The Evolution of Hominin Diets

Vertebrate Paleobiology and Paleoanthropology Series

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The Evolution of Hominin Diets

Integrating Approaches to the Study of Palaeolithic Subsistence

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A three-dimensional photosimulation produced from a point cloud of an area of the occlusal surface of a human molar. The area was scanned at 100 times magnification using a Sensofar μ Confocal Imaging Profiler at the Paleoanthropology Laboratory, University of Arkansas at Fayetteville.

Microgravette point from the Gravettian site Grub/Kranawetberg (Austria) representing possible hafted tip of hunting weapon, illustration by: Walpurga Antl-Weiser (Naturhistorisches Museum, Vienna)

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Preface

Michael P. Richards and Jean-Jacques Hublin

The study of hominin diets, and especially how they have evolved throughout time, has long been a core research area in archaeology and paleoanthropology, but it is also becoming an important research area in other fields such as primatology, nutrition science, and evolutionary medicine. Although this is a fundamental research topic, much of the research continues to be undertaken by specialists and there is, with some notable exceptions (e.g., Stanford and Bunn, 2001; Ungar and Teaford, 2002; Ungar, 2007) relatively little interaction with other researchers in other fields. This is unfortunate, as recently it has appeared that different lines of evidence are causing similar conclusions about the major issues of hominid dietary evolution (i.e., the recognition of the important role of meat eating in brain evolution in early Homo, as well as the subsistence strategies of Neanderthals). However, multidisciplinary or integrated, approaches to the study of hominid diets remain rare. Therefore, we wanted to address this issue through a symposium we organized at the Department of Human Evolution in the Max-Planck Institute for Evolutionary Anthropology in Leipzig from May 17th to 21st 2006.

The symposium had two main goals. The first was to bring together key researchers to provide a current state-of-the-art report of their research area. The second and main goal of the symposium was to bring together researchers who may not normally meet, as they work in different regions, on time periods, and with different analytical tools. With this meeting we aimed to address three main issues of dietary evolution:

(a) Meat eating: when did it start and how did it intensify?
(b) Hunting technologies: What is the first evidence of hunting, and how did it develop over time?
(c) Resource intensification: When did this first occur, and how do the species chosen for intensification differ over time and between regions (i.e., use of marine/aquatic resources, small mammals).

To do this, we invited participants from different fields who all had researched these topics, or some aspects of them. These four general research areas were (1) modern studies (primates, modern humans), (2) faunal and plant studies, (3) archaeology and paleoanthropology, and (4) isotopic studies.

This volume therefore presents research articles by most of these participants that are mainly based on their presentations at the symposium. As can hopefully be seen in the volume, these papers provide important reviews of the current research in these areas, as well as often present new research on dietary evolution.

In the section on modern studies Hohmann provides a review of the diets of non-human primates, including an interesting discussion of the role of food-sharing amongst these primates. Snodgrass, Leonard, and Roberston provide a review of the evidence for the change in brain size of the earliest hominids and how this is linked with diet quality and body composition. Lucas presents an informative look at the mechanics of food processing in the mouth and how this may have changed over time related to differing foods used by different hominins. Finally, Lindeberg presents the evidence for hominin dietary evolution based on the studies of modern human nutrition and health, arguing that many modern diet-related diseases are linked with a mismatch between the diets we should have based on our dietary evolution (lean animal protein and simple carbohydrates) the diets most people have (fatty animal foods and complex carbohydrates).

In the faunal and floral research section, Villa and Lenoir provides a summary of the faunal evidence for diets in Lower and Middle Paleolithic Europe. Comparisons between Middle Paleolithic (or Middle Stone age) and Late Paleolithic (or Late Stone Age) assemblages are proposed for different geographical areas. Hoffecker explores Neanderthals and modern human diets in the Late Pleistocene environments of Eastern Europe. Gaudzinzki-Windhauser and Niven provide a review of the faunal evidence for subsistence in the Middle Paleolithic and Upper Paleolithic of Europe, focusing on reindeer exploitation. Steele and Klein review the available zooarcheological data documenting the "transition" from the Middle to the Late Stone Age in South Africa. They examine how subsistence changes relate to demographic changes and models of modern human origin. Adler and Bar-Oz conduct a

comparison between Neanderthal and the first modern human game exploitation in Southern Caucasus and conclude they occupied the same ecological niche with clear consequences regarding mutual exclusion. Munro presents a synthesis of the evidence for changes in dietary adaptations towards smaller game and intensification in South-West Asia in the later Paleolithic, and Stiner and Kuhn move beyond discussion of the faunal evidence directly to discuss the implications of this work and especially division of labor between males and females in Paleolithic Mediterranean Eurasia. Jones provides a useful review of the (limited) evidence for the exploitation of plant foods in the European Paleolithic.

The archaeological and paleoanthropological data also contribute to a better understanding of food acquisition by ancient hominins. Alemseged and Bobe use a paleoenvironmental approach to infer possible dietary adaptation of two hominin genera: *Paranthropus* and *Homo*, particularly in the way they could exploit fallback resource. Shea analyzes the emergence of long range projectile technology likely in Africa at approximately 50–100 Ka and its subsequent spread into Eurasia. Churchill and Rhodes' review of the anatomical features related to the development throwing bring support to the claim that projectile weapons arose in the African later MSA and moved into Europe in the hands of modern humans. However Villa and Lenoir also provide possible evidence for the use of stone-tipped spears by Neanderthals in Western Europe. MacDonald, Roebroeks, and Verpoorte examine the Neanderthal archaeological record and how energetic issues in the use of space may in part explain it.

Finally, in the isotopic studies section Schoeninger provides a review of the small number of studies on the isotopic evidence for the diets of living non-human primates and critically relates it to the isotopic evidence for the diets of early hominins. Sponheimer and Dufour provide a critical assessment of the isotopic evidence for diets of early hominins with a focus on whether there is evidence for increasing dietary breadth in australopithecines and early Homo. Bocherens presents a selection of the isotopic data for European Neanderthals, emphasizing the importance of large herbivores in Neanderthal diets. Finally, Richards provides a summary of the isotopic evidence for Upper Paleolithic humans in Eurasia that also shows the dietary importance of animal foods, including small game such as aquatic foods.

This wide range of papers will hopefully be of interest to researchers who work in dietary evolution to provide a current account of the field, and will provide an introduction into the research that is being undertaken into this topic in fields that are not the reader's own. The research on dietary evolution continues, and hopefully through further interdisciplinary forums such as this we can come closer to knowing how hominin diets changed and evolved over time, as well as learning how to use this knowledge to help us understand the origin and implications of the range of diets of modern humans living in different parts of the world today.

Acknowledgments. We are grateful to the Max Planck Society for funding the workshop, as well as all of the participants for agreeing to take part in this, which we hope they found as interesting and enjoyable as we did. We are especially grateful to Diana Carstens and Silke Streiber as well as to Michelle Hänel, Jörn Scheller, and Annette Weiske for assistance in organizing the workshop. Allison Cleveland and Stefanie Altman played an essential role in the preparation of this volume.

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1. The Diets of Non-human Primates: Frugivory, Food Processing, and Food Sharing

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Keywords Primates • diet composition • frugivory • provisioning • meat eating

Abstract Most nonhuman primates have a mixed diet that consists of a wide spectrum of plant foods and a relatively small spectrum of animal foods. Patterns of food selection shift in relation to seasonal changes in food availability. Food habits may also vary within and between groups of the same species for other reasons, such as inter-specific competition and local traditions. Primates practice various forms of food processing and by doing so modify the physical structure of food. Food processing is likely to affect food intake rate, passage time, and nutrient absorption. The diets of Hominids (*Pan*, *Gorilla*, and *Pongo*) are dominated by plant foods. In some species, food sharing is habitual. Food may be transferred between mature individuals (e.g., chimpanzee, bonobo) or from mature individuals to immatures (e.g., bonobo). Consumption of animal food is widespread, but may vary considerably between species. Except for bonobos, insectivory is common among Pongids, and except for gorillas and orangutans, consumption of vertebrate meat is habitual. Hunting and meat eating occurs equally in forests and in open habitats. In forest populations, hunting increases at times when plant food is highly abundant, suggesting that hunting activities are triggered by high energy intake from plant foods. Patterns of meat sharing by chimpanzees and bonobos differ: in chimpanzees, the majority of the prey is consumed by adult males and adult females. In bonobos, adult females control access to carcasses and share meat among each other and with immatures. Information from bonobos and chimpanzees suggest that neither food sharing nor provisioning is causally related to hunting and meat eating. Instead, evidence suggests that food sharing and provisioning have developed in the context of frugivory when primates consume fruits that are large and/or difficult to process. Patterns of food sharing by bonobos offer a model for how a change in the diet of adults could have precipitated to immatures.

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Introduction

Tree branches intertwine overhead, arching high above the forest floor. Multiple layers of leaves keep the sun out, making the air on the forest ground remain humid and cool. Not far away, work is in progress. The sound of hammers carries through the green light. Their echoes duplicate the original sounds and create an acoustic ambience reminiscent of carpenters constructing the roof truss of a new building. Only the whistles and voices of the craftsman are missing. Not surprisingly, the sounds come from a group of chimpanzees cracking *Coula* nuts. To access the nutritional seeds, chimpanzees place the nuts on a rock and use clubs or stones to open the hard shell. Watching nut-cracking chimps is like zooming back into a world without human primates. Is this how our ancestors branched out of the line of nonhuman primates? Patterns of dentition of australopithecines have been interpreted as adaptations to nut-cracking (Peters, 1987). Nuts provide high-quality food that preserves well and can bridge lean seasons when other plant foods are scarce. In some species, density of fat is high and converts into metabolic energy to a high degree (Peters and O'Brien, 1981). The technology to open the shells is relatively simple, but tools are not always available at the food patch. Chimpanzees have been seen carrying tools from far away, suggesting that they prepare for the task of nut cracking long before they arrive at the food patch (Boesch and Boesch, 1983). Studies of chimpanzees at Taï have demonstrated that acquisition of the hammer-anvil technique involves both learning and teaching (Boesch and Boesch, 1984), and it is easy to imagine how extractive feeding and tool use could have pushed the development of primates from nonhuman species to ancestral hominins (Peters, 1987). However, while nut cracking by primates is a remarkable pattern of food acquisition, alternative models of human evolution associate the dietary shift from non-human apes to ancestral hominins with the consumption of meat (Dart, 1953; Lee and DeVore, 1968), changes in nutrient density in plant foods (Conklin-Brittain et al., 2002), or foraging style (O'Connell et al., 2002). While the discussion about meat versus plant foods continues (e.g., Bunn, 2007), there is large agreement that the split between nonhuman primates

and proto-hominins was marked by a shift in diet composition (Leonard, 2002). Most models associate this development with a series of environmental changes that transformed tropical forest into savannah woodlands (review by Reed and Rector, 2007). It is thought that as a consequence of climatic changes, frugivore primates faced longer periods of reduced food abundance and were forced to use alternative sources such as meat, nuts, or underground storage organs of plants (Tooby and DeVore, 1987; Bunn and Ezzo, 1993). In contrast to models that associate the shift in diet with a particular diet component (e.g., meat), and a specific habitat (dry savannah), it has been proposed that subsistence patterns of early hominins were more flexible and adapted to a variety of environmental conditions and food sources (Ungar et al., 2006).

Models of feeding patterns of early humans use various sources of information; data from nonhuman primates is one source. The construction of conceptual models has a long history in research on human and nonhuman primates, and has turned out to be very useful for testing the causality of links between ecology, behavior of contemporary species, and fossil evidence (Tooby and DeVore, 1987; McGrew, 1992; Milton, 1999; Leonard et al., 2003). The strength of such models depends on the data that are fed into the model. As new information accumulates, the database requires updates.

The goal of this paper is to review recent reports on primate feeding ecology, focusing on three corresponding topics. It begins with a summary of published information on dietary composition and its variation between and within populations. This is followed by a section on how food items are processed prior to ingestion and how food is distributed among group members. Given the prominent role of animal matter in the diet of early humans, the final part focuses on the role of fauna in the diet of primates.

Diet Composition: Variation Between and Within Species

Nonhuman primates exploit a variety of food sources, including reproductive and non-reproductive plant parts, exudates of plants, invertebrates, and the meat of vertebrates. Notable exceptions to the average primate diet are species which have specialized in the consumption of secretions from insects (e.g., *Microcebus*), the ingestion of lichen (e.g., *Pygathix bieti*), needles from conifers (e.g., *Macaca sylvanus*), and species that depend heavily or exclusively on insects and other animal food, such as *Tarsius* and many Galagos (Harcourt and Nash, 1986; Bearder, 1987; Richard et al., 1989; Bennett and Davies, 1994; Mittermeier et al., 1994).

Primate omnivory can be portrayed as a mixture of a large number of plant food species and a small number of animal foods (Milton, 1987). This classification is not unjustified, but does not account for the extensive variability of food habits. Considering the proportions that different plant food items contribute to diet and/or feeding time, one item dominates all others: fruit.

From the species listed in Table 1.1, the majority (N = 90, 73%) have a food repertoire that includes some fruit; in 49 species (40%), fruit contributes 50% or more of the diet. In addition, the diet is often skewed towards a few species of fruit (Table 1.2). Black howler monkeys consume fruit and leaves from various sources, but more than 80% comes from a single species. The diet of the bamboo lemur is dominated by shoots and leaves of bamboo (Wright and Randrimanantena, 1989), and in gelada baboons 90% of the food comes from seeds, leaves, and bulbs of monocotyledons (Dunbar, 1977). In some cases like gelada baboons, the diet composition reflects ecological constraints. In some Malagasy lemurs, variation of the concentration of macronutrients narrows the niches that are exploited by different species (Ganzhorn, 1988), and the same may apply to other sympatric primate communities (Terborgh, 1983). Hanuman langurs, crab-eating macaques, and olive baboons are able to sustain themselves on sources that are nutrient-poor and difficult to digest (Koenig and Borries, 2001), and respond flexibly to environmental changes by switching to novel food sources that are highly nutritious (Richard et al., 1989).

The diets of chimpanzees and bonobos are dominated by ripe fruit and complemented by leaves, flowers, and animal food. Comparative nutritional analyses of samples from Salonga bonobos and Gashaka chimpanzees showed that the food items of both species contain similar amounts of nutrients (Hohmann et al., 2006). Plant food samples from the two sites differed in terms of associations of nutritionally relevant components. In chimpanzee samples, anti-feedants such as tannins and phenols were found to be associated with lipids whereas in the food samples eaten by bonobos, concentration of lipids was independent of tannins and phenols. Another difference was that ambient levels of tannins and phenols were significantly higher in the habitat of chimpanzees (Hohmann et al., 2006). However, food samples from both species contained very similar amounts of these anti-feedants, suggesting that chimpanzees are more selective in choosing food plants than bonobos. The effects of these differences are still unknown, but they are likely to be reflected in species-specific patterns of food selection, food processing, and/or digestion.

The dietary patterns shown in Table 1.1 depict major trends of food selection, but these patterns do not account for extensive intraspecific variability. Some of the variation between populations of the same species is probably based on differences in ecology. Hanuman langurs occupy a variety of different habitats, and dietary composition tends to correlate with the abundance of young leaves, flowers and fruit, while the intake of mature leaves is considered to be independent of forest productivity (Newton, 1992). In rich habitats, common langurs concentrate on high quality food and have relatively large food repertoires (Koenig and Borries, 2001).

Early field studies on woolly spider monkeys, the largest New World primate, suggested that the species adapted to a low quality diet dominated by leaves (Milton, 1984). More recent work revealed that some populations are highly

TABLE 1.1. Size of food repertoire of primate species, proportions of different food components in the total diet, and body mass (kg) (From Rowe, 1996).

							Body mass	
Species	Food	Fruits	Leaves	Flowers	Seeds	Animal prey	Female	Male
Prosimians								
Arctocebus aureus		14				85		
Arctocebus calabarensis						100	0.31	0.32
Loris tardigradus						99	0.26	0.29
Nycticebus coucang		50				30	1.20	1.21
Perodicticus potto		65				10	1.08	1.02
Euoticus elegantulus		5				20	0.27	0.30
Galago alleni		73				25	0.27	0.23
Galago senegalensis						52	0.19	0.21
Galagoides demidoff		19				70	0.07	0.08
Galagoides zanzibaricus		30				70	0.14	0.15
Otolemur garnettii		50				50	0.72	0.82
Phaner furcifer							0.40	0.44
Lepilemur leucopus							0.58	0.54
Lepilemur mustelinus							0.62	0.59
Lemur catta		70	25	5			2.68	2.71
Eulemur rubriventer	67						2.14	2.27
Hapalemur aureus							1.50	1.66
Hapalemur griseus							0.89	0.94
Hapalemur simus							2.40	2.15
Propithecus diadema		20	26	3	25		7.50	7.50
Propithecus tattersalli		37	39					
Propithecus verreauxi	102						3.48	3.64
Indri indri	62	25	50–75		19		7.14	5.83
Tarsius bancanus						100	0.11	0.12
Tarsius dianae						100	0.11	0.09
Tarsius pumilus						100		
Tarsius spectrum						100	0.11	0.13
Tarsius syrichta						100	0.12	0.13
New World Monkeys								
Callithrix flaviceps	30	14				20		
Callithrix humeralifer	52	83					0.31	0.28
Callithrix kuhlii		67						
Callithrix penicillata		30					0.18	0.23
Callithrix pygmaea	38						0.13	0.13
Saguinus bicolor	21	96					0.43	0.43
Saguinus fuscicollis		96					0.40	0.39
Saguinus geoffroyi		60				30	0.54	0.55
Saguinus imperator		97		4				
Saguinus nigricollis	41						0.48	0.47
Leontopithecus rosalia		78					0.58	0.57
Aotus nigriceps		65–75	5–30			5–20	0.94	0.94
Aotus trivirgatus							0.92	0.95
Callicebus brunneus		47	28	2		15	0.85	0.85
Callicebus moloch		54	28			17	0.86	1.00
Callicebus personatus	91	81				0	1.38	1.27
Callicebus torquatus	57	65	15			16	1.31	1.30
Cebus albifrons	68	53			42		1.81	2.48
Cebus paella	96	66			25		2.39	3.05
Cebus capucinus	119	65	15			20	2.67	3.87
Saimiri boliviensis		18				82	0.80	1.03
Saimiri oerstedii							0.70	0.85
Saimiri sciureus							0.95	0.85
Pithecia albicans	81	34	10	7	46			
Pithecia monachus		55	4	3	38		1.90	2.80
Pithecia pithecia		60		7	30		1.26	1.73
Chiropotes albinasus		54		3	36		2.51	3.02

(continued)

TABLE 1.1. (continued)

Species	Food	Fruits	Leaves	Flowers	Seeds	Animal prey	Body mass	
							Female	Male
Chiropotes satanas	86	30		3	66		2.60	3.10
Cacajao calvus		18		6	67	5	2.88	3.45
Alouatta caraya		24	76				4.61	6.64
Alouatta fusca		2–29	66–77	6–20			4.55	6.23
Alouatta palliata	100	13	70	18			5.35	7.15
Alouatta seniculus	195	42	53	5			5.60	7.20
Ateles belzebuth	33	83	7	1			9.85	8.53
Ateles chamek		80	17	2				
Ateles geoffroyi		78	8	13	11	1	7.46	8.21
Ateles paniscus	171	83	6	6			8.75	7.34
Lagothrix lagotricha	225	68	14	3	7		5.00	6.80
Brachyteles arachnoides		32	51				9.45	12.13
Old World Monkeys								
Macaca fascicularis		64					4.10	6.50
Macaca fuscata	192						13.15	14.50
Macaca mulatta	92						7.65	8.25
Macaca nemestrina	160	74	5	4		12	7.80	10.35
Macaca nigra	120						6.60	10.40
Macaca radiata	39	47–53					4.17	7.13
Macaca sinica		75	23				3.85	6.40
Macaca sylvanus	100						10.60	16.15
Papio hamadryas cynocephalus	180						12.30	24.89
Papio hamadryas papio							13.00	26.00
Mandrillus sphinx	113	92					11.50	26.90
Theropithecus gelada					90		11.70	20.00
Cercocebus galeritus	61	73–78	11–14	1		1–3	5.40	10.20
Lophocebus albigena		59	5	3		11	5.67	7.26
Allenopithecus nigroviridis		81	2				3.70	5.95
Miopithecus talapoin		43					0.78	1.27
Cercopithecus ascanius	104	62	7			25	3.30	4.21
Cercopithecus cephus	47	78	7			15	2.90	4.10
Cercopithecus mitis		55	19			17	4.23	7.35
Cercopithecus neglectus		74	9	3		5	4.46	7.55
Cercopithecus nictitans		90					4.08	6.35
Colobus polykomos							8.30	9.90
Procolobus pennantii		6	72	12			7.00	10.50
Procolobus rufomitratus		25	63	6				
Procolobus verus		3	73	7	14		4.20	4.70
Presbytis comata	64	14	65	7	1		6.67	6.40
Presbytis femoralis		49						
Presbytis hosei	47	30	65	2			5.57	6.20
Presbytis melalophos	55	24	40	12	25		5.80	5.90
Presbytis potenziani		32	55				6.40	6.50
Presbytis rubicunda		19	37	11	30	1	5.70	6.22
Semnopithecus entellus		24	45	20		3	11.20	18.30
Trachypithecus auratus		35	47	7		1		
Trachypithecus cristatus	94	10	90				5.70	6.60
Trachypithecus johnii	114	25	58	9			10.90	12.71
Trachypithecus obscurus		35	58	7			6.60	7.32
Trachypithecus phayrei		24	68				6.95	7.93
Trachypithecus vetulus		28	60	12			6.30	7.55
Pygathrix nemaeus	50						8.20	10.90
Nasalis concolor		25–30	60				7.10	8.75
Nasalis larvatus		17	44	3	2	1	10.00	21.20
Apes								
Hylobates agilis		58	39	3		1	5.70	6.00
Hylobates concolor		21	72	7			5.80	5.60
Hylobates hoolock		65	13	17		5	6.10	6.90

(continued)

TABLE 1.1. (continued)

Species	Food	Fruits	Leaves	Flowers	Seeds	Animal prey	Body mass	
							Female	Male
Hylobates klossii		70	2			25	5.90	5.70
Hylobates lar		50	29	7		13	5.60	6.29
Hylobates muelleri		62	32	4		2		
Hylobates pileatus		71	11	15		2	7.50	9.16
Hylobates syndactylus		31	59	8	3		10.57	13.52
Pongo abelii	200							
Pongo pygmaeus	400	60					37.00	77.50
Gorilla gorilla beringei	145	2	86	2		0	97.70	159.2
Gorilla gorilla gorilla		67	17			3	71.50	169.5
Gorilla gorilla graueri	102						80.00	175.2
Pan troglodytes	250	45–76	12–45	1–18	1–11	0–5	39.50	50.00

TABLE 1.2. Number of main food items in relation to total food repertoire, the proportion of main food items in the total diet, or the time spent feeding on main food items (From Rowe, 1996).

	Total repertoire	Number of main food items	Proportion of diet (%)	Feeding time (%)
Eulemur fulvus	57	10	60	
Eulemur rubriventer	67	10	50	
Indri indri	62	5	50	
Pithecia pithecia		2	49	
Alouatta pigra		1	86	
Cercocebus galeritus		1	61	
Colobus angolensis	46	5	47	
Colobus guereza		1	69	
Trachypithecus pileatus	35	2		30
Nasalis larvatus	55	4	60	

frugivorous, and it seems that the proportion of fruit in the diet of woolly spider monkeys increases whenever the forest offers sufficient resources (Strier, 1991; Talebi et al., 2005).

Data from chimpanzees also indicate that populations in wet forest habitats have a larger food repertoire than those living in dry forest (Hunt and McGrew, 2002; Pruetz, 2006). This difference is considered to reflect variation in the abundance of fruit in relation to climatic factors but may also be related to the quality of food sources. Another force that has been found to affect food choice is the presence of competing species. Where chimpanzees coexist with gorillas, dietary patterns may reflect niche separation (Yamagiwa et al., 1996) or geographic differences in forest vegetation (Ganas et al., 2004). In Western gorillas, differences between populations are most prominent in terms of fruit consumption (Rogers et al., 2004). Flexibility of food choice is not restricted to natural sources, but extends to cultivated plants. Some populations of baboons, macaques, chimpanzees and gorillas have adapted well to exploit human crops (Naughton-Treves et al., 1998), and translocation of wild communities has shown that some species are able to switch to a completely different set of foods (Silver and Marsh, 2003).

Even in areas where climatic conditions are relatively stable, fruit production is a seasonal phenomenon and fruiting intervals are often separated by several years, making the availability of certain species difficult to predict (Leigh and Windsor, 1982). When preferred food sources are scarce, most species turn to foods that are not used at other times of the year. The type of fallback food varies between, and sometimes also within species. Cercopithecines and chimpanzees of Kanyawara Community, Kibale forest, Uganda, both have a diet that is dominated by fruit. At times when ripe fruit are scarce, cercopithecines turn to unripe fruit, leaves, and other food sources while chimpanzees maintain feeding primarily on ripe fruit (Wrangham et al., 1998).

Data from sympatric populations of gorillas and chimpanzees show variation in terms of dynamics of diet composition during lean seasons. In the lowland forest of Lope, Gabon, gorillas focus on leaves of dicotyledons while chimpanzees maintain a high intake of fruit throughout the year (Tutin and Fernandez, 1993). In the montane forest of Kahuzi Biega, D.R. Congo, gorillas stick to a folivore diet while chimpanzees turn from fruit to monocotyledon herbs when fruit becomes scarce (Basabose, 2002).

Comparison of data from two populations of orangutans provides a particularly interesting example of the nutritional consequences of differences in the availability of fallback foods. In both populations, food availability is affected by a

community-wide fluctuation of fruiting in which brief periods of high fruit abundance are separated by long periods of low fruit availability (Medway, 1972). At times of food shortage, Borneo orangutans are forced to use cambium of trees, a food that is characterized by very low nutrient concentration and high fiber content, as fallback food. Urine samples collected during the lean season contained high concentrations of keton, suggesting that subjects had lost body mass because of a lack of energy (Knott, 1998). Orangutans from Sumatra experience a similar fluctuation in fruit abundance. However, due to the higher density of *Ficus* trees, fruit availability does not reach the low level recorded at Borneo (Wich et al., 2004). Instead, measurements of social parameters (e.g., group size) and energy constitution (e.g., keton excretion) suggest that individuals from Sumatran population are able to maintain body mass during the lean seasons by using fig trees (Wich et al., 2006).

Digestive Strategies

The variation in diet composition between species reflects to some extent the functional morphology of the digestive tract (Chivers and Hladik, 1980). Omnivore generalists like macaques, baboons, and chimpanzees have a simple digestive tract that facilitates digestion of various types of food. In capuchins and other fruit eaters, small intestines make up a large proportion of the digestive tract, but in most species the volume of large intestines exceeds that of the small intestines. Species that depend largely on a diet of leaves and other non-reproductive plant parts show adaptations to ferment food in the stomach or in the large intestines (Milton and McBee, 1983). Evidence suggests that adaptations in gut morphology constrain flexible responses to changes in diet in terms of digestive kinetics and digestive efficiency. The diet of howler monkeys is dominated by leaves, and nutrient extraction is enhanced by fermentation in the large intestines and slow passage rate of ingesta (Milton et al., 1980). Whenever available, howlers increase intake of fruit, but feeding experiments suggest that this change in diet composition does not shorten gut passage time (Milton, 1981). In this case, the digestive morphology seems to relate to the dominant section of the diet and not to sporadic bursts of frugivory. Woolly spider monkeys show a strong tendency to feed on fruit whenever resources are abundant, but are also able to sustain themselves on a highly folivore diet when fruit is scarce. However, unlike howlers, woolly spider monkeys have a rapid passage rate (Milton, 1984), suggesting that their digestive system is adapted to a diet that is dominated by fruit (Strier, 1991).

In a long-term study on red colobus monkeys, Chapman et al. (2002) found that diet composition changed on a spatial and a temporal scale. While all groups focused on vegetation, the proportion of different food items varied within and across groups.

Although the diets of chimpanzees and orangutans are characterized mainly by ripe fruit, the large intestines remain spacious. Analyzing data on food intake and nutritional quality of foods eaten by chimpanzees at Kanyawara, Uganda, Conklin-Brittain et al. (2006) found that at times when ripe fruit is in short supply, individuals with a particularly high energy demand (e.g., lactating females) would not be able to cover their energy requirements without fermentation. Similarly, the long passage of digesta by orangutans is seen as an adaptation to the high concentration of fermentable fibers in the natural food of this species (Caton et al., 1999).

The examples given above do not necessarily contradict the predicted relationship between diet and digestive system (Chivers and Haldik, 1980). However, the flexibility of diet composition indicates that gut size alone does not allow for inferences about the nature and quality of food items. Temporary changes in diet composition may affect parameters such as intake rate, transit time, gut motility, and digestive efficiency of nutrients and other food components. So far, the digestive physiology of primates remains largely unexplored and offers a challenging field for future studies.

Processing Plant Foods

As do other frugivores, primates deal with items that are often difficult to access because of hardness, protective structures like spines and thorns, or large size (Leighton and Leighton, 1983). Moreover, accessibility of nutrients is not homogenous, but is concentrated in certain parts of fruit (e.g., mesocarp, exocarp, arille). Seeds and other parts of the fruit are usually protected from consumption by secondary compounds (Levey and Cipollini, 1998). Because of this, consumption of fruit requires some kind of processing. Many species of the Old World have cheek pouches. Cheek pouches serve as containers for storing food, which allows individuals to collect food as they move and exposes food items to salivary enzymes that extract part of the nutrients. Storage of food in cheek pouches also promotes retention of seeds (Corlett and Lucas, 1990) and in this way, affects the structure of ingesta, and has important consequences for factors such as digestive kinetics and nutrient absorption (Lambert, 1998). However, inter-species differences in seed handling are not always linked to cheek pouches. Comparing feeding behavior of woolly monkeys and spider monkeys, two frugivore species from the neotropics without cheek pouches, it was found that woolly monkeys, like cheek-pouched monkeys of the Old World, remove most seeds from fruit while spider monkeys ingest fruit together with seeds (Dew, 2005).

Another form of oral food processing occurs in orangutans and the two *Pan* species. When eating ripe fruit, individuals may compress fruit pulp into wedges that are chewed on for extended periods of time (Fig. 1.1). Small parts of the wedge are probably ingested, but the majority is discarded after chewing. This type of food processing is usually seen when fruit crop has reached an advanced stage of ripeness, suggesting that wedging serves to avoid certain components

FIG. 1.1. Male chimpanzee from Ngogo (Uganda) chewing on a wadge of *Ficus mucuso* (photograph by K. Langergraber).

such as non-digestible fibers that are not so prominent at an earlier stage.

In addition to oral food processing, primates have a tendency to process food manually, including removal of spines and thorns, breaking hard shells by smashing fruit on hard surfaces, and washing food items (Boesch and Boesch, 1990; Panger et al., 2002). Panger et al. (2002) compared food processing techniques performed by different populations of wild capuchin monkeys and found that 16 types (80%) of processing involved processing of fruit and four of animal foods. Other taxa well known for investing in manual food processing are orangutans and chimpanzees. Orangutans have exceptional manipulative skills that are habitually used for food preparation. These include the use of leaves as gloves to assist manipulation of spiny fruit, and use of extractive tools to access the hard shelled nuts of *Nesia* fruit (van Schaik et al., 1996).

The catalogue of food processing behaviors by chimpanzees is impressively large and biased towards tool use (McGrew, 1992; Matsuzawa, 1994; Whiten et al., 1999). Long-term studies of nut cracking by chimpanzees at Taï, Ivory Coast, and Bossou, Guinea, indicate that consumers know about material characteristics of both food items and tools (Boesch and Boesch, 1983, 1984; Matsuzawa, 1994). Reports on other types of plant food processing by chimpanzees are rare and anecdotal (Nishida et al., 1983). At Lope, Gabon, chimpanzees were seen to remove the stingy hairs from the skin of *Diospyros* before feeding (Tutin et al., 1996). Perhaps the most detailed analysis of food processing has been made by Corp and Byrne (2002), who investigated techniques of manual food processing of leaves that are physically defended. Comparing manipulation of defended and undefended leaves, the study revealed not only the complexity of manual skills but also the hierarchical organization of different actions.

Dividing Plant Foods

Most fruits eaten by primates are small compared to the body mass of the consumers. Small size promotes an individualistic style of feeding; that is, food items are collected and consumed by the same individual, and competition occurs over food patches rather than food items. However, some species of trees and climbers produce larger fruit that can not be consumed in a single bite. For example, Asian breadfruit trees carry fruit that weigh up to 10 kg (Fig. 1.2). The fruit is rich in nutrients but difficult to process. Lion tailed macaques are eager to feed on these fruit but it seems that only males with their long canines are able to open the tough outer skin (own observations). After opening a fruit, males and females alternate in extracting the sweet husk covering each single seed. This type of communal feeding requires social tolerance but does not include food sharing. Division of plant food has been reported from both marmosets and chimpanzees (Feistner and McGrew, 1989) and was thought to be most frequent among females sharing fruit with dependent offspring (McGrew, 1975; Silk, 1978). In addition to provisioning kin with nutrients, the transfer of food from the mother to her infant is an important way to transfer information about what and what not to eat. During the dry season, chimpanzees at Tongo (D.R. Congo) are reported to dig for tubers to obtain the moisture as an alternative source of water (Lanjouw, 2002). Digging for one tuber takes up to 15 minutes, and immatures may dig for their own food or beg for a share from older individuals. Given that all sources of surface water disappear during this period, division of tubers may be under strong selective pressure. In bonobos, division of plant food seems to be more frequent than in other hominoids, resembling meat sharing in many ways (see below). Bonobos share fruit from a number of species; one species, African bread fruit, *Treculia africana* (Fig. 1.3), seems

FIG. 1.2. Liontailed macaque feeding on Asian breadfruit, *Artocarpus heteropyllus* (photograph by G. Hohmann).

FIG. 1.3. Wild fruit of African breadfruit, *Treculia africana*, may weigh up to 30 kg and are consumed by bonobos, chimpanzees, gorillas and humans (photograph by G. Hohmann).

to be more important than others (Hohmann and Fruth, 1996). Fruit of *Treculia* are consumed by all African ape species living in forested habitats and is also widely used for production of human food (Akubor and Badifu, 2004). Ripe fruit can weigh up to 30 kg; they are rich in protein, unstructured carbohydrates, and lipids. Using nutritional data from samples collected at the site of Lui Kotal, a 10 kg *Treculia* provides up to 20,000 calories. Given that consumption of this resource does not require climbing or other forms of locomotion, it is reasonable to assume that the nutritional reward is likely to be unusually high. At Lomako, bonobos consumed, on average, one fruit per week and in the majority of cases, the fruit was shared with other adult and immature individuals (Fruth and Hohmann, 2002). In most cases, females were in control and shared with other adult females and immatures. While access of other adult females was often constrained, females were usually very tolerant towards immatures independent of their kin relationships, and it was obvious that substantial amounts of food were consumed by members of this age class (Fruth and Hohmann, 2002). The mode of food division included tolerated theft, delivery of partly processed food items, and handouts of fresh food (Hohmann and Fruth, 1996).

Faunivory

Animal matter is a common component in the diet of nonhuman primates. Most species select some kind of fauna, some depend entirely on animal food (Table 1.1); missing scores in Table 1.1 are more likely to reflect a lack of observation than a strict vegetarian life style. The data compiled by Rowe (1996) suggest that there are few species that have been studied intensely and long enough without providing any evidence for using sources of animal food (e.g., *Cercopithecus mitis*, *Trachypethecus christatus*).

Looking at the nature of animal foods, insects dominate all other sources (McGrew, 1992). In spite of the importance of insects in the diet of primates, little is known about the nutritional value of insects and evidence from other species is somewhat contradictory. Some studies found that ants and termites yield few calories in relation to volume and are often difficult to digest because of high concentrations of secondary compounds (McNab, 1984). However, insects that are eaten by humans have relatively high levels of crude protein and fat, and they also contain some essential amino acids and therefore remain important supplements in the diet of many populations (Bukkens, 2005). Given the wide use of insects as food source, it is reasonable to assume that nonhuman primates are equally selective in feeding on species that are relatively easy to digest and/or have behavioral or physiological adaptations that enable them to reduce the negative effects of secondary compounds. Most primates browse for insects while moving on the ground or through the canopy. Prey is sometimes processed (with or without tools) in order to remove parts containing toxic compounds before ingestion (Panger et al., 2002). Hominoids differ from many other primates because they focus on social insects such as ants, bees, and termites that occur in large patches, and chimpanzees enhance collection of insects further by using probes and other tools for "fishing." Similar reports from bonobos are missing, raising the question on whether or not the two *Pan* species have access to the same resources. In a recent study at Salonga National Park, McGrew et al. (2007) found that insect species known to be eaten by chimpanzees at other sites are also available to bonobos. Consequently, there must be other reasons for the absence of ants and termites from the diet of bonobos.

Evidence for the consumption of marine animals is rare and limited to some populations of capuchins, macaques, and baboons inhabiting natural or cultivated shoreline habitat (Freese and Oppenheimer, 1981; Napier, 1981 cited in Rowe, 1996). Swamp monkeys, crab eating macaques, and dwarf guenons are well adapted to life in swamp areas, and anecdotal evidence suggests that lakes, rivers, and streams are commonly used as sources for animal foods, but this has been studied for very few species and the significance of aquatic animals in the diet of nonhuman primates remains anecdotal and fragmentary.

The third type of fauna that primates consume is the meat of other vertebrates. Occasional consumption of the meat has been reported from various taxa, but most reports are restricted to few species: capuchins (Perry and Rose, 1994), baboons (Strum, 1981), and chimpanzees (Teleki, 1973). One trait that these species have in common is that they prey on vertebrates that are relatively large in relation to the body size of the predator. Often, acquisition of prey is described as being opportunistic (catching a prey upon encounter) and individualistic (prey taken by one individual) but chimpanzees may also actively search for prey (Boesch, 1994b).

Evidence for cooperative hunting is still rare, and comparison of different sites shows large variation in hunting frequency, strategies for obtaining prey, and temporal fluctuation of meat eating (Stanford, 1996; Watts and Mitani, 2002). While intra-specific variability of hunting by chimpanzees offers a fascinating model on how environment and sociality affect hunting and meat consumption in hominoids, it should be noted that most data are biased to one prey species, the red colobus monkey, and also to hunting by males. Much less is known about acquisition of other vertebrate species known to be eaten by *Pan*, and information on hunting by female chimpanzees is almost nonexistent. The recent report from Fongoli, Senegal, by Pruetz and Bertolani (2007) is a notable exception. The study provides rare evidence for the use of tools in the context of vertebrate hunting. As interesting as the tool use is that the tool-aided prey acquisition was mainly by adult females and immatures.

With this note of caution in mind, one can ask how differences in ecology and social behavior influence hunting frequency, hunting success, meat acquisition and meat sharing. One critical issue that has been raised in many empirical and theoretical studies is the question of whether hunting is a means to procure food when other sources are scarce, or whether hunting activity is restricted to times of high food supply (Stanford, 1996). Evidence from the field is mixed. Observations of chimpanzees at Gombe and Mahale suggest that hunting and meat consumption coincides with temporal shortages of plant foods (Takahata et al., 1984; Stanford, 1996). In contrast, data from Taï and Ngogo show that hunting occurs most frequently, and is most successful, at times when fruit are abundant (Boesch, 1994b; Watts and Mitani, 2002).

Hunting success seems to be triggered by social and ecological variables. At Taï it increases with the number of adult males, but data from other sites indicates that this is not always the case. Another variable that seems to influence the chance of catching prey is forest structure: hunting success is highest in areas with broken canopy where escape routes are limited; travel patterns of hunting parties suggest that chimpanzees are aware of the spatial constraints (Boesch et al., 2002; Watts and Mitani, 2002).

Meat Sharing

The proximate goal of hunting is acquisition of meat. Figures from Gombe chimpanzees suggest that during the dry season, adult individuals consume between 33 and 98 g of meat per day (Stanford, 1996). At Taï, the average daily intake of meat is estimated to be 186 g for adult males and 25 g for adult females (Boesch and Boesch-Achermann, 2000). Although such an amount seems to be small, it may still be an important source for nutrients that otherwise would be difficult to obtain. And still, is the nutritional pay-off sufficient to compensate for the energetic costs of hunting? To answer this question, a number of variables have to go into the equation: time and energy required to search and capture the prey, the probability of obtaining a share, and the energetic reward. Evidence from the field demonstrates that some individuals gain more than others. In chimpanzees, it is usually one of the hunters controlling access of other group members to the food source, but members of a hunting group who have not contributed to make the catch may also obtain meat (Boesch 1994a, b). Figure 1.4 shows that adult males and cycling females are the preferred beneficiaries of meat sharing, while younger individuals receive very little (Boesch and Boesch-Achermann, 2000). Estrus females are more likely to receive meat than non-estrus females (Stanford, 1996) suggesting that the nutritional benefits from meat consumption may offer reproductive advantages. Indeed, McGrew (1996) found that females who obtain meat from males had a higher reproductive success than females who received meat rarely or not at all. The chimpanzee model fits nicely with what one would predict: close relatives (males) cooperate in hunting, cooperation raises the per capita intake of meat, and meat sharing with females increases mating success and reproductive success of males. Bonobos provide an interesting case that shows how prey capture and meat sharing may have evolved in a different way. Combined information from Lomako (Hohmann and Fruth, 1996) and Lui Kotal (G. Hohmann and Fruth 2008) indicates that duikers, solitary living forest antelopes, are the major prey, and that meat consumption always involves meat sharing. Current evidence suggests that most if not all hunts are opportunistic actions by single individuals. The adult sex ratio within bonobo parties is female biased (Hohmann and Fruth, 2002) and therefore, one would assume that females catch prey twice as often as males. Direct observations on prey acquisition are rare and do not allow estimates of hunting success. However, observations from Lomako and Lui Kotal show that it is almost always adult females who control the prey (Hohmann and

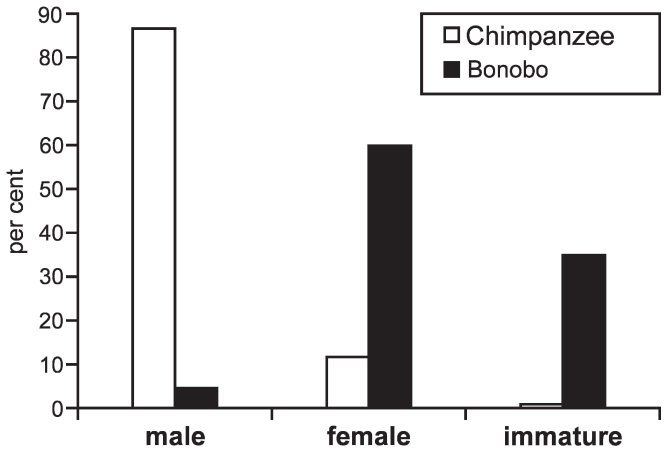

FIG. 1.4. Distribution of meat among chimpanzees and bonobos. Data of chimpanzees are from Taï forest, Ivory Coast, published by Boesch and Boesch-Achermann (2000, Table 8.4, p. 165). Data from bonobos are from Lomako, DRC, published by Fruth and Hohmann, 2002.

Fruth, 1996). Female prey owners share with other adult females and immatures, and both classes receive substantial shares from the prey (Fig. 1.4). Males also make efforts to get some meat but receive nothing or very little. In this regard, the bonobo model does not fit predictions: close relatives (males) do not cooperate in hunting and, although larger than females, are unable to obtain a share of meat. Instead, unrelated females cooperate in monopolizing the catch and divide the source with other females and immatures. Given the energetic demands of pregnancy, lactation, and infant transport on one hand, and the low cost of catching terrestrial prey, the gain from a portion of meat by females will certainly compensate for any costs deriving from catching and processing the food. Meat consumption by immatures seems to be mainly constrained by the toughness of meat and by the physical difficulties to remove meat from bones. Our observations from bonobos at Lomako and Lui Kotal suggest that independent of kinship, females may assist immatures by handing out or offering partly processed pieces of meat, and by fixing the carcass when immatures try to remove meat.

Inferences on the Feeding Behavior of Early Hominins: A Primate Perspective

The diet of any species depends on the types of resources that are available in the habitat at a given time. Analyzing lists of plant food species eaten by hominoids suggest that consumers take food from whatever plant taxa are available (Rodman, 2002). The picture changes immediately when variation in abundance of different plant species is taken into account. Data on diet composition such as those published by Rowe (1996) demonstrate that the time individuals allocate to feed on different food sources is skewed and that preferred foods are rarely the most abundant species. Distinctions between what is eaten and what is not are probably based on the nutritional quality, the density and distribution of resources, and food selection of other species with a similar diet.

In addition to selecting certain species, primates use various techniques of external food processing to modify food items in a way that is likely to enhance digestion. This allows exploiting items that are physically or chemically protected or dissecting items of very large size. Whether or not the food processing abilities of primates exceed those of other species remains to be explored, but the combination of dental features, functional morphology of hands and feet, and cognitive abilities provides a set of tools to improve the quality of what is ingested.

As in other vertebrates, food acquisition is mainly individualistic. However, in some species food sharing is habitual, and the mode of distribution may vary consistently between different species (Fig. 1.5). Data from chimpanzees show that food sharing mainly involves meat and that acquisition of meat does not only benefit the hunter, but also adult females. If food sharing has the potential to promote the reproductive

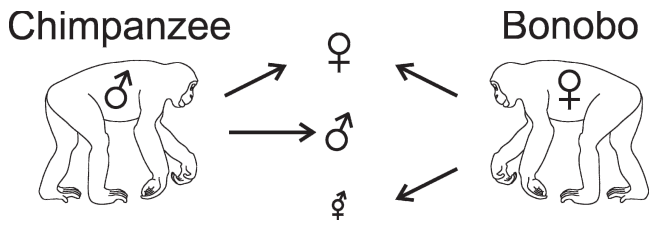

FIG. 1.5. Differences in ownership of divisible food and directions of food sharing in chimpanzees and bonobos. Arrows indicate the major trajectories of food transfer.

success of females, and if males share food preferentially with mating partners, the behavior has an immediate selective advantage in terms of reproductive performance. Bonobos add another component to the primate model: food is controlled by females and distributed to other females *and* to immatures. Food sharing involves large fruit and the meat of vertebrates. Provisioning is not a daily behavior and it is not known how critical it is for the survival of the young. Still, if the tendency to provision offspring varies between individuals – a question that needs to be explored – even modest differences in the nutrition of offspring could influence physical fitness and life history parameters.

Communal feeding, food sharing and provisioning are common practice in other mammals like social carnivores (Pusey and Packer, 1994; East and Hofer, 2002). Nevertheless, for good reasons it is assumed that these behaviors became prime movers during early stages of human evolution (Milton, 1999; O'Connell et al., 2002). Models such as the one proposed by Lovejoy (1981) assume that the behavioral suite of (a) hunting (or scavenging), (b) meat eating, and (c) food sharing emerged when hominins lived in dry habitats where plant food was often in short supply and where vertebrate prey was permanently or temporarily abundant. This implies that meat served as a fallback food during periods in which plant food was not abundant. However, evidence from recent studies of *Pan* differs from these assumptions. First, hunting and meat eating occurs equally in forests and in open habitats. Second, food sharing may have evolved independently of meat eating. Third, at least in some populations, hunting and meat consumption increase at times when plant food is highly abundant, suggesting that hunting activities are triggered by high energy intake from plant foods. The sources that provide high energetic rewards are usually the fruit of forest trees, and not roots and tubers. In sum, evidence from primate studies differs to some extent from predictions made in the models on human evolution. This is not to say that primate studies are irrelevant for modelling human evolution. What it suggests is that the common ancestor of *Pan* and *Homo* engaged already in food sharing, hunting, meat eating, and provisioning, and that this behavioral suite was later modified when populations of forest apes moved into open and dry areas. Communal attacks of other predators and the defense of stolen carcasses may have set the direction for a divergent development that gradually led into independence of subsistence on forest fruit.

Given the fact that hunting and meat sharing of chimpanzees is biased to red colobus, a forest species that does not occur in dry savannah habitat, and given the behavioral diversity of food sharing and provisioning within the genus *Pan*, there is room for refinement of existing models on hunting and meat eating in early hominins. Three topics, amongst others, are likely to provide useful hints: hunting of terrestrial prey, prey acquisition and food sharing by females, and scavenging by contemporary human populations.

Nonhuman primates are not an ideal model for reconstructing the evolution of a tribe that became extinct a couple of million years ago (Wrangham, 1987). Most species have adapted to niches that may not have existed before. However, nonhuman primates are the best model that we have. Moreover, primates offer a view on the behavioral ecology of species that are closely related to us, not only with their genes, but also in their ability to copy and transmit technical and behavioral innovations of others.

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2. The Energetics of Encephalization in Early Hominids

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Abstract Bioenergetics, the study of the use and transfer of energy, can provide important insights into the ecology and evolution of early hominids. Despite a relatively large brain with high metabolic demands, contemporary humans and other primates have resting metabolic rates (RMRs) that are similar to those of other mammals. As a result, a comparatively large proportion of their resting energy budget is spent on brain metabolism among humans (~20–25%) and other primates (~8–10%) compared to other mammals (~3–5%). To understand this shift in energy budget, Aiello and Wheeler's Expensive Tissue Hypothesis (ETH) posits a metabolic trade-off – a reduction in gut size with brain size increase – to explain this phenomenon. Here, we explore the interrelationships between brain size, body size, diet, and body composition using comparative data for humans, non-human primates, and other mammals. Among living primates, the relative proportion of energy allocated to brain metabolism is positively correlated with dietary quality. Contemporary humans fall at the positive end of this relationship, having both a high quality diet and a large brain. Thus, high costs associated with the large human brain are supported, in part, by energy-rich diets. Although contemporary humans display relatively small guts, primates as a group have gut sizes that are similar to non-primate mammals. In contrast, humans and other primates have significantly less skeletal muscle for their size compared to other mammals. These comparative analyses suggest that alterations in diet quality and body composition were necessary conditions for overcoming the constraints on encephalization. Fossil evidence indicates that brain expansion with the emergence of *Homo erectus* at about 1.8 million years ago was likely associated with important changes in diet, body composition, and body size.

Introduction

Bioenergetics, the study of the use and transfer of energy, can provide important insights into the ecology and evolution of early hominids. Energy dynamics represent a central interface between an organism and its environment; how

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