12 *Energetic responses to food availability in the great apes: implications for hominin evolution*

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Introduction

The past 40 years of great-ape field research have seen the accumulation of a wealth of data that can be used to make predictions about the behavior of early hominins. We have only just begun, however, to undertake great-ape field studies that incorporate a physiological component in the wild. Understanding how the energetic and reproductive systems of living hominoids respond to environmental variation allows us to build more informed models with which to reconstruct the behavior, morphology, and responses to ecological pressures that were present in great-ape and human ancestors.

Fruit is the favored, although not always the most common, food of the great apes, and all ape populations that rely on fruit experience fluctuations in its availability. Given the importance of fruit in ape diets, such fluctuations are likely to have a major impact on these animals' biology and behavior. The primary goal of this chapter is to discuss how differences in overall fruit availability and fallback foods play a central role in shaping energetic and reproductive responses of the great apes, and then to examine the implications of this for hominin evolution.

A review of the literature reveals that relatively few studies present quantitative data on changes in diet or energetics over time. Descriptions are more likely to be statements about how diet or behavior changes in response to fluctuations in food availability. Thus, a secondary aim is to suggest ways in which data from both previous and future research can be presented in order to facilitate truly comparative studies of food availability and energetics.

Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates, ed. Diane K. Brockman and Carel P. van Schaik. Published by Cambridge University Press.

Fluctuations in fruit availability: continental differences

Despite popular misconceptions, the rainforests of the world do not produce a constant cornucopia of fruit. The availability of food, especially fruit, fluctuates in all tropical forests where apes live. However, the extent and severity of fluctuations experienced by different species and populations vary. There appear to be some fundamental differences in forest fruit production patterns that may have affected ape evolution in each region.

In Southeast Asian forests, three major features characterize the pattern of fruiting. First, there are dramatic supra-annual peaks in fruit availability (Medway 1972; Appanah 1985; van Schaik 1986) known as mast fruitings. Many forests in this region are dominated by trees in the Dipterocarpaceae family, which is distinguished by its unusual reproductive pattern. Triggered by climatic events, these trees fruit and flower on an irregular basis, once every two to ten years (Ashton *et al.* 1988). They are joined by other tree families, resulting in a phenomenon in which more than 90% of trees produce fruit during these "mast" fruiting events (Medway 1972; Appanah 1981; van Schaik 1986). This provides an overabundance of fruit for animals, such as orangutans, during these periods. Second, Dipterocarpaceae dominance means that a significant portion of the plant biomass is non-reproductive during most years, lowering baseline fruit productivity. Appanah (1985) demonstrated that this results in lower overall productivity of these forests, meaning that they can support substantially less animal biomass than do other tropical rainforests. Due to the concentration of plant reproductive effort during masts, these synchronized fruiting events are often followed by long periods of low fruit availability (Appanah 1985). Third, these supra-annual peaks, and the subsequent extended low-fruit periods, are irregular and unpredictable (Ashton *et al.* 1988).

African forests do not experience this kind of unpredictable community-wide mast fruiting (see Chapter 2). Instead, the predominant pattern of fluctuation in fruit availability is within-year seasonal variation in response to the more pronounced wet and dry seasons compared with Southeast Asia. Fruit availability, of course, also varies from year to year in Africa, but as pointed out in Chapter 2, the pattern is one of more constant higher fruit production with occasional bust years compared with the opposite pattern of generally low fruit production with occasional boom years in Southeast Asia.

Thus, while annual and supra-annual variation in fruit production does occur in African forests, the interannual variation in fruit production is significantly greater in Asia compared with the other tropical regions (see Chapter 2). It is not only that the mast fruitings provide such a superabundance of fruits when they occur, but also that the intervening periods of low fruit availability often tend to be much longer and more severe than those in Africa. Fleming *et al.* (1987) conclude that this fruiting pattern in Southeast Asia leads to forests in which fruit availability is more temporally and spatially patchy than in other tropical forests. Another important continental difference may be that African apes have higher-quality fallback foods to rely on during low-fruit periods, as discussed later in this chapter. This could temper the effects of low-fruit periods on apes in Africa. These differences between continents may help us to understand some of the unique features of orangutans compared with the African apes and may be particularly important for understanding reproductive patterning (van Schaik & van Noordwijk 1985; Knott 1999, 2001).

Energetic adaptations to fruit availability

Fluctuations in the availability of fruit are important because of the responses that they may elicit in their consumers (see also Chapter 3). Given that the focus here is on the energetic and physiological ramifications of such fluctuations, we can predict a number of energetically sensitive responses. Many factors are involved, including the magnitude and duration of the period of fruit scarcity or abundance, the availability of fallback foods, the social structure, and physiological adaptations and limitations. The quality, in addition to the quantity, of the food, is also important. If less fruit is available but it is of higher quality, then foraging time may not need to increase to maintain dietary adequacy. Below is a survey of the responses that have been observed in great apes, focusing particularly on energetic shifts and then moving on to reproductive ramifications.

Changes in diet composition and energy intake, and the impact of fallback foods

Most ape populations incorporate a high percentage of fruit in their diet when it is available. The fruits that are preferred, however, vary between species. Chimpanzees prefer succulent fruit (Wrangham 1977; Basabose 2002). Orangutans also show a high preference for succulent fruit (Leighton 1993), but they particularly value energy-rich fruits and thus may prefer lipid-dense seeds over succulent fruits if they are higher in calories. Another contrast is that Western lowland gorillas always seem to incorporate large amounts of foliage in their diet, even when sympatric chimpanzees are eating an entirely frugivorous diet (Tutin *et al.* 1991).

When preferred fruit is scarce, apes incorporate fallback foods into their diet. Fallback foods are those that are permanently or frequently available but usually are ignored (Tutin *et al.* 1991) (see also Chapter 3). For apes, such foods include leaves, pith, terrestrial herbaceous vegetation (THV), bark, some insects, and less preferred fruits such as figs (see Table 12.1). These fallback foods are normally lower in quality than preferred foods, being more fibrous (Knott 1998; Tutin *et al.* 1991; Doran *et al.* 2002), lower in carbohydrates (Knott 1998), and/or lower in lipid (Knott 1998). Staple foods are those that are frequently available but form a more regular part of the diet and are adequate nutritionally to allow the animal to subsist on them. In some cases, a food may be a staple, such as figs at particular sites, but also may be used as a fallback food.

It is important to note that some ape populations show little reliance on fallback foods, especially when there is a high herbaceous component to the diet. In particular, mountain gorilla diet does not vary significantly over time, except for increased bamboo eating by some groups when new shoots are put out (Watts 1984, 1998). Bonobos at Lomako (White 1998) do not show significant differences between months in their time spent feeding on fruits, figs, pith, leaves and flowers, and meat. Thus, despite fluctuations in fruit availability, bonobos do not appear to need to rely on certain foods as fallback resources. Taï chimpanzees also seem to be well buffered against seasonality because they have a more diverse set of high-quality preferred foods, including nuts (Boesch & Boesch-Achermann 2000). However, Doran (1997) found that when fruit abundance was unusually poor, Taï chimpanzees showed similar responses to those seen in east African populations.

Data on dietary composition, however, provide limited information on variation in the quality of the diet. We need nutritional analyses of the foods eaten to be able to report quantitatively on differences and assess their significance. This work has been done at a small number of ape study sites. Dietary quality (or, the amount of energy that a diet provides, and how easily it can be extracted) is measured by the relative percentages of nutrients in the diet, with high-quality diets being low in fiber and high in carbohydrates and lipids (Conklin-Brittain *et al.* 1998; Knott 1998).

Complete macronutrient analysis of the diet has been done for chimpanzees (Conklin-Britain *et al.* 1998) and for orangutans (Knott 1998, 1999). Two gorilla studies (Rogers *et al.* 1990; Remis *et al.* 2001) and one

Table 12.1 *Fallback foods eaten by great apes*

Species/study site	Fruits (including seeds)	Leaves and Stems	Pith	Bark	Insects
Orangutans					
Borneo					
Gunung Palung, Indonesia	Some figs	Yes	Yes	Yes	Yes
Kutai, Indonesia	Figs important	Yes	Yes	Yes	Sometimes
Tanjung Putting, Indonesia	No (figs rare)	Yes	Yes	Yes	Yes
Ulu Segama, Malaysia	Some figs	Yes	Yes	Yes	Sometimes
Sumatra					
Ketambe, Indonesia	Figs important	Yes	–	Yes	Yes
Gorillas					
Mountain gorillas					
Karisoke, Rwanda	No fallback foods used	–	–	–	–
Lowland gorillas					
Bai Hokou, CAR	*Duboscia*	Yes	Yes	Yes	No
Lopé, Gabon	Fibrous fruit *Duboscia*	*Zingiberaceae* *Marantaceae*	Yes	Yes	No
Mondika, CAR and/or RC	*Duboscia, Tetrapleura tetraptwra Klainedoxa*	Yes	Yes	Yes	No
Ndoki, Congo	*Duboscia*, figs	Yes	Yes	Yes	No
Kahuzi-Biega, DRC	No fallback foods	–	–	–	–
Bonobos					
Lomako, DRC	No fallback foods used	No	No	No	No
Wamba, DRC	None	Yes	Yes	–	No
Yalosidi, DRC		Yes (stems, shoots, sedges)	Yes	–	No
Chimpanzees					
East Africa					
Budongo, Uganda	Figs eaten as staple – no period of scarcity seen				

Table 12.1 (*cont.*)

Species/study site	Fruits (including seeds)	Leaves and Stems	Pith	Bark	Insects
Gombe, Tanzania	–	Yes	Oil-palm pith Some THV	–	–
Kalinzu, Uganda	*Musanga leo-errerae* Figs eaten as staple	Some	No THV eaten as staple	No	–
Kanyawara, Uganda	Figs	No	Yes (THV)	No	–
Mahale, Tanzania	–	Yes	–	Yes	–
Central Africa					
Ipassa, Gabon	–	Yes	Yes	Yes	Yes
Kahuzi-Biega, DRC	Figs eaten as staple	Yes (herbaceous)	Yes (THV)	No	Yes
Lopé, Gabon	*Duboscia macrocarpa* *Elaeis guineensis*	*Zingiberaceae* *Marantaceae*	Yes	Yes	Yes
Ndoki, Congo	*Duboscia*, *Ficus*	Yes	No	No	No
West Africa					
Bossou, Guinea	*Musanga cecropioides* Oil-palm (*Elaeis guineensis*) nuts	No	Oil-palm pith	Yes	No
Taï, Ivory Coast	Fibrous fruit, *Duboscia viridifolia, Klainedox gabonensis*	Yes	–	–	–

CAR, Central African Republic; DRC, Democratic Republic of Congo; RC, Republic of Congo; THV, terrestrial herbaceous vegtation.

References: Bai Hokou (Goldsmith 1999; Remis *et al.* 2001); Bossou (Yamakoshi 1998; Sugiyama & Koman 1992); Budongo (Newton-Fisher 1999; Newton-Fisher *et al.* 2000); Gombe (Wrangham 1977; Hladik 1977; Goodall 1986); Gunung Palung (Knott 1998, 1999); Ipassa (Hladik 1977); Kahuzi-Biega, chimpanzees (Basabose 2002); gorillas (Goodall 1977); Kalinzu (Furuichi *et al.* 2001); Karisoke (Fossey & Harcourt 1977; Vedder 1984; Watts 1984, 1988, 1998); Kanyawara (Wrangham *et al.* 1991, 1993, 1996; Conklin-Brittain *et al.* 1998); Ketambe (Sugardjito *et al.* 1987; Rijksen 1978; Utami 2000); Kutai (Rodman 1977; Leighton 1993); Lopé (Tutin *et al.* 1991; Tutin & Fernandez 1993; Rogers *et al.* 1990; Williamson *et al.* 1990); Lomako (Badrian *et al.* 1981; Badrian & Malenky 1984; White 1998); Mahale (Nishida 1974); Mondika (Doran *et al.* 2002); Ndoki (Nishihara 1995; Kuroda *et al.*

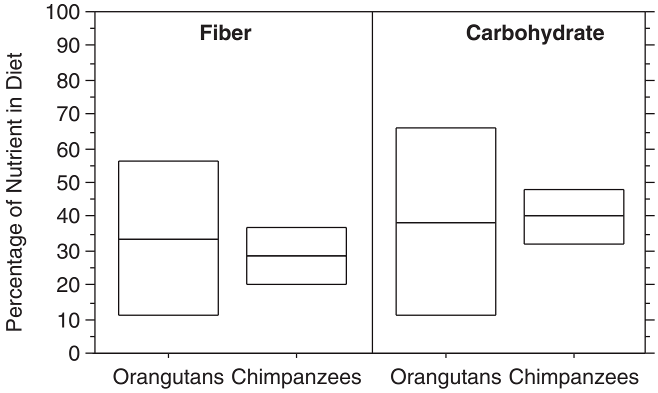

Figure 12.1 Box-plot comparisons of range and mean of percentages of fiber and carbohydrate in the diet of Gunung Palung orangutans (Knott 1999) and Kanyawara chimpanzees (Conklin-Brittain *et al.* 1998).

other orangutan study (Hamilton & Galdikas 1994) have examined some of the macronutrients but not seasonal differences. For chimpanzees at Kanyawara, ripe fruit availability was associated with a significant increase in consumption of lipid, free simple sugars, and total non-structural carbohydrates. Protein content of the diet did not vary seasonally. Of the fiber portion of the diet, neutral detergent fiber (NDF) did not vary significantly over the year. During the high-fruit period, the orangutan diet was significantly higher in lipid and carbohydrate and lower in fiber (NDF) compared with in the low-fruit period. Similar to the diet of chimpanzees, protein content did not significantly vary.

Thus, the general nutrient composition of the diet changes in similar ways in these two ape populations. However, the degree of variability in nutrient composition differs between the Kanyawara chimpanzees and the Gunung Palung orangutans. The percentage of carbohydrate and fiber showed a much wider range of variation in the orangutans (Fig. 12.1). Thus, compared with chimpanzees, orangutans ate a much higher-quality diet during some months and a lower-quality diet during other months. Calorific intake has been extrapolated for orangutans, and the data show a dramatic response, with as much as five times the calories consumed during the high-fruit period compared with in the fruit-poor period (Knott 1998, 1999). It is unknown whether chimpanzees do the same and, if so, to what extent.

Thus, the nature of the fallback food helps explain energetic differences between orangutans and chimpanzees. In this case, the calorific content of the fallback foods and the severity and length of the fruit-shortage period are particularly important. Wrangham *et al.* (1991) show that chimpanzees in Kanyawara, and at many other sites, rely on THV or pith as an importantfallback food. Pith appears to be a calorie-rich fallback food resource (Wrangham *et al.* 1991). Orangutans do consume pith, but this is not a prime backup food; instead, leaves and bark are the most important during fruit-scarce periods. These foods have about half the calories, and are much higher in fiber and lower in carbohydrate, than their preferred foods (Knott 1998). It may be that the greater availability of pith in African rainforests is an important difference between the two ape habitats, allowing chimpanzees to enjoy the energetic benefits of a better fallback food.

Energy expenditure and energy balance

Studies of the relationship between primate diet and foraging effort suggest that primates that eat high-energy foods with high spatiotemporal patchiness, such as fruit, have longer day ranges than do primates that eat more evenly distributed low-quality foods, such as leaves (Milton & May 1976; Clutton-Brock & Harvey 1977). Thus, we would predict that when diets become more folivorous, apes would decrease their range use, and this does appear, in general, to be the case. Goldsmith (1999) found that Western lowland gorillas responded to decreasing fruit availability by increasing their consumption of leaves, stems, and bark and by decreasing daily path length. Orangutans also conformed to this pattern (Galdikas 1979; Knott 1999). At Gunung Palung, male orangutans significantly decreased their travel time, and both sexes decreased their day range during the period of lowest fruit availability (Knott 1999). This was possible because they shifted to a more folivorous and evenly distributed diet during the fruit-poor period. When fruits are scarce, male chimpanzees also reduce their range size (Wrangham 1977). When food was plentiful, chimpanzee females at Mahale increased their day range (Hasegawa 1990). During the months with highest fruit production, Taï chimpanzees ranged the farthest, whereas they ranged the least during the month of highest *Coula* nut production (Boesch & Boesch-Achermann 2000) and during periods of particular fruit scarcity or when figs with large fruit crops were fruiting (Doran 1997).

How does general activity level, as opposed to travel, respond to changes in food availability? Surprisingly, this has been little studied in apes. Doran (1997) examined the question in chimpanzees at Taï and found that these apes spent more time feeding during the period of fruit scarcity. Data from our study of wild orangutans (Knott 1998, 1999) show that orangutans expended more calories during the fruit-rich period. This is explained by a significant increase in calorific expenditure due to travel. Conversely, relying on more abundant leaves and bark and shortening their day range were effective energy-conservation strategies for orangutans during fruit-poor periods.

Energy balance is the difference between energy intake and energy expenditure and indicates whether energy intake during a given period is adequate to meet an organism's needs. Weight data on chimpanzees from Mahale and Gombe show that these animals lose weight when fruit is scarce (Wrangham 1977; Uehara & Nishida 1987), although provisioning may have affected these observations. No weight data are available for wild gorillas or orangutans.

Ketones, excreted in urine, are produced when an organism is metabolizing its own fat deposits in order to meet its energy needs. Chimpanzee researchers at Kanyawara (Wrangham, unpublished data) and Mahale (Huffman, unpublished data) have never detected systematic ketone production. While chimpanzees in these forests are likely experiencing decreases in energetic status during fruit-poor periods, it appears that their energy deficits do not reach the "starvation level" indicated by ketosis. In contrast, during months of severe fruit shortage, ketones do appear in a large proportion of orangutan urine samples at Gunung Palung (Knott 1998). They are totally absent during periods of high fruit availability. These results indicate that during fruit-poor periods, orangutans are metabolizing their fat reserves to make up for insufficient energy intake. However, because the presence of ketones is indicative of starvation, they are unlikely to reveal small weight losses and it is noteworthy that we have not detected ketones during less severe periods of fruit shortage.

When kilocalories consumed were compared with those expended in orangutans, the mast fruiting was shown to lead to a daily calorific intake that exceeded energy requirements by several thousand calories (Knott 1999). This excess indicates that the orangutans were gaining weight during these periods. Correspondingly, during this period, energy balance was negative, indicating that the orangutans were losing weight, a conclusion supported independently by the ketone analyses.

Reproductive responses to energetic status

We know from the considerable body of work on human reproduction (e.g. see Ellison *et al.* [1993]) that human ovarian function is best understood within an ecological context in which female reproductive hormones respond to changes in nutritional intake, energy expenditure, and energy balance. Explicit studies of primate reproductive ecology are only just beginning (Ellison 2001), but these suggest that the same factors are important in understanding non-human primate, and particularly ape, reproductive functioning as well (Bentley 1999; Knott 2001).

Like humans, apes have long interbirth intervals and exhibit high investment in single offspring. Furthermore, because of the unpredictability of fruit resources, apes such as the orangutan cannot time their births to coincide with peaks of fruit availability. Thus, Knott (2001) has argued that apes have evolved, as did humans, to time reproduction so that conception is more likely during periods of positive energy balance. Van Schaik & van Noordwijk (1985) make the argument that non-seasonally breeding primates, such as great apes, should time reproduction to coincide with periods of high food availability in order to store reserves that can be drawn on later during pregnancy. As suggested by Ellison (1990), if the initiation of reproduction during a state of positive energy balance is associated with improved reproductive outcome, then it should be favored by natural selection. Thus, we should expect female reproductive physiology in the apes to be influenced strongly by energetic factors resulting from fluctuations in food availability. This is in contrast to many seasonally breeding monkeys, where increased food supply is tied to the season of lactation rather than conception (Van Schaik & van Noordwijk 1985; Lindburg 1987).

Evidence of this ecological influence on reproductive timing – the "Ecological Energetics Hypothesis" – is mounting (Knott 1999, 2001) (see Table 12.2) (see also Knott [2001] for a discussion of alternative hypotheses). At Gunung Palung, Knott (1999) found that estrone conjugate (E1C) levels in orangutan urine were significantly lower during the fruit-poor period as opposed to the mast fruiting period. Additionally, matings occurred only during the high-fruit period. This suggests that orangutans responded to the low-fruit period physiologically as well as behaviorally by not investing in reproduction. In captivity, Masters and Markham (1991) showed that E1C levels in orangutans are also associated with energy balance. As in humans, orangutans appear to modulate the probability of conception so that it will be more likely to occur when there are sufficient energy reserves for gestation and lactation.

Several lines of evidence suggest that nutrition is also an important factor in regulating chimpanzee reproduction. First, chimpanzees in captivity – where, presumably, access to energy is more than adequate at all times – that are allowed to keep their babies with them have dramatically shorter interbirth intervals, earlier age at menarche, and earlier age at first birth compared with their wild counterparts (Tutin 1994) (reviewed in

Table 12.2 *Reproductive and ovarian responses to changes in fruit availability from sites where data are available.*

Species and site	Ovarian response: Fruit-rich period	Ovarian response: Fruit-poor period	Other responses associated with fruit/food availability
Orangutans			
Gunung Palung, Indonesia	Higher estrone conjugates All conceptions	Lower estrone conjugates No conceptions	
Tanjung Putting, Indonesia	More conceptions		
Gorillas			
Karisoke, Rwanda	None	None	
Chimpanzees			
Gombe, Tanzania	Increased overall conceptions All postpartum conceptions First full swellings in adolescents Maximal swelling in cycling females Resumption of cycling after weaning Peak number of swellings		High-ranking females with access to best foraging areas reach sexual maturity sooner, and have higher offspring survival, higher annual production of offspring, and shorter interbirth intervals
Kanyawara, Uganda	Increased conceptions		
Mahale, Tanzania	First postpartum swelling One conception peak (of two)		

References: Gombe (Tutin 1975; Goodall 1986; Wallis 1995, 1997; Pusey *et al.* 1997); Gunung Palung (Knott 1999, 2001); Karisoke (Watts 1998); Kanyawara (Sherry 2002); Mahale (Nishida *et al.* 1990); Tanjung Putting (Galdikas 1979, 1988).
Fruit availability was not measured directly at Gombe and Mahale.

Knott [2001]). Second, Wallis (1997) points out in her review of reproductive parameters from chimpanzees at Gombe that the individuals with the shortest interbirth intervals were all descendants of Flo. These family members were the most frequent visitors to the banana feeding station and Wallis speculates that they may have received better nourishment. Additionally, Pusey *et al.* (1997) show that Flo and her family occupied the most productive home range in Gombe.

Finally, seasonality in conceptions has also been reported at Gombe, with the majority of conceptions occurring during the dry season, which is associated with higher fruit availability (Wallis 1997), a finding that Wallis (1997) speculates may have been due to changes in diet. Sherry (2002) (reviewed in Chapter 13) has shown a significant relationship between increased food supply and conception in Kanyawara chimpanzees.

The influence of energetic status on reproduction in gorillas is less clear. Gorillas in captivity often have problems reproducing, and thus any influence of the improved energetic status of captivity on reproduction is obscured. Mountain gorillas have been studied most extensively, but they do not show seasonality in their reproductive parameters, which is not surprising given their unusually stable food supply. Mountain gorillas may maintain reasonably good energetic status year round and thus be reproducing at their full potential (Knott 2001). Future studies of lowland gorillas that focus on the relationship between energetics and reproduction in more seasonal environments should help to clarify this.

Summary of energetic and reproductive responses

The review presented above indicates that the nature of the food supply is one of the key variables determining the energetic and reproductive responses of the great apes to fluctuations in food abundance. Thus, if sufficient variables are considered, then apes can be seen to respond in logical and predictable ways to changes in the food supply. In evaluating why energetic and reproductive responses may differ between ape species and populations, several key conclusions can be drawn: (i) the temporal availability, distribution, and patch size of preferred and fallback foods play a critical role in ranging and grouping patterns; (ii) the calorific content of the diet during high-fruit periods is critical in determining overall energetic adequacy as well as the ability to store excess energy; (iii) the nutritional value of the fallback foods and the efficiency with which nutrients can be extracted from them determine the extent to which energy is suboptimal during fruit-poor periods; (iv) the proportion of the diet that is made up of fallback foods influences the extent to which the fallback diet will be adequate; and (v) the length and severity of the period during which fallback foods are relied upon plays a key role in determining the nature and extent of physiological responses. The energetic responses elicited by apes to these conditions range from modifying ranging patterns and activity budgets to selecting superior fallback foods to storing up energy as fat and then catabolizing it. The reproductive responses mirror the severity of the energy deficits that the population experiences, with interbirth intervals growing as populations experience longer and more extreme periods of scarcity.

Comparison of the Bossou chimpanzees with other east African chimpanzees is particularly illustrative of these points. The three fallback foods eaten by chimpanzees at Bossou – Musanga fruits, oil palm nuts and pith – appear to be very calorie-rich (Hladik 1977; Yamakoshi 1998). Bossou chimpanzees also have much smaller home ranges and thus can, presumably, meet their calorific requirements while expending much less on travel. Thus, the nature of the Bossou food supply, and the animals' ability to access very high-quality fallback foods, means that they should be able to maintain a particularly favorable energy balance compared with other chimp populations. This very high energetic status is also correlated with the shortest interbirth interval of any chimpanzee population and is consistent with the "ecological energetics" model of primate reproductive ecology (Knott 2001).

At the other end of the spectrum sit orangutans, whose fallback foods are so energy-poor that ketonic starvation is sometimes widespread in a population. The energetic inadequacy of the fallback resources, coupled with the temporal extent of fruit scarcity, is such that these apes have had to evolve, or at least call in to action, other physiological responses to weather such crises. Their ability to store fat during seasons of abundance and then catabolize these stores is essential to their survival. The other important part of this physiological response lies in the fact that the fruit-rich periods allow excess energy consumption; orangutans spend more time feeding than would be predicted just to satisfy their subsistence needs (Knott 1999). This extreme variability in the food supply experienced by orangutans is also associated with the longest interbirth interval of the primates (Galdikas & Wood 1990; Knott 2001) (see also Table 12.3).

Table 12.3 compares the general relationships between fallback foods, energetics, and reproduction in ape populations. The contrast between orangutan and African ape populations is striking. Whereas orangutans, in general, increase their feeding time when fruit is abundant, the opposite finding or more complex results often are reported for chimpanzee and gorilla populations. Orangutans seem to be taking advantage of periods of high fruit abundance to eat as much as possible and put on fat reserves. This is necessitated by the irregular nature of the fruiting peaks, the long periods of very low food availability, and their need to rely on very low-quality fallback foods. Gorillas and chimpanzees, in contrast, may sometimes decrease time spent feeding when fruit, or other preferred food, is abundant. For example, Watts (1988) shows that gorillas at Karioske

Table 12.3 *Relative fallback food quality with energetic responses and associated interbirth intervals*

Species/study site	Quality of fallback foods	Total time feeding		Daily distance traveled		Interbirth Interval (years).
		High fruit	Low fruit	High fruit	Low fruit	
Orangutans						
Borneo						
Gunung Palung, Indonesia	Poor	Increase	Decrease	Increase	Decrease	7.0
Kutai, Indonesia	Poor	Increase (variable)	Decrease (variable)	Increase variable	–	–
Tanjung Puting, Indonesia	Poor	Increase	Decrease	–	Decrease	7.7
Ulu Segama, Malaysia	Poor	Increase	Decrease	–	–	–
Sumatra						
Ketambe, Indonesia	Poor	Increase[a]	Decrease[a]	Decrease[a]	Increase[a]	8.6
West Langkat, Indonesia	–	–	Decrease	–	Increase	–
Gorillas						
Mountain gorillas						
Karisoke, Rwanda	None	Decrease (when bamboo shoots abundant)	–	Decrease (when bamboo shoots abundant)	–	3.9
Lowland gorillas						
Bai Hokou, CAR	Good	–	–	–	Decrease	–
Kahuzi-Biega, DRC	None	–	–	Increase (when eating *Myrianthus holstii*)	Decrease (when bamboo shoots abundant)	–
Lopé, Gabon	Good	–	–	Increase	Decrease	–
Mondika, CAR and RC	Good	–	–	Increase (prediction)	Decrease (prediction)	–
Bonobos						
Lomako, DRC	Good/excellent	–	–	–	–	8.0
Wamba, DRC	Good/excellent	–	–	–	–	4.5

Chimpanzees						
East Africa						
Budongo, Uganda	None	–	–	–	–	–
Gombe, Tanzania	Good	Increase when fruit high and low; decrease when intermediate (data from males)		Increase	Decrease	5.5
Kanyawara, Uganda	Good	No relationship with time spent eating non-fig fruit[c]		–	–	6.2
Mahale, Tanzania	Good	–	–	Increase (females)	Decrease (females)	6.0
West Africa						
Bossou, Guinea	Excellent	Increase	Decrease	–	–	5.1
Taï, Ivory Coast	Excellent	Decrease	Increase	Increase (except when eating *Coula* nuts or large fig crops)	Decrease	5.8

CAR, Central African Republic; DRC, Democratic Republic of Congo; RC, Republic of Congo.

References: Bai Hokou (Goldsmith 1999; Remis *et al.* 2001); Bossou: (Yamakoshi 1998; Sugiyama & Koman 1992); Budongo (Newton-Fisher 1999); Gombe (Wrangham 1977; Goodall 1986); Gunung Palung: (Knott 1998, 1999); Kanyawara (Wrangham *et al.* 1991, 1993, 1996; Conklin-Brittain *et al.* 1998); Karisoke (Vedder 1984; Watts 1984, 1988); Ketambe (Utami 2000; van Schaik 1986; te Boekhorst *et al.* 1990); Kahuzi-Biega (Goodall 1977); Kutai (Rodman 1977; Mitani & Rodman 1979); Lomako (Badrian *et al.* 1981; Badrian & Malenky 1984; White 1998); Lopé (Tutin 1996; Tutin *et al.* 1991; Tutin & Fernandez 1993; Tutin 1996; Rogers *et al.* 1990; Williamson *et al.* 1990); Mahale (Hasegawa 1990; Nishida 1974); Mondika (Doran *et al.* 2002); Taï (Doran 1997; Boesch & Boesch-Achermann 2000); Tanjung Putting (Galdikas 1979, 1988); Ulu Segama (MacKinnon 1971, 1974); Wamba (Kuroda 1979; Kano 1992); West Langkat (MacKinnon 1974). Reproductive parameters from Knott 2001. Relative fruit variability and quality of fallback foods are based on a qualitative cross-site comparison of authors' reports.

[a] Flanged and unflanged males; no data from females;

[b] Fruth unpublished data;

[c] Wrangham personal communication.

decreased total time spent feeding in areas where food abundance was high because they were able to satisfy their subsistence needs quickly.

Why would not all apes eat as much as they possibly can when preferred food is abundant? This has not been measured directly for most populations, but we would predict that all apes likely *do* increase their calorific intake when fruit (or preferred food) is abundant, even if they decrease total time spent feeding. But, there are tradeoffs between eating and other activities that animals can engage in. More time spent feeding means less time for mating, grooming, hunting, fighting, and other social activities. Goodall (1986), for example, reports that party size, competition for estrus females, and patrol activities tend to decrease the time spent feeding for chimpanzees at Gombe. Costs such as toxin load and limitations on gut and digestive capacity also must be figured in. Thus, how long an animal should keep eating beyond the point when it has met its daily energetic needs may depend largely on the probability that its energetic requirements can be met readily in the future. If fruit availability is unpredictable, if fruit scarce seasons can extend for many months, and if fallback foods are inadequate or too low in nutritional quality to survive on for the long term, then an increase in maximization of energy intake, such as that seen in orangutans, makes sense. In contrast, if the availability and distribution of food are fairly consistent and predictable, such as observed in mountain gorillas, then we would not expect huge increases in feeding time during food-rich periods. Large-scale differences in the patterning of resource availability between continents may indeed have selected for some of the differences in feeding behavior seen between the Asian and African apes.

A second major finding from this review is that in most ape populations, daily travel distance is increased when fruit availability is high and decreased during fruit-poor periods. However, this is not the case when high-fruit periods are associated with especially dense or concentrated resources that do not require much travel. For example, travel distance in Taï chimpanzees is decreased when eating rich Coula nuts and when feeding in very large fig crops (Boesch & Boesch-Achermann 2000; Doran 1997). This also may be the explanation for the decrease in travel during high-fruit periods at Ketambe, where huge fig trees form an important part of the diet (Sugardjito *et al.* 1987; Utami *et al.* 1997).

Several additional factors may obscure the above relationships in some ape populations. Party composition in chimpanzees has been shown to fluctuate with resource distribution (Chapman *et al.* 1995). Thus, chimpanzees can use their fission–fusion social behavior to cope with varying resource conditions and may not need to modify other energetic variables. Doran *et al.* *(*2002) predict that lowland gorillas should modify their group composition based on resource distribution. Second, Goodall (1986) has shown that differences in processing times between different foods are a major determinant of time spent feeding for Gombe chimpanzees. This may be particularly important in ape populations that habitually use tools. Third, competing social factors may influence energetic variables (Goodall 1986). Additionally, a high-versus-low-fruit comparison may be too simplistic at many sites. The temporal and spatial distribution of food, the size of food patches, and the calorific and nutrient content of preferred and fallback foods may not co-vary in the same way between different periods. This is well described for lowland gorillas at Mondika by Doran *et al.* (2002), who divided the year into three distinct periods based on the size, density, and distribution of gorillas foods and predicted differences in ranging and group cohesion based on these differences.

Interbirth intervals also appear to be associated with the degree of fruit fluctuation and the quality of the fallback foods. Orangutans have the longest interbirth intervals, and the data reviewed above suggest that this may be linked to very high variability and unpredictability in fruit production, long periods of low fruit availability due to mast fruiting, and a lack of high-quality fallback foods during these periods. The extent to which conceptions at a given site are concentrated during fruit-rich periods also may prove to be determined by the degree of dietary fluctuation.

Our ability to assess energetic variables in comparable units across sites will make significant progress towards explaining interpopulation and interspecies variation. The importance of continuing long-term studies of individual populations is clear, as data sets will need to be analyzed over multiyear periods to capture the range of supra-annual variation experienced at each site.

Recommendations for comparative studies

This review reveals that our ability to make direct quantitative comparisons of ape food availability between sites is limited due to a lack of comparable data. There are a number of reasons for this. First, ape field studies normally are carried out by primatologists or anthropologists who are not trained botanists or plant ecologists. Thus, the plant phenological component of a study is usually a supplement to the main behavioral data collected and, given limited funds, it is often not feasible to gather the depth of botanical and phenological information needed to make studies comparable. Secondly, tropical rainforest plant communities are extremely complex. To identify and monitor all species eaten by apes within a single locale may not be feasible. This is particularly true of Southeast Asia rainforests, where one study site can have thousands of tree species. The unfortunate consequence of these factors is that although it is now routine practice to gather phenological data, those data usually are only relative measures that can be used to demonstrate fluctuations in fruit availability at a single locale but do not provide quantitative data necessary for comparisons between sites. Although relative measures tell us how apes in a particular population are responding, comparisons among sites and between ape species are essential for understanding the differences observed.

A literal "common currency" of fruit availability is needed to compare between sites. Such a measure needs to take into account not only the quantity but also the quality (value) of fruit available at a given time. We suggest that *kilocalories of ape fruit available/hectare* could be such a comparative measure. To calculate this, we need to be able to do the following: (i) identify accurately the species eaten using long-term data; (ii) monitor the fruiting pattern of a representative sample of fruit species eaten by apes; (iii) count or estimate the absolute crop size of monitored trees as they fruit; (iv) determine the density of each of the species eaten within the home range(s) of the apes in question; (v) weigh each fruit type to determine the grams/fruit; and (vi) analyze the nutrient and calorific content of the fruits that are eaten. This would allow us to compare directly the temporal variability and the quality of ape fruits. Other factors such as patch size, distances between patches, toxin levels, foraging efficiency, and digestibility also could be factored in, but the above comparison would be a good first step.

Finally, it is important that researchers do not use "wet" or "dry" seasons as proxies for fruit availability, since fruit production is not associated consistently with one or another of these seasons but varies markedly from site to site (see Chapter 2). Rainfall may have no relationship to fruit abundance, as White (1998) found at Lomako. Year-to-year variation may be such that "dry-season" months in one year may have more rain than "wet-season" months in other years (White 1998).

Additionally, great potential exists for future studies of reproductive ecology in the apes and other primates. Most of the existing data were not gathered with this question in mind and thus do not have the precision needed to address this issue fully. In particular, we need more studies that examine the calorific content of the diet and its effect on reproductive hormones. Quantitative changes in food supply, or a simple dry season/wet season analysis, may not be a precise enough indication of the actual energetic intake that we expect reproductive physiology to respond to.

Ovarian function needs to be compared with actual feeding behavior, ideally calorific intake, to properly gauge the effect of nutritional status on reproductive functioning. Future analysis of data on seasonal fluctuations in phenology, calorific intake, energetic patterns, and reproduction should yield further insight into these relationships among the apes.

Implications for hominin evolution

Changes in environmental conditions have been proposed as catalyzing agents during critical junctures of human evolution (Vrba 1985a, 1985b, 1989; Rogers *et al.* 1994). Environmental fluctuations have become more and more extreme since the Miocene Epach (Potts 1998). Starting at six million years ago, deep-sea cores reveal an isotopic record of oxygen enrichment, indicating a marked global cooling trend with accompanied drying (deMenocal 1995). This general trend, however, is characterized by a two- to threefold increase in the degree of environmental fluctuations during the period of most recent hominin evolution (Potts 1998). The most extreme climatic oscillations seem to have occurred around 2.5, 1.7, and 1.0 Ma (deMenocal 1995; deMenocal & Bloemendal 1995). The implication of this is that early hominins probably experienced increasingly dramatic seasonal fluctuations in food availability. Using our knowledge from great apes, we can now look at the adaptations of early hominins in light of the energetic challenges that such seasonality would have posed.

Dental microwear studies suggest that fruits represented a significant component of the australopithecine diet (Teaford *et al.* 2002). The importance of fruit likely varied from site to site and through time, but, with the possible exception of *Paranthropus*, the austrolipithecine-grade hominins appear to have relied heavily on fruit and therefore would have been faced with very real energetic challenges as the availability of these resources became more patchy in both time and space. Thus, the fallback foods of these hominins would have played a central role in shaping these species' adaptations and evolution.

The dental anatomy of the australopithecines suggests that their fallback foods were significantly harder, tougher, or more gritty than fruit (Teaford *et al.* 2002). These hominins show a consistent and increasingly marked posterior megadontia accompanied by thickened molar enamel. The exact nature of the foods to which these teeth were designed has been the subject of considerable debate in the literature and remains enigmatic. However, it seems unlikely that these fallback resources were the same as those exploited by extant apes, since the thickened enamel and large flat molar crowns displayed by these hominins are very different from the thinner-enameled, more sharply cusped molars of the living apes. There is increasing evidence that underground storage organs (USOs), such as roots, tubers, and rhizomes, may have been selected as fallback foods by australopithecines and paranthopines (Hatley & Kappelman 1980; Wrangham *et al.* 1999; Conklin-Brittain *et al.* 2002). Interestingly, Conklin-Brittain *et al.* (2002) argue that the substitution of USOs for THV and other ape piths as fallback foods would have substantially increased the overall quality of the hominin diet over that of the chimpanzee's. Energetically, if early hominins did indeed adopt a more calorifically adequate, abundant, and spatiotemporally reliable fallback food, then the impact of fruit fluctuations would have been reduced significantly. Thus, even though periods of food scarcity were likely longer and more severe than those experienced by extant apes, these early, hominins may have uncovered – literally – a way to moderate the fluctuations in the quality and energetic adequacy of their diet.

As in the apes, a second response of hominins may have been to modify their activity budgets and ranging behavior. This is especially interesting given the fact that one of the major morphological shifts characterizing the australopithecines is a switch to bipedal locomotion. As a way of saving energy, the adoption of bipedality may have represented a major energetic victory in coping with a changed resource base; movement between more distant energy-rich fruit patches would have been increasingly feasible (Rodman & McHenry 1980; Leonard & Robertson 1995, 1997a, 1997b) (see Steudel-Numbers [2003] for an alternative view).

The advent of the genus *Homo* might instructively be seen here as the time when hominins developed even more effective means of buffering themselves from perturbations in their food supply. Unlike the poor-quality, calorifically marginal fallback foods exploited by most great apes, members of the genus *Homo* increasingly exploited high-quality, energy-rich alternatives to seasonal fruit, including both difficult-to-process plant foods, such as nuts and tubers, and meat (Milton 1999; Kaplan *et al.* 2000). Other technological advances in food processing, such as tool use and cooking (Wrangham *et al.* 1999; Knott 2001), would have further enhanced this pattern of improved resource quality and better access to energy at all times of the year.

Adopting new resources and restructuring energy budgets and ranging costs might not have been the only ways in which *Homo* responded to periods of low fruit availability. It is possible that they, like orangutans, were able to store fat during periods of abundance, which could then be drawn upon during lean periods. While there is no direct evidence for fat-storage abilities in early hominins, modern humans clearly possess this trait. However, since chimpanzees and gorillas do not tend to store large amounts of fat during seasons of plenty, the time at which fat storage evolved is debatable.

Although they had adopted and refined a suite of behaviors that improved access to high-quality fallback foods, this does not mean that these hominins were never subjected to periods of calorific scarcity. However, the extent to which the lean seasons caused energetic shortfalls is unclear. Indeed, the evolution of increasingly larger brains within the human lineage may signal that energy availability was no longer limited or unreliable in the way that it had been in early hominins. Brains are costly to grow and to maintain, and thus buffering mechanisms – of a dietary, technological, or physiological nature – must have been in place to ensure that this critical organ had reliable access to the energy it constantly demands. Fat storage may have been one of those brain-buffering mechanisms.

Reconstructions of hominin evolution tend to focus on food acquisition, ranging patterns, tool use, etc. These are assuredly important variables. Leonard and Robertson (1997a, 1997b), for example, argue that hominin energetic needs increased dramatically with the advent of the genus *Homo*. However, lacking from these descriptions is a discussion of how reproduction, particularly female reproduction, would have been affected by changing energetic status caused by fluctuations in the food supply. Data from great apes and modern humans (see Chapter 13) tell us that maintaining positive energy balance in order to achieve conception would have been an important part of the equation (Knott 2001).

The interaction between food, food acquisition, and reproduction may have been particularly important in changing the dynamics of the hominin interbirth interval. If *Homo* females were able to buffer more effectively against food seasonality and energy fluctuations and thus maintain a higher energetic status, this could have been one important factor in the shortening of the interbirth interval in humans as compared with great apes (Knott 2001). Changes in the food supply, food-acquisition techniques, offspring provisioning, and social structure would have made shorter interbirth intervals possible through allowing for the production of overlapping nutritionally dependent offspring for the first time in hominoid history (Lancaster & Lancaster 1983; Knott 2001). These adaptations would have allowed our ancestors to reproduce more rapidly and perhaps less seasonally. Additionally, if part of the human adaptation that allowed us to evolve large brains is due to the ability to switch to a lower-fiber, higher-quality diet (Aiello & Wheeler 1995), then it also may have increased the need to maintain positive energy balance in females to nourish developing human brains. Thus, even in the face of an increasingly variable environment, hominins appear to have circumvented the "energy crisis" that these environmental fluctuations would have posed for other apes.

Acknowledgments

I would like to thank Diane Brockman and Carel van Schaik for asking me to be part of this book and for their constructive comments on the text. Tim Laman and Nancy Conklin-Brittain provided useful comments and discussion. I wish to particularly thank Catherine Smith for her assistance in reviewing the literature and editing the manuscript.

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