Potassium Iodide Distribution

The News and Comment briefing "Potassium iodide and nuclear accidents" (19 Mar., p. 1485) by Constance Holden misrepresents my congressional testimony. At the hearing, I made it absolutely clear that I was quoting from a report issued by the American Thyroid Association on 18 September 1981. This organization represents the leading experts in the field of thyroid disease. Their report said that "evidence from subjects exposed to relatively large amounts of diagnostic [iodine-131] in Sweden and carefully followed suggested no increase in thyroid tumor incidence in populations exposed to about 100 rads (adults) or 159 rads (persons under 20 years of age). For these reasons, projected thyroidal doses from radioiodine as high as 500 rads have recently been proposed as a realistic threshold for the institution of blocking counter-measures in the event of a reactor accident releasing radioiodines into the environment. . . . The projected absorbed dose of 10–30 rads recommended by NCRP [National Council on Radiation Protection and Measurements] 55 as the threshold for the institution of iodine blockade in the event of a reactor accident is overly conservative. Based upon available data, it would seem unlikely that clinically significant thyroid disease would result from individual thyroid exposure of less than 100 rads." Frank von Hippel and Sydney Wolfe challenged this position and stated that I had not published in this field. Their challenge is irrelevant since I was simply quoting from the experts. I was not reporting from my experience, as the briefing states.

The briefing also states: "If the lineup at the hearing is any indication, it would appear that the main opponents of general distribution of KI are also the strongest nuclear power enthusiasts." The American Thyroid Association's report concluded that data are not now available to define more precisely the relative risks of radioiodine exposure and of short-term iodide therapy and recommended the appointment of a national task force of appropriate specialists to consider the problem. One can hardly characterize the members of this association as "the strongest nuclear power enthusiasts." It simply consists of the most knowledgeable thyroidologists in the country.

Representative Edward Markey (D–Mass.), who called the hearing and who was the only member of the Committee on Interior and Insular Affairs present, favors distribution of KI, and all but one of those invited to testify reflected this point of view. Holden's statement that " . . . the preponderant scientific opinion—judging from recent hearings in the House—is that KI should be made available to people who live near reactors" leaves the impression that this reflects preponderant scientific opinion rather than the viewpoint of a single congressman and the witnesses he called who reinforce that viewpoint.

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Models of Human Evolution

C. Owen Lovejoy's article, "The origin of man" (23 Jan. 1981, p. 341), offers a series of interesting suggestions regarding possible sequences of change in human evolution and the natural selection pressures which may have brought them about. However, a general scientific readership that is not acquainted with details of the state of inquiry in the study of human evolution should be aware that a number of the assertions incorporated in Lovejoy's argument are in fact uncertain, and several are currently under investigation.

1) In a discussion of human evolution one should be concerned with demographic patterns without agriculture. Although reliable data on human birth spacing are scarce, those cases that have been reported are inconsistent with Lovejoy's estimate of 2.5 years and imply values for spacing that are as high or higher than those estimated for apes (*1*).

2) It is not clear that, before the spread of agriculture and firearms, the great apes were precariously poised on the brink of extinction (*2*). Presumably the ultra-*K* selective reproductive strategy of apes is derived, rather than primitive, and it would be important to assess the adaptive qualities of the ape strategy.

3) There are serious difficulties with the suggestion that among incipient hominid populations some nonbipedal males improved their reproductive success by gathering nonmeat foods in order to provision their mates and offspring. The transport of sufficient nuts, berries, and insects poses problems even if one assumes a simple bark tray was used as a carrying device. The difficulties seem particularly acute if, as implied, the incipient hominids were not yet bipedal. The feasibility, energy potentials, and energy costs of such provisioning in savanna environments can and should be measured.

4) Lovejoy is dealing mainly with evolutionary events that occurred just before 4 million years ago. He specifically discounts the possibility that meat was involved in hominid feeding systems of those times. While this may be correct, readers should be aware that a shift into an adaptive pattern involving food transport and provisioning would be greatly facilitated if highly portable, high-quality food such as meat were a component of diet. I know of no a priori reason why meat, whether secured by hunting or scavenging, could not have been important and think that Lovejoy's model would have been strengthened by having had this possibility left open for further investigation.

It would certainly have been relevant to have drawn readers' attention to the fact that, by 2 million years ago at the next stage of human evolution, there is strong archeological evidence for hominid consumption of meat from the carcasses of much larger animals than are eaten by any living ape. Equally, there is archeological evidence from the same time range (which many researchers would regard as consistent with Lovejoy's central hypothesis) that food began to be transported at an early stage in evolution (*3*). While this archeological evidence relates to the time range following that which is the focus of concern, it is germane to an assessment of Lovejoy's arguments and is compatible with it.

Archeological indications from 2 million years ago are fully consistent with the most important part of Lovejoy's overall scenario—namely, his suggestion that pair-bonding and provisioning were shifts that occurred early on in human evolution. The crucial next step is to separate out testable components and implications from Lovejoy's scenario and to test them.

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Lovejoy proposes that the "unique" sexual and reproductive behavior of the human female can be explained by, and used as evidence for, a history of pair-bonding in emerging hominids. Flexibility in the timing of sexual activity is a characteristic shared with many Old World monkeys and apes (*1*) and probably evolved in a context other than the pair-bond or the nuclear family.

Lovejoy states birth intervals in humans to be 2.5 years and in pongids to be 3 years. The origin of the 2.5-year estimate for humans is unclear, as no source is cited. In some noncontracepting, nonabstinent human populations where late weaning is the custom, birth intervals are longer than 3 years (*2*). Early weaning and the resulting shorter birth intervals in humans are undoubtedly recent phenomena historically (*3*). For the apes, data are available for the gorilla, whose birth intervals are from 3 to 5 years ($\bar{x}$ = 3.75 years), when the infant survives to at least 3 years (*4*). Rough estimates of orangutan birth intervals vary from 3 to 7 years (*5*) to 4 to 5 years (*6*).

Lovejoy presents birth interval data only for the common chimpanzees from the Gombe Stream Reserve, in spite of the fact that the model depends on comparisons of all pongids. If the birth intervals of the gorilla and orangutan are included in the comparison and the estimate for humans corrected, no extreme differences between hominid and pongid birth intervals can be seen.

According to Lovejoy, "continual sexual receptivity" and "sequestration" of ovulation were necessary preconditions for pair-bonding in early hominids. The statement that human females are continually sexually receptive is not referenced, and a personal communication from D. C. Johanson is unacceptable as evidence (*7*). Peaks in human female autosexual and female-initiated sexual behavior around the time of ovulation have been reported (*8*), and cyclicity in nonsexual behavior is well documented (*9*). In addition, there is no evidence to indicate that mammalian pair-bonds are maintained by increased sexual activity or attraction between the pair. In a recent review of monogamy in mammals, it is concluded that "sexual behavior occurs infrequently and thus must play a minor role in pair bond maintenance" (*10*). The author continues, "there are no more intense socio-sexual interactions in species exhibiting long-term pair bonds than in polygamous forms" (*10*). These statements apply to the pair-bonding apes—the siamang and the gibbon. In the siamang (*Symphalangus syndactylus*), copulations occur only during a 4- to 5-month period every 2 to 2.5 years. These copulations are clustered around the time of ovulation (and genital swelling) at monthly intervals (*11*). In the gibbon (*Hylobates lar*), sexual activity "is not a prominent feature of the animal's behavior in the laboratory" (*12*).

A relationship between flexibility in the timing of sexual behavior and the stability of male-female bonds becomes even less tenable if data from the great apes are taken into consideration. The gorilla (*Gorilla gorilla*) exhibits the most stable social groupings of all the great apes (*4*). Copulations are limited to a period of 1 to 4 days out of the menstrual cycle in both the field (*13*) and laboratory (*14*). In the common chimpanzee (*Pan troglodytes*), described as living in poorly coordinated but stable groups, copulations occur predominantly during a 10-day period, when the perineum is maximally tumescent (*15*). In the laboratory, copulations occur throughout the reproductive cycle (*16*). Although data are limited, the pygmy chimpanzee (*Pan paniscus*) copulates at any stage of the menstrual cycle in captivity (*17*). The orangutan (*Pongo pygmaeus*) may also copulate at any stage of the reproductive cycle in both the field (*5, 6, 18*) and the laboratory (*19*). This ape exhibits no external signs of ovulation (*20*) and cycle length must be determined by noting menses (*19, 21*). Orangutan social organization is described as solitary, with no long-term associations between adult males and females (*5, 6, 18*). These data indicate that continual sexual activity and attraction between a pair are not necessary preconditions for the maintenance of long-term bonds between males and females in the apes. It can be argued that the opposite correlation exists (*19, 22*).

If reconstruction of early hominid behavior is to be productive, one cannot selectively omit available evidence from our closest living relatives, the apes.

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20. It must be noted that, of all the hominoid primates, including humans, only the chimpanzees exhibit pronounced genital swellings at mid-cycle, around the time of ovulation. The gibbon and gorilla show only small and inconspicuous swellings. However, female chimpanzees, gorillas, orangutans, and possibly humans, like most female mammals, exhibit an increase in solicitations of the male for copulations at mid-cycle.
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Lovejoy argues that (i) compared to pongids, hominids exhibit delayed reproduction, requiring higher total fertility to maintain population size or growth rate; (ii) higher fertility has been achieved in hominids by shortening birth intervals; (iii) hominids are more "*r*-selected" than pongids; and (iv) the increased population growth potential and colonizing ability associated with this reproductive shift are largely responsible for the present widespread distribution of hominids and the severely restricted distribution of pongids. All but the first of these assertions are either contradicted by empirical evidence or inconsistent with demographic theory.

Table 1 summarizes several demographic features of chimpanzees and hu-

Table 1. Comparative data on chimpanzee and human reproduction (females only) (*1, 2, 10, 11*).

Reproductive trait	Chimpanzee	Human
Age at menarche (years)	8.8	15.5
Postmenarchic sterility (years)	1.0 to 1.5	2 to 4
Age at first reproduction (years)	11.8	19 to 20
Length of gestation period (days)	227	267
Normal litter size	1	1
Mean birth interval (years)	3.2	3 to 4
Age at last reproduction (years)	30 to 35	40
Total fertility rate*	5.8	5.6†
Total length of reproductive span (years)	20 to 25	20 to 25
Length of generation (years)	19.6	20 to 25

*The mean number of offspring produced by females who survive to the end of the reproduction span.
†Weighted mean of data on 48 nonindustrial populations (*10*).

mans relevant to points (ii) and (iii). Lovejoy states (without citing a source) that the typical birth interval in humans is 2.5 years; the literature on modern tribal and hunter-gatherer populations indicates a mean interval closer to 3.5 years (*1*), somewhat longer than the relevant estimate for chimpanzees (*2*). In this and all other respects in which the two species appear to differ (Table 1), humans differ in the direction predicted by models of *K*-selection (*3*). They reproduce later, produce fewer offspring, have longer pregnancies and birth intervals (and so, presumably, longer periods of parental care), and have longer generations. The differences between the two species are minor, however, except for one: humans begin reproducing about 8 years later than chimpanzees. Since delayed reproduction is considered the sine qua non of *K*-selection (*3*), humans appear to be even more *K*-selected than chimpanzees.

Lovejoy poses an important theoretical question: by how much must total reproductive output be increased to compensate (in terms of population growth potential) for the delay in reproduction that distinguishes humans from chimpanzees? The equations on page 344 of Lovejoy's article do not provide the answer. The quantity given by his equation 1 is not Fisher's reproductive value, but a demographic non sequitur equal to $R_0 l(\alpha)$, where R_0 is the population's net reproduction rate and $l(\alpha)$ is the probability of surviving from birth to age α, the age at first reproduction. This quantity bears only a tenuous and nonmonotonic relationship to the population's rate of increase, which is approximately $\ln R_0 \times (\text{mean generation length})^{-1}$ (*4*). Moreover, Lovejoy introduces two simplifications that further reduce the utility of this equation. First, he assumes that $l(x) = \kappa^x$ throughout the life-span, where x is age and κ is some constant. Second, $b(x)$ the probability of producing a same-sex offspring at age x, is written $1/\beta$, where β is the length of the period between successive births (also assumed constant). Thus mortality and fertility are assumed to be constant and independent of age, contrary to what is found in both chimpanzees and humans (*2, 5*). Lovejoy's equation 4 is thus of limited value, and the usefulness of his table 1 is correspondingly diminished.

It is possible, nonetheless, to answer Lovejoy's question. Consider the Lotka-Euler equation relating population growth, fertility, and mortality in a population with a stable age distribution

$$1 = \int_\alpha^\omega e^{-rx} b(x) l(x) dx \qquad (1)$$

where r is the instantaneous rate of population increase, ω is the age at last reproduction, and all the other parameters are as defined above (*4*). Without making any untoward assumptions about the distributions of $b(x)$ and $l(x)$, what would happen if we delayed reproduction by some quantity Δ, so that $b(x) = 0$ in the interval $(\alpha, \alpha + \Delta)$? By how much would we need to change the other parameters of Eq. 1 to maintain r at its original value? This question was recently answered for a discrete time version of Eq. 1 by Caswell and Hastings (*6*). These authors show that, if sexual maturation is shifted by Δ years, then overall fertility must be multiplied by a factor of approximately

$$\Phi_\Delta = (e^r/\bar{p})^\Delta \qquad (2)$$

to compensate for the reduction in population growth, where $\bar{p}$ is the mean probability of surviving each year during the reproductive span.

Suppose we observe a protohominid population in demographic equilibrium ($r = 0$) among whom $\bar{p} = 0.95$, a reasonable figure for both chimpanzees and primitive humans (*2, 7*). Then suppose we delay the onset of reproduction in this population by 8 years, a value of Δ suggested by Table 1. Substituting these values in Eq. 2, we obtain $\Phi_\Delta \simeq 1.5$. That is, the observed delay in sexual maturation among humans relative to modern pongids would have to be countered by a 50 percent increase in overall fertility just to maintain the population at its former size. As the figures in Table 1 show, no such increase has occurred; if anything, the evidence suggests a general *lowering* of fertility among humans.

A similar argument applies to Lovejoy's suggestion that hominids are more *r*-selected than pongids. If "*r*-selection" means anything, it means that the parameters of Eq. 1 are evolutionarily adjusted to maximize the value of r. As several analyses have shown, the most effective way to increase r is to reduce the age at first reproduction, unless the population is actually declining in size (*6, 8*). Caswell and Hastings' conclusions are pertinent here, since a reduction in α equal to Δ increases r by an amount equivalent to multiplying total fertility by Φ_Δ. According to the numerical results given here, chimpanzees must again be considered more *r*-selected than humans because of the earlier age at which they begin reproducing.

MacArthur and Wilson (*9*) have shown that maximization of r also maximizes the colonizing ability of the population and minimizes its chances of becoming extinct. All things being equal, then, chimpanzees should have higher population growth rates and lower extinction rates, be better colonizers, and thus have a wider geographical distribution than humans. Obviously, all things are *not* equal. Lovejoy's thesis notwithstanding, the evolutionary success of humans cannot be explained solely in reproductive terms.

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Lovejoy traces human bipedal origins to a "demographic dilemma." We note the following problems with his scenario.

1) The chimpanzee interbirth interval and generational length utilized by Lovejoy are derived from studies at Gombe. However, this population was undergoing demographic changes associated with provisioning and epidemics of paralytic and respiratory diseases (*1*, table 9). Sugiyama and Koman (*2*) worked with a nonprovisioned group of chimpanzees and suggest an interbirth interval closer to 4 years, which allows a female to replace herself and a male in about 18 years. Thus, it seems unlikely that chimpanzees were forced to retreat into forested areas in the face of a demographic dilemma.

2) In his table 1, Lovejoy gives the "maximum life potential" of humans as 60, the age of sexual maturity as 15, and the interbirth interval as 2.5 years. However, most demographic models (*3*) use 15 and 45 as the age of sexual maturity and menopause, respectively. Use of the latter figure would greatly alter the reproductive values presented in Lovejoy's table 1. In equation 4, Lovejoy assumes that each taxon reproduces at a constant rate from age of sexual maturity to "maximum life potential." This assumption does not seem valid for humans (*3*) and may not be true for other primates (*4*). These considerations cast doubt on the reproductive values calculated by Lovejoy.

3) Lovejoy states that human females are continually sexually receptive; no scientific evidence demonstrates this, and studies (*5–6*) mentioned by Lovejoy indicate the contrary. Beach (*6*, pp. 354–355) writes, "No human female is 'constantly sexually receptive' (Any male who entertains this illusion must be a very old man with a short memory or a very young man due for a bitter disappointment)."

Where Lovejoy postulates concealed ovulation as a means of maintaining the pair-bond, Symons (*7*) suggests human females concealed ovulation to allow them to sneak copulations with males "fitter" than the mates with whom they were paired. Moreover, Symons argues that the human family is not a sexual but an economic union, a position supported by the fact that marriages in extant hunter-gatherer groups are alliances of families that extend social networks. Food-sharing in these networks is a partial insurance against future starvation (*8*).

4) In response to Lovejoy's argument that early hominids evolved dual parental care in order to increase reproductive output, it should be noted that *r*-selected species usually do not exhibit extended or extensive parental care. When offspring disperse and thus compete for first access to resources, selection favors low investment per offspring. It is only when offspring do not disperse and interact competitively for resources that selection favors large investment in the young (*9*). Thus, it seems unlikely that early hominids became biparental in order to increase *r*-selected traits.

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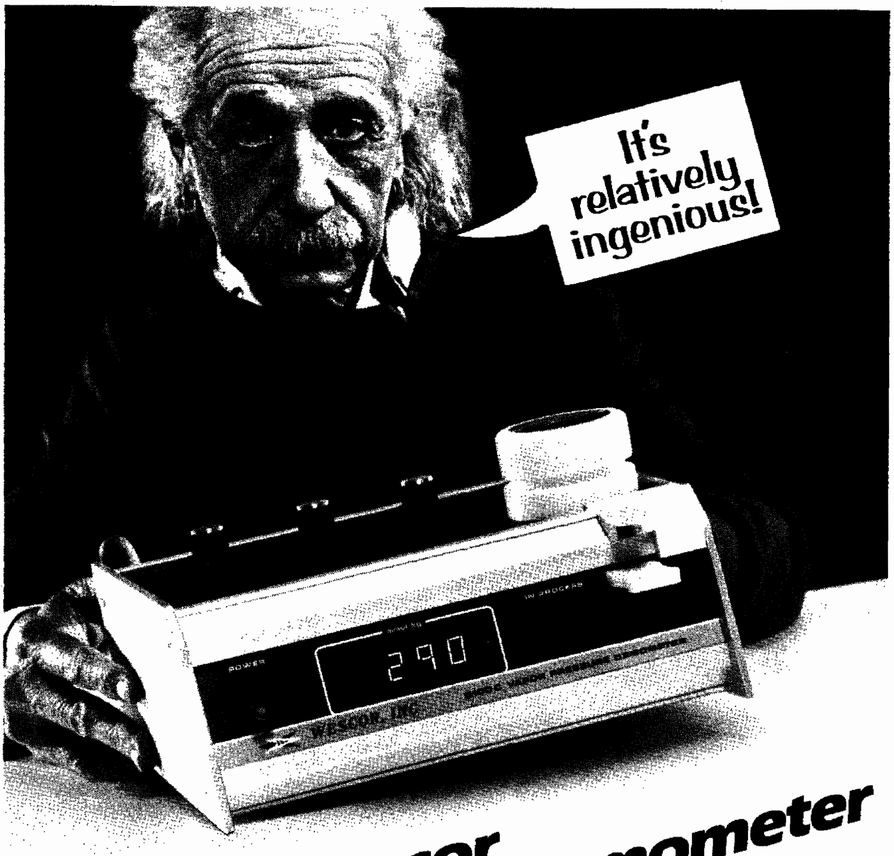
Lovejoy proposes that human bipedalism arose as a consequence of natural selection on males: a male that was bipedal could carry more food to his mate and her offspring (and this would give the offspring an advantage over those from families in which the adult male was quadrupedal). A problem with this proposal is that the male could not be sure the offspring were his. By contrast, his mate, however promiscuous, would know her own offspring. Since males are never as sure of their paternity as females are of their maternity, selection on male behavior would be less efficient than selection on female behavior (*1*).

Therefore, it is important to give more consideration to the role of females in the origin of human bipedalism. One evolutionary model states that bipedalism arose because of the advantage it gave to females in the transport of infants (*2*). This model is appealing because it depends on the most important bond in mammalian groups, that of the mother and her dependent offspring. Upright walking, originally adaptive in infant transport, would confer the added ability to carry food and would contribute to infant care.

Although the material model states that, above all other considerations, human females would be selected for behavior associated with better infant care, they must still be both sexually attractive and sexually receptive at times if the species is to survive. Females who possess the ability to refuse unwanted sexual advances would be at an advantage, since they could provide environments for infant care away from the tense approaches of strange males. An obvious way for females to choose when and with whom they will mate is to conceal the outward signs of the estrous cycle.

In our maternal model, estrus is not concealed so as to prolong female sexual attraction. It is reduced and hidden in order to protect immature troop members, dependent for long periods of time on their mothers, from the constant social upheavals accompanying mating behaviors in those primates with prominent estrus. Its concealment is the ultimate expression of female choice. Mothers with these abilities are more likely to rear offspring who will survive preferentially the lengthy trials of troop socialization.

No particular mating pattern need result from the maternal model, in contrast to the paternal model, which is tied to an assumption of monogamy. Diversity in the organization of human societies today reflects precisely this point. We caution against interpreting the fossil record



in terms of Western cultural standards and hope that paleoanthropologists will remember their own best advice: the present may not be the key to the past.

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References and Notes

1. G. Orians, *Am. Nat.* **103**, 589 (1969); R. Trivers, in *Sexual Selection and the Descent of Man*, B. Campbell, Ed. (Aldine, Chicago, 1972), p. 136.
2. Females have long been under intense selection for efficient infant transport. See F. A. Hassan [in *Biosocial Mechanisms of Population Regulation*, M. N. Cohen, R. S. Malpass, H. G. Klein, Eds. (Yale Univ. Press, New Haven, Conn., 1980), pp. 311–314] for discussion of nutritional load in transport versus pregnancy.
3. We thank G. Barlow, D. Boaz, L. Brunker, S. Carr, D. Dobson, P. Dolhinow, S. Ferris, S. Geary, V. Sarich, R. T. White, T. D. White, R. Wilson, and J. Wyles for comments.

Two recurrent themes require special comment before I address specific questions raised above. The first is a consistent reference to the social and reproductive behavior of living hunter-gatherers. Modern human social behavior is completely irrelevant to that of emergent hominids. Humans are products of at least 2 million years of intense social evolution (*1*). Their mating and reproductive behavior are saturated with religious, symbolic, and relational strictures. Almost no vertebrate species is less suited to the reconstruction of early hominid behavior.

A second theme is the 2.5-year human birth interval used in my table 1. My use of a 3.0 chimpanzee birth interval is systematically ignored. Both figures were stated as conservative minima for comparison with Old World monkeys. My conclusions from that table were as follows:

> It can be seen . . . that both chimpanzees and humans have considerably lower reproductive values than Old World monkeys for low values of $l(x)$ [survivorship at age x] . . . the existence of successful hominid clades in Pliocene mosaics suggests that both birth space reduction and elevation of survivorship had probably been accomplished.

Several respondents contradict my conclusions by citing !Kung birth intervals. These have a "modal length" of "about 4 years" and occur in a population whose fertility is "considerably lower than any other population known that is practicing natural fertility" (*2*). To the contrary, in orangutans "birth intervals. . . exceed five years and probably average six or seven years" (*3*). In chimpanzees, "the mean interval between births of surviving offspring at Gombe was 5 yr 10 mo" (*4*). The interval "between surviving offspring in the Virunga study groups was about 4½ years . . . but in the whole Virunga population was nearer 8 years (*5*). Thus even if the extreme case of the !Kung is used for humans, the pongid-hominid birth interval ratio remains significantly greater than that which I used. In any case, my discussion was directed at an explanation of hominid demographic success relative to that of other hominoids and viewed in the context of Old World monkey expansion in the Mio-Pliocene (*6*). No physiological adaptations bearing on reproductive rate were suggested; rather, both birth space reduction and elevation of survivorship were accounted for by behavioral modifications. Wood inverts my hypothesis. His arguments further *accentuate* the difficulty of accounting for early hominid success without positing a reproductive strategy not found in other, relict hominoids. How could such a K-selected species succeed in demonstrating r-type characters (for example, the ability to radiate and colonize unstable and novel environments), when other hominoids could not? The primary elements of the model (provisioning, home-basing, monogamy, and increased infant care) are *intensifications* of K strategy. Their ultimate effect was the elevation of the reproductive rate, however, which is more typical of r strategists. He concludes that "chimpanzees should have higher population growth rates and a wider geographical distribution than humans." What more dramatic case can be made for the existence of a novel reproductive strategy in hominids? Wood does not address bipedality, feminization of the male canine, sequestration of ovulation, occupation of an almost global terrestrial niche, and the most elaborate epigamic adornment of any primate (including monomorphic as well as dimorphic characters). Are these to be regarded as tangential to the biological history of hominids (*7*)?

Harley states that I proposed continual sexual receptivity and sequestration of ovulation as "preconditions" for pair-bonding. I made no such proposition. I modeled the evolutionary development of monogamous pair-bonding in a social species. Obviously, the behavior (pair-bonding) and its physiological correlates (sequestration of ovulation, epigamic adornment, and extension of estrus) would evolve in concert; complex adaptations do not arise de novo. One cannot selectively ignore the critical difference between hominid monogamy and that in other mammals and primates. The monogamous species to which she refers are pair-dwelling and defend a proscribed territory. In such cases complex sexual mechanisms are obviously not required to reinforce pair-bonds. On the other hand, sequestration of ovulation absolutely obligates copulatory vigilance as a compensatory mechanism and would only be adaptive in a social species. Her suggestion that ovulation is functionally recognizable in human females is unacceptable (*8*). In polygynous species, male strategy favors consort only with ovulating females, and during such time (estrus) "there is no doubt that sexual factors play the greatest part in male-female associations" (*9*, p. 108). Last, she states that orangutans "exhibit no external signs of ovulation." Must one not consider dramatic proceptivity and intensive approach to long-calling males as external signs? As Galdikas points out, "Orangutan females are never in a situation where vivid visual signals of sexual receptivity might give them an immediate advantage" (*3*). In summary, because early hominids were unquestionably group-dwelling, simple analogy is insufficient for the analysis of their origin and evolution. Data from other monogamous mammals and primates cannot be simply extended without regard for their ecological and selectional bases.

Cann and Wilson suggest that sequestration of ovulation is an expression of "female choice" (*10*). The supposed selective value of such "choice" was the rejection of "tense approaches of strange males." Bipedality is accounted for by infant transport. This model contains a number of logical and biological incongruities. Hominid ovulation is hidden from *both* sexes: it cannot reflect female "choice." To the contrary, female proceptivity, as found in all other living hominoids, is the most direct possible expression of female-initiated sexual behavior. In the provisioning model, those females selecting mates that reliably provision would be most capable of meeting their nutritional requirements and those of their offspring; that is, a female's reproductive success would be the direct consequence of her mate selection. In addition, if "female choice" were the selective agent responsible for loss of external signs of ovulation, why are hominid female epigamics permanently displayed? Additional incongruities of the "maternal model" include (but are not limited to) the following: (i) dependent offspring are protected by estrous cycling; prominent estrus only occurs in nonlactating females, and its absence in females with dependent offspring is a protective mechanism; (ii) in a polygynous mating system loss of external signs of ovulation would dramatically reduce individual fertility and be counterselected at maximum intensity; (iii) polygynous mating systems yield solitary males and high intermale competition, which in turn lead to infanticide (*11*), rape (*12*), and highly aggressive male behavior directly dangerous to infants (*13*); (iv) in a social, pair-bonded species, male-male aggression is reduced and male behavior directly enhances infant survivorship; (v) adoption of bipedality eliminates the grasping ability of the infant foot, thereby increasing the difficulty of infant transport and reducing access to arboreal food sources. It requires an enlarged foraging range (*11*) and higher search time while reducing speed and agility, thus increasing the dangers of predation. The effects of the "maternal model" are directly *opposite* those suggested by its proponents.

Wolfe *et al.* offer a series of specific criticisms that contain factual and conceptual errors. (i) I did not use the Gombe birth interval. As noted above, I used 3.0 years. (ii) 60 years was used because it is a conservative "maximum life potential." The object of my calculations was to demonstrate the need by hominoids to elevate survivorship in order to obtain reproductive values competitive with those of Old World monkeys. Using 45 years intensifies this need and further accentuates the (unmodified) hominoid reproductive disadvantage. (iii) Proceptivity is a physiological component of estrus—not a cognitive drive. (iv) Of what value are "sneaked copulations" with "more fit males" (the definition of "fitness" is exceedingly hazy here) if there is no indication of ovulation to either sex? (v) Of course the human family is an "economic" union (*14*). Once and for all, let us agree, emergent hominids were not human! (vi) I do not posit "community" food sharing. Such behavior requires either group selection or a complex extension of kin selection; I posit only the common mammalian and avian phenomenon of mate and offspring provisioning. (vii) I did not state that early hominids were "*r*-selected." I stated, quite clearly, that they show more *r*-related characters than other hominoids despite their intensified *K*-type physiology.

Only one primary point introduced by Isaac is not covered in the above discussion. This concerns the possible role of hunting and dietary "meat" in emergent hominids. I did not discount meat protein, which is a significant dietary item of most primates (*15*); I discounted hunting. The a priori reason by which hunting may be discounted is hominid bipedality; no form of primate locomotion could be less suited to the tracking and capture of large prey, prior to the evolution of relatively advanced material culture and social cooperative behavior. While "food sharing" would be consistent with the model, I did not consider present evidence for it sufficiently strong to include it in my original discussion (*16*).

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References and Notes

1. Present-day hunter-gatherers are the product of the global period of sociocultural evolution commonly referred to as the upper Palaeolithic, one aspect of which was essential self-domestication. Thus the behavior of living human populations cannot be viewed as even approximating that of early *Homo sapiens*, much less that of *H. erectus* or the australopithecines. For an archaeological chronicle of these highly significant changes, see L. G. Freeman, in *Omniverous Primates: Gathering and Hunting in Human Evolution*, R. S. O. Harding and G. Teleki, Eds. (Columbia Univ. Press, New York, 1981), pp. 104–165; see also R. G. Klein, in *ibid.*, pp. 166–190.
2. N. Howell, in *Kalahari Hunter-Gatherers*, R. B. Lee and I. DeVore, Eds. (Harvard Univ. Press, Cambridge, Mass. 1976), p. 145. R. B. Lee [*The !Kung San: Men, Women, and Work in a Foraging Society* (Cambridge Univ. Press, Cambridge, 1979), p. 442] comments that "Among the !Kung infanticide is rare; instead, long-term lactation and the consequent suppression of ovulation serves to delay reconception in nomadic !Kung females for 24 to 36 months after the birth of a previous child. The result is an average birth interval of 3 to 4 years between successive live births." He also points out that "there is an 8-month difference in mean birth interval between more nomadic and more sedentary mothers (44 vs. 36 months). At one water hole, birth intervals have dropped to as short a period as 20 months. . . ."
3. B. M. F. Galdikias, in *Reproductive Biology of the Great Apes*, C. E. Graham, Ed. (Academic Press, New York, 1981), pp. 283–300.
4. C. E. G. Tutin and P. R. McGinnis, in *ibid.*, pp. 243–264.
5. A. H. Harcourt, D. Fossey, K. J. Stewart, D. P. Watts, *J. Reprod. Fertil. Suppl.* **28**, 59 (1980). The birth interval irrespective of survival of the offspring was 3.8 years. Wood comments that birth intervals between all offspring, not just surviving offspring, are the most appropriate data for analysis. This is incorrect. Average birth space, independent of mortality, is appropriate for estimates of population stasis and stability. The point of my original discussion, however, was not population dynamics, but the time period required to successfully raise a single infant to parental independence (allowing birth of a second). As a measure of this factor, only successful birth intervals can be considered. Furthermore, since all present hominoid populations have been substantially disturbed by recent human activity, mortality has decreased the relative birth space (for example, at Gombe). The birth interval data can be effectively corrected, however, if such artificial mortality is removed by using the average successful birth space.
6. P. Andrews and J. A. H. van Couvering, in *Approaches to Primate Paleobiology*, F. S. Szaley, Ed. (Karger, Basel, 1975), pp. 62–105; E. Delson, in *ibid.*, pp. 167–217.
7. Wood states that the quantity given by my equation 1 is "not Fisher's reproductive value, but a demographic non sequitur. . . ." This is not so. My equation 1 is exactly and precisely R. A. Fisher's definition of reproductive value [R. A. Fisher, *Genetical Theory of Natural Selection* (Clarendon, Oxford, 1930), pp. 25–30]. Since my intention is only to compare the qualitative nature of the interaction of survivorship, birth space, and age of first reproduction, I have introduced the simplifications of $r = 0$ (zero population increase), constant fertility dependent only on birth space (certainly, decreased birth space elevates fertility), and constant probability of surviving from one year to the next. Under these simplifying assumptions, the effect of birth space on the relative reproductive values of a model hominoid population and emergent hominid population depends only on the ratio of the birth-space values for the two populations. Wood's calculation of rates of natural increase based on modern hunter-gatherers and relict pongids bears no relation to the points raised in my article, nor at any point did I ask, as he suggests, "by how much must total reproductive output be increased to compensate . . . for the delay in reproduction that distinguishes humans from chimpanzees?" Not only can such a question not be answered for emergent hominids, it is irrelevant to a model of reproductive behavior. No matter what model is posited for hominid bioecological success, its primary focus must be individual male and female selective mechanisms affecting reproductive success. Without this focus, simple manipulation of population parameters (especially of living populations unrepresentative of earlier evolutionary conditions) leads directly to group selection, which is the effect of Wood's arguments. This leads to Wood's ultimate evolutionary non sequitur: "the evolutionary success of humans cannot be explained solely in reproductive terms." All evolutionary success can only be explained in reproductive terms!
8. Burley writes, "That ovulation is well-concealed is well-evidenced. Not until 1930 was there accurate, scientifically established information concerning its timing. . . . Prior to this some doctors and biologists believed that women could conceive throughout the menstrual cycle; others felt that conception was most likely to occur near or during menstruation. . . ." [N. Burley, *Am. Nat.* **114**, 835 (1979)]. For additional discussion, see references therein.
9. T. Noshida, in *The Great Apes*, D. A. Hamburg and E. R. McCown, Eds. (Benjamin Cummings, Menlo Park, Calif., 1979), pp. 73–121.
10. For authors who stipulate "caution against interpreting the fossil record in terms of Western cultural standards," the use of the term "choice" would seem ill-advised. It implies cognition, which is irrelevant to primates other than modern *H. sapiens* (and serves as further evidence that human social behavior must not be used to reconstruct that of earlier hominids). No primate female is able to "choose when and with whom they will mate." Rather, they demonstrate partner preference under the hormonal drive of estrus. However, all three living hominoids already demonstrate this behavior, so it is difficult to understand the primary premise of the "maternal model."
11. A vivid example was observed in hanuman langurs: "The new harem leader gained exclusive right to his females. Then he commonly bit young infants after the takeover. Their mothers hung them on a branch to die and came into estrus, ensuring an even higher proportion of the new lord's children" [A. Jolly, *The Evolution of Primate Behavior* (Macmillan, New York, 1981), p. 181].
12. J. R. Mackinnon, *Anim. Behav.* **22**, 3 (1974); R. D. Nadler, *Arch. Sex. Behav.* **6**, 457 (1977).
13. Fossey notes that, within her study area for Virunga gorillas, the only directly observed cases of infant death were the direct or indirect result of aggressive behavior of nonmember silverback males. See D. Fossey, in *The Great Apes*, D. A. Hamburg and E. R. McCown, Eds. (Benjamin Cummings, Menlo Park, Calif., 1979). pp. 139–184.
14. At the same time it should be pointed out that all birds and mammals that adopt a monogamous, pair-bonding, reproductive strategy are doing so as an "economic adaptation" in the sense that they are maximizing the ability to effectively reproduce given their particular ecological circumstance. The "economic union" cited by Wolfe *et al.*, however, is a social phenomenon and not an ecological one, is peculiar to *H. sapiens*, and is irrelevant to the arguments concerning the selective forces acting on emergent hominids.
15. L. Binford, *Bones: Ancient Men and Modern Myths* (Academic Press, New York, 1981).
16. C. E. Graham, *Reproductive Biology of the Great Apes* (Academic Press, New York, 1981).
17. I thank T. D. White, D. C. Johanson, T. J. Barton, R. Mensforth, L. Skvarch, R. S. Meindl, R. Walker, W. Kimble, and B. M. Latimer for helpful comments and criticism.