

COMMENTARIES

Demography and Human Origins

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Lovejoy's (1981) recent discussion of hominid origins is an important contribution to the growing understanding of this critical event in human evolution. It is a major development in the incorporation of paleodemography into general paleoanthropological thinking, a process begun by Mann (1973) and Weiss (1973). However, we take exception to several aspects of the theory Lovejoy developed. We contend that alternative interpretations fit the evidence equally well, and provide the basis for a more realistic explanation of the events surrounding the earliest phases of human evolution. In particular, we believe it is important to examine three issues: (1) whether there is any evidence that a demographic shift was associated with human origins or occurred early in human evolution; (2) whether monogamy was associated with such a shift; (3) and whether such a shift was *the* fundamental cause of human origins.

EVIDENCE FOR A DEMOGRAPHIC SHIFT

Lovejoy's model for the causes of the speciation event leading to the establishment of the hominid lineage rests on the supposition that a critical demographic shift occurred among the middle Miocene hominoids. Lovejoy proposes that Miocene prehominids found themselves in an increasingly unpredictable and patchy environment while they were still characterized by a reproductive pattern like that observed today among the Gombe Stream chimpanzees (Teleki, Hunt, and Pfifferling 1976), involving long periods between births and low infant survivor-

ship. This resulted in what Lovejoy terms a "demographic dilemma," which on the one hand played a role in the widespread extinctions of Miocene apes, and on the other, resulted in a unique hominid adaptation.

According to Lovejoy, the development of monogamous pair bonding overcame the "demographic dilemma" for the emerging hominids by encouraging a more effective use of resources and reducing competition between the sexes, thus improving diet and survivorship. This maximized the reproductive capacities of females by permitting shorter birth spacing and increased survivorship of the offspring, allowing populations to colonize new regions.

But was there a "demographic dilemma"? The demographic pattern of any Miocene ape species is a matter of pure speculation; there is no known fossil evidence that supports any assumption about the reproductive strategy of Miocene hominoids. We specifically question the assumption that the Gombe chimpanzee reproductive pattern (long birth spacing and low infant survivorship) necessarily represents the Miocene ape condition.

The first concern is whether recent pongids can generally be characterized by the elongated birth spacing of the Gombe chimpanzees. We believe that currently available data do not clearly support this contention. For instance, *Pongo* seems to exhibit a very humanlike variation in birth spacing which according to MacKinnon (1979) is density dependent. In the two groups he studied, one had an average live birth spacing of three years, while the other was approximately eight years.

Among the African pongids, a study of two gorilla groups inhabiting nearby sections of the Virunga Volcano region suggests differences in average birth space (Harcourt and Fossey 1981; Harcourt, Fossey, Stewart, and Watts 1980). While the data reported are not fully comparable, it is of some interest to examine the various birth space estimates. In the disturbed habitat of the western Virungas, the interval between consecutive offspring surviving to one year was estimated at 8 years (Harcourt and

Fossey 1981). As calculated from Schaller's (1963) earlier study of this region, the actual average birth space (all births) was 6.15 years. In contrast, the relatively undisturbed eastern section was characterized by a live birth space average of 4.75 years.

Data for chimpanzee groups indicate an even more variable range of birth space averages. Data published by Tutin (1980; Tutin and McGinnis 1981) on the Gombe sample confirm the Teleki calculations used by Lovejoy, indicating a birth space average at least a year greater than that of the eastern Virunga gorillas. Nishida (1979) suggests a slightly shorter interval for the Mahale Mountain chimpanzees. In contrast, Sugiyama and Koman (1979) indicate a considerably smaller birth space average for the Bossou chimpanzee population. Similarly, a short interval has been reported for a pygmy chimpanzee group (Kano 1980). Clearly, chimpanzees have the physiological potential for a very short birth interval. This is indicated by the average of 3.5 years reported for captive chimpanzees (Savage, Temerlin, and Lemmon 1973).

In sum, it would appear that long average birth intervals only characterize chimpanzees (or indeed the great apes in general) under certain conditions. These primates are physiologically capable of markedly altering the birth intervals in response to a variety of ecological and/or demographic circumstances without genetic change. Thus, the evidence suggests that the reproductive capacity of these apes does not differ from that of living humans (Keyfitz and Flieger 1971; Weiss 1973) and this (rather than long birth intervals) is therefore the most likely assertion that could be made about the last common ancestor of humans and the African apes. Making this minimum assumption, we regard it as impossible to ascertain whether a Miocene hominoid population suffered a "demographic dilemma" such as Lovejoy describes, without specific knowledge of factors ranging from ecology and habitat to age structure and population density. Moreover, because of the sensitivity of a pongid (or human) pattern of birth interval regulation, we question whether such a dilemma would likely be long term.

Finally, it may be productive to examine evidence provided by the fossil record itself. Although the demography of Miocene prehomonids and the earliest hominids (*Australopithecus afarensis*) is unknown, there are some demographic estimates that might be ascer-

tained for the later South African *Australopithecus africanus* sample (Wolpoff, as discussed in Waterfall 1979). This sample may confirm one of Lovejoy's assertions about early hominid demography. Assuming the sample approximates a stable and stationary population (Birch 1948), this australopithecine species seems to combine a high birth rate, as predicted by Lovejoy, with a fairly high mortality rate in the subadults and young adults. For instance, at Sterkfontein the general fertility rate is about 40 per 1,000 compared with about 20 per 1,000 in Teleki's chimpanzee sample. One important consequence of this combination is the likelihood of a high orphaning rate. Under the stable and stationary population assumptions and following Deevey's procedure (1947), it can be calculated that the probability of a mother's death by the time her first born has reached sexual maturity approximates 0.7 in the *A. africanus* sample, as compared with about 0.3 in the Gombe chimpanzee sample with its lower young adult mortality rate. If these estimates are even approximately correct, there may indeed have been a "demographic dilemma" early in hominid evolution but it may not have involved only fertility. Instead, the real problem may have been in low adult survivorship and consequently in the maintenance of parental care in a slowly maturing species. If so, any broad-based kinship system providing for an increase in the number of adults in addition to the parents concerned with the survival of an infant would be populationally adaptive.

THE MONOGAMY SOLUTION

Our second concern has to do with Lovejoy's solution to the "demographic dilemma"—monogamy. He asserts that this mating system would result in the improvement of provisioning strategy and survivorship (as discussed above), and assure a male's participation in the family group through his efforts to maximize his inclusive fitness (see Melotti 1981).

Monogamy, however, is not the only possible model that would fit these requirements. There is no theoretical reason to assume that monogamy is the most likely system that would apply even if the demographic conditions Lovejoy posits actually existed. Although pair bonding appears to be a common human behavior, a survey of contemporary preurban societies (Murdock 1953) provides no basis for the contention that exclusive long-term monogamy is or ever was the only bonding pattern for humans.

We feel that other mating systems may not only improve provisioning strategy and consequently survivorship, but may also be more in accord with what we know of both modern human and chimpanzee societies (Wrangham 1979a). Chimpanzee social structure is based on a "community" of 15 to 80 individuals of all age-sex classes sharing a single home range (Wrangham 1979b). Anestrous female chimpanzees with offspring spend over 80% of their time either alone with their offspring or in nursery parties. Males rarely spend time alone, tending to associate with all-male groups or with groups of mixed composition (Wrangham and Smuts 1980). While successful reproductive behavior is not always the result of the enthusiastic promiscuity noted by earlier observers (van Lawick-Goodall 1968), its structuring is quite variable, responding to a variety of different circumstances. For instance, mating between close kin is avoided (Pusey 1979, 1980). Females may exercise some degree of choice of partner through avoidance or lack of responsiveness (Tutin 1979), but under other circumstances copulations may be restricted to the most dominant male when he remains in close proximity to an estrous female and interrupts the courtship attempts of other males (McGrew 1981). Yet, in one study it was observed that about half the successful impregnations resulted from intense short-term pair bonds (up to 28 days) during which the male, female, and her dependent children avoid the social group (Tutin 1979). Exclusive long-term monogamy would require a considerable shift from these disparate patterns if it characterized the prehomínids.

If we assume, as Lovejoy does, a prehomínid mating system and social structure analogous to that seen in the Gombe chimpanzees, it is reasonable to ask what less dramatic shifts in strategy might resolve the "demographic dilemma." For example, one alternative to monogamous male participation for improving infant survivorship might have been for early homínids to incorporate kinship-based female participation in already existing nursery parties. A group of related females has several potential advantages over a single female, including predator avoidance, exchange of information concerning resources, and transmission of learned behavior (Lancaster 1976). In addition they would improve their own inclusive fitness through mutual care of the offspring. Interestingly, chimpanzees show continuous food sharing which is almost always among groups of related females (McGrew 1979). However, in this respect female

chimpanzee behavior differs from homínids in that female-collected foods are generally not shared with the males (McGrew 1981). While male chimpanzee hunting does result in provisioning the females (Galdikas and Teleki 1981), distribution of meat is not necessarily along lines of biological relationship (Teleki 1973).

The modification of the chimpanzee pattern that we suggest would allow for the sex-based division of labor that Lovejoy posits. The key to the modification we propose goes beyond the recognition of kinship, a phenomenon observed in chimpanzees (Goodall 1976; Riss and Goodall 1977; Bygott 1979). We suggest that the early appearance of formalized behavioral expectations and ultimately of social organization was based on recognized kinship relations. At the origin of this development may well lie the formalization of reciprocal food sharing along lines of biological relationship. Each homínid male, by assuming responsibility for provisioning a kinship group, would assume a parental role and enhance the survival of his relatives. Recognition of *specific* paternity would not necessarily be of particular importance, because the kinship recognition we propose as the structural basis for formalizing these groups would provide for a parental role. At the same time, male assumption of provisioning responsibility would fulfill the requirement of ensuring that males increase their inclusive fitness. Such a paternal role could be viewed as an intermediate step in the development of specific paternity recognition.

More than one male may have provisioned a single kinship group. The collective exploitation and defense of an area greater than the total area of individual territories would give each male reproductive advantages (such as access to more females) through cooperation (Emlen and Oring 1977). Moreover, if chimpanzees are the appropriate model, it is interesting that they are the only nonhuman primate to show long term male-male social relationships (McGrew 1981). Male groups cooperate in controlling large areas (Wrangham 1979a) as well as in hunting activities (Teleki 1973). Thus, we posit that male groups may also have been fundamental in early homínid social organization.

At the same time, the increased predictability of male provisioning and the formalization of other ties following from kinship recognition would help establish reciprocity in food sharing on the part of the females (although among the earliest homínids other factors such as the development of simple containers would also be im-

portant in this behavioral change; see Tanner and Zihlman [1976]). In turn, increased group reliance on plant foods gathered and shared by females would provide a firm adaptive basis for the further development of the less predictable hunting of larger game (Lee 1968). Together, these provisioning strategies would result in a more effective use of a wider range of resources (Isaac 1978). Finally, this arrangement would enhance the opportunities for social behavior that Lovejoy argues is so important to the evolution of the intellect by providing a wider but more rigorously structured social milieu.

Other models, then, may fit the data at least as well, if not better, than the monogamous one. For instance, there are some indications that polygamy might be a better justified model for the early hominids. These are found in the prominent epigamic characters discussed by Lovejoy, as well as in the marked degree of sexual dimorphism suggested by direct studies of early hominid skeletal morphology (Wolpoff 1976; Johanson 1980), a point that Lovejoy ignores. In contrast, "in species exhibiting long term pair bonding, there is often a reduction in the degree of sexual dimorphism, both behavioral and morphological" (Kleiman 1977).

Similarly, we feel that the Emlen and Oring (1977) model was inappropriately used. Lovejoy argues that because the environmental conditions for polygamy were *not* fully met in the reconstructed Miocene ecosystem, monogamy must have resulted. While it is uncertain that critical food resources were not sufficiently clumped to argue strongly for a pattern of resource monopolization by the males that would result in a polygamous mating structure, it is equally uncertain whether one can argue the converse as Lovejoy does. Mobile feeding by a generalized primate does not necessarily lead to exclusive, long-term pair bonding. We believe that a firm connection between ecology and mating structure cannot be made in this case.

The possibility of mating structure models other than monogamy also follows from the Emlen and Oring discussion of the temporal distribution of female receptivity. If all the females in a population become sexually receptive in unison, there is little potential for individual males to monopolize multiple females. This is especially true if each female is sexually active for only a brief period. With increasing degrees of asynchrony among females, the potential for individual males to accumulate more than one mate increases. The develop-

ment of constant receptivity in human females maximized the potential for asynchronous mating. While this could form the basis of monogamous grouping, it could as easily support the maintenance of polygynous groups.

Viewing the problem another way, there are distinct disadvantages to exclusive long-term pair bonding. Given Lovejoy's model of a female of limited mobility with dependent offspring (obviously several at a time, if her reproductive potential is realized), and a mate foraging far afield to reduce feeding competition with her, the only major contribution that the male can make is via provisioning. Because of the time and energy spent by a monogamous male during provisioning, other aspects of male participation in raising the young would be sacrificed. Yet the demographic reconstruction of the South African *A. africanus* sample indicates that the likelihood of orphaning is probably high enough to question whether a monogamous mating system, even with a full-time foraging husband, could ensure the demands of infant care in the event of the death of either mate.

Lovejoy does not specify in his model whether he believes that monogamy implies isolated nuclear families. This is a serious omission, as it could lead to radically different interpretations of his model. If the nuclear family were isolated, then the prolonged absence of the male would leave the female and offspring more vulnerable to predation. Lovejoy notes that a smaller foraging area for the female would reduce exposure to predators. However, predators would probably take advantage of the fact that she would be unable to protect her dependent offspring as efficiently by herself.

If Lovejoy does *not* consider the monogamous pairs as isolated, but rather as forming groups, the next question becomes: What is the basis of *this* grouping? Again, we believe that kinship is the most reasonable answer. If this is so, one might well ask which is more important—the mating system or the grouping? In failing to elaborate on this aspect of his model, Lovejoy has left a number of important questions unanswered.

Finally, it is not completely clear that monogamy could necessarily ensure a male's participation by improving his inclusive fitness. Monogamous pair bonding could be particularly difficult to maintain if the foraging space for each mate is separate. The male, spending most of the day far from the home base, would be unable to repel the advances of other males

toward his mate. It is hard to see how "cheating" could have been avoided. Modern "monogamous" societies are not always successful in maintaining marital fidelity (Kinsey et al. 1953), even with the elaborate controls of a complex cultural system. As the dramatic increase in hominid intelligence took place much later in human evolution (Washburn 1960), at best only moderately effective social controls were possible at the time of the hominid divergence. There would be a less risky payoff for a male, in terms of his inclusive fitness, if he participated in either an extended family based on maternal kinship, or if he joined with other related males in providing for, or defending, the entire group.

Thus, we conclude that to the extent that there was a demographic shift involved in hominid origins, a variety of kinship-based mating systems might have underlain the consequent social restructuring. Rather than postulating a particular mating system, we would point to the use of kinship recognition as the formal basis for social *grouping*, regardless of its specific form. Based on the several alternative models we have suggested, it seems reasonable that a matrifocal kinship system might have been the basis of this grouping. In fact, however, *there is no reason to suppose that any specific mating system characterized all populations and even if only one did, there is ample reason to posit that exclusive long-term monogamy was not necessarily the one.*

A CAUSE OR THE CAUSE?

Our final concern also proceeds from the assumption that there was a demographic dilemma, and is independent of which consequent mating system(s) actually evolved. This concern arises from our belief that there is a fundamental fallacy in assuming a *single cause* model for hominid origins (Mann 1972; Wolpoff 1980). While Lovejoy systematically dismisses all but the demographic variable, we argue that this is neither realistic nor justified.

In fact, the causes and conditions surrounding the *actual speciation event* that founded the hominid lineage will probably always remain unknown, and there is no reason to assume that these bear any necessary relation to the subsequent evolutionary trends within the lineage (Mayr 1963). Hominids became recognizable with the advent of these trends, and thus it is the *adaptive shift*, rather than the actual speciation event, that should be the focus of discus-

sions of hominid origins. This shift must be viewed in its ecological context (Bartholomew and Birdsell 1953) and it almost certainly involved an interrelated complex of adaptive behaviors. It is the development of this *complex*, and not any particular behavior or associated morphology, that is the key to understanding the adaptive shift associated with hominid origins, and this complex may involve no, or only a few, unique elements. Instead, it is likely that the adaptive shift was mainly based on a change in emphasis and importance for behaviors already within the repertoire of the prehomínids.

A single cause approach to the origins problem must necessarily ignore this, because by emphasizing uniqueness, the single cause approach requires a dismissal of the importance of any aspect of behavior or biology shared with our closest relatives. This has resulted in a list of possible causes for the hominid-pongid divergence that shrinks as our knowledge of pongids increases.

We contrast this with an approach that emphasizes the ecological shift associated with hominid origins. Such an approach does not rest solely on unique hominid characteristics, but may also stress *shared* behaviors or morphologies whose importance stems from the adaptive changes they allow. For instance, consider the problem of tools and human origins. The potential importance of technology is dismissed by Lovejoy through the observation that the earliest stone tools are only about 2.5 million years old, although just above this statement are admissions that the earliest tools "will have left no record" and that "tool use is a general capacity of pongids." Since tool use is common to both homínids and extant pongids (van Lawick-Goddard 1970, 1973; Teleki 1974; Sabater Pi 1974; McGrew, Tutin, and Baldwin 1979), it is likely that this behavior existed before their divergence. We submit that these considerations fail to eliminate the possibility that technology (although not necessarily *lithic* technology) was an important component in homínid origins (Isaac 1981). Studies of later australopithecines providing evidence of delayed maturation (Mann 1973) and neural reorganization (Holloway 1969) suggest the possibility that technology played a critical role in behaviors ranging from defense to gathering and preparing food. Thus, we contend that the series of adaptive changes leading to early homínid population expansions and occupation of novel niches might well have relied on the in-

creased adaptive capacity allowed by tool use in gathering and processing foods and protection from predators in a new ecological context such as open grasslands.

Similarly, Lovejoy dismisses the dental evidence for a dietary factor in the hominid adaptive complex. He regards the dentition of *A. afarensis* as generalized, with molars of only moderate size relative to body size compared with later hominids. The basis for this statement escapes us, since comparison with the few human fossil specimens that allow for determination of both molar and body size indicate that *A. afarensis* was very megadont.¹ We therefore suspect that an adaptation to diets requiring powerful masticatory forces, as further indicated by the megadont character of the later australopithecine dentitions (Wolpoff 1973) may also be a significant aspect of hominid origins (Jolly 1970) although like toolmaking it may have evolved earlier (Wolpoff 1981). We regard such an adaptation, along with tool use, as an important factor underlying the increased dietary range (Wolpoff 1980) and consequent adaptability of the earliest hominids. These are adaptive characteristics that Lovejoy ignores because they are shared (tool use) or because he does not recognize that they characterize the earliest hominids (adaptation to dietary items requiring powerful masticatory forces).

The one morphological complex Lovejoy does focus on is bipedalism, a morphological complex and behavior which he has shown to be fully developed in the earliest hominids. Yet even this discussion, of a complex whose analysis in fossil hominids is primarily the result of Lovejoy's own original work (Lovejoy 1974; Lovejoy, Heiple, and Burstein 1973), suffers from the same single cause approach that we believe it is necessary to reject. Over the years, arguments about the adaptive significance of bipedalism have ranged across a wide spectrum of behaviors: seeing over tall grass, carrying weapons for defense, freeing the hands for tool use, the energy efficient use of long distance stride, and others. Lovejoy's contribution to the debate focuses on carrying the immature (which by his model would be numerous), and foods for provisioning. We believe that to attempt to choose between these single causes misses the entire point of early hominid social organization. A group of hominids would be able to do all of the above. We assert that the adaptive importance of bipedalism stems from the numerous advantages this behavior would confer on a group. In our view, a kinship-based organiza-

tion for such a group would markedly expand the adaptability that bipedalism could provide precisely because the structure of the group would ease the organization of differing adaptive behaviors within it.

In conclusion, we wish to focus on a number of behavioral and morphological changes that are associated with the ecological event of hominid origins when a shift in the *adaptive complex* of locomotor, dietary, technological, and reproductive behaviors probably occurred. Our point is that demographic changes are not the only ones that serve to explain the subsequent pattern of hominid adaptability. We tend to view the problem of origins in a broad ecological context, involving the adaptive separation of hominid and African pongid lines. We propose that the emerging (probably terrestrial, open country based) adaptability in the hominid line should be understood in parallel with the developing forest frugivorous adaptation in the African pongids, and that these differing adaptations might well have been the consequence of niche divergence in (what were then) two similar species. In our view, there is a complex of behaviors associated with the emerging hominid adaptive pattern, many of which were (and are) shared with the contemporary pongids but as part of a different behavioral pattern expressed in increasingly different ecological conditions.

We have focused on the adaptive implications of formalized behavioral structures based on kinship recognition in early hominid groups. This is one specific aspect of a more general behavioral pattern in the hominids which at some point became recognizable as cultural (Durham 1979). We argue that the subsequent increased complexity of structured learned behavior (Holloway 1969; Hollowell 1961; Wolpoff 1980) had even more general consequences for the earliest hominids than shortening of birth spacing and the appearance of male parenting. We believe that it is this early cultural adaptation that underlies the unique direction of subsequent hominid evolution.

Notes

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¹ For instance, the ratio of the area of the mandibular molars (mm^2) to estimated body height (cm) in the *A. afarensis* specimen "Lucy"

is .38, *exactly the same* as for the only usable *A. africanus* specimen (STS 7) and markedly contrasting with the much smaller teeth of *Homo erectus* (the ratio for the Baringo specimen is .24) or archaic *Homo sapiens* (the Spy 2 ratio is .25).

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On Williams's Review of *Evolutionary Biology and Human Social Behavior*

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In his review (*AA* 84:416-418, 1982) of *Evolutionary Biology and Human Social Behavior* (N. A. Chagnon and W. Irons, eds.), B. J. Williams states: "The theoretical background . . . is the weakest part of the book in that it has carried with it uncritical acceptance of . . . hypotheses in sociobiology. . ." (p. 417). The following facts call this assessment into question:

1. A primary goal of the book is to carry forward the task of theory evaluation through hypothesis testing (pp. xii, 2-3, 10, 39, 78, 85, 89, 127-128, 132, 184, 213, 215-216, 248-249, 252-257, 272, 273, 287, 290-293, 370-372, 409-412, 417-418, 420-421, 468-470, 509, 525-526).

2. Several chapters (8, 9, 10, 12, 15, 18) are devoted primarily to reporting tests of hypotheses, and much of the rest of the book lays the groundwork for future testing by deriving testable predictions from sociobiological hypotheses.

3. Most of the tests reported confirm theoretical predictions, but one definitely does not (chapter 12), and the authors reporting these falsifying results suggest a need for theory modification. Authors who do report confirming results continually caution that more tests are needed before the hypotheses can be accepted (pp. xvi, 2-3, 4, 39, 55-57, 78, 127, 139, 144, 177, 207, 213, 214, 237, 241, 248-249, 256-257, 272, 288-289, 320, 367, 369, 401, 486, 509, 525-526).

It is hard to see how testing equates with "uncritical acceptance"—especially when those conducting the tests suggest modifying theory when they get disconfirming results, and continually caution that more tests are needed when they get confirming results. The "theoreti-