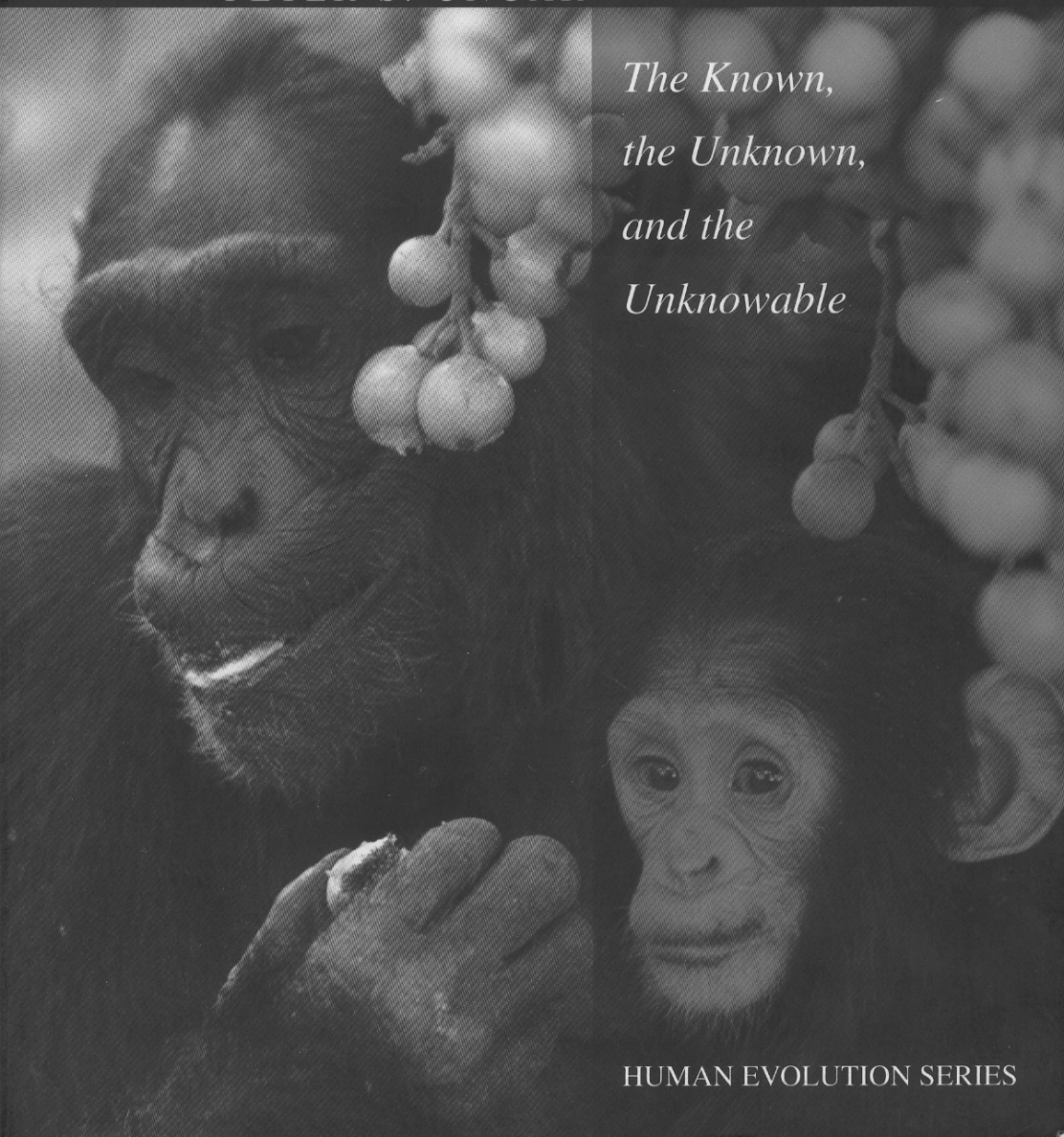


# Evolution of the Human Diet

EDITED BY PETER S. UNGAR

*The Known,  
the Unknown,  
and the  
Unknowable*

HUMAN EVOLUTION SERIES



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# Seasonality, Fallback Strategies, and Natural Selection

## *A Chimpanzee and Cercopithecoid Model for Interpreting the Evolution of Hominin Diet*

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JOANNA E. LAMBERT

### **Introduction: The Known, Unknown, and Unknowable**

*Natural selection, acting in various guises at various levels, seems together with genetic drift to account for almost all features of organisms once the appropriate raw material has arisen by mutation and recombination.*

—(Futuyma, 1979, p 438)

Within this evolutionary framework, we can reasonably assume that feeding-related features observed in extant primates should be, at least in theory, demonstrably the result of natural selection. It is the *demonstrable* aspect of this important assumption that those concerned with dietary adaptations in the present and in the evolutionary past must confront. In addition to information derived from morphology, it is a truism that scientists studying extant primates have the luxury of observing the function of diet-related anatomy via direct observation of a feeding animal, while those scientists evaluating fossil species do so in the absence of such data (Kay, 1984). Yet, both scientists confront a similar challenge, and in evolutionary terms yield comparably synchronic interpretations; the ghost of selection past haunts us all. Hence, our use of the powerful combination of comparative models, extant species analogs, and correlative evaluations as tools for interpreting changes in form and function over evolutionary time.

It is exceedingly doubtful that tropical habitats are, or ever have been, in any form of equilibrium (Maley, 1996; Newberry, Songwe, and Chuyong, 1998). Indeed, the most useful models for evaluating both plant and faunal adaptations are those that admit *disequilibrium* and environmental change, often as a function of

climate and rainfall (Newberry, Songwe, and Chuyong, 1998; Potts, 1998). From the perspective of a plant-eating animal, climate shifts and their impact on food resource availability and abundance vary in predictability. For example, longer-term (e.g., glaciation) or more extreme (e.g., monsoons) shifts are relatively unpredictable and can have important evolutionary consequences, particularly with regard to speciation and extinction (Foley, 1994; Vrba, 1995). Conversely, climate shifts can also be more predictable, especially in terms of rainfall seasonality. Indeed, while obfuscating myriad details of ecological specificity and variability, a shorthand reference to habitat type is commonly made in terms of habitats being either seasonal or nonseasonal as a function of broad patterns of latitude, land area, and, most importantly, rainfall (Rathcke and Lacey, 1985; van Schaik, Terborgh, and Wright, 1993; White, 1998a; references in Fleagle, Janson, and Reed, 1999). This dichotomy is realistically best viewed as being the two ends of a complex continuum of relative degrees and intensity of seasonality (e.g., strongly seasonal, less seasonal, etc.).

Evaluations of climate, seasonality, and concomitant shifts in food availability and abundance have been central to hypotheses regarding the origin and extinction of hominin species, as well as evaluations of hominin feeding-related adaptations (Foley, 1993; Vrba, 1995; Reed, 1997; Potts, 1998; Teaford and Ungar, 2000; Ungar, 2004). With regard to the latter, most models have historically evaluated form-function relationships in light of the frequency with which that animal exploits favored, preferred foods. Such categorization occurs with extant and extinct animals at both species (e.g., a species is a frugivore because it spends most of its time eating fruit; Chivers and Hladik, 1980) and community levels (e.g., percentage of total frugivory in a species community; Fleagle and Reed, 1996).

But foods are not created equally. Some are intrinsically more nutrient dense, while others less so, and either can differ in their chemical and mechanical defense. Extrinsic factors such as effect of season and habitat also influence a food's value to a consumer as they strongly influence overall and relative availability and abundance of that food (Oates, 1987; Janson and Chapman, 1999; Lambert, 2007). As such, species exhibit an array of behavioral and anatomical adaptations for exploiting foods that are of limiting importance during periods when other, either more nutrient dense, more abundant, or less-protected foods are scarce. This suggests differences in degree of natural selection pressure, and highlights an interpretation of anatomy that shifts the lens away from frequency to critical function (*sensu* Rosenberger and Kinzey, 1976; Rosenberger, 1992). That is, a traits' function is critical to the harvesting or ingestion of a particular resource (fallback foods); the crucial or "critical" aspect of this argument relates not to the overall utility of this feature for consuming a food type in high quantity or in high frequency, but that it instead has extreme utility under particular—limiting—environmental circumstances, during which time an animal must fall back on foods that are uncommonly consumed (Robinson and Wilson, 1998).

It is increasingly evident that understanding the use of fallback foods and the evolution of fallback strategies are key to understanding dietary adaptations, in both extant and extinct species, including those within our own lineage (Wrangham et al. 1999, Ungar, 2004; Laden and Wrangham, 2005; Ungar et al., 2006). However, researchers vary in their use of the term "fallback" and differentially focus on one or

another of the variables important to optimal feeding and foraging, including inherent energy yield of food (nutrient density), search time, and handling time (MacArthur and Pianka, 1966). In theory, an animal should exhibit preference for the most profitable (in terms of energy yield) foods, that is, foods that are nutrient dense, easy to find, and easy to access. Foods that are either less nutrient dense, harder to find, or more difficult to access are presumably less profitable and thus less preferred. As such, “fallback” is used variously as an indicator of food preference, as an index of fallback food availability, either in absolute abundance or relative to preferred foods, or to simply refer to the absolute inherent quality and nutrient density of the food (Gautier-Hion and Michaloud, 1989; Wrangham et al., 1996; Tutin et al., 1997; Yamakoshi, 1998; Wrangham et al., 1999; Gursky, 2000; Furuichi, Hashimoto, and Tashiro, 2001; Fox et al., 2004; Lambert et al., 2004; Ungar, 2004). Variability in how this term is used also often relates to habitat differences in food abundance and availability, which strongly influence search time (Malenky and Wrangham, 1994; White, 1998b; Furuichi, Hashimoto, and Tashiro, 2001; Laden and Wrangham, 2005).

My discussion is not novel in its evaluation of the importance of fallback foods. Rather, my purpose here is to refine our understanding of the types of fallback foods animals rely on during periods of potentially more intense selective pressure, and how these differences can relate to a species’ overall fallback strategy and evolution of feeding related traits. In this discussion, I place fallback *foods* into two broad categories that ultimately relate to different fallback *strategies*, including (i) fallback foods of lower nutritional density (lower inherent energy yield). These foods typically, although not always, comprise nonreproductive plant anatomy such as bark, leaves, petioles. Such foods often have the advantage of being more abundant (less search time); however, they inherently require more processing on the part of the animal (more handling time). It is in the use of these fallback foods where we tend to see anatomical adaptation (e.g., thicker dental enamel, longer molar shearing crests, longer digestive retention times); extant Cercopithecoidea and *Gorilla* spp. are good examples of this strategy.

Alternatively, (ii) fallback foods can be of higher nutritional density (greater inherent energy yield). These foods are commonly, although not exclusively, reproductive plant parts such as fruit and seeds. The advantage of these foods is that they can facilitate the maintenance of a high-energy-yield diet throughout the year. However, they often carry with them the disadvantages of being mechanically protected (longer handling time; e.g., palm nuts, termite mounds) and difficult to find (more search time). It is these foods where we may observe behavioral innovation and tool use for coping with seasonal shortages—*Pan troglodytes* and *Cebus* spp. are examples of such a strategy.

It should be noted that neither strategy precludes the other, so that, for example, species that use tools to access a high energy, but mechanically protected, food may also have thick dental enamel and a robust masticatory apparatus (e.g., *Cebus* spp.). This classification facilitates evaluation of differences between sites because food abundance and availability are heavily influenced by habitat and season; resource availability strongly influence search time, which, in turn, directly affects a food’s profitability (MacArthur and Pianka, 1966). With this framework in mind, my goals in this chapter are as follows:

1. To discuss how species relying on a plant-based diet in habitats that vary in their seasonality must evolve strategies to cope with periods of preferred food scarcity (*known*), and that this can result in the adoption of morphological and/or behavioral adaptations that facilitate the consumption of fallback foods which differ in chemical, mechanical, nutritional, and ecological properties (*known and knowable*).
2. To argue that the evolution of such strategies is influenced by the likelihood of an environment undergoing periods when food availability shifts (critical periods), and that environments differ in this regard as a function of latitude, altitude, rainfall and area—with some habitats being more inherently vulnerable (*known*).
3. To evaluate how Cercopithecoidea and African apes (*Gorilla* and *Pan* spp.) have adapted to consuming fallback foods. I suggest that cercopithecoids and gorillas have evolved a set of anatomical and physiological adaptations for facilitating a fallback strategy that relies on more abundant but lower-quality foods. Alternatively, *P. troglodytes* has evolved behavioral means by which to maintain key, higher-quality foods during such shortages. *Pan paniscus*, however, is distributed throughout relatively uniform, less-seasonal habitat, and a restricted geographical range; while we observe behavioral mechanisms in this species for reducing stress and intragroup competition over ripe fruit, critical periods are less extreme for this species than in monkeys, chimpanzees, and gorillas, and selection for adaptations for fallback foods relaxed.

### Anatomical and Physiological Solutions for Falling Back on Lower-Quality Foods

Although the myth of “stable forests” persists (Janson and Chapman, 1999), primates have evolved in inhospitable habitats, both in terms of availability of preferred resources, and the not unrelated facts that plants have evolved myriad chemical and mechanical mechanisms to protect themselves from plant predators. As such, there is ample evidence that primates are extremely selective feeders and consume only a fraction of the plant species available to them in a habitat (Oates, 1977, 1987; Glander, 1978; Milton, 1984). Selective-feeding behavior is also exhibited in terms of the times of day a primate will consume a given plant species (quantity/quality of toxins and antifeedants in a plant ebb and flow throughout the day), as well as which portions of the plant (e.g., leaf tips or petioles but not the entire leaf), and the total quantity of a particular plant food that is consumed (Glander, 1978; Struhsaker, 1978; Oates, 1987). In addition to behavioral adaptations, like all herbivorous animals, primates have also evolved anatomical and physiological solutions for dealing with plant defenses and fiber.

Periods of preferred food scarcity differ in duration and intensity as a function of habitat type and seasonality. During such periods, species have the option of switching to foods that are more abundant but may require more dental and digestive processing because they are either less nutrient dense, higher in secondary metabolites and/or fiber, or more mechanically defended. Alternatively, species can fall back on foods that are either difficult to find or that may be of less-nutrient density than most preferred items but do not influence the overall quality of diet because the profitability of that food is relative to other foods in an already high-quality diet. Examples of



Figure 17.1 *Lophocebus albigena* consuming *Ficus* fruit in Kibale National Park, Uganda. Photo courtesy of Alain Houle.

both strategies are found among primates. For example, Wrangham, Conklin-Brittain, and Hunt (1998) and Conklin-Brittain, Wrangham, and Hunt (1998) have demonstrated the different ways in which cercopithecines respond to periods of seasonal scarcity relative to sympatric *P. troglodytes* in Kibale National Park, Uganda. While the monkeys tended to fall back on foods that were higher in digestion inhibitors and toxins, in this study, the chimpanzee fallback food (pith) did not significantly negatively influence their overall high-quality diet in terms of fiber or secondary metabolites. While pith of different plant species differs, they are overall higher than leaves in more readily digested fiber fractions (hemicellulose; Wrangham et al., 1991; Conklin-Brittain, Wrangham, and Smith, 2002). In addition, these authors found that chimpanzees maintained more ripe fruit throughout the year than did the cercopithecines and did not consume more fiber. Since *P. troglodytes* is roughly an order of magnitude larger than the monkeys, these were unexpected results based on body size predictions.

Primates that fall back on foods that differ from preferred or more commonly consumed foods in their chemical, mechanical, nutritional, and ecological characteristics are expected to evolve solutions (anatomical, physiological, behavioral) to the particular challenges presented by those fallback foods. For example, *Lophocebus albigena* (fig. 17.1) has among the thickest dental enamel in the order Primates, and thick enamel is generally argued to have been selected for (at some point in the evolutionary past) because of its function in facilitating the frequent consumption of hard foods (Kay, 1981; Dumont, 1995; Teaford, Maas, and Simons, 1996). Lambert et al. (2004) evaluated the hardness of foods consumed by *L. albigena* and sympatric *Cercopithecus ascanius* during a dry El Niño season in the Kibale National Park, Uganda (1997). During the study period, ripe fruit and other preferred, softer, and



more commonly consumed foods were unavailable to these two species. The study animals instead consumed fallback foods, which were not only different in form and type, but also hardness. We found no difference in dietary hardness when the puncture resistance of all fruit (over 1991–1997) consumed by the two species was compared. However, when the hardness of only fallback foods (1997) was evaluated, *L. albigena* exploited a diet with greater resistant to puncture and crushing than *C. ascanius*. This difference was largely explained by the higher percentage of bark and seeds consumed by the *L. albigena* during this period. The diet of these two species can have high overlap, and *L. albigena* can be highly frugivorous; however, *L. albigena* fall back on very hard foods, while the guenon increases leaf intake. Bark is a highly lignified and particularly hard resource, and these results corroborate the hypothesis that it is not so much what is consumed most commonly (i.e., soft, fleshy fruit) that selects for enamel thickness but the hardness of foods that are consumed during critical periods, when other more preferred foods are not available.

Like many primates, including chimpanzees, lowland gorillas overall show a preference for ripe, soft fruit (Remis, 1997; Remis et al., 2001). Nishihara (1995), for example, has found that western lowland gorillas (*Gorilla gorilla gorilla*) spend 63% of their feeding time on fruit. And, in a recent review that included data from all long-term western lowland gorilla sites, Rogers et al. (2004) documented that these apes will maintain fruit in their diet throughout the year; the authors indeed call *G. gorilla gorilla* “fruit pursuers, with strong preferences for particular and often rare fruit species, for which they will incur significant foraging costs” (p 175). However, as noted by Ungar (2004), the dietary differences between gorillas and chimpanzees become most apparent in analyses of their fallback foods, such that during periods of preferred fruit scarcity, gorillas will tend to fall back on tougher, more fibrous foods than those consumed by chimpanzees. Rogers et al. (1994), for example, argue that the bark of *Milicia excelsa* is an important fallback resource for *G. gorilla gorilla* in Lope Reserve, Gabon, during seasons of low fruit availability. Ungar (2004) argues that it is the key differences in the mechanical properties of the fallback foods that can account for the longer shearing crests and steeper cusps in gorillas and flatter molar surfaces in chimpanzees.

Gorillas are argued to be able to consume their lower-quality fallback foods as a consequence of the aforementioned dental adaptations, as well as a high number of cellulose digesting ciliates and overall body size, which facilitates the slower digestive processing required for fermenting fiber (Demment and van Soest, 1983; Collet et al., 1984; Remis et al., 2001).

But, cercopithecoids do not have the body size advantage of gorillas. In addition to the case study of thick dental enamel in *Lophocebus*, are there other anatomical and/or physiological solutions that can be identified? The degree to which fiber (nonsoluble structural carbohydrates) of plant cell walls can be used as an energy source depends in part on the length of time that these components are retained in the fermenting chamber(s) of the gastrointestinal tract. Longer digestive retention times result in higher levels of fermentation, and many plant parts require considerable fermentation before they are useful as an energy source (Milton, 1981, 1984; 1986; 1993; Lambert, 1998; Remis, 2000). It has long been presumed that smaller mammals have (both absolutely and relatively) faster food passage rates than larger species, which limits their capacity to ferment fibrous plant components (Parra,

1978; Kay, 1985; Cork and Foley, 1991; Kay and Davies, 1994; Van Soest, 1994). Yet, as it turns out, both cercopithecoid subfamilies have relatively longer digestive retention times than the much larger African apes (Lambert, 2002a). This is to be expected among the Colobinae, who have specialized, sacculated, and alkaline stomachs for consuming a diet high in fiber. On average, their mean digestive retention times range from roughly 40 to 60 h (refs in Lambert, 1998; Caton, 1999). Neither cercopithecines nor hominoids exhibit such derived stomach anatomy (Chivers and Hladik, 1980; Milton, 1987). Yet, in an analysis regressing digestive retention times as a function of body size, Lambert (1998) found that the cercopithecines in the analysis were significantly further above the regression line than any other primate taxon. Indeed, despite being on average an order of magnitude smaller than African apes, all tested cercopithecines do exhibit mean digestive retention times averaging 31 h (*P. troglodytes*: 31.5–48 h; *Gorilla gorilla*: 36.5–61.9 h) (Milton and Demment, 1988; Maisels, 1993; Lambert, 1998, 2002a; Remis, 2000). These digestive results have important implications for understanding how monkeys can consume either similar or greater levels of fiber than larger-bodied apes and rely on higher-fiber fallback foods during critical periods (Lambert, 2002a).

In addition to fiber, cercopithecoid fallback foods are often higher in toxins than those consumed by *Pan* (Wrangham, Conklin-Brittain, and Hunt, 1998) and must be detoxified either by microbial activity in a specialized stomach or microsomal enzymes activated in the liver (Freeland and Janzen, 1974). Although we know extremely little about microbial detoxification in colobines, the potential of the specialized stomach with a diverse and dense microbial community to act as a detoxification chamber has been demonstrated in ruminating ungulates (Keeler et al., 1978; Waterman and Kool, 1994). All noncolobine primates rely not on bacterial activity, but on microsomal enzymes (Freeland and Janzen, 1974), the production of which scales allometrically. Walker (1978) has demonstrated that rates of enzymatic activity scale negatively with mammal body size (Walker, 1978; Freeland, 1991). Freeland (1991) thus suggests that smaller mammals are at an advantage for detoxifying plant secondary metabolites and that the larger the mammal, the greater the preference for foods with low amounts of toxic plant metabolites. Cercopithecines, on average, are smaller than apes, which may facilitate their consumption of chemically defended plants not available to apes, and only available to colobines as a consequence of their specialized stomach.

Thus, cercopithecoids deal with the higher fiber and defenses of their fallback foods via dental and digestive adaptations. These adaptations for consuming less-nutrient dense foods as a fallback strategy may well have evolved at some time in the mid- to late Miocene. Most explanations for the evolutionary success of Cercopithecoidea (over apes) suggest that they adopted a more efficient strategy in competing for increasingly rare resources (Andrews, 1981; Temerin and Cant, 1983). The actual mechanisms of how these monkeys accomplished this have received less attention, although I have argued elsewhere that a combination of long retention times and digestive flexibility, a capacity to detoxify plant compounds (either by bacteria in the case of colobines, or microsomal enzymes in the case of cercopithecines), uriposia, and cheek pouches (which in cercopithecines facilitates fast harvesting) gave monkeys a competitive edge over ape counterparts in allowing them access to lower-quality food resources. These anatomical and physiological

mechanisms facilitate access to a set of fallback foods not consumed by apes that are more abundantly distributed in a habitat and also less vulnerable (say, than fruiting phenology) to climate perturbations (Lambert, 1997, 2000, 2002a, 2002b, 2005; Lambert et. al., 2004; Lambert and Whitham, 2001). Smaller body size (along with its associated faster life history strategies and shorter generation times) is also correlated with greater potential for speciosity (Cowlshaw and Dunbar, 2000).

### Maintaining Higher-Quality Foods during Critical Periods

Rather than switching to alternative, lower-quality foods, other species exhibit adaptations for coping with environmental fluctuations and scarcity of preferred food types by evolving behavioral mechanisms to maintain particular foods in the diet throughout the year regardless of their availability. *Pan troglodytes* stand out as an excellent example of such a strategy (fig. 17.2). Although their colon is proportionately larger than what is seen in *Homo sapiens*, chimpanzees have digestive retention times that are comparable to those of humans and, contrary to what might be predicted for their body size, consume an unexpectedly high-quality diet (Milton, 1999). Behavioral adaptations (e.g., fission-fusion social structure) that facilitate the maintenance of ripe fruit in the diet throughout the year, in addition to tool use, which can facilitate the consumption of foods that are high in nutrient density (but often mechanically protected), are behaviors that are key to their fallback strategy. For example, several authors (Chapman, White, and Wrangham, 1994; Wrangham et al., 1996) have demonstrated the correlation between fruit availability and the fissioning-fusing of chimpanzee feeding-party size; essentially as fruit becomes



Figure 17.2 *Pan troglodytes* consuming *Ficus* fruit in Kibale National Park, Uganda. Photo courtesy of Alain Houle.

scarce, feeding parties become smaller, and animals will increase day range to maintain fruit in the diet. In this way, the total yield of a food consumed during seasonal scarcity is influenced by the cost of searching time but not that of handling and processing time.

So, given that a foraging primates' diet comprises some number of foods, some of which are more profitable than others, when does it make sense for an animal to add the next most profitable item, with profit in this case influenced by handling time, rather than search time? It is under these circumstances where we observe the use of feeding-related tool use that facilitate consumption of resources that are mechanically protected (which increases handling time) but that have the potential to yield high amounts of energy (e.g., termite mounds, hard nuts; McGrew, 1992). Chimpanzees will use a variety of tools regardless of overall food availability (Whiten et al., 1999), but of interest here is what the selective advantage for this behavior was in the first place. Procuring requisite nutrients and calories is critical to the survival of every animal, with more successful foragers assumed to have greater fitness. At some point, costs incurred from increasing day range, regardless of party-size fissioning, will outweigh the benefits from consuming that food. The balance of this equation will vary by habitat, season, and rainfall and hence potential for selective pressure. For example, the chimpanzee (*P. troglodytes*) community at Bossou, Guinea, lives in a seasonal habitat characterized by low rainfall, low resource availability, and high seasonality of fruit availability (Yamkoshi, 1998). This forest is also isolated and discontinuous from other forest fragments; this essentially means that the chimpanzees are unable to expand their day and home range in search of readily accessed high-quality foods. Chimpanzees in this forest employ a number of feeding-related tools, including hammer and anvil, pestle pounding, and ant dipping. Most important, tool use in these chimpanzees facilitates the consumption of two important, nutrient-dense fallback resources: oil palm nuts and palm pith. Both resources are mechanically protected and cannot be exploited without the use of tools (Yamkoshi, 1998). During periods of extreme resource scarcity, nut cracking and pestle pounding for pith increase dramatically, providing critically needed calories from lipids and carbohydrates.

Such observations suggest that fission-fusion and foraging-related tool use can serve critical functions and are advantageous during critical periods when more profitable and preferred foods are not available. In the case of tool use, cognitive function is a necessary precursor, suggesting that in these cases, the critical, limiting habitats in which chimpanzees found themselves resulted in a situation that promoted innovation of these behaviors. Indeed, while he did not discuss critical function or fallback foods, Potts (2004) has recently proposed a "fruit-habitat hypothesis" that suggests the evolution of the relatively very large brains of great apes and their concomitant cognitive capacity, can be explained by a "causal connection between ape ancestral diets, habitats, and environmental history" (p. 224). In short, he argues that as preferred fruit resources became increasingly rare as a function of forest reductions and climatic shifts in the African Miocene, ancestral apes were under extreme selective pressure for evolving cognitive means (e.g., complex mental representational ability) to deal with food source uncertainty.

Although not directly related to diet and feeding, the recent observation (Pruetz, 2005) of cave use by western populations of *P. troglodytes* living in the hottest, most

extreme habitat of its range, fits this same pattern of behavioral innovation under extreme environmental circumstances. Chimpanzees living in very dry areas will also dig drinking holes, or wells (Matsuzawa, 2002). These behaviors represent behavioral solutions to intense selective pressure that is more likely to occur in seasonal habitats. These examples pose a critical question: Can we use our understanding of fallback strategies in apes and Cercopithecoidea to explain the evolution of feeding related adaptations in *Pan* spp.—and by analogy and extrapolation—early hominins?

### The Role of Critical Function and Environmental Shifts in *Pan* spp. Adaptations

I turn now to the oft-cited differences between our two closest living relatives: *P. troglodytes* and *Pan paniscus*. Despite glossing over myriad details and decades of research, it is evident with regard to the discussion of feeding-related adaptations and the environment, these two species differ in their: (1) total species distribution, (2) total range in their use of habitat types, and (3) proclivity for tool use and composition of toolkit.

Habitats differ in their patterning of rainfall and its impact on seasonal availability of foods; this not only has extreme effects on habitat carrying capacity but also, as argued, on the degree of potential for periods of intense selection as a consequence of environmental fluctuations. Indeed, Potts (1998) has evaluated the impact of variable selection in widely fluctuating circumstances on hominin evolution. He suggests that the environmental circumstances in which hominins evolved were particularly inconsistent, with episodic and extensive change in vegetation, water, and other resources. Habitats are on a continuum, as are species distribution with regard to habitat types, with habitats at the periphery of a species' distribution tending to be more challenging from the animal's perspective; it is indeed at the edges of species distributions where we see most evolution (Cowlshaw and Dunbar, 2000). Of the two *Pan* species, *P. troglodytes* is by far the more widely distributed—in discontinuous populations from East to West Africa, north of the Congo River. This wide distribution across much of equatorial Africa encompasses a diversity of habitat types, including less seasonal wet lowland forest; relatively more seasonal habitats, such as moist montane forest, savanna, and gallery forest; and highly seasonal, arid, and open woodland (fig. 17.3).

*Pan paniscus*, conversely, lives in a much smaller region south of the Congo River, with a distribution that is delineated on all sides by rivers. Increasing total species distribution is not an option for this species as its movement is impeded by the presence of large, impassable rivers (Eriksson et al., 2004). This region is characterized as being relatively undisturbed, lowland, climax-moist forest and is commonly commented on as being markedly less seasonal than the habitats used by *P. troglodytes* (Malenky, 1990; Foley, 1993; White, 1998b; Doran et al., 2002). Overall, the bonobo is argued to live in habitats where food resources are spatially and temporally more abundant than those of common chimpanzees (Malenky and Wrangham, 1994; Thompson, 2003). For example, in a comparison of *P. troglodytes* in Kibale National Park, Uganda, and *P. paniscus* in Lomako, Democratic Republic of Congo, White

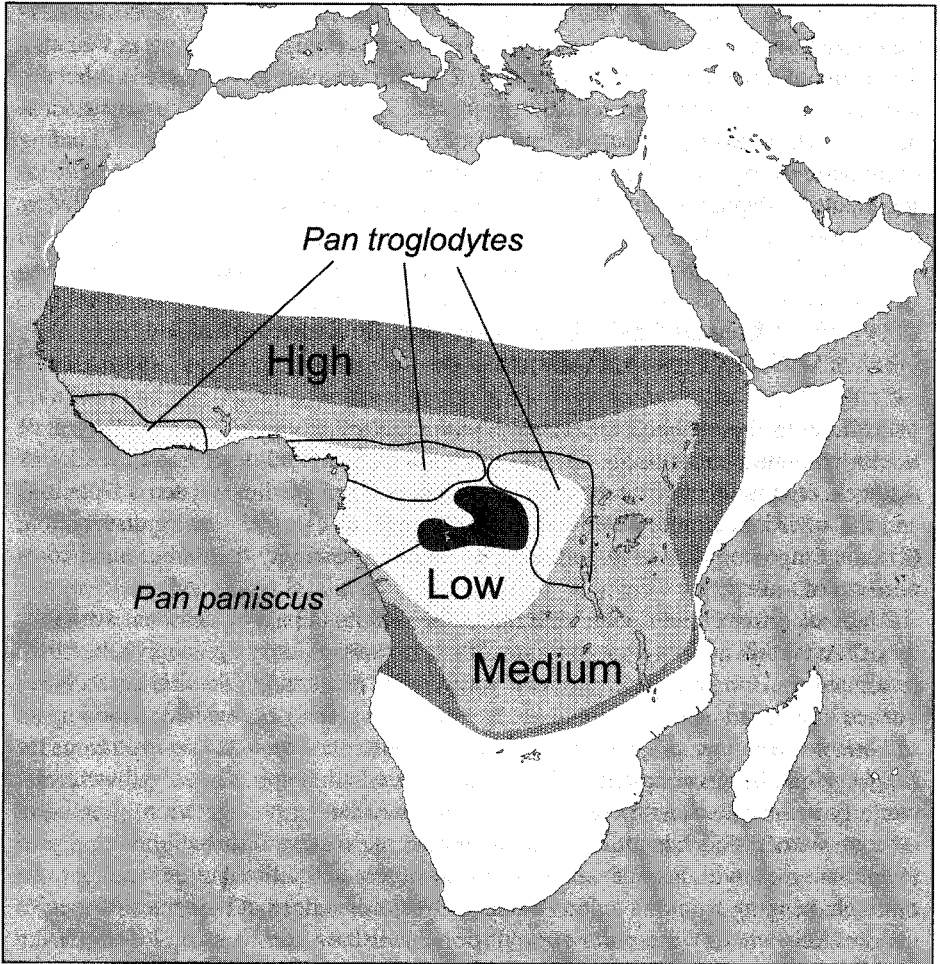


Figure 17.3. Map of Africa, indicating: (i) patterns (low, medium, high) of rainfall seasonality and (ii) geographic distribution of *Pan paniscus* and *Pan troglodytes*.

(1998b) suggests “there is more variation in food and distribution for *P. troglodytes* than is experienced by *P. paniscus*, suggesting that it is the level of variation in food availability rather than the absolute amount that is the critical difference selecting for differences in social organization in these two species” (p 38).

*Pan troglodytes* can be found in habitats at the other extreme of the seasonality continuum: in savanna woodland habitats in both Eastern and Western regions of the continent. These habitats differ in many respects from the moist forests of the Congo Basin. Indeed, relative to the forests in Democratic Republic of Congo, savanna woodland is drier with more seasonal rainfall patterns, has xeric-adapted plant species with hard-shelled seed or nuts and underground storage organs, and has more patchily distributed preferred resources as a function of greater seasonality (Moore, 1996).

The common chimpanzee is also well known for its diverse toolkit, while feeding-related tool use in wild populations of *P. paniscus* has not been reported (Boesch, Hohmann, and Marchant, 2002; McGrew, 1992). Are these facts related? Moreover, can we use this information to interpret patterns in early hominins and the stimuli for tool use? We have entered the world of the unknown, but are still—potentially—within the realm of the knowable. Jim Moore (1996, p. 275) writes: “many a great ape grant proposal has waxed on about insights that the proposed research would provide into the behavioral ecology of our early ancestors, and the term ‘model’ is ubiquitous in the resulting literature.” It is difficult to not fall into this trap, but my primary point here is not so much using these two *Pan* species as a model of what may or may not have happened some millions of years ago but, instead, to consider the evolution of particular traits as a function of periods of food scarcity when animals need to rely on less-profitable resources. Specifically, I am referring to interpreting the evolution of behaviors as a response to critical periods (more seasonal habitats) and, which, in the case of *P. troglodytes*, resulted in a fallback strategy that facilitated the maintenance of foods that are nutrient dense, despite being mechanically defended.

The most common explanation of speciation imputes a disruption of gene flow by geographical isolation of a previously panmictic population into two or more disparate population, thus allowing for the accumulation of change and divergence into separate species (Futuyama, 1979; Eriksson et al., 2004). One of the most striking examples of this is the distribution of *Pan paniscus* and *Pan troglodytes*. My model, evolutionary scenario, analog—whatever one wants to name it suggests the following:

1. Some ancestral proto-*Pan* population was isolated by changes in the course of the Congo River—this is not a new argument and is well supported by genetic and biogeographic evidence (Bradley and Vigilent, 2002; Thompson, 2002, 2003).
2. Early *P. troglodytes* was able to increase its range through equatorial Africa, while *P. paniscus* was not because of the numerous large impassable rivers—again these are not new arguments and are well-supported aspects of *Pan* spp. biogeography (Thompson, 2002, 2003; Eriksson et al., 2004).
3. As the distribution of *P. troglodytes* expanded across equatorial Africa, this species encountered increasingly more seasonal and unpredictable environments, and, with increasing seasonality, came increased potential for disruptive critical periods of intense selective pressure. Innovative behaviors in early *P. troglodytes* were selected for because of their utility during these critical times for maintaining a diet that was relatively high in quality.

It is part 3 of this argument that is potentially of interest to paleoanthropologists, as it arrives at the question of why *P. troglodytes* uses tools, while *P. paniscus* does not. Ancestral and extant populations of *P. paniscus* occupy a restricted, relatively less seasonal habitat, suggesting that this species is less likely to be presented with critical periods resulting in either fallback strategy; although, given the inherently more labile nature of behavior over, say, evolution of dental traits, it might be expected that on those occasions where food may be limiting, behavioral solutions might arise. In the case of *P. troglodytes*, concomitant to range expansion came an increasing likelihood of critical periods. But, why not adopt a fallback strategy that

relies on more abundant albeit lower-quality foods, which is seen in Cercopithecoidea? Indeed, the body size of *P. troglodytes* would predict such a strategy, and yet the opposite is true: Despite their smaller size, Cercopithecoidea are generalist, eclectic feeders with an array of anatomical and physiological adaptations (dental, digestive, enzymatic, etc.) for consuming high-fiber plant foods replete with toxins that are not tolerated by sympatric chimpanzees. This suggests that as *P. troglodytes* expanded its ranges into increasingly seasonal habitat, the trophic space that included consumption of lower-quality food was occupied by monkeys who were simply better at it and had been since at least the end of the Miocene. No room at the inn. Gorillas, with their absolutely larger body size, proportionately larger and more ciliated gut, and higher molar-shearing blades and cusps, could use higher-fiber foods than common chimpanzees. Thus, selection on *Pan troglodytes* resulted in another strategy, namely, behavioral strategies for shifting feeding-party size and using feeding-related tools.

It is of note that the genus *Cebus* is known both for its tool use in the wild and has a relatively unspecialized digestive strategy. Relative to similarly sized cercopithecoids, capuchins have fast digestive times, which limits their ability to ferment fiber. For example, *Cebus apella*, weighing only 3.5 kg, has a transit time (TT) of 3.5 h, while *Cercopithecus pogonias* and *Cercopithecus ascanius* have species average weights of 3.75 kg and 3.6 kg, respectively, and have TT of 16.6 and 19.7 h (Milton, 1984; Maisels, 1993; Lambert, 1998, 2002a). At the same time, capuchins have been demonstrated to use tools to facilitate access to resources during periods when preferred foods were not available. Moura and Lee (2004) argue that “energy bottlenecks” create contexts for capuchins (*C. apella*) to derive benefits from tool technology. In the Caatinga dry forest of northeastern Brazil, capuchins have been observed to commonly use tools and do so during the extended dry season of this region. During such times, the resources that are available without tool use are not sufficient for nutritional requirements and the capuchins forage terrestrially. Several tools and tool-facilitated behaviors have been found in four habituated capuchin groups foraging in these areas, including digging for tubers with stones, cracking open seeds and branches with stones, breaking tubers with stones, and using stones as hammers in combination with wooden anvils to crack seeds. These monkeys consume forty-one plant species as food; tool use increases the use of at least three of these species. The researchers argue that *Cebus* foraging for embedded and mechanically defended resources in habitats that experience energy bottlenecks is facilitated by innovative tool use (Moura and Lee, 2004). A similar argument is made for *C. apella* in another dry region of Brazil, where capuchins commonly use hammer-and-anvil technology to crack nuts during the dry season when preferred resources are scarce (Fragaszy et al., 2004).

This chimpanzee model is directly testable by observing the behavior of *P. paniscus* in its most southern limit of its extant distribution, which is described as “transitional grassland habitat” (Thompson, 2003). This southern region is characterized by different soils and a marked seasonal distribution of rainfall. *Pan paniscus* are known to move through and feed in these areas. At least three grassland species have been consumed by *P. paniscus*, and there are behavioral correlates of being in a different habitat type, too, including no vocalizations (Thompson, 2003). It is exactly in this inherently more seasonal and less-predictable



habitat where we might observe innovative solutions related to feeding on foods during crunch times.

### Conclusions and Implications: Using What We Know

*Pan paniscus* has classically received less attention in reconstructions of early hominin behavior for exactly the reason that I employ it here: it is distributed in much less seasonal habitats than those are associated with early hominin sites (Moore, 1996; Hunt and McGrew, 2002). Foley (1993) argued that hominin origins are closely linked to the development of increasingly seasonal conditions; he also argues that differences among African ape species were driven by the degree to which their ancestral and extant environments are seasonal and differences in the selection for traits for dealing with food scarcity in more seasonal habitats. He purposely ruled out *P. paniscus* in his evaluation because this species is found in less-seasonal habitats. He instead applied data from *P. troglodytes* day range, time spent feeding, and feeding party size to an understanding of early hominin behavior and adaptations.

I suggest that the *P. troglodytes*–*P. paniscus* comparison, along with knowledge of cercopithecoid and gorilla feeding, can lend insight into the evolution of behavioral solutions to facilitate a fallback strategy on relatively high-quality foods. By analogy from this comparison, as early hominins expanded into increasingly seasonal habitats, the potential for critical periods of selection increased as well. We cannot observe behavior in the past (the unknown) directly, but we can document fine details of climate via ever increasingly sophisticated archaeological and geological methods, and we can use models derived from nonhuman primate models, which can illuminate the timing and rate of natural selection pressure on feeding adaptations. Moreover, we can evaluate distribution patterns and the degree to which habitats are marginal. *Pan troglodytes* occupy habitat that can have upward of five to seven dry (rainfall <100 mm) months/annum; *Australopithecus afarensis* has been found in habitats that probably had even more dry months (Foley, 1993; see Reed and Rector, chapter 14, in this volume). This suggests extreme potential for critical periods, which may select either for adaptations to lower-quality foods or adaptations for innovative behaviors—such as flexibly sized feeding parties and tool use—that maintain a higher-quality diet or some combination of both. As suggested earlier, it is not necessarily an either-or situation, and neither strategy precludes the other. *Cebus* spp., for example, have both thick dental enamel for exploiting hard foods, as well as tools to access high-quality, but protected fallback foods.

With regard to hominin diet and adaptations, Scott et al. (2005) have recently argued that there is greater dietary overlap and variability in *Paranthropus* and *Australopithecus* than previously thought. They indeed suggest “early hominin diet differences might relate more to microhabitat, seasonality, or fallback food choice than to oversimplified, dichotomous food preferences” (Scott et al., 2005, p. 694). I agree, but I would add another degree of complexity: there are differences among both fallback *foods* and, more importantly, overall fallback *strategies*. On the basis of the above framework, we can envisage a continuum of fallback strategies: at one

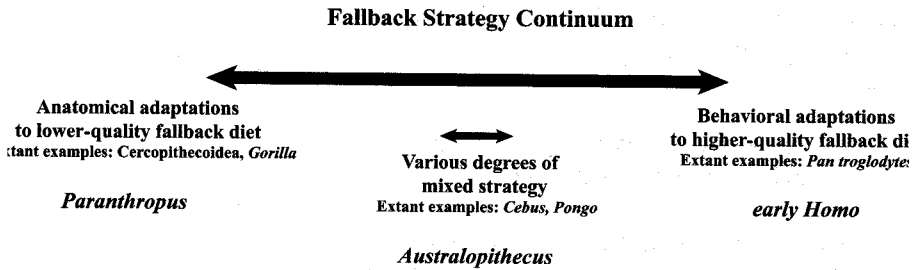


Figure 17.4 Graphic depicting the continuum of fallback strategies observed in extant primates, with implications for interpreting hominin diet-related adaptations.

end, we see the evolution of *anatomy* to exploit *lower-quality* (less nutritionally dense) foods; at the other end, we see evolution of *behavioral* mechanisms for maintaining *higher-quality* foods, with various degrees of a mixed strategy in between (fig. 17.4). Only in relatively aseasonal habitats like that of *P. paniscus* would we see relaxed selection for fallback strategies. We know that the evolution of hominin species is closely related to increasing seasonality, so some fallback strategy at a point along this continuum is expected. In the case of a comparative *Paranthropus*, *Australopithecus*, early *Homo* evaluation, we might expect, based on anatomy alone, for *Paranthropus* to be at one end of the continuum, early *Homo* at the other, and *Australopithecus* somewhere between the two.

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