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Hunting and Human Evolution

Recent fossil evidence coupled with new ethnographic data stimulate this reappraisal of the role of hunting in hominid evolution. Figures are assembled on modern primate diets including those of human foragers, which indicate the distinctive importance of hunting in human adaptation. Guided by current theory in evolutionary ecology, a scenario for hominid divergence is developed which is consistent with (a) the latest fossil evidence, (b) data available on the behavior of modern non-human primates, (c) archaeologically detectable traces of hominid behavior, and (d) modern hunter-gatherer ethnography.

1. Introduction

Recently discovered fossil evidence of early hominids in East Africa (Johanson *et al.*, 1978), has provided the data base necessary to formulate a picture of some of the morphological changes that characterized the early hominids during the late Miocene and early Pliocene. Now that some of these morphological changes are documented, we are in a position to address the questions of how and why such changes took place, and what selective pressures are likely to have produced them. Four areas of investigation seem most likely to provide valuable information concerning these questions. They are: (1) the fossil record; (2) behavioral studies of our nearest primate relatives; (3) archaeology of hominid activity sites; and (4) studies of modern human hunter-gatherers. Studies of particular animal behaviors which have been selected in conditions that are thought to be applicable to early hominids should provide valuable clues as well.

Any evolutionary scheme proposed to account for the changes seen in the fossil record should be firmly based in the neo-Darwinian principles of natural selection. Proposed speciation and subsequent divergence should be consistent with current models from evolutionary biology in which traits are favored that increase the fitness of the individual bearer and close kin (Williams, 1966; Hamilton, 1964), unless alternative mechanisms of evolutionary change can be demonstrated. Models should be supported by data from *all* the relevant areas of investigation.

The longest standing explanation for hominid divergence is the reliance on tools proposed by Darwin (1871). Later well accepted theories included the importance of hunting (Dart, 1953; Washburn & Lancaster, 1968), savannah dwelling (Kortlandt, 1962) and reliance on seeds (Jolly, 1970). The most recent theory (Lovejoy, 1981) sees a change in reproductive strategy as the important factor in hominid divergence, while dismissing both tools and hunting as playing no part in the process. According to Lovejoy, the key behavior evolved to achieve this switch in reproductive strategy is male provisioning and monogamous pair bonding. Male provisioning and sharing has also been stressed heavily by Isaac (1978) although he has not explicitly distinguished the role it might play in the divergence of hominids from its role in their subsequent evolution. Other recent authors (see Harding & Teleki, 1981) join with Lovejoy in dismissing the importance of subsistence behavior in hominid evolution but do not propose any specific alternatives.

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The recent increasing trend to reject dietary specialization, and, specifically, hunting, as a key step in human evolution, seems to originate primarily with two events. First, the "Man the Hunter" symposium organized in 1965 emphasized the importance of plant foods in modern hunter-gatherer diets. For the first time, quantitative data demonstrated that plant foods were indeed important in the diet of some modern human foragers. Lee (1968) went so far as to generalize about the priority of plants in the diet for all human groups except those living in high latitudes. Second, an increasing awareness of a male-bias in data collection led many scholars to believe that this might seriously distort the types of evolutionary models proposed. The so-called "hunting hypothesis" was a prime suspect in the search for male bias, and the aggressive tendencies that it was supposed to imply were found very distasteful.

The purpose of this paper is to set aside questions of bias or moral implications and examine whether the rejection of hunting, as a key behavior in human evolution, has been premature. An analysis of the relevant data available to date demonstrates that an hypothesis of hominid divergence based on hunting is:

- (a) consistent with the data on modern primates, including human foragers;
- (b) consistent with general principles of evolutionary ecology;
- (c) consistent with fossil evidence now available.

2. Speciation, Divergence and Feeding Strategy

Evolutionary change within a species can take place in various ways such as adaptation to a different set of food resources, different climactic or weather patterns, a different set of predators, or by an adaptive change in overall life cycle and reproductive strategy. These changes may seem sufficiently great as to define a new species with respect to the original, since all of these pressures may require different behavior or morphology for maximum efficiency. But, speciation refers literally only to reproductive isolation. With such isolation, no other changes are implied as causal in a speciation event. It is not, however, the case that reproductive isolation alone will always allow two groups of organisms to coexist geographically.

It has been observed in ecological studies that two morphologically distinct species rarely occupy precisely the same niche. Thus, two contemporaneous species are usually isolated geographically, or they do not exploit the same set of food items. In the case of two morphologically distinct species competing for the same food resources, one variant would frequently eliminate its competitor. Therefore, any adaptive changes not accompanied by changes in feeding strategy would rarely lead to speciation where two species overlap geographically. One of the two divergent lines would usually become extinct in the zone of geographical overlap. On the other hand, if a subpopulation changes its feeding strategy, it can coexist side by side with the original population and neither will necessarily eliminate the other. Unless a long period of geographical isolations is assumed between pongids and hominids, there was probably divergence in feeding strategy between the two at an early date.

3. Diets of Foraging Peoples and Non-human Primates

Until recently, it seemed a well accepted fact that human foragers relied mainly on meat for subsistence. Quantitative data collected by Lee demonstrated clearly that this is not

always the case, and in fact, shed some doubt about whether it had ever been the case for humans in the tropical and temperate latitudes. Likewise, chimpanzees and baboons were classified as herbivores until Goodall (1963) and DeVore & Washburn (1963) provided accurate reports of meat eating for these primates. Unfortunately, the reaction to this new data produced a belief that was as extreme as the previously accepted ideas about primate diets. Human and non-human primates alike found themselves lumped as omnivores, and the dietary differences between the two were downplayed (i.e., Harding & Teleki, 1981). This omnivorous label obscures striking differences with important biological consequences.

Table 1 is a summary of some data available concerning the importance of meat (mammals, fish, reptiles and birds) in the diet for various primates, carnivores and human groups with little or no agriculture as well as a comparison of relative efficiencies of meat acquisition for each. The reader must be cautioned that some of the data are crudely measured or calculated, and further research would add greatly to confidence in the

Table 1

Forager	Hunting efficiency		Meat consumption				Reference
	(1) Kg meat/hour foraged	(2) Kg meat/consumer day	(3) Kg Average adult weight	(4) ($\times 10^{-2}$) Kg meat (daily)/kg body wt.	(5) Percentage of daily calories provided by meat	(6) Ratio of meat/vegetable items in scats (%)	
Wolf		4.5	32	13-19			Mech (1970)
Coyote		1.0		11-16		78/36*	Hilton (1978)
Dog (very active)		1.7		4.6		67/33*	Mayer (1953, quoted in Mech, 1970)
African Wild Dog	1.9	3.8	19	20.0	100		Estes & Goddard (1967)
African Wild Dog	2-9 kg/day				100		Schaller (1972, quoted in Mech, 1970)
Raccoon Dog						94/6*	Stroganov (1969)
African Dog				15.0		38/62*	Wright (1960)
Brown Bear						36/64*	Stroganov (1969)
Black Bear						27/73*	Stroganov (1969)
Spotted Hyena	0.53	1.5-1.8*	52	3.8	100	17/83*	Stroganov (1969)
Polecat		3.4*				2/98*	Kruuk (1972)
Lion	7.0	7.8	145	5.4	100	88/12	Stroganov (1969)
Lion				11-13			Schaller (1972)
Leopard		7.0	60	11.7	100		Wright (1960)
Cheetah	10 kg/day	4.0			100		Schaller (1972)
Bobcat				4.8-6.1*			Schaller (1972)
				10-12*			Golley <i>et al.</i> (1965, quoted in Mech, 1970)

Table 1 continued

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	(1) Kg meat/hour foraged	(2) Kg meat/consumer day	(3) Kg Average adult weight	(4) ($\times 10^{-2}$) Kg meat (daily)/kg body wt.	(5) Percentage of daily calories provided by meat	(6) Ratio of meat/vegetable items in scats (%)	
Yellow Baboon (adult male)	0.006	0.036	35	0.1	3		Hausfater (1975)
(whole troop)	0.001	0.008	25	0.03	1		
Anubis Baboon (adult male)	0.003–0.026	0.084–0.238	35	0.2–0.7	8–22		Strum (1981)
(troop minus infants)	0.002–0.004	0.016–0.032	25	0.06–0.13	2–5		
Chimpanzee (whole troop)		0.027	35	0.08	3		Wrangham (1975, quoted in Teleki, 1981)
Ache (bow)	0.53	1.78	55	3.2	80		
Ache (hands only)	0.27						Hill & Hawkes (in press)
Yanomamo (bow)	0.48–1.35	0.41–0.49	44	0.93–1.11	33		Hawkes <i>et al.</i> (in press)
Yanomamo (bow)	0.57						Saffirio & Hames (n.d.)
Yanomamo (bow)	1.0	0.21–0.44	44	0.48–1.00	16–27		Hames (1979)
Kung (bow)	0.60–0.66	0.46	44.1	1.04	29		Lizot (1977)
Kung (bow)		0.19	45.3	0.42	12		
Gwi (bow)	0.47	0.34	44.1	0.77	25		Lee (1979)
Gwi (bow)	0.22	0.30	52.1	0.58	18		Wilmsen (pers. comm.)
Mbuti Net Hunters (with nets)	0.12	0.37					Silberbauer (1981)
(with bow)	(both sexes)	0.17					Tanaka (1980)
Total		0.54	40	1.35	44		Harako (1981)
Mbuti Archers (with bow)	0.11	0.11					Harako (1981)
(with spear)	0.63	0.22					
Total		0.33	40	0.83	27		Harako (1981)
Mbuti Net Hunters (both sexes)	0.22	0.45	40	1.1	35		Hart (1978)
Yanomamo (bow)		0.43	44	1.0	32		Chagnon & Hames (1979)
Bari (bow)	0.16–0.25	0.39					Beckerman (1980)
Mbuti Net Hunters (both sexes)	0.38	1.06	40	2.7	86		Tanno (1976)
Anbara		0.55	40	2.7	26		Meehan (1977)
							Yost (in press)

Kg meat/h foraged and kg meat/consumer day are both 100% of live weight and subtract nothing as waste. Average adult weight is taken as the mean of the average adult male and adult female weights reported.

Table 1 *continued*

* Cases in which different numbers have been reported for different seasons of the year. Numbers presented are derived as follows:

- Wolf*: Mech (1970). (2) P. 284. (3) Item (4) divided by item (2). (4) P. 184.
- Coyote*: Hilton (1978). (2) P. 226. (4) P. 226. (6) P. 223.
- Dog*: Mayer (1953 quoted in Mech (1970)). (2) P. 183 in Mech. (4) P. 183 in Mech.
- African Wild Dog*: Estes & Goddard (1967). (1) From p. 63 plus 40% that was subtracted as waste, divided by two hours per day foraged (p. 62). (2) From p. 63 plus 40% that was subtracted as waste. (3) Estimated from data on p. 61 and 63. (4) Item (2) divided by item (3). (5) There is no mention of vegetable items in the diet.
- African Wild Dog*: Schaller (1972). (1) Quoted in Mech (1970, p. 184).
- Raccoon Dog*: Stroganov (1969). (6) P. 72.
- African Dog*: Wright (1960). (4) Pp. 1-15.
- Brown Bear*: Stroganov (1969). (6) P. 128.
- Black Bear*: Stroganov (1969). (6) P. 141.
- Spotted Hyena*: Kruuk (1972). (1) Kg meat per day from p. 77. Approximately 3-8 h/day spent foraging (p. 213). Assume all consumers are foragers. (2) P. 77. (3) Estimate from p. 211. (4) Item (2) divided by item (3). (5) There is no mention of vegetable items in the diet.
- Polecat*: Stroganov (1969). (6) P. 390.
- Lion*: Schaller (1972). (1) Kg meat/day from p. 278. Two hours per day spent foraging (p. 121). (2) P. 00. (3) Estimate from p. 210; (5) there is no mention of vegetable items in the diet.
- Lion*: Wright (1960). (4) Pp. 1-15.
- Leopard*: Schaller (1972). (2) P. 292. (3) Estimate from p. 291. (5) There is no mention of vegetable items in the diet.
- Cheetah*: Schaller (1972). (1) P. 314. (2) P. 314. (5) There is no mention of vegetable items in the diet.
- Bobcat*: Golley *et al.* (1965) quoted in Mech (1970). (5) From Mech, p. 183.
- Yellow Baboon* (adult male): Hausfater (1975). (1) Assumes males caught all prey, and average prey weight is 2.5 kg 45 items \times 2.5 kg divided by 2519 h \times 7.5 males (p. 45); (2) estimate males consumed 75% of all prey taken. (3) Estimate. (4) Item (2) divided by item (3). (5) Assumes daily caloric needs at 50 cal/kg. body weight (estimate from table III, Bilby, 1968, Zoological Society of London, Symposia 21), edible portion 65%, and 2500 cal/kg meat.
- Yellow Baboon* (whole troop): Hausfater. (1) 45 items \times 2.5 kg divided by 2519 h \times 32.7 individuals (p. 45). (2) Estimate 8 h foraging day. (3) Estimate. (4) Item (2) divided by item (3). (5) Assume daily caloric needs at 50 cal/kg body weight (as above), edible portion 65%, and 2500 cal/kg meat.
- Anubis Baboon* (males): Strum (1981). (1) From data given in tables 8.1, 8.2, 8.4, and 8.11. Assume average prey weight at 2.5 kg. (2) Assume 8 h foraging day and males consume 75% of prey by weight. (3) Estimate. (4) Item (2) divided by item (3). (5) Assume daily caloric needs at 50 cal/kg body weight (as above), edible portion 65%, and 2500 cal/kg meat.
- Anubis Baboon* (troop minus infants): Strum (1981). All items from tables 8.1, 8.2, 8.4, and 8.11 or as specified above.
- Chimpanzee*: Wrangum (1975), quoted in Teleki (1981). (2) Wrangum (1975); 4.34 quoted in Teleki, p. 327. (3) Estimated from p. 322. (4) Item (2) divided by item (3). (5) Assume daily caloric needs at 50 cal/kg body weight (as above), edible portion 65%, and 2500 cal/kg meat.
- Ache* (bow): Hill & Hawkes (in press), Hawkes & Hill (n.d.). (1) In first reference, p. 28. (2) From tables 2 and 3 in second reference. (3) Unpublished data. (4) Item (2) divided by item (3). (5) Table 2 in second reference.
- Ache* (hands only): Hill & Hawkes (in press). (1) P. 28.
- Yanomamo* (bow): Saffirrio & Hames (n.d.). (1) Table 9. Table 13. (3) From Lizot (1978, p. 512). (4) Item (2) divided by item (3). (5) Mean consumption 0.45 kg per day. Assume caloric needs at 50 cal/kg body weight, edible portion 65%, and 2500 cal/kg meat.
- Yanomamo* (bow): Hames (1979). (1) P. 243.
- Yanomamo* (bow): Lizot (1978). (1) From p. 507, average 4.4 kg (gutted)/av. 6.0 h hunting. Add approximately 30% to get live weight. (2) P. 508 gives number of consumers and number of days observed. Table 8 gives weight of meat and fish consumed. (3) P. 512. (4) Item 2 divided by item (3). (5) From table 9, p. 512, but using 2500 cal/kg meat rather than 1460 cal/kg as Lizot.

Table 1 *continued*

- Kung* (bow): Lee (1979). (1) 7900 cal/day divided by 3000 cal/kg meat (p. 270) divided by 8 h per day hunting = 0.33 kg/day $\times 2$ to get live weight from edible portion of 50% (table 8.1 and 8.4). (2) From table 9.7 (p. 271) 690 cal/person divided by 3000 cal/kg meat multiplied by 2 to get live weight. (3) From table 10.9. (4) Item 2 divided by item (3). (5) From table 9.9, p. 271.
- Kung* (bow): Wilmsen (pers. comm.). (2) From table 10, 244 cal/day divided by 2500 cal/kg meat multiplied by 2 to get live weight. (3) From table 9. (4) Item (2) divided by item (3). (5) Table 10.
- Gwi* (bow): Silberbauer (1981). (1) From p. 483, estimate that an average of 16 men hunt an average of 7 hours on 50% of the days of the year. Annual kill was 8632.8 kg, add 12.5% to get live weight (from table 12.3). (2) From p. 486, add 12.5% to get live weight. (3) Estimate weight same as reported for *Kung* by Lee (1979). (4) Item (2) divided by item (3). (5) Assume daily caloric needs at 50 cal/kg body weight (as above), edible portion 65%, and 2500 cal/kg meat.
- Gwi* (bow): Tanaka (1981). (1) From p. 70, 300 g per capita/day and represent 22% of the population (p. 74), therefore each man kills 1.36 kg/day. From p. 76, men hunt 6.2 h/day on the average. (2) P. 68. (3) P. 15. (4) Item 20 divided by item (3). (5) From p. 74, ratio of calories from vegetable; meat is 5.7:1.
- Mbuti Net Hunters* (with nets): Harako (1981). (1) From p. 522, hunting returns average 1.06 kg/person day divided by an average of 8.4 h hunting per day (p. 521). (2) P. 534. (3) Estimate. (4) Item 20 divided by item (3). (5) Assuming caloric requirements at 50 cal/kg body weight day (as above), edible portion 65%, and 2500 cal/kg meat.
- Mbuti Net Hunters* (with bow): Harako (1981). (2) From p. 534.
- Mbuti Archers* (with bow): Harako (1981). (1) From p. 528, 4.4 kg/day killed by hunters. From p. 508, there are 10 hunters in the population of average band of 39 people (p. 528), and they hunt an average of 3.9 h/day (p. 525). (2) P. 534. (3) Estimate. (4) Item 20 divided by item (3). (5) Assume caloric requirements at 50 cal/kg body weight daily (as above), edible portion 65%, and 2500 cal/kg meat.
- Mbuti Archers* (with spear): Harako (1981). (1) P. 529 shows 11 hunts. Total game killed calculated from species weights in table 13.11 is 640 kg. Average of 10 men per hunt (p. 508) and average duration of hunt is 9.2 hours (table 13.8).
- Mbuti Net Hunters* (with net): Hart (1978). (1) From table V, average of 25.4 kg per net hunt. Add 20% to get live weight. From table III, average 6.0 h/hunt and 20 participants. (2) P. 340. (3) Estimate. (4) Item (2) divided by item (3). (5) Assume daily caloric requirements at 50 cal/kg body weight (as above), edible portion 65%, and 2500 cal/kg meat.
- Yanomamo* (bow): Chagnon & Hames (1979). (2) From p. 911 table I, 260 g/day plus 40% to get live weight. (3) Estimate. (4) Item (2) divided by item (3). (5) Assume daily caloric requirements at 50 cal/kg body weight (as above), edible portion 65%, and 2500 cal/kg meat.
- Bari* (bow): Beckerman (1980). (1) From p. 97, edible portion unknown. (2) From p. 101, edible portion unknown (note that the majority of this is fish.).
- Mbuti Net Hunters* (with nets): Tanno (1976). (1) From p. 117, average 63 kg/day. From 112, table III, average 12.3 men. Add 10 women (estimated from page 114) to each hunt. Hunt duration average 7.5 hours (table III). (2) From p. 119, 63.3 kg meat daily divided by an average of 60 people (p. 107). (3) Estimate. (4) Item (2) divided by item (3). (5) Assume daily caloric requirements at 50 cal/kg body weight (as above), edible portion 65%, and 2500 cal/kg meat.
- Anabara*: Meehan (1977). (2) Pp. 367 and 368 (note that this is primarily fish. (5). P. 368 (note that this is primarily fish).

interpretation. Nevertheless, the overall pattern of consumption is quite instructive and some of the studies were carefully carried out and give a very precise answer about the dietary importance of meat. Comparison of efficiency levels is somewhat more difficult, as few good measurements are available.

It is very difficult to answer *conclusively* whether or not humans (1) are more efficient predators than other primates and (2) depend more heavily on meat than other primates primarily because the data relevant to this question have not been collected by primate researchers. It is somewhat disconcerting, therefore, that some of these same investigators (Harding & Teleki, 1981, p. 9; Teleki, 1981, p. 306) should conclude that humans

show no significant dietary differences relative to chimpanzees or primates in general. There are, in fact, no careful measurements on meat returns per foraging hour or percentage of the diet (in calories) derived for meat for chimpanzees. Calculations shown in Table 1 for chimpanzees make several assumptions and are, therefore, quite rough. Baboon data is somewhat better but calculations should also be considered rough estimates.

Two important points are demonstrated from the data in Table 1. First, as far as one can be confident in the estimates from primates, humans are much more efficient hunters as measured in kg meat killed per hour spent foraging, than are either baboons or chimpanzees. Second, *all* human hunter-gatherers monitored get a much greater proportion of their daily food requirements from meat than do any other primates thus far reported.*

Hunting returns for hunters using traditional technology are from 10 to 200 times greater than that observed for baboons, with an average of about 30-fold higher returns for male human hunters than adult male baboons. Although the return rate from chimpanzee hunting cannot be calculated, it would appear from descriptive accounts of Teleki (1973) that chimps get hunting returns much lower than those reported for baboons.

A striking finding in this context is that Ache hunters in eastern Paraguay obtain 0.27 kg of meat per hour foraging using no weapon or tool but their bare hands and occasionally a digging stick (Hill & Hawkes, in press). This is a return rate an order of magnitude higher than any ever reported for adult male baboons, and 25-fold higher than the average predation return rate for baboons. (The calculation does not subtract out the time that Ache men spend hunting with bow and arrow, and thus an even higher overall rate would result if hunters concentrated only on hand-killed prey while foraging). Time studies are also instructive but less precise measurements of actual foraging returns. The human extreme is shown by the Chippewayan (Irimoto, 1981, p. 144) who spend only 1.4% of their foraging time (for both males and females) gathering plant items and 98.6% of their time obtaining meat and fish. The reverse is true for baboons who spend 99% of their foraging day eating plant items and only 1% obtaining and eating meat (Post, n.d.).

Carnivore data are also somewhat rough, but instructive. Spotted hyenas get hunting returns in the range of human hunters, whereas African hunting dogs and lions get returns (kg/foraging hour) 2–10 times higher.

If we examine the amount of meat consumed per day per kg body weight of consumer, we find humans once again intermediate between non-human primates and carnivores. The human hunter-gatherers studied so far eat about 10 times as much meat per kg of body weight as do chimps or baboons. During the year of highest predation recorded for baboons (Strum, 1981), if we assume adult males eat 75% of all meat killed, they fall into the lower part of the range for human rates of meat consumption. (It is notable that these baboons live in an area in which many other predators have been eliminated). Most carnivores on the other hand, consume 5–10 times as much meat per kg body weight

* The Tasaday may not have eaten significantly more meat than do some primates, however, the entire diet of the Tasaday is not completely known and the partial monitoring of the diet does not allow one to be confident about amounts of meat that they consumed regularly.

as do the average human hunter-gatherers. Rough calculations concerning the percentage of the diet (in calories) which is provided by meat, shows that human hunter-gatherers range widely showing extremes of 12% and 86% in measured studies. Non-human primates studied thus far fall well below this level, averaging about 3%. It can also be seen that some carnivores such as coyotes probably eat as much vegetable matter as do some human groups, and some bears probably eat more vegetable matter than any human hunter-gatherers reported.

The data indicate that although humans are omnivores, they generally subsist on much greater amounts of meat than any other primate. Indeed, the use of the word omnivore to describe a feeding pattern is so vague as to be almost valueless. The wide range of dependency on meat for different human groups, as well as the dietary differences between such organisms as chimpanzees, humans and coyotes are senselessly obscured by such a broad label. Diets consisting of 1%, 40% and 95% meat can all be called omnivorous, but the labeling begs the important question of the significance of these diets to the adaptive differences of the organisms.

A second important difference between human and pongid feeding strategies is the extensive use of tools for obtaining and processing food items. Although this difference should be considered and examined as closely as that of hunting behavior, it will not be thoroughly discussed in this paper. The evolutionary scheme that will be presented in a later section suggests that increase in tool use was very important in subsequent hominid evolution, but not in the original divergence between pongids and hominids. It is important to note, for example, that more than 50% of the game killed by the Ache of eastern Paraguay is killed by hand, and yet hunting success is still far greater than that of any non-human primate.

A third important difference between modern human foragers and non-human primates is the pronounced sexual division of labor, and redistribution of food resources. It is instructive that primate researchers have described predation as primarily a male activity (e.g., Teleki, 1973; Strum, 1981). A shift to increased hunting for humans may provide the key to understand sexual division of labor, which is much more difficult to explain if one assumes no shift in feeding strategy. Similarly, the increased incidence of "sharing" seen at predatory events among chimpanzees and baboons (e.g., Teleki, 1973; Strum, 1981) suggests that increased meat eating may be very important to understanding human resource sharing. The causal connection between meat eating and these behaviors is by no means clear, however, explaining the origin of the behaviors without an hypothesized change in feeding strategy appears even more difficult.

Recent archaeological evidence supports the proposal that early hominids were more dependent upon meat for subsistence than are the extant pongids (see Isaac 1981a). It is notable that Bunn (1981) after demonstrating that many early fossil bone deposits found in East Africa show stone tool cut marks, concluded:

This direct evidence of early hominid diet enables us to dismiss models of human evolution which do not incorporate meat eating as a significant component of early hominid behavior (Bunn, 1981, p. 576).

Unfortunately, any attempt to demonstrate whether or not early hominids ate meat by these direct indicators or how much they might have eaten, is not generalizable. If we find little evidence of meat eating at another hominid site, what do we conclude about hominid diets, and how can we predict the diet at a third site? Only when the underlying

principles of foraging behavior are understood will we be able to explain both the observed differences in modern hunter-gatherer diets, and the dietary pattern for early hominids.

Optimal foraging theory derived from evolutionary biology has been used to explain the foraging behavior of several human groups (Hawkes & O'Connell, 1981; Hawkes *et al.*, in press; Hill & Hawkes, in press; O'Connell & Hawkes, 1981; Winterhalder, 1977; Jones, 1981; Beckerman, in press; Smith, in press) and includes an attempt to make the type of behavioral generalization most likely to illuminate precisely what the early hominid diet was like. The direct archaeological approach alone is a lot like looking for archaeological evidence that apples fell to earth 3.5 million years ago. The problem is much more simply and completely solved by understanding that a law of gravity applies to all objects with mass and that apples and the earth both have this property. We must then discuss whether apples existed 3.5 million years ago, knowing that if they did, they certainly fell to earth whether or not direct archaeological evidence of the event can be found. Without an understanding of the principles of how gravity works, it would be a weak argument to simply claim by analogy that if apples fell at one point in time and space, they must have fallen at another. Searching for direct archaeological evidence of diet is a useful test of any behavioral theory, but will not by itself provide a strong basis to make predictions about what hominids must have been eating under various circumstances.

Only by understanding the underlying principles of foraging decisions for observable human groups (and other organisms) will we be able to understand why or why not early hominids might have eaten meat, and how much. If, as current data suggest, human groups primarily exploit resources according to the energy returns they can get for the time they invest,* we can predict the diet of early hominids in any ecological circumstance or point in time from the array of available resources.

4. Hominid Characters

Two separate but related processes must be addressed in any coherent scheme of hominid evolution. First, a speciation event took place, perhaps as early as the late miocene, that produced the divergence of the two lines leading to extant pongids and *Homo sapiens*. Second, continued adaptive change through time produced important differences between earlier and later hominids. This paper deals primarily with the first step. The similarities of the hominids and pongids both genetically (Goodman, 1977) and morphologically (Le Gros Clark, 1962) point to a relatively recent common ancestor. It is also notable that the crown component measurements and canonical variates analyses of McHenry & Corrucini (1980) led them to conclude that "In fact, the lower molars of *A. Afarensis* are more similar to modern *Pan* than they are to *Ramapithecus*, particularly the relative expansion of the talonoid" (1980, p. 1104). Possibly the common ancestor of hominids and pongids is more recent than current fossil evidence suggests. In any case, there are some clear differences between the earliest fossil types classified as hominid and all other apes living or extinct. Since living apes have all of the basic

* Other parameters of fitness may, of course, occasionally override the decision to forage optimally.

characteristics of the fossil apes in the miocene, it is safe to assume that it was the hominids that diverged and changed somehow from their previous form. The remaining apes very likely underwent little or no significant change at the time of hominid speciation.*

If one compares the earliest well-described hominid fossils (Johanson *et al.*, 1979) to the extant pongids, a set of attributes which characterize this divergence emerge. These early hominids were bipedal with long legs and a human-type foot. Hominid dentition shows canine reduction and an increase in molar size. The arms are shortened relative to the trunk, and hands are much closer to the modern human type. Finally, the body and size appears smaller than *Pan troglodytes*, but with greater sexual dimorphism and a cranial capacity in the same range as extant Pan.

A second set of characters that differentiate *Homo sapiens* from extant pongids cannot be determined at present from the fossil record, but should also be considered. These are *not necessarily relevant* to the original divergence of the two lines as they may have developed well after that event, however, they are certainly possible candidates for use in any explanation of hominid origins. Primary among these are: (1) increased male parental investment; (2) loss of overt signs of ovulation and continual female sexual receptivity; (3) female menopause; (4) intensified reciprocal behavior and food sharing; (5) secondary sex characteristics such as enlarged mammary glands; and hair growth patterns; (6) frequent tool use; (7) extensive use of syntactically organized vocal symbols for communication; (8) relative hairlessness; (9) changes in life history strategy.† Some other authors (i.e., Alexander & Noonan, 1979) have proposed several other traits separating humans from pongids, however, the confirmation of these at present is premature.

Once hominid and pongid lines diverged, at least one and possibly several other branchings in the hominid line occurred with both new lines showing geographical overlap in their home ranges. It is not clear, however, whether the line leading to *Homo sapiens* underwent any changes as a result of these events, or whether alternative "off-shoot lines" simply specialized away from the main hominid line. It is clear, however, that during the past 3.5 million years, a progression took place in which the body grew

* The point is made that no living ape is ancestor to man. While this is indeed true, very little evidence is available demonstrating that modern chimpanzees differ significantly from the hominid-pongid common ancestor. Ideally, any theory assuming differences or similarities between modern pongids and our common ancestor, should justify those assumptions. In this paper, the common ancestor is assumed to be very similar to Pan, but slightly smaller in size. The assumption of similarity is based on the scant evidence and the fact that the environment of modern chimpanzees, and the environment of their ancestors are very similar. For the moment at least, it is not clear what selective pressures might have produced changes in Pan over the past several million years. An increase in body size is assumed in order to simplify the hominid model (so hominids do not reduce and then increase body size) but no selective pressure for producing this increase in body size of Pan can be offered at present.

† The best demographic study on human foragers is that by Howell (1979). When data from the !Kung bushmen are compared to data on chimpanzees published by Teleki *et al.* (1976), age at menarche is greater for humans, and average lifespan is longer. The difference in average birth interval is small, and due to the small sample size for chimpanzees, may not be significant.

in size, and the cerebral cortex expanded disproportionately.* Other morphological changes included changes in dentition, jaw and oral cavity, shape of the female pelvis and further modification of the hands. Deposits of manufactured items can be detected possibly as early as 2.75 million years ago (Isaac, 1981*b*, p. 15). However, the number of types of tools as well as absolute numbers increases greatly, especially in the latest phases of hominid evolution.

Complete evolutionary schemes should account for all these factors at some point between the miocene and the present, however, which items on the lists are important in the original process of hominidization must be inferred since direct evidence is not readily available. The timing proposed for the emergence of each trait should be consistent with hypotheses about the immediate fitness advantage to its bearer of each additional trait. Large interconnecting feedback loops with multiple vague connections are usually untestable and bring us no closer to explaining this divergence. Great importance should be placed on demonstrating why a trait should have been advantageous in the hominid case but not for the pongids.

5. A Current Model of Hominid Origins

Owen Lovejoy (1981) recently proposed an evolutionary scheme that represents a great step forward in its approach. It is an attempt to apply current evolutionary thinking to the problem of hominid divergence, and transcends fossil evidence alone to also incorporate important differences in human physiology and behavior. Because of this new perspective, it is richer than older theories of tool use and hunting. Although the new approach is a welcome improvement, the scheme as presented has serious flaws.

Isaac (1981*b*) has criticized the theory because of its failure to deal with available archaeological data, however, far more serious problems concern the theory's inability to stand up to rigorous application of the principles of natural selection, and its lack of agreement with life history theory from evolutionary biology. It is based on the incorrect belief that K reproductive strategies are locked in by feedback loops that do not allow a reversal toward r strategies (Johanson & Edey, 1981, p. 326), that crude mortality rate and longevity are independent (Lovejoy, 1981, p. 343), that reproductive value can only be adjusted by changing birth interval (*ibid*, p. 344) and that hominid traits will arise that function to "increase the social harmony of the group" (Johanson & Edey, 1981, p. 334). This last argument is evoked specifically to produce pair bonding, which is a necessary condition according to the model, in order to increase male confidence in paternity and male provisioning (the most important steps in the model). It implies that natural selection is acting at a level higher than the individual, and thus presents many difficulties (Williams, 1966). The statements about longevity and lifespan contradict current life history theory (see Stearns, 1974 for review). Empirical demonstrations of the correlation between brain and body weight to aging (Cutler, 1976) and life history parameters (Blueweiss *et al.*, 1978) suggest that early hominids with brain and body weights similar to *Pan* would show no difference in these parameters.

In addition to the problems mentioned, Lovejoy's model fails entirely to deal with several important early fossil features of hominids. These are (1) Early modification of

* The ratio of brain weight/body weight for most organisms increases at a relatively fixed rate (see Jerison, 1973) as size increases are observed throughout the vertebrates.

the hominid hand to a more human shape; (2) Possible increased brain/body weight ratio; and (3) Increased molar dominance and change in overall jaw structure. Regardless of all these problems, Lovejoy has suggested many useful ideas to be considered in evolutionary schemes for hominids.

The proposed scheme below has borrowed heavily from Lovejoy (1981), Isaac (1978), Darwin (1871) and others and attempts to put together the most evolutionarily consistent scheme possible. It is, of course, a crude attempt, but it is intended to generate useful comments as have the earlier schemes, that will bring us one step closer to understanding our past.

6. An Alternative Model of Hominid Origins Based on Divergence in Feeding Strategy

Hunting has long been considered as a possible hominid specialization that could account for various other hominid characters (Dart, 1953; Washburn & Lancaster, 1968). It has not, however, been clear exactly *why* hunting should be so important to human groups or even if hunting really is important in human subsistence. Optimal foraging theory, derived from evolutionary biology, and its accompanying optimal diet model (Charnov, 1976; Charnov & Orians, 1973; MacArthur & Pianka, 1966; Pulliam, 1974; Pyke *et al.*, 1977) have recently been used to explain why and under what conditions humans will hunt rather than gather plant resources (Hawkes *et al.*, in press). This model suggests that the explanation is a single attempt to maximize the returns (in calories) that organisms will get from each hour that they spend foraging.

The model points out that hunting may be favored because it provides a far greater number of calories per unit of time invested than does gathering vegetable items for organisms with certain physical abilities or technology and under certain ecological conditions. This is possibly the important pivotal point to understanding why and under what conditions we might expect early hominids to specialize as predators.

Late Miocene apes inhabited the various new ecosystems that were emerging around the previously tropical parts of the old world. It is hypothesized that one subpopulation of the common ancestor to pongids and humans found itself in an ecotype where foraging returns from hunting were quite high either due to a lack of other predators, an abundance of some game type (or types) that were easily killed by this ape, or some other factor. This subpopulation began to rely more heavily on predation to meet its nutritional requirements.

Strum (1981) reported the highest hunting returns for non-human primates so far, among a group of anubis baboons in an area in which man had eliminated many of the natural predators. From the optimal diet model, one expects that when encounter rates for high return items increase, lower ranked resources will be dropped from the diet. Thus, if prey items give higher returns than any other resource for baboons, and their availability increases, the amount of predation will also increase. From the data presented in Strum (1981), one calculates that these baboons got an average of 1894 calories/forager hour* upon encounter with a prey item. From Harding (1975) one

* From table 8.1, average of two males in pursuit, which lasts an average of 50 minutes (table 8.3). Table 8.7 shows an average of 51 minutes for consumption and an average of four consumers per carcass. I assume two consumers eating at any one time. Therefore, $2.5 \text{ kg} \times 2500 \text{ cal/kg}$ divided by 3.3 predator hours.

calculates predatory returns for adult males at 3337 calories/hour* upon encounter with prey. This is almost certainly higher than the returns for any plant item exploited by these baboons (they could meet daily energy requirements in 0.5–1.0 hours) and thus as the encounter rate with prey items increases, game should become a more important part of the diet. During one year that Strum observed this group of baboons, it can be calculated that adult males consumed about 0.25 kg of meat per day, which would provide about 22% of their daily calorie requirements (see Table 1). This observations meets predictions of the optimal diet model and demonstrates that under the *right ecological conditions* (e.g., no competing predators) other primate species will rely as heavily on meat to fulfil their nutritional requirements as do some human groups.

If a subpopulation of the common ancestor to pongids and hominids found itself in an environment where returns from predation were, for example, tenfold higher (because of an increase in encounters with vulnerable prey) than for other subpopulations of the species, some important changes might take place. Since both the chimpanzee (Teleki, 1973) and baboon (Strum, 1981; Hausfater, 1975) data indicate that hunting is almost strictly a male activity (probably due to differences in physical ability and the female's parenting role) males in this subpopulation would be able to meet their own nutritional requirements in a very short time each day, whereas females would continue to forage the whole day as meat resources would not be easily available to them. Males would then have much free time each day, and new strategies might evolve in an attempt to use this free time to increase fitness.

One strategy that might be very successful for males would be to continue hunting during the day, and provide females with food resources in an attempt to increase the probability of copulation with receptive females. The pattern of males hunting while females continued to forage primarily for plant items, would be the beginning of sexual division of labor.

It has been noted in both chimpanzees (Teleki, 1973, p. 162) and baboons (Strum, 1981, p. 271) that estrous females receive a greater percentage of the meat from a kill made by males than do non-estrous females. Specific accounts of males allowing females access to meat in exchange for copulation are also given (Strum, 1981, p. 271; Teleki, 1973, p. 73). The widespread reports in ethnographic literature (e.g., Rasmussen, 1931; Balicki, 1970; Holmberg, 1950; Hart & Pilling, 1960; Neel *et al.*, 1964; Hames, pers. comm.; Woodburn, 1968; Clastres, 1972; Gregor, 1973; Siskind, 1973) that human males frequently trade meat for sexual access or that good hunters obtain more wives suggest that this is the optimal solution for "hunting apes" to increase their fitness. Males, after meeting their own nutritional requirements, would spend the remainder of their foraging day obtaining food items which could be traded to females for sex privileges (see Symons, 1981 for further discussion). This provisioning of females would primarily be in the form of meat. Wild vegetable items come in small packages and are frequently low in calories. High calorie items such as nuts require tools and often fire to process.

Table 2 shows calorie returns upon encounter for some vegetable and animal items. It is clear that if animal items are present at any reasonable density, they usually provide

* 1032 hours observation, and 2% of foraging time spent in predation. The four males, therefore, spent 82.4 predator hours and killed 44 animals which I estimate weighed an average of 2.5 kg. Therefore, $44 \times 2.5 \text{ kg} \times 2500 \text{ cal/kg}$ divided by 82.4 predator hours. This number assumes males consumed all prey.

Table 2(a) **Vegetable items**

Group	Food item	Returns* cal/h	Extraction Tools†	Processing	Reference
Batak	Discorea H. (tuber)	1739‡	d, c	Slice, leach, cook	Eder (1958, p. 61)
Batak	Discorea I. (tuber)	484‡	d, c	Cook	Eder (1968, p. 61)
Paiute	Typha sp. (cattail)	128	d, c	Pound, leach, cook	Jones (n.d.)
Paiute	Oryzopsis sp. (seed)	336	c	Winnow, grind, cook	Jones (n.d.)
Paiute	Pinus m. (pine nut)	1080	s, c	Roast, crack, grind, cook	Jones (n.d.)
!Kung	Mongongo nut	875-950	c	Roast, crack, pound	Lee (1979) as recalculated in Hawkes & O'Connell (1981)
Alyawara	Ipomea c. (tuber)	6252	d, c	Cook	O'Connell & Hawkes (1981)
Alyawara	Solanum c. (fruit)	5984	c	None	O'Connell & Hawkes (1981)
Alyawara	Cyperus sp. (corn)	4435	d, c	Cook	O'Connell & Hawkes (1981)
Alyawara	Acacia c. (pod)	4333	—	None	O'Connell & Hawkes (1981)
Alyawara	Vigna l. (tuber)	1724	d, c	Cook	O'Connell & Hawkes (1981)
Alyawara	Cossid (larvae)	1486	d, c	Cook	O'Connell & Hawkes (1981)
Alyawara	Acacia c. (seed)	646	c	Crack, grind, cook	O'Connell & Hawkes (1981)
Alyawara	Acacia a. (seed)	580	c	Winnow, grind, cook	O'Connell & Hawkes (1981)
Alyawara	Grass seeds	575	c	Winnow, grind, cook	O'Connell & Hawkes (1981)
Alyawara	Acacia c. (seed)	552	c	Winnow, grind, cook	O'Connell & Hawkes (1981)
Alyawara	Acacia (other)	538	c	Winnow, grind, cook	O'Connell & Hawkes (1981)
Ache	Orange	5071	c	None	Hawkes <i>et al.</i> (in press)
Ache	Honey	3266	a, c	None	Hawkes <i>et al.</i> (in press)
Ache	Palm larvae	2367	a, c	None	Hawkes <i>et al.</i> (in press)
Ache	Palm heart	1526	a	None	Hawkes <i>et al.</i> (in press)
Ache	Palm fiber	1200	a	Squeeze	Hawkes <i>et al.</i> (in press)
Ache	Palm fruit	946	a, c	Pound	Hawkes <i>et al.</i> (in press)

Table 2(b) **Game items**

Group	Food item	Returns* cal/h	Extraction tools†	Processing	Reference
Ache	Collared peccary	65000	b, d	Butcher, cook	Hawkes <i>et al.</i> (in press)
Ache	Deer	27000	b	Butcher, cook	Hawkes <i>et al.</i> (in press)
Ache	Paca	6964	—	Butcher, cook	Hawkes <i>et al.</i> (in press)
Ache	Coati	6964	—	Butcher, cook	Hawkes <i>et al.</i> (in press)
Ache	Armadillo	5909	d	Butcher, cook	Hawkes <i>et al.</i> (in press)
Ache	Snake	5882	d	Butcher, cook	Hawkes <i>et al.</i> (in press)
Ache	Bird	4769	b	Butcher, cook	Hawkes <i>et al.</i> (in press)
Ache	White-lipped peccary	2746	b	Butcher, cook	Hawkes <i>et al.</i> (in press)
Ache	Monkey	1215	b	Butcher, cook	Hawkes <i>et al.</i> (in press)
Alyawara	Lizards	4200	d	Butcher, cook	O'Connell & Hawkes (1981)

* Calories divided by time necessary to extract and process an item once it has been encountered.

† d—digging stick; c—container or basket; a—axe; b—bow; s—hooked stick.

‡ Some search time included in calculation.

much higher overall foraging returns than plants because the average returns upon encounter are so much higher. Secondly, it can be seen that almost all high calorie or high return plant items used by human foragers require several tools for exploitation. An example taken from the Ache of Eastern Paraguay demonstrates this point clearly. Both paca and oranges can be obtained and consumed without the use of any tools. Foragers average about 7000 cal/h upon encounter with paca, and only 5000 cal/h upon encounter with oranges (Hawkes *et al.*, in press, table III). These oranges are of domestic origin and represent the highest return vegetable item in the Ache diet by more than a factor of three (wild fruits and vegetables are usually considerably smaller and lower in calories than similar domesticated items). They also give higher returns than most other vegetable items reported in hunter-gatherer literature. Ache hunters, on the other hand, kill pacas, coatis, armadillos, snakes and a variety of other small animals either by hand or with a stick, and *all* of these items give higher returns upon encounter than do oranges.

It is the ability to carry the resource, however, that greatly overshadows the differences in returns. A forager with no carrying implements returning some distance to women and children might be able to carry about 800 calories of oranges (10 items), but could carry 39,000 calories of paca (two items). This convenient package of calories provided by game is very important to understanding the widespread sharing of killed game observed in chimpanzees (Teleki, 1973) and baboons (Strum, 1981). It is no evolutionary accident that provisioning behavior is not important among chimpanzees. The contribution from vegetable items brought back to females or offspring would simply not be worth the effort. The possible contribution that can be provided with game items is of a different magnitude.

Other hypotheses about the importance of provisioning (e.g., Lovejoy, 1981) in hominid evolution see the provisioning of mates, and especially offspring, as important. In order to increase one's own inclusive fitness, however, males should only provision offspring when confidence in paternity is high. The model proposed here does not envision high confidence in paternity at this stage of hominid evolution and thus, it would *not* be advantageous for males to provision offspring directly. We might, however, expect females to use some of their surplus food resources to feed their own offspring. Males would directly increase their fitness primarily by increasing opportunities for copulation. This strong selective pressure would then produce the ability to carry items back to the location of females, hence bipedality.

It is frequently assumed (for example Lovejoy, 1981) that bipedality is a giant step backwards for any organism intending to specialize as a predator, but bipedality is not necessarily a disadvantageous form of locomotion for hunting. Human hunters (and presumably early hominids) rarely attempt to simply run down a prey item and kill it with their teeth. In analysing the costs of bipedality it is incorrect to apply the carnivore hunting strategy to humans as their respective abilities are very different. Humans (and chimps) are very efficient at killing prey that they are able to isolate in trees (this is not an ability of canids or large cats, for example). They are also quite capable of extracting burrowing animals, obtaining water-dwelling creatures, and outsmarting animals much swifter than themselves. In short, bipedality, although disadvantageous for simple and direct pursuit, does not necessarily eliminate a creature with hominid abilities from becoming an efficient predator.

Schaller & Lowther (1969) have demonstrated that a bipedal organism with human

capabilities but no tools, would have little trouble obtaining meat on the African Savannah. Their study probably represents a conservative estimate of the game that could be taken, because life-long human foragers are considerably more skilled at detecting and pursuing game than are anthropologists.

In a very different ecological setting, Hill & Hawkes (in press) report that Ache men while bow hunting acquire 0.27 kg of meat per hour using only their hands. In addition, some of the animals killed with the bow could probably be killed by hand (especially young animals) if bows were unavailable. Subtracting out the pursuit time that men spend in bow hunting each day (0.2 h/h foraged spent in direct pursuit with bow) increases this return to 0.34 kg/h if foragers were using only their hands (and possibly a digging stick). About 2.7 kg of meat can be obtained per 8 h foraging day or about 5300* edible calories per day. This demonstrates that an Ache forager hunting only with his hands could almost completely feed one other person per day besides himself. In other words, he would have plenty of meat left over each day to trade to females for copulation.

This scheme specifically envisions high variability in male reproductive success. High sexual dimorphism is seen to be a result of this competition plus a difference in energy acquisition and requirements (see Post, 1980). Males would not fully provision females and would thus have a greater number of calories available to them because of the difference in foraging returns for the two sexes.

As males began to hunt and carry prey items bipedally back to females to trade for copulations, estrous females would have received the largest portion of meat at any point in time. It would then have been to the females' advantage to mimic an estrous state by becoming continually sexually receptive. This continued receptivity would allow the female greater access to game killed and returned by males. It is most important to note that it is also to the females' advantage to trade copulations for provisional resources. This is not only due to the favorable energy input, but more importantly, the male who provisions most adequately is often the most fit male in the population and it is to the females advantage to copulate most frequently with him.

Bipedality, once established, might then allow an emphasis on tool use because tools could be *carried* until needed. This would be especially true if the use of a very simple tool such as a digging stick could greatly increase returns from either plant or animal resources in an area where sticks for immediate use were not available. For example, the advantage of the simplest wooden tool in the middle of a large grassland area surrounded by forest might increase the fitness immensely of an animal who can both make and carry around such a tool without difficulty. The modern shape of the earliest hominid hands suggests that once hominids were able to carry tools everywhere without undue difficulty (unlike chimpanzees) they became more adept at making tools that allowed them any kind of fitness advantage.

Early hominids were probably isolated from the common ancestor that led to the pongids for only a very short period. Their drastic changes in morphology and behavior because of their specialization to hunting eliminated the probability of cross-breeding. More importantly, pongids were not competed to extinction only because hominids had

* 0.2 hours of each hour foraged are spent in direct pursuit of game with bow, therefore, actual returns are 0.27 kg/0.8 h, or 0.34 kg/h. In an eight-hour day assuming 65% edible portion and 3000 cal/kg (the meat of these items is quite fat), this is 5304 calories/day.

begun to exploit new food resources. Hominids quickly concentrated on prey and vegetable items (i.e., roots and nuts) which gave much higher foraging returns than any of the items exploited by the pongids, but often required the ability to carry tools around in order to exploit them.

We might consider why pongids did not begin to use tools extensively. Clubs and spears are very useful for hunting, but low encounter rates with prey items, and the difficulties of carrying tools through the forest while walking quadrupedally, do not allow chimpanzees to take advantage of this possibility. Once bipedality had been selected because of an ability to bring back food items, the problems of carrying around potentially useful tools are greatly diminished, even if encounter rates for prey items are low. The same argument holds for the digging stick, and the exploitation of roots or other items. It is probably not worth the effort for a chimpanzee to carry a digging stick, as the energetic price paid might outweigh the daily increase in returns, however, once bipedal for another reason, the energetic price of carrying tools is not so great and even if they are used rarely at first, they might be worth the minimal effort of carrying. Additional lower return items would begin to be ignored as foraging returns increased with tool use.

According to this argument, tool use would probably never select for bipedality and Lovejoy (1981) is probably correct in looking to male provisioning for the key. However, once bipedal, increased tool use would arise, not so much from a greater ability to make or use tools, but since they could be carried, the payoff for making and using them would enormously increase. The change in the early hominid hand is most likely the result of the new positive selection pressure for tool manufacturing ability.

The cranial capacity of *A. afarensis* specimen No. AL-45-133 has been estimated at 500 ml (Holloway, pers. comm.). This cranial capacity falls at the uppermost extreme of the range measured for chimpanzees (a sample of 29 *Pan troglodytes* endocasts shows a range of 334 to 474 ml (Holloway, 1973, p. 23) and by most reasonable body weight estimates for *A. afarensis* gives a brain/body weight ratio larger than chimpanzees but smaller than *Homo sapiens*. The data suggests that cranial expansion may have already begun prior to *A. afarensis*.

It has been noted by Jerison (1973) that predators show significantly higher brain/body weight than do non-predators. It might be suggested that an increase in cranial capacity seen among even the earliest hominids was produced by the change to a greater dependency on predatory ability and a slight increase in tool use as described above.

Upon first examination, the hominid tooth pattern may seem an unlikely step for an animal that has become increasingly predatory. True carnivores have large sharp teeth to effectively hold and kill their victims. It should be noted, however, that hominids do not kill prey with their teeth as do other carnivores and thus, should not show a similar dental pattern. From Teleki's reports it seems that chimpanzees most frequently kill their victims by slamming them against the ground (i.e., Teleki, 1973, pp. 51, 133) in a manner identical to that used by the Ache (Hill & Hawkes, in press, table II) for some prey items. Hominid teeth might seem rather inefficient for eating raw meat. Carnivores with their large sharp teeth tear off huge chunks of meat and bone, swallowing them whole. However, in order to process these chunks of prey efficiently, carnivores have developed strong enzymes that are sometimes capable of dissolving cartilage and bone (Kruuk, 1972, p. 108). Apes have no such enzymes nor would they need to develop them if they had efficient dentition for chewing meat into small, well-masticated pieces.

Teleki (1973) provides several excellent descriptions of the difficulties that chimpanzees have in dividing and consuming their prey. He reports that it takes an average of eight chimpanzees an average of over three and a half hours to consume a single prey item. This is in contrast to only eleven minutes on average (1973, p. 56) to capture and kill the prey. Carnivores have no such difficulty in consuming prey. This difficulty in consuming prey might select for strong incisors and large molars to tear off and thoroughly chew raw meat into small pieces. Szalay (1975) hypothesized that hominid dentition is in fact an adaptation to increased meat consumption. As the hands, and simple tools in them, were used more and more exclusively as weapons, canines became unnecessary. Canine interference in the thorough mastication of meat and new vegetable items exploited with simple tools would provide the selection pressure to reduce their size.

Male provisioning would allow females a greater freedom to concentrate on careful parental care without having to maximize foraging efficiency. This change would probably reduce infant mortality considerably, and thus, the *average* life span would increase. More importantly, with a greater number of organisms living to older ages, the advantages that could be obtained from averting causes of death later in life (aging) would increase greatly and thus provide the selection pressure for greater longevity. Organisms with a longer juvenile developing period might then be more able to out-compete others in adulthood (through learning, etc.), but such a longer period of development would necessitate an *increase* in the birth interval. This long period of juvenile dependency would, however, have an even more important consequence. If juvenile offspring had a very low probability of surviving their mothers' death at, for example, under ten years of age, it would be an unwise strategy for a female to continue to bear offspring when the probability of her death within the next ten-year period was quite high. Old females with a low probability of surviving another ten years should shift their reproductive strategy. The optimal strategy for a female under these conditions is to assist in the parental care of her own daughters' offspring, and to cease reproductive effort herself. This is a probable cause of human female menopause. The fact that males do not show the same physiological adaptation probably indicates that direct parental care of a males' own infant offspring was not critically important in the hominids.

The scheme presented attempts only to explain the characteristics of the earliest fossil hominids, and those behaviors which are inferred to have necessarily accompanied such characteristics. It does not attempt to explain the subsequent evolutionary trajectory taken by the hominids, but can be useful as a starting point. It is also likely to contain many errors which will have to be corrected as new fossil, archaeological and behavioral data emerge. Nevertheless, I hope the significant contribution of the scheme is to emphasize the use of an evolutionary framework based on changes that can demonstrably increase an organisms' inclusive fitness.

7. Conclusion

I have tried to emphasize several points about what seems to be lacking in current thought about hominid evolution. These points are the following: (1) That use of *all* data, fossil, archaeological, and behavioral are necessary in order to formulate a coherent evolutionary scheme for hominids. Unfortunately, many authors of recent theories have concentrated primarily on the data from one specialty field to the exclusion of important data from other areas. A well co-ordinated team effort of investigators with various

specialities would probably be most successful in this endeavor; (2) Changes in hominid diet at the time of pongid hominid divergence seem to be indicated on both theoretical and empirical grounds. Because of its primary importance in the fitness of any organism, subsistence strategy must be considered seriously in any evolutionary scheme; (3) Any evolutionary scheme presented must be consistent with our current understanding of how natural selection operates. All traits hypothesized to have arisen must increase the inclusive fitness of the bearer of that trait, and at the point in time that the trait is hypothesized to have arisen (not further down the line after other traits are present in a "positive feedback loop"). Two traits, both dependent upon the presence of the other in order to increase inclusive fitness, are unlikely to have arisen simultaneously at any point in the evolution of hominids. If a single tendency by itself cannot be shown to be beneficial without subsequently adding another trait as well, such a tendency will probably not be favored through natural selection.

Finally, I have presented an alternative hypothesis that takes into account *all* known properties of the earliest hominids, and is evolutionarily consistent. Traits are seen to have arisen (though not necessarily fully developed) in a chronological fashion such that each change will increase the inclusive fitness of the organism undergoing the change. Although feedback between some traits may be seen to increase the degree of development of those traits, the origin of every trait is specified without resort to vague feedback loops. The scheme presented can be chronologically summarized as follows:

- (1) A subpopulation of miocene apes found itself in an ecozone where the ease of acquiring prey items made it advantageous for them to begin to specialize as predators.
- (2) Males, because of their greater efficiency as hunters, were able to more easily meet their nutritional needs even as the organism reached maximum density for female survival. Males used free time during the day to acquire food items (primarily meat) which they traded to estrous females for copulation privileges. It was advantageous for females to receive such food items, and copulating with the best provider also ensured offspring of highest fitness. Monogamy is not implied and females were not fully provisioned, thus sexual dimorphism is great.
- (3) Increasing use of hands as a weapon decreased the usefulness of large canines. The need to efficiently chew raw meat and new tougher vegetable resources exploited with crude tools made large canines disadvantageous.
- (4) Longer and longer periods of "estrous" were selected in females, obscuring ovulation and resulting in receptivity to copulation.
- (5) The increase in fitness from such provisioning behavior selected for bipedal locomotion and the ability to easily carry food items to females.
- (6) The ability to easily carry items swayed the balance between the costs and benefits of making more elaborate tools to be used on rarely encountered, but high return resources. Increased tool manufacture and use selected for changes in hand morphology.
- (7) Frequent tool use and predatory behavior (especially upon other primates) gave great advantages to more intelligent organisms and produced a slight increase in brain/body weight ratio. This also would select for reorganization of the central nervous system.

- (8) The reduction in infant mortality brought about through provisioning allowed for an increase in longevity, and a lengthening of the juvenile dependency period. This in turn made grandmother-parental care advantageous and produced female menopause. Grandmother care of infants along with male provisioning to families, allowed for a slight shortening of the birth interval.

It should be noted that the final step in the above scheme did not necessarily have to have taken place by the time of *A. afarensis*. Further understanding of subsequent steps in human evolution, as well as an increase in our overall understanding of the evolutionary process will probably shed considerable light on the behavioral traits that are difficult to determine from the fossil and archaeological record.

It should be emphasized that this scheme leads to an organism which is far from being human. The scheme specifically avoids dealing with some human behavioral traits which probably did not arise until other physical changes had taken place (specifically, changes in the central nervous system). It is presented only in an attempt to explain pongid-hominid divergence, and leaves a great deal of room for further evolutionary changes to have taken place in the past three million years.

If the scheme is roughly correct, it suggests that accounting for changes subsequent to *A. afarensis* may be considerably more difficult than explaining the changes necessary to get *A. afarensis* from the hypothesized common ancestor. The explanation of human intelligence is still a most difficult problem. The solution of this problem, too, will require data from the fossil record, non-human primate behavior, archaeology and hunter-gatherer ethnography. Since we know that the primary physical change in hominids during this period was the expansion and reorganization of the neocortex, the behavioral contrast between pongids and foraging humans is of utmost importance. The archaeological residues of hominid activity represent an enormous wealth of information on hominid behavior during this period, but only if they can be interpreted. This interpretation must be based on an understanding of the principles that underlie human behavior, and the assemblage patterns that different behaviors leave in the ground.

Energy acquisition is the major activity in terms of time expenditure for both human hunter-gatherers and their nearest primate relatives. Dietary differences are of key importance in the process of divergence and the data demonstrate that such changes have taken place between living pongids and hominids. It must, therefore, be concluded that the recent trend to dismiss subsistence strategy as irrelevant to hominid evolution is a theoretical and empirical step backwards in the process of illuminating our evolutionary pathway.

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