



## Evolutionary Consequences of Fallback Foods

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**Abstract** Primatologists use the term fallback foods to denote resources of relatively low preference that are used seasonally when preferred foods are unavailable. We examine the assumption that fallback foods play an important role in shaping morphological adaptations, behavior, and socioecology in primates. We discuss operational definitions of preferred and fallback foods and suggest that the evolutionary importance of fallback foods applies more to adaptations for processing than for harvesting foods. Equally, we propose that preferred resources tend to drive adaptations for harvesting foods. We distinguish 2 classes of fallback foods according to their roles in the diet and their evolutionary effects. Staple fallback foods are available year-round, tend to be eaten throughout the year, and seasonally can constitute up to 100% of the diet. Filler fallback foods never constitute 100% of the diet, and may be completely avoided for weeks at a time. We suggest that the availability of the 2 classes of fallback foods have different effects on the socioecology of primate species.

**Keywords** diet · fallback foods · feeding ecology · resource selectivity · seasonality

### Introduction

Most primate species experience periodic food shortages during which their diets shift substantially. The foods that primates utilize during periods of low food availability

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are frequently called fallback foods (FBFs). Several primatologists have hypothesized that the ecological characteristics (e.g., hardness, patch size, dispersion) and patterns of availability—both temporally and spatially—of FBFs shape the physiology, socioecology, and behavior of a wide range of primate species. For example, Lambert *et al.* (2004) suggested that the unusually thick dental enamel of gray-cheeked mangabeys is an adaptation to the relatively great hardness of their FBFs. Likewise, the specialized digestive physiology of colobines allows them to fall back on low-quality foliage that cannot be readily exploited by monogastric primates (Bauchop 1971, 1977; Chivers and Hladik 1984). The ability of colobines to exploit a superabundant FBF has led to the hypothesis that folivorous primates experience dampened feeding competition compared with frugivorous primates (Isbell 1991; Steenbeek and van Schaik 2001; Yeager and Kool 2000). Others have argued that the quality and distribution of FBFs constrain group cohesion (Tutin *et al.* 1991; Wrangham 1980, 1986), which may have substantial effects on levels of intragroup aggression and rates of affiliative interactions (White 1998; Wrangham 1986).

Although many consider the concept of FBFs to be important for understanding primate evolutionary ecology, the term fallback foods is absent in the wider literature on vertebrates and little examined even for primates.

We therefore assess current knowledge of primate fallback foods. Specifically, our goals are 1) to clarify the definition of FBFs and preferred foods; 2) to explore the significance of FBFs for the evolution of morphology, socioecology, and behavior of extant primates; and 3) to propose that 2 distinct classes of FBFs occur, with different effects.

## What Are Fallback Foods?

Although FBFs are not always operationally defined, the term most often refers to items assumed to be of relatively poor nutritional quality and high abundance, eaten particularly during periods when preferred foods are scarce (Hanya 2004; Knott 2005; Laden and Wrangham 2005; Lambert *et al.* 2004; Ungar 2004, Yamakoshi 2004a). Accordingly, one can operationally define FBFs as foods whose use is negatively correlated with the availability of preferred foods (*cf.* Altmann 1998; Conklin-Brittain *et al.* 1998; Doran *et al.* 2002). Two points about the concept should be stressed.

First, the definition of fallback foods implies a distinction between preference and importance. Whereas preference is a matter of dietary choice, importance is a measure of dietary composition. For example, the importance of a particular item might refer to its use as a proportion of total caloric intake, or the percentage of total feeding time spent eating it. Although preferred foods are in some circumstances important, they need not be, as illustrated in Table I. Similarly, high importance of an item in the diet does not necessarily imply positive selectivity or high preference. Fallback foods tend to be foods of low preference but of high importance seasonally.

Second, it is useful to distinguish a fallback food from a keystone resource, even though the 2 terms are sometimes treated as equivalents (Tutin *et al.* 1997; Ungar 2004; White 1998; Yamakoshi 1998). Accordingly, FBFs are the resources a species utilizes during periods when preferred foods are scarce, while the term keystone foods applies to communities. Paine (1969) originally applied the term keystone to

**Table 1** The difference between dietary preference and importance

		Preference	
		High	Low
Importance	High	High-quality foods that comprise a substantial part of the diet during some seasons e.g., ripe fruit for chimpanzees at Kanyawara <sup>1</sup> , fleshy, nonfig fruits for orangutans at Kutai <sup>2</sup>	Low-quality foods that form major part of diet during some periods (FBFs) e.g., bark for orangutans at Gunung Palung <sup>3</sup> , terrestrial herbs for gorillas at Lopé <sup>4</sup>
	Low	High-quality foods that are eaten rarely e.g., monkeys for chimpanzees at Ngogo <sup>5</sup> , <i>Dehassia</i> fruits for red leaf monkeys at Gunung Palung <sup>6</sup>	Low-quality foods that comprise a small percentage of the diet e.g., <i>Pternandra</i> fruits for gibbons at Gunung Palung <sup>6</sup> , mature leaves for red leaf monkeys at Sepilok <sup>7</sup>

The 2 major axes by which one can categorize food items are illustrated. Preference is a measure of selectivity and indicates disproportionate use relative to availability. High preference items are also those of high perceived quality to the organism, with quality typically defined as rate of energy return. Importance is a measure of dietary preponderance, such as the proportion of feeding time spent on a particular item. FBFs are typically items of low preference and high importance. We expect that foods of both low preference and low importance have little effect on fitness and therefore are unlikely to exert strong selective pressures on primates.

References: 1, Wrangham *et al.* 1998; 2, Leighton 1993; 3, Knott 1998; 4, Tutin *et al.* 1991; 5, Watts and Mitani 2002; 6, Marshall 2004; 7, Davies *et al.* 1988.

predators in rocky tidal communities, but its use has since been expanded considerably (Mills *et al.* 1993; Paine 1995; Terborgh 1986). The essential element underlying the concept of a keystone species is that its removal will have powerful cascading effects on a wide range of species within an ecosystem (Power *et al.* 1996). In the context of our discussion, a keystone resource by that definition would be a plant resource that is eaten by several species, and whose loss would have a negative impact on the community much larger than would be predicted from its abundance (Leighton and Leighton 1983; Peres 2000). Primate FBFs can on occasion be keystone resources for a larger vertebrate community (Leighton and Leighton 1983).

### What Are Preferred Foods?

Because our definition of FBFs depends on the meaning of preferred foods, it is necessary to define preference. We advocate a classic definition: preferred items are overselected. In other words, preferred food items are selected disproportionately often relative to their abundance within the population's habitat (Leighton 1993; Manly *et al.* 2002). Thus, preference is defined as the relationship between 2 parameters: availability and usage. Neither rarity nor frequent utilization is alone sufficient to characterize a food as preferred.

Unfortunately, the operationalization of selection and abundance can vary because of the nature of different ecological systems (Cock 1978; Lechowicz 1982; Manly *et al.* 2002), which means that even with the definition of preference as overselection, comparing the utilization of preferred foods across studies can be complicated by

variation in the specific methods for calculating preference (Chesson 1978, 1983; Johnson 1980). Two such problems are prominent for studies of primates, due to their generalist feeding strategies and the heterogeneous environments in which they live. Both concern the magnitude of the sampling effort required to assess preference.

First, selectivity is ideally assessed from a large number of independent feeding samples gathered from a representative set of individuals and age-sex classes and over a sufficiently long period to encapsulate the full range of temporal variation in food availability. But because in many primate field studies researchers gather data on a limited number of individuals, and often for extended periods, e.g., full-day follows, instead of by unbiased sampling, they can be vulnerable to pseudoreplication. Similarly, most primate field studies last for only 1–2 yr, durations insufficient to capture the full range of temporal variation in many habitats. This means that even large numbers of observations can generate an inadequate sample size for characterizing the true preference ranks of all foods. For example, McConkey *et al.* (2002, 2003) provide a careful analysis of gibbon feeding selectivity in central Borneo based on the use and availability of foods over 12 mo. However, they noted that because many plants in the Bornean forest fruit on much longer cycles, e.g., mast fruiting taxa (Marshall and Leighton 2006), they could not include a range of gibbon fruits in their analysis.

Second, when the number of food items that is available simultaneously is large, it is difficult to assess their abundance. Many preferred food items may be so rare that a realistic assessment of abundance requires intense sampling effort. In addition, even for common species, the time required for a complete phenological analysis is often prohibitively high. Investigators therefore commonly employ low-cost indices derived from monitoring only a selection of the major food items, or from walking fruit trails designed to catch more abundant food species. These methods have various shortcomings (Blake *et al.* 1990; Chapman *et al.* 1994). For example, many do not control for the density of food trees, meaning that the relative contribution of certain species to estimates of food availability correlate poorly with their relative availability in the forest (Doran *et al.* 2002; Tutin *et al.* 1997). Although such indices provide valuable relative measures of intrahabitat food availability, estimates of total food availability in a habitat, which are necessary to calculate preference values or compare food availability between sites, are impossible.

Given the need for both extensive spatial sampling and intensive temporal monitoring to characterize resource availability adequately, and the requirement of a large set of independent, unbiased feeding samples, it is understandable that primate studies rarely permit the quantitative assessment of feeding preference. However, the few researchers who have systematically sampled the range of important variables and analyzed them via appropriate multivariate techniques have provided valuable insights into the causal factors influencing primate fruit selection (Altmann 1998; Janson *et al.* 1986; Leighton 1993).

## **Foods as Selective Forces**

All organisms, whether generalist or specialist, exhibit a wide range of adaptations to their foods. We consider whether, because preferred foods and FBFs differ in their

quality, availability, and patterns of usage, they consistently exert different selection pressures.

The reason that particular resources are preferred is generally that they provide high-quality food, i.e., they allow a fast intake of calories (Krebs and Stephens 1986). While preferred foods thus tend to require relatively little manual or masticatory processing, the fact that they are costly for plants to produce means that they normally are rare in the environment. Accordingly, we suggest that the adaptive challenge for obtaining preferred foods generally tends to be the problem of searching over a wide area and reaching them rapidly. This means that preferred foods should be associated with adaptations for harvesting, i.e., for detecting foods at a distance and for efficient locomotion between food patches (Gaulin and Konner 1977). For primates, ripe fruits are the classic example of preferred foods that are rare and associated with harvesting abilities. For example, sympatric species tend to converge in their diets more when ripe fruits are abundant than when they are scarce (Guillotin *et al.* 1994; Waser 1987, Wrangham *et al.* 1988). Further, species that eat relatively more fruit for their body size show adaptations for traveling fast and far, e.g., atelines and apes (Temerin and Cant 1983). In cases where preferred food sources, e.g., fruit trees, are clumped, travel costs between successive trees are presumably substantially reduced, but travel required for movement between patches remains high.

FBFs, by contrast, are typically abundant—and easy to locate—but are hard to process, and therefore provide low rates of energy gain, when compared to preferred foods. Thus, they should promote enhanced processing abilities, e.g., accessing physically defended foods, mastication, and digestion. In line with the requirement for specialized processing, within guilds species tend to have more divergent diets when preferred foods are less abundant (Schluter 1994; Schoener 1982; Waser 1987).

In sum, feeding adaptations can be divided into 2 categories, those associated with increased harvesting ability and those associated with enhanced processing abilities (Gaulin and Konner 1977). The dichotomy is summarized in Table II. We consider examples of adaptations using this framework.

We do not claim that all foraging-related behaviors or morphological structures fit the expected pattern. For example, some argue that the relatively large incisors of frugivores are adaptations for processing large fruits, which are presumably preferred foods (Goldstein *et al.* 1978; Hylander 1975; but Ungar (1996a) found no relationship between incisor size and diet in 4 sympatric Sumatran primates). Likewise, Ungar (2004) argued that early *Homo* had relatively long shearing crests that were adapted to chewing meat. Although Ungar (2004) argued that meat was a FBF for

**Table II** Proposed framework for consideration of preferred and fallback foods as selective forces

Preferred foods	Fallback foods
Feeding adaptations	
Food harvesting	Food processing
General cognitive abilities	Dental topography
Spatial navigation	Enamel thickness
Locomotion	Gut length and morphology
Visual acuity	Body size
Olfaction	Tool use
Other effects	
Reproductive cycles	Social cohesion

early *Homo*, we would argue that it was more likely a preferred food. The idea that teeth were adapted to processing meat would therefore run against our general expectation for primate digestive adaptations. Similarly, although primatologists often consider color vision in Old World primates to be an adaptation to finding ripe fruits (Regan *et al.* 2001; SurrIDGE *et al.* 2003) —as our framework would expect, because vision can be viewed as a harvesting adaptation— a plausible case can be made to support its evolution for finding young leaves, which may be FBFs (Dominy and Lucas 2001; Dominy *et al.* 2003; Lucas *et al.* 1998, 2003). We suggest that such cases may represent exceptions to the general claims that preferred foods are processed easily whereas fallback foods are found easily. Primates positively select most preferred foods precisely because they provide high rates of energy return and require little specialization to process. However, when preferred foods require specialized adaptations that do not impose strong costs on the ability to exploit FBFs, adaptations to process preferred foods are expected. Such instances are sufficiently rare in primates to accommodate our general framework.

## Preferred Foods and Adaptations for Harvesting

Traits that affect harvesting efficiency may include several general categories (Table II). Here we discuss 2: cognition and locomotion.

### General Cognitive Abilities

Some authors have proposed that primate cognitive evolution has primarily taken place in the context of foraging (Russon and Begun 2004; Tomasello and Call 1997; Yamagiwa 2004). Most discussions of the role of foraging in shaping primate cognitive evolution focus on the patchiness of plant food resources most primates utilize (Milton 1981; Potts 2004). Highly dispersed foods supposedly promote the cognitive abilities of primates, resulting in enhanced cognitive abilities in primates whose food resources exhibit a higher degree of patchiness (Clutton-Brock and Harvey 1980; Milton 1988). As most preferred primate foods are more patchily distributed than FBFs, such arguments therefore concern the importance of general cognitive abilities, i.e., intelligence, for the harvesting of preferred foods, not the processing of FBFs. In other words, the pressure to harvest preferred foods efficiently may have resulted in many of the advanced cognitive skills possessed by extant primates, e.g., spatial navigation, cognitive mapping, and memory.

### Locomotor Adaptations

Although a variety of selection pressures probably created the wide diversity of locomotor adaptations among extant primates, e.g., predator avoidance, finding mates, territorial defense, the need to travel efficiently between food patches must have been a primary force shaping locomotor adaptations (Fleagle 1984). As preferred foods are less common and more patchily distributed in space than FBFs are, we expect locomotor adaptations to be solutions to the problem of maximizing the harvesting efficiency of preferred foods more than FBFs. For example, Isbell *et al.* (1998)

argued that the need to travel efficiently between widely distributed patches of preferred foods was the primary selection pressure for increased lower limb length in patas monkeys (*Erythrocebus patas*). Similarly, in a comparison of the locomotor behavior of gibbons (*Hylobates agilis*) and macaques (*Macaca fascicularis*), Cannon and Leighton (1994, 1996) showed that the increased travel efficiency of gibbons allowed them to exploit small, dispersed patches of high-quality fruit that were unavailable to the less efficient macaques. Chimpanzee locomotor anatomy shows clear adaptations for accessing preferred fruits in trees at the expense of morphological adaptations that would allow them to travel efficiently between patches of terrestrial FBFs (Pontzer and Wrangham 2004).

## FBFs and Adaptations for Processing

Periodic resource scarcity can result in elevated mortality or morbidity in a range of primate species (Dittus 1979; Lee and Hauser 1998). During such times, selection probably acts relatively intensely on traits that confer a survival advantage on individuals that possess them (Boag and Grant 1981), producing phenotypic adaptations for processing nonpreferred FBFs that are crucial for survival during these periods (Kawecki 1995; Robinson and Wilson 1998). We consider 3 types of adaptations for processing FBFs: dental adaptations, digestive adaptations, and tool use.

### Dental Adaptations

Correlations between primate dentition and mechanical properties of foods suggest functional relationships between dental morphology, e.g., enamel thickness, tooth shape, and the ability to exploit different types of plant foods (Lucas 1979; Lucas and Peters 2000). However, high dietary overlap between species with different dental morphologies (Dumont 1995; Maas and Dumont 1999; Ungar 1996b; Wrangham *et al.* 1998) and the seemingly counterintuitive observation of primates frequently avoiding foods to which they seem well adapted, e.g., low rates of folivory in some Asian colobines (Marshall 2004; Yeager and Kool 2000) appear to undermine the argument that dental morphology reflects adaptations to specific diets. One can solve the paradox of species with highly specialized foraging adaptations exhibiting generalist feeding behavior—Liem's paradox (Robinson and Wilson 1998)—by distinguishing between preferred foods and FBFs.

Food items preferred by primates, e.g., ripe fruits, require little specialization, and species with a wide range of masticatory anatomies can process them. In contrast, FBFs, such as leaves or seeds, are less easily processed and therefore require more specialized dental morphology, suggesting that adaptations for FBFs impose few costs to the utilization of preferred foods while providing an important advantage during periods of food scarcity. Thus, dental morphology should reflect adaptations to FBFs, not preferred foods (Robinson and Wilson 1998; Rosenberger and Kinzey 1976; Rosenberger 1992). In support of this notion, Yamashita's (1998) analysis of the functional dental morphology of 5 lemur species demonstrated that the hardest and strongest foods eaten, i.e., FBFs, have higher correlations with dental features than the most commonly eaten foods.

Field studies of sympatric primate species further support the claim that dental morphology reflects adaptations to processing FBFs rather than preferred foods. Kinzey (1978) showed that 2 species of titi monkeys (*Callicebus torquatus* and *C. brunneus*) exhibit divergent dental adaptations for processing different FBFs (leaves vs. insects), despite sharing a predominantly frugivorous diet. Similarly, Lambert *et al.* (2004) found that during periods of food abundance there was no difference in the hardness of foods eaten by gray-cheeked mangabeys (*Lophocebus albigena*) and red-tailed guenons (*Cercopithecus ascanius*) despite substantial differences in tooth enamel thickness between them. However, during periods of fruit scarcity, the thick-enameled mangabeys were able to utilize hard foods inaccessible to the more thin-enameled guenons (Lambert *et al.* 2004). Ungar (2004) also concluded that differences in dental topography between sympatric gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes troglodytes*) reflected different adaptations to FBFs, not preferred foods.

### Digestive Adaptations

Several primatologists have conducted research relating various aspects of primate digestive physiology to dietary intake (Chivers and Hladik 1984; Milton 1998). Variation between primate species in digestive retention times (Lambert 1998, 2002; Milton and Demment 1988), gut surface area and volume (Chivers and Hladik 1984; Kay and Davies 1994), relative lengths of portions of the gut (Chivers and Hladik 1980; 1984), and gut microbial communities (Bauchop 1971; Bauchop and Martucci 1968) correlate well with dietary specializations. Accordingly, as with dental adaptations, digestive adaptations may be best viewed as adaptations to process FBFs, not necessarily the most commonly eaten, i.e., important, foods in the diet of a primate species. Preferred foods are of relatively high quality, i.e., low-fiber, high-energy, few antifeedants, and therefore short, relatively undifferentiated guts can process them. In contrast, primates typically require more gastrointestinal specialization to process FBFs, which typically contain more fiber, fewer readily available calories, or higher levels of antifeedants. For example, the large body size, longer gut, and correspondingly longer gut retention times in gorillas presumably account for their ability to rely far more heavily on low-quality FBFs than do chimpanzees, which have shorter gut retention times (Remis 2000; Remis *et al.* 2001; Tutin *et al.* 1991). Similarly, forestomach fermentation allows colobines to fall back on low-quality mature foliage that is unavailable to sympatric monogastric primates (Davies 1994; Kay and Davies 1994), which must use other resources as FBFs. More broadly, large-bodied primates with correspondingly long digestive systems are generally better able to process low-quality foods than small-bodied primates are (Hemingway and Bynum 2005; Janson and Chapman 1999; Kay 1984; but body size does not fully explain all variation: Conklin-Brittain *et al.* 1998; Hemingway and Bynum 2005), allowing them to rely heavily on FBFs during periods of food shortage in ways that smaller primates cannot.

### Tool Use

As primates typically use tools to obtain and to process food (van Schaik *et al.* 1999; Yamakoshi 2004b), it is reasonable to examine whether tool use occurs primarily in

the context of feeding on preferred foods or FBFs. Researchers have given the issue little direct attention, although it is logical to hypothesize that tool use will occur primarily in the context of feeding on FBFs. Preferred foods, such as ripe fruits, are favored owing to their relatively high rates of energy return per unit time and low levels of chemical or physical defenses (Leighton 1993). The items typically have short handling times and require unsophisticated feeding techniques. In contrast, because some fallback fruits are produced during periods of relative food scarcity when seed predation is likely to be relatively intense, we expect that these fruits will have evolved more substantial defenses than those produced during periods of high fruit availability (Marshall and Leighton 2006). Selection pressure to acquire energy during periods of low food availability may lead primates to manufacture and to use tools to process FBFs during these periods.

Some observations of tool use in wild primates support this notion. Yamakoshi (1998) reported that 2 of the 3 main FBFs for the Bossou chimpanzees were available to them through the use of tools. Tool-use was strongly negatively correlated with the abundance of preferred foods. He therefore argued that tool use is a key adaptation enabling the chimpanzees to access FBFs during periods of fruit scarcity (Yamakoshi 1998). Similarly, de A. Moura and Lee (2004) argued that food shortages were primarily responsible for the routine use of stone tools by capuchins to access buried or physically defended foods in the dry forests of northeastern Brazil. In addition, van Schaik and Knott (2001) reported that tool use enabled Sumatran orangutans to access highly nutritious seeds from *Neesia cf. malayana* during periods of fruit scarcity. Yamagiwa (2004) suggested that tool use in chimpanzees and orangutans allows them to utilize higher quality FBFs than gorillas and bonobos do.

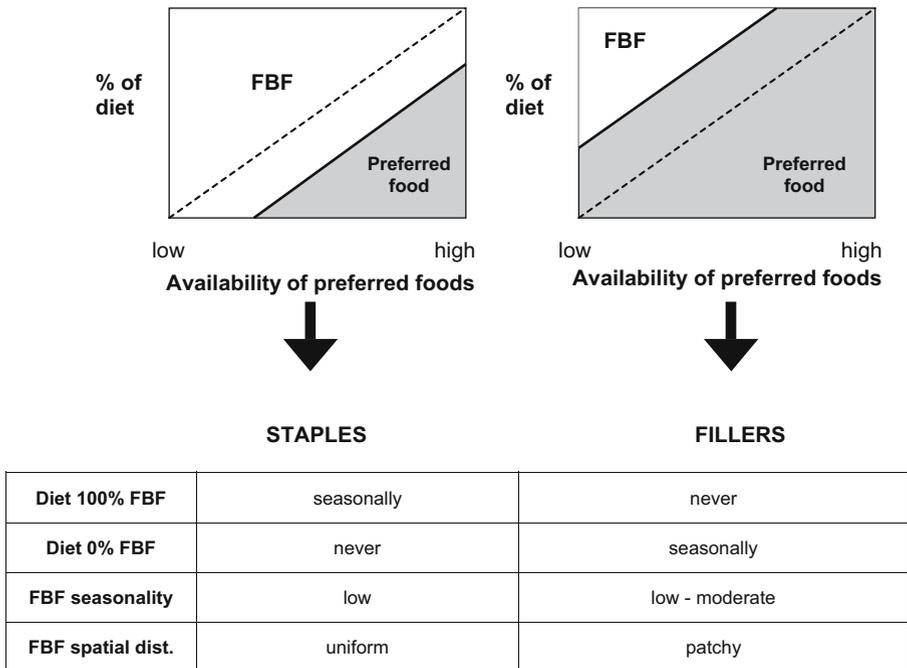
As FBFs are ecologically important to a wide range of non-tool-using primates, as not all tool use occurs in the context of feeding, and as tools are not required to access many FBFs, seasonal reliance on FBFs cannot fully explain the observed variation between primate species and populations in patterns of tool use (Whiten *et al.* 1999; van Schaik *et al.* 1999, 2003). However, further research is needed to test the hypothesis that tool use is primarily an adaptation to FBFs in species containing the preconditions for tool use (*sensu* van Schaik *et al.* 1999).

### Staple vs. Filler FBFs

FBFs vary widely in their total contribution to the diet, from providing only a limited proportion of food even during their heaviest period of use, to providing all of the diet for short or even extended periods. For example, consider the difference between the roles of cambium in orangutan diets, vs. foliage in gorilla diets. When little else is available, orangutans rely heavily on tree cambium as a FBF, but the proportion of feeding time never reaches 100% ( $\leq 37\%$  of feeding time): Gunung Palung (Knott 1998), Kutai (Leighton 1993), and Tanjung Puting (Galdikas 1979). By contrast, gorillas utilize pith and leaves as FBFs, and during periods of fruit scarcity these items can comprise virtually all of the diet: Lopé (Tutin *et al.* 1991), Bai Hokou (Remis *et al.* 2001), and Mondika (Doran *et al.* 2002). Indeed, such foliage almost completely dominates the annual diet of mountain gorillas (Watts 1984, 1998).

In recognition of this variation, we suggest that it is useful to classify FBFs according to whether the species or population ever utilizes the FBF for 100% of the diet. We depict the distinction between the 2 classes of FBFs in Fig. 1. We define pure examples of staple FBFs as those that can seasonally serve as the sole food resource during periods of low preferred food availability, in line with the definition of FBF. That staple FBFs can seasonally constitute the entire diet implies that they are capable of sustaining the physiological maintenance functions of individuals, even if they are inadequate for reproduction. Therefore, we expect that the digestive system and socioecology of species eating staple FBFs is importantly adapted to them.

In contrast, filler FBFs never constitute the entire diet, and presumably could not maintain the individuals feeding on them in the absence of other food resources. Therefore, the socioecological consequences of filler FBFs represent a trade-off between preferred and FBF foods. Accordingly, we predict that the degree of physiological, behavioral, and ecological adaptation is less complete in response to filler FBFs than to staple FBFs. The relationship between the influences of preferred foods and filler FBFs depends on such factors as their relative importance in the diet and their similarity or difference in such factors as distribution and ease of processing.



**Fig. 1** Two proposed classes of FBFs. Left: Species that utilize staple FBFs. The graph shows how the composition of the diet during a given month or season relates to the phenological availability of preferred foods during that period. Right: The same relationship for species that are unable to utilize staple FBFs, and instead use filler FBFs. The dotted line in each graph represents the boundary between the 2 proposed classes of FBFs. Species for which the solid line is below the dotted line have staple FBFs (left), those with the solid line above the dotted line have filler FBFs (right). Characteristics of the 2 types of feeding adaptation are shown under each graph.

We suggest that one can readily recognize the distinction between staple and filler FBFs. Cases of staple FBFs include leaves for proboscis monkeys (*Nasalis larvatus*) at Tanjung Puting (Yeager 1989), young leaves for *Indri indri* at Mantadia (Powzyk and Mowry 2003), and leaves for howlers (*Alouatta palliata*) at Santa Rosa (Chapman 1987). Examples of filler FBFs include mature leaves for banded leaf monkeys (*Presbytis melalophos*) at Kuala Lompat (Davies *et al.* 1988), palm nuts for brown capuchins (*Cebus apella*) at Cocha Cashu (Terborgh 1983), and fungus for Goeldi's monkeys (*Callimico goeldii*) at San Sebastian (Porter 2001). Because the nature of a FBF depends on the digestive ability of the species eating it, the same food type may act as a staple for one species and a filler for another. For example, terrestrial herbs and pith serve as staple FBFs for gorillas (Remis *et al.* 2001; Tutin *et al.* 1991), but as filler FBFs for chimpanzees (Basabose 2002; Wrangham *et al.* 1998).

Some authors have identified staple foods as a category of food resources distinct from FBFs because they are utilized year-round (Doran *et al.* 2002; Knott 2005; Newton-Fisher 1999). We would argue that year-round use does not preclude a food item serving as a FBF; indeed many FBFs habitually comprise at least part of the diet. The key issue is whether food use correlates inversely with the availability of preferred foods. In one case, a staple food appeared to conform to this definition of a FBF (Newton-Fisher 1999) and in a second it did not (Doran *et al.* 2002). To avoid confusion, we therefore use the term staple FBF to differentiate it from the simple term staple in the literature.

As a preliminary proposal for differences between the consequences of adaptation to staple vs. filler foods, we suggest 4 points.

- 1) One can distinguish species by whether they are adapted to staple or filler FBFs because the ability to thrive on a staple FBF alone depends on specific digestive (processing) adaptations that have far-reaching implications for evolutionary ecology.
- 2) The principle that species can be distinguished as staple FBF-feeding species versus filler FBF-feeding species has different implications for the ecological constraints on the geographic distribution of each species. Specifically, staple FBF-feeding species are more constrained by the availability of staple foods, whereas filler FBF-feeding species are more constrained by the availability of preferred foods because there are times of year when each of the food categories — staples for staple-FBF-feeders and preferred foods for filler-FBF-feeders — constitute 100% of the diet (Fig. 1). They are therefore critical food types that must be present in abundance to allow each type of species to colonize given habitats.
- 3) We expect species that utilize filler FBFs to experience more pronounced fluctuations in resource availability than those utilizing staple FBFs, following from the fact that species that utilize filler FBFs are subject to substantial variation in food abundance imposed by the preferred component of the diet. Accordingly, we expect that species utilizing filler FBFs have differences in ecology and life history that reflect a less predictable food supply, compared to those that can subsist on staple FBFs. The prediction is similar to those concerned with the difference between frugivorous and folivorous species (Janson and van Schaik 1993; Leigh 1994). In line with the frugivore-folivore distinction, therefore, it

suggests that species that utilize only filler FBFs have relatively slower life histories. Specifically, they will grow more slowly, reproduce more slowly, and die later than those utilizing staple foods, as occurs with chimpanzees compared to gorillas (Knott 2001).

- 4) Species that utilize staple FBFs experience reduced feeding competition compared to those utilizing filler FBFs because during periods of reliance on staple FBFs we expect food abundance to be relatively high compared to the preferred foods that are necessary for species without access to staple FBFs. As a corollary, we expect that species with staple FBFs generally form more stable groups, with cascading effects on social dynamics.

## Discussion

We agree with authors who have suggested that it is useful to distinguish FBFs as a special category of the primate diet. However, we also suggest that current usage of the term fallback food includes definitions that are not strictly comparable. We therefore propose a method of operationalizing FBFs intended to be robust, logically consistent, and comparable across studies.

Our definition draws attention to the hypothesis that different degrees of reliance on FBFs are characteristic of different species, and that it is useful to distinguish between filler FBFs and staple FBFs. We expect staple FBFs to have stronger evolutionary and ecological influences than filler FBFs, because during the period when they are being eaten, staple FBFs are the only food type exerting a selective pressure. The distinction comes close to replicating the traditional classification of species into frugivores and folivores. However, we regard it as a more coherent distinction, because it resolves how species that eat leaves but are capable of eating much fruit should be classified. For example, there has been debate as to whether primatologists should classify gorillas as frugivores or folivores (Remis *et al.* 2001, Rogers *et al.* 1990, Tutin *et al.* 1991). A focus on the filler-staple distinction makes clear that gorillas fall into the staple FBF category, and suggests that many of their digestive, behavioral, and life-history adaptations can be understood as consequences of the importance of this food category.

## Conclusion

- 1) When operationalizing fallback foods (FBFs), it is necessary to distinguish the concepts of preference and importance, to assess the spatial and temporal availability of food in an unbiased way, and to collect or subsample data in a way that ensures the independence of observations.
- 2) We propose that differences in the selection pressures primates incur while eating preferred vs. fallback foods tend to lead to differences in foraging adaptations. We hypothesize that preferred foods primarily drive harvesting adaptations, while fallback foods shape processing adaptations. Explicit consideration of the different selection pressures of these resource types may help to advance our

understanding of the ways in which seasonality in resource availability affects both extant primate populations and extinct species.

- 3) We propose that 2 distinct classes of fallback foods be considered, staple FBFs and filler FBFs, and that they shape life history and socio-ecology in different ways.

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