the precise interpretation of the Pliocene-Pleistocene African localities with associations of bones and stone tools (*59*), there is general agreement that by 1.6 million years ago, contemporaneous with the appearance of *Homo erectus*, hominids were processing animal tissue at a higher level than is known for any extant nonhuman primate species (*60*).

While the causes of meat-eating are ecological, the consequences would be distributional and social. Increased meat-eating leads to larger home range size and longer day ranges, given the patchy distribution of prey items and scavengeable carcasses. Under these conditions, male cooperation in food acquisition would be advantageous. While individual defense of females by a male would be increasingly difficult, especially if differences in male and female foraging behavior become more pronounced, cooperative defense of groups of females would minimize the loss of females to roving or intruding males. Territorial exclusion, given the size of area involved, would be difficult, and hostile intergroup encounters would again involve alliances of males rather than individual defense. Such a pattern of behavior would enhance male kin associations within and between groups as a means of coping with high levels of intergroup competition and interactions.

Factors other than seasonal stress and resource availability influence the socioecology of the genus *Homo*. Principal among these are the higher levels of maternal reproductive costs associated with greater encephalization, slower infant growth rates, delayed maturity and independence, and infants at an additional risk from nonnutritional mortality as a result of predation, inter-group encounters, and infanticide. The effect of all these would be to increase the frequency, intensity, and stability of male-female associations. As a means of decreasing foraging costs through provisioning or scrounging, and reducing mortality risks, a stronger bond between particular males and females would be advantageous.

One alternative mode of meeting these reproductive costs would be to increase female kin-bonding and use other females as providers and protectors. Again, shifting to matrilineality would be possible under the model, but would be difficult to establish, given ecological and demographic constraints. Associations of mothers and daughters would require resources that could be defended by female coalitions, a demographic context where females did not sustain costs of inbreeding, and dispersal of young males associated with low mortality and a high probability of subsequent breeding. Such conditions were unlikely to be met in the environments of *H. erectus*, but may be associated with rapid demographic and range expansions and high quality, abundant foods among later *Homo*.

The result of a specific environmental stress (seasonality), a shift in resource base, and changing life history parameters associated with the costs of producing offspring for *H. erectus* would be the simultaneous buildup of male kin alliances (competitive and cooperative inter-group effects) and specific male-female links (polygamous rather than monogamous) resulting in a higher level of complexity of both inter- and intra- (specifically male) sex relationships.

Modern humans. Where do modern humans fit in with this pattern? Essentially the trend observable in the divergence from the African hominoids, and in the evolution of the genus *Homo*, shows a strengthening of male kin relationships. The most significant aspect of this process would have been greater levels of kin-biased behavior and recognition; greater longevity would extend this to lineages of adjacent generations (patrilines) and create the potential for lineage recognition through space, structuring relationships between groups over the long term. In the model, hominids and modern humans have made the transition from social state 3 to 4. The other change is stronger associations between specific males and females (facultatively polygynous). On these grounds it may be argued that polygynous male family groups occurring within larger male kin lineages characterized the social organization of the ancestors and earliest representatives of modern humans. From this social state the development of stronger female kin systems (social states 12 and 28) can be reached. Polyandry (social state 12) is adjacent to social state 4, while the pathway to social state 28 has a more complex route through transitory relations with males. Environmental, social, economic, and political factors may have constrained or made available new pathways for modern humans.

REFERENCES AND NOTES

1. O. Lovejoy, *Science* **211**, 341 (1981).
2. G. L. Isaac, *Sci. Am.* **238**, 90 (April 1978).
3. N. Tanner, *On Becoming Human* (Cambridge Univ. Press, Cambridge, 1981).
4. W. C. McGrew, in *Woman the Gatherer*, F. Dahlberg, Ed. (Yale Univ. Press, New Haven, 1981), pp. 35–73.

5. J. Tooby and I. DeVore, in *The Evolution of Human Behavior: Primate Models*, W. G. Kinzey, Ed. (SUNY Press, New York, 1986), pp. 28–47.
6. R. Foley, *Another Unique Species* (Longman, Harlow, 1987).
7. J. A. H. van Couvering, in *Fossils in the Making*, A. K. Behrensmeyer and A. P. Hill, Eds. (Univ. of Chicago Press, Chicago, 1980), pp. 272–297.
8. R. L. Bernor, in *New Interpretations of Ape and Human Ancestry*, R. L. Ciochon and R. S. Corruccini, Eds. (Plenum, New York, 1983), pp. 149–164.
9. B. A. Wood and A. T. Chamberlain, *J. Human Evol.* **16**, 625 (1987).
10. H. M. McHenry, *ibid.* **15**, 177 (1986).
11. F. C. Howell, in *The Evolution of African Mammals*, V. Maglio and H. B. S. Cooke, Eds. (Harvard Univ. Press, Cambridge, MA, 1978), pp. 154–248.
12. R. E. F. Leakey and A. C. Walker, *Am. J. Phys. Anthropol.* **76**, 1 (1988).
13. C. B. Stringer, *J. Hum. Evol.* **16**, 135 (1988).
14. I. Tattersall, *ibid.* **15**, 165 (1986).
15. R. W. Wrangham, *Behaviour* **75**, 262 (1980).
16. Stable associations between males and females can include short-term male tenure or tenure over the reproductive lifespan; both types are subsumed under the term "stable."
17. R. Dawkins, *The Blind Watchmaker* (Longman, London, 1987).
18. See "adaptive landscapes"—S. Wright, *Proc. 11th Int. Congr. Genet.* **1**, 356 (1939).
19. J. J. Bull and E. L. Charnov, *Evolution* **39**, 1149 (1985).
20. W. Hennig, *Phylogenetic Systematics* (Univ. of Illinois Press, Chicago, 1966).
21. See also M. Ridley [*Anim. Behav.* **34**, 1848 (1986)] for an example of this approach applied to primate mating systems.
22. A. E. Pusey and C. R. Packer, in *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, T. T. Struhsaker, Eds. (Univ. of Chicago Press, Chicago, 1987), pp. 250–266.
23. F. J. White and R. W. Wrangham, *Behaviour* **105**, 148 (1988).
24. T. Nishida and M. Hiraiwa-Hasegawa, in (*22*), pp. 165–177.
25. Although it is assumed that character states can only change singly, this does not imply that the length of time a population spends at each point in an evolutionary pathway is equal. Some may be inherently more unstable than others depending on changes in behavior and relationships, and so several character changes may occur in rapid succession allowing for a more dynamic system.
26. W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964).
27. K. J. Stewart and A. H. Harcourt, in (*22*), pp. 155–164.
28. S. B. Hrdy, *The Langurs of Abu* (Harvard Univ. Press, Cambridge, MA, 1977).
29. J. Terborgh and A. W. Goldizen, *Behav. Ecol. Sociobiol.* **16**, 293 (1985).
30. R. I. M. Dunbar, *Reproductive Decisions* (Princeton Univ. Press, Princeton, NJ, 1984).
31. D. L. Cheney and R. M. Seyfarth, *Am. Nat.* **122**, 392 (1983).
32. C. P. Groves, in *Comparative Primate Biology*, D. R. Swindler and J. Erwin, Eds. (Liss, New York, 1986), vol. 1, pp. 187–217.
33. P. Andrews and L. Martin, *J. Human Evol.* **16**, 101 (1987).
34. M. M. Myiamoto, J. L. Slightom, M. Goodman, *Science* **238**, 369 (1987).
35. C. G. Sibley and J. E. Ahlquist, *J. Molec. Evol.* **20**, 2 (1984).
36. R. A. Foley, in *Comparative Socioecology*, V. Standen and R. A. Foley, Eds. (Blackwells, Oxford, in press).
37. R. W. Wrangham, in (*5*), pp. 51–71.
38. M. P. Giglieri, *J. Hum. Evol.* **16**, 319 (1987).
39. A. Hill, *ibid.*, p. 583.
40. E. S. Vrba, in *Ancestors: The Hard Evidence*, E. Delson, Ed. (Liss, New York, 1985), pp. 63–71.
41. A. Hill *et al.*, *J. Hum. Evol.* **14**, 759 (1985).
42. B. Patterson, A. K. Behrensmeyer, W. D. Sill, *Nature* **226**, 918 (1970).
43. M. D. Leakey, *Laetoli* (Clarendon, Oxford, 1987).
44. B. T. Gray, thesis, Case Western University (1980).
45. T. H. Clutton-Brock and P. H. Harvey, *J. Zool. London* **183**, 1 (1977).
46. R. I. M. Dunbar, *Primate Social Systems* (Croom Helm, London, 1988).
47. D. C. Johanson and T. D. White, *Science* **203**, 321 (1979).
48. W. H. Kimbel, T. D. White, D. C. Johanson, in (*40*), pp. 120–137.
49. H. McHenry, quoted in E. Delson (*53*).
50. P. S. Rodman and J. C. Mitani, in (*22*), pp. 147–154.
51. B. Senut and C. Tardieu, (*40*), pp. 193–201.
52. T. Olson, in (*40*), pp. 94–101.
53. See, for example, E. Delson, *Nature* **327**, 654 (1987).
54. F. E. Grine and R. F. Kay, *ibid.* **333**, 765 (1988).
55. A. C. Walker, *Philos. Trans. R. Soc* **B292**, 57 (1981).
56. T. G. Bromage and M. C. Dean, *Nature* **317**, 525 (1985).
57. M. C. Dean, *J. Hum. Evol.* **16**, 197 (1987).
58. T. J. Case, *Q. Rev. Biol.* **53**, 243 (1978).
59. R. Potts, in *Hominid Evolution and Community Ecology*, R. Foley, Ed. (Academic Press, London, 1984), pp. 129–166.
60. See L. R. Binford and H. T. Bunn and E. Kroll [*Current Anthropol.* **27**, 431 (1987)] for two divergent views in this controversy.
61. I. DeVore and S. Washburn, in *African Ecology and Human Evolution*, F. C. Howell and F. Bouliere, Eds. (Methuen, London, 1963), pp. 335–367.
62. K. Hill, *J. Hum. Evol.* **11**, 521 (1982).
63. S. T. Parker, *Hum. Evol.* **2**, 235 (1987).
64. See (*22*), table A-1, for primates; M. V. Flinn and B. S. Low, in *Ecological Aspects of Social Evolution*, D. I. Rubenstein and R. W. Wrangham, Eds. (Princeton Univ. Press, Princeton, NJ, 1986), pp. 217–243.
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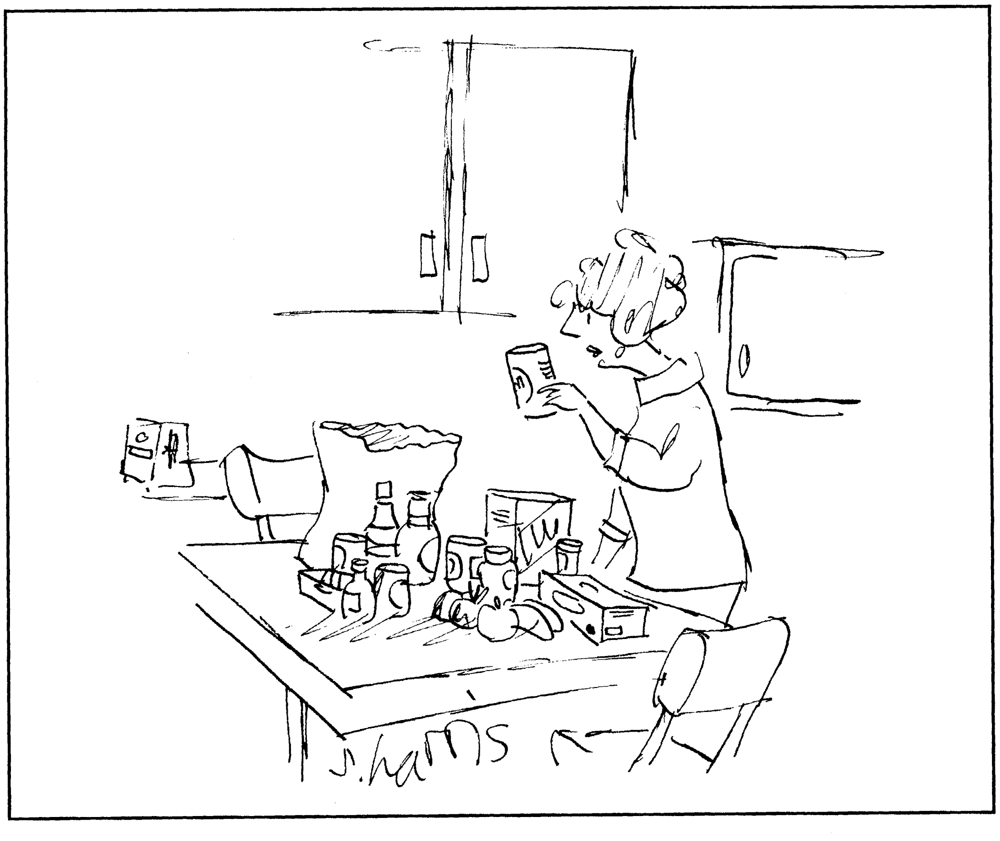

" Caution: This tomato soup combined with our chicken noodle soup can form a lethal nerve gas."