

Defining Fallback Foods and Assessing Their Importance in Primate Ecology and Evolution

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ABSTRACT Physical anthropologists use the term “fallback foods” to denote resources of relatively poor nutritional quality that become particularly important dietary components during periods when preferred foods are scarce. Fallback foods are becoming increasingly invoked as key selective forces that determine masticatory and digestive anatomy, influence grouping and ranging behavior, and underlie fundamental evolutionary processes such as speciation, extinction, and adaptation. In this article, we provide an overview of the concept of fallback foods by discussing definitions of the term and categorizations of types of fallback foods, and by examining the importance of fallback foods for primate ecology and evolution. We begin by comparing two recently published conceptual frame-

works for considering the evolutionary significance of fallback foods and propose a way in which these approaches might be integrated. We then consider a series of questions about the importance of fallback foods for primates, including the extent to which fallback foods should be considered a distinct class of food resources, separate from preferred or commonly eaten foods; the link between life history strategy and fallback foods; if fallback foods always limit primate carrying capacity; and whether particular plant growth forms might play especially important roles as fallback resources for primates. We conclude with a brief consideration of links between fallback foods and primate conservation. *Am J Phys Anthropol* 140:603–614, 2009. © 2009 Wiley-Liss, Inc.

Food is a fundamentally important resource that strongly influences primate individuals, groups, populations, and species in a variety of ways. For example, an individual's ability to safely harvest and process sufficient food to fulfill its requirements for growth, maintenance, and reproduction are key determinants of fitness (Altmann, 1988, 1991; Koenig et al., 1997). The availability of food also typically determines a species' geographical range and limits its population density (Cant, 1980; Chapman and Chapman, 1999; Stevenson, 2001). In addition, the morphological, mechanical, and biochemical properties of foods are important selective forces that shape a species' anatomical traits (Chivers and Hladik, 1980; Rosenberger, 1992; Robinson and Wilson, 1998; Yamashita, 1998). Finally, the distribution and abundance of food are thought to be the fundamental ecological forces shaping primate grouping and social systems (Wrangham, 1980; Isbell, 1991; Sterck et al., 1997; Koenig et al., 1998).

Results from early field studies suggested that different types of food systematically differ in both their quality and patterns of distribution in space and time. On the basis of these differences, several scientists hypothesized that different types of food may exert distinct selection pressures on primate populations (Milton and May, 1976; Clutton-Brock and Harvey, 1977, 1980; Hladik, 1978; Milton, 1981a). Initial discussions characterized these differences using fairly gross categories, hypothesizing fundamental ecological differences between folivores and frugivores based on their diets (Clutton-Brock and Harvey, 1979; Johns, 1988; Anthony and Kay, 1993; Janson and van Schaik, 1993; Leigh, 1994; Yeager and

Kirkpatrick, 1998; Godfrey et al., 2001). More recent work has focused on identifying important functional categories that more explicitly consider the evolutionary and ecological importance of different classes of foods (Rosenberger, 1992; Taylor, 2002; Lambert et al., 2004; Laden and Wrangham, 2005; Marshall and Leighton, 2006; Vogel et al., 2008).

In this work, we discuss fallback foods, a class of resource that has received considerable attention in recent years (Altmann, 1988; Wrangham et al., 1998; Laden and Wrangham, 2005; Lambert, 2007; Marshall and Wrangham, 2007). Where applicable, we highlight results from our own studies of Southeast Asian primates to illustrate more general principles. In particular, we discuss the results of a long-term study of gibbons (*Hylobates albibarbis*) and leaf monkeys (*Presbytis rubi-*

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cunda rubida) at Gunung Palung National Park, West Kalimantan, Indonesia (GPNP).

DEFINITION AND CATEGORIZATION OF FALLBACK FOODS

Although there is some variation in its precise application (Lambert, 2007), the term fallback foods is generally used to refer to abundant foods of relatively low quality that are used during periods of low overall food availability (Wrangham et al., 1998; Hanya, 2004; Lambert et al., 2004; Yamakoshi, 2004; Knott, 2005; Laden and Wrangham, 2005). The most commonly applied operational definition of fallback foods describes them as foods whose use is significantly negatively correlated with the abundance of preferred foods (Wrangham et al., 1998; Doran et al., 2002a; Marshall and Wrangham, 2007). For example, our studies of gibbons at GPNP demonstrate that figs are a major fallback food for this taxon. Fig consumption varies substantially over time, between 0 and 75% of monthly independent feeding observations (Marshall and Leighton, 2006). Fig consumption is highest during periods of low preferred food availability and drops substantially when more prized resources are abundant, conforming to the operational definition of a fallback food (see Fig. 1).

Although discussion of the concept of fallback foods is becoming increasingly common among evolutionary anthropologists, use of the term “fallback foods” is not universal. For example, in an informal survey of recent papers on primate feeding ecology ($n = 51$), we found that the term is fairly common in papers published by researchers working in Africa and Southeast Asia (i.e., the term is explicitly mentioned in roughly one-third of papers addressing primate feeding ecology), less common in publications from South and Central America (i.e., the term is explicitly mentioned in 10–25% of such papers), and largely absent from papers published by our colleagues working in Madagascar (i.e., less than 5% of such papers). Whether this disparity reflects the fact that the concept has less utility in the New World and Madagascar, whether it represents slow diffusion of a generally useful concept, or whether it simply reflects use of distinct terminology among primatologists working in geographically separated areas remains unclear. In support of the last of these three possibilities is our observation that, particularly in the Americas but also in Madagascar, the terms “keystone” or “staple” are frequently used to refer to resources that generally conform to the operational definition of a fallback food. This indicates that the concept does have broad utility for primate species across the tropics, despite variation in terminology. The fact that the majority of published uses of the specific term “fallback foods” are found in a single journal (*International Journal of Primatology*, 60% of 62 papers between 1993 and 2008) suggests that limited diffusion within the field of evolutionary anthropology may explain some of the patterns of its use. We advocate more general use of the term “fallback food” when referring to foods that are consumed by a particular taxon in inverse proportion to the availability of their preferred foods. We feel this would avoid confusion that might arise from the fact that the term “keystone,” as applied by some primatologists to foods used by a particular species, is a misuse of a term that had an earlier and different meaning among ecologists and primatologists, one that related to interactions among species, typically

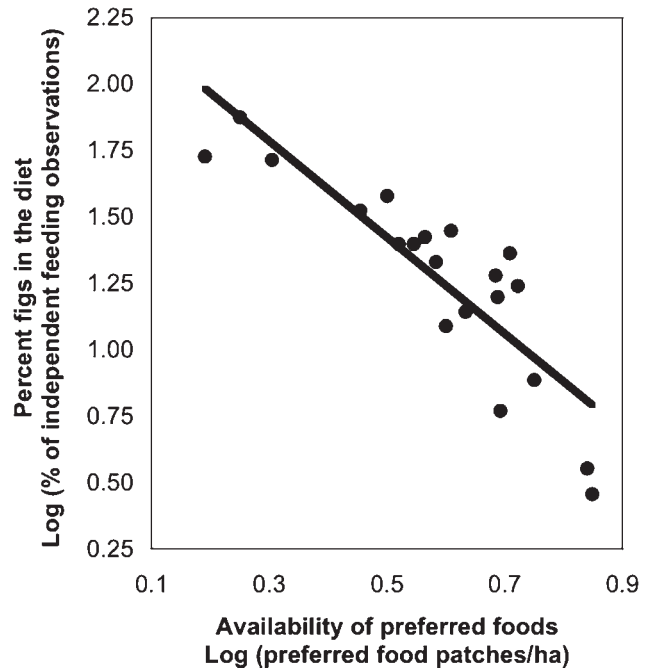


Fig. 1. Figs are fallback foods for gibbons at GPNP. This figure shows that fig consumption (log of the percent of all independent feeding observations that are of fig feeding) is significantly negatively correlated with the availability of preferred foods (log of preferred food patches per ha; $r^2 = 0.75$, $P < 0.0001$, $n = 20$ periods). Data were gathered between January 1986 and March 1991 and are lumped into 20 three-month periods to reduce the effects of sampling error associated with small sample sizes.

across multiple trophic levels (Paine, 1969; Hemingway and Bynum, 2005; Marshall and Wrangham, 2007) and the fact that, in contrast to the use of the term “staple” in common parlance, fallback foods may be completely ignored for extended periods (Marshall and Wrangham, 2007).

Discussion of the importance of fallback foods rests implicitly, sometimes explicitly, on the concept of ecological crunch periods. In this context, ecological crunches—sometimes alternatively referred to as “bottlenecks,” or “critical use times”—are periods of extreme food scarcity, during which heightened resource competition imposes substantial mortality (Boag and Grant, 1981). This competition is generally assumed to be intraspecific, although interspecific competition for resources during ecological crunches may also be intensified (Peres, 1996; Marshall et al., 2009b). Such periods are typically rare relative to the lifespan of the organism in question but are thought to exert a disproportionately large influence on morphology (Rosenberger and Kinzey, 1976; Rosenberger, 1992; Lambert et al., 2004), socioecology (Wrangham, 1986; Yamakoshi, 2004), and macroevolutionary phenomena, such as speciation and extinction (Potts, 1998; Ungar, 2004; Laden and Wrangham, 2005).

In recognition of this presumed importance, two recent publications have attempted to provide an overview of the topic of fallback foods (Lambert, 2007; Marshall and Wrangham, 2007). Each proposes a framework for classifying fallback foods in a way that highlights the evolutionary significance of different dietary strategies. Here,

we briefly summarize each framework and consider ways in which they might be complementary.

High-quality versus low-quality fallback foods and strategies

Lambert's (2007) classification focuses on the quality of fallback foods and is explicitly tied to distinct fallback strategies. She describes a continuum of fallback strategies; at one end are species whose fallback diets are composed of relatively abundant, low-quality foods (e.g., leaves and bark) and at the other end are species that fall back on higher quality, less-abundant fallback foods (e.g., fruit and seeds). Lambert (2007) argues that low-quality fallback foods are harder to process, and therefore species require specific anatomical adaptations to eat them (e.g., specialized dental or digestive characteristics). In contrast, rare, high-quality fallback foods drive behavioral adaptations (e.g., fission-fusion social systems and tool use). Which end of this continuum a particular species (or population) occupies depends on habitat type and morphology, among other things (Lambert, 2007). This conceptual framework usefully distinguishes the low-quality fallback strategies employed by gorillas and Cercopithecoid monkeys from the high-quality fallback strategies typical of common chimpanzees. In addition, it provides a valuable framework from within which to generate hypotheses about the evolution of the human diet.

Staple versus filler fallback foods

Marshall and Wrangham (2007) classify fallback foods based on their importance in the diet, suggesting that a useful distinction can be drawn based on whether or not a fallback food resource seasonally comprises 100% of the diet or nearly so. They use the term "staple fallback foods" to describe resources that can seasonally serve as the sole food supply during periods of low-preferred food availability. In contrast, "filler fallback foods" are defined as resources that never comprise the entire diet. This distinction implies that staple fallback foods are sufficiently abundant to at least sustain physiological maintenance functions in the absence of other food resources, whereas filler fallback foods are not. On the basis of this framework, Marshall and Wrangham (2007) proposed a number of preliminary hypotheses related to the ecological and evolutionary implications of the use of these distinct types of fallback food. For example, they hypothesized that species using staple fallback foods would experience reduced intraspecific feeding competition, undergo less pronounced fluctuations in resource availability, live in more stable groups, and have "faster" life histories relative to those using filler fallback foods.

Comparing classification schemes

Although the two frameworks described above were developed independently and approach the classification of fallback foods from a somewhat different perspective, they are largely complementary (see Fig. 2). We expect that filler fallback foods (see Marshall and Wrangham, 2007) are generally seen in species using a high-quality fallback strategy (see Lambert, 2007), while staple fallback foods are generally seen in taxa using low-quality fallback strategies, although we imagine that this characterization is not universally true. While the poorest quality filler fallback foods are probably of higher quality

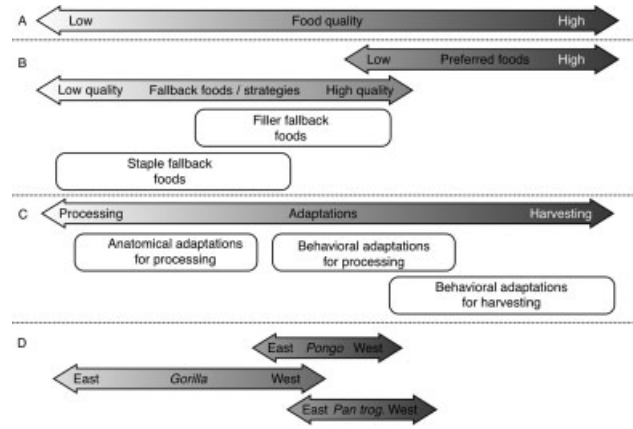


Fig. 2. A proposed way to unite two fallback food classification schemes proposed by Lambert (2007) and Marshall and Wrangham (2007). Figure based on Lambert (2007: 338; Fig. 17.4) and Marshall and Wrangham (2007: 1223 and 1228; Table II and Fig. 1). **A:** All items in a primate species' diet can be ranked along a continuum of quality that reflects rates of nutrient return. On the right side of the figure are high-quality items, which tend to be rare in the environment; on the left side are low-quality items, which tend to be more common. **B:** Preferred foods and fallback foods can be placed along this gradient, we subdivide the latter into high- and low-quality fallback foods. As indicated, staple and filler fallback foods may be only loosely related to fallback food quality. **C:** Relatively high-quality foods tend principally to drive behavioral and harvesting adaptations, while low-quality foods exert an important selective force on anatomical and processing adaptations. **D:** Gorillas, orangutans, and chimpanzees occupy distinct positions along this continuum. Interestingly, there appears to be a consistent east to west gradient within each taxon, with populations to the west enjoying relatively higher overall diet quality and engaging in high-quality fallback strategies compared to populations in the east.

than the poorest staple fallback foods, and the highest quality fillers are expected to be of higher quality than the highest quality staples, we anticipate substantial overlap between these two classes (Fig. 2B). This is partly due to the fact that the same food item might serve as a staple fallback for one taxon and a filler fallback for another taxon based on the primate species' anatomy and physiology (i.e., have a different perceived quality for the consumer, cf. THV for gorillas and chimpanzees), and also because fallback strategies are expected to vary based on habitat type, area, and the degree of seasonality (Lambert, 2007; Marshall and Wrangham, 2007).

Both schemes hypothesize that relatively high-quality foods drive harvesting adaptations while relatively low-quality foods drive processing adaptations and that low-quality foods are disproportionately important in determining anatomical traits, while high-quality foods are more implicated in behavioral adaptations (Fig. 2C). The proposed inflection point between behavioral and anatomical adaptations, and between harvesting and processing adaptations, differ between the two schemes. Lambert (2007) suggests that this distinction falls between the two ends of her continuum of fallback strategies, while Marshall and Wrangham (2007) suggest that this division falls between preferred and fallback foods. Despite this difference, the conceptual point is the same: some foods have short search times but long handling times, while others require long search times but

short handling times, and we expect these differences to have important consequences for primate adaptation.

Finally, both frameworks can be used to explain variation within and among extant primate taxa. Here, we note three examples from the great apes, although we anticipate that the conceptual points discussed here would apply across a broader range of primate taxa. Some gorilla populations are able to subsist on abundant, low-quality, staple fallback food resources for extended periods (Harcourt and Stewart, 2007). As noted earlier, while these resources are of relatively low quality compared to fallback foods used by some taxa, the specialized digestive and masticatory adaptations of gorillas enable them to extract sufficient nutrients from these resources to sustain themselves (Lambert, 1998; Remis, 2000; Taylor, 2002). The extensive use of low-quality fallback foods is exemplified by mountain gorillas (*Gorilla beringei beringei*: Watts, 1984), although generally it appears to be more true for Eastern Gorillas (*Gorilla beringei* subsp.) than Western Gorillas (*Gorilla gorilla* subsp.: Doran and McNeilage, 2001; Doran et al., 2002a; Harcourt and Stewart, 2007). Chimpanzees, in contrast, use higher quality, filler fallback foods, maintaining a higher diet quality than gorillas, even in times of preferred fruit scarcity (Tutin and Fernandez, 1985; Tutin et al., 1991; Wrangham et al., 1998; Yamagiwa and Basabose, 2003). As with gorillas, there appears to be a similar gradient from east to west, with chimpanzee taxa in East Africa (*Pan troglodytes schweinfurthii*) experiencing more extreme seasonality and using a relatively lower quality fallback strategy than Western chimpanzees (*P. t. verus*: Doran et al., 2002b). As Lambert (2007) suggests, orangutan fallback strategies lie somewhere in between those of gorillas and chimpanzees. Orangutans use filler fallback foods, yet as with gorillas and chimpanzees, there is substantial variation among taxa across an east to west gradient. Eastern Bornean orangutans (*Pongo pygmaeus morio*) have poorer quality fallback foods than western Bornean orangutans (*Pongo pygmaeus wurmbii*), and Sumatran orangutans (*Pongo abelii*) have the highest quality fallback foods of all (Morrogh-Bernard et al., 2009; van Schaik et al., 2009). Figure 2D schematically represents the relative position of these three taxa and indicates the variation within each taxon. The gradients of variation in fallback food quality, and ultimately fallback strategies, may underlie substantial differences in life history and sociality between and within these taxa (Doran et al., 2002b; Wich et al., 2004b; Knott, 2005; Lambert, 2007; van Schaik et al., 2009).

The placement of bonobos along this continuum is problematic. The staple-filler framework would group them with gorillas as species using staple fallback food resources, suggesting that they should be placed toward the left side of Figure 2. This placement, however, seems unrealistic, because bonobos are thought to have relatively high-quality fallback foods, which suggests that they should be situated to the right of common chimpanzees on the diagram. This implies that the integrated framework described here does not apply well to bonobos. This may be because bonobos are largely released from the selection pressures of fallback strategies as they inhabit relatively aseasonal forests, as Lambert (2007) suggests. Alternatively, it may be because the two classification systems that we have attempted to integrate here do not cleanly map onto one another, despite general concordance. Specifically, as noted earlier, the

relationship between a fallback food item's nutritional quality (stressed by Lambert, 2007) and its dietary importance (stressed by Marshall and Wrangham, 2007) may not be consistent across primate taxa. Finally, it may be that the proposed explanatory framework does not include the full range of parameters necessary to adequately characterize the ecological significance of fallback foods for primates. Application of this framework to other primate species should help clarify these issues.

We conducted an extensive review of the primate feeding ecology literature to test the applicability of the proposed framework but were surprised to find that very few published papers provide sufficient data to empirically identify fallback foods and even fewer provide detailed information on their quality or temporal variation in their use or availability. For example, summary data tables rarely explicitly report variation in the importance of a particular food item over time (e.g., by presenting the range of values for monthly importance) nor do they present detailed phenological data on a representative sample of individuals from a particular plant taxon necessary to assess changes in availability. We are confident that while these data are not generally published in raw form, many of our colleagues have information on the nutritional quality and monthly use and availability of different foods that would permit the identification of fallback foods, their classification as either staples or fillers, and an assessment of their quality. Collaborative compilation of these data sets would provide an excellent opportunity for comparative tests of the ecological importance of fallback foods and to examine hypotheses about potential ties to socioecology and life history.

CONSIDERING THE IMPORTANCE OF FALLBACK FOODS FOR PRIMATE ECOLOGY AND EVOLUTION

Fallback foods are becoming increasingly invoked as key selective forces that determine masticatory and digestive anatomy, influence grouping and ranging behavior, and underlie fundamental evolutionary processes such as speciation, extinction, and adaptation. Here, we consider several basic questions about the importance of fallback foods for primate ecology and evolution. This is not an exhaustive list of important questions about fallback foods nor does it constitute a comprehensive review of the topic; rather, we discuss several questions related to fallback foods that we find particularly interesting and have data to address.

Are fallback foods a distinct class of food resources?

Fallback foods are often argued to be a distinct class of food resources that exert evolutionary and ecological pressures on primate populations in ways that other types of food do not. Dental morphology is one domain in which this distinction is pronounced. Building on early analyses by Rosenberger and Kinzey (1976), there is mounting evidence that aspects of dental morphology, such as enamel thickness, topography, and jaw robusticity, are best viewed as responses to evolutionary pressures imposed by fallback foods and not other classes of food (Kinzey, 1978; Yamashita, 1998; Lambert et al., 2004; Ungar, 2004; Taylor, 2006; Vogel et al., 2008).

Our own work on the population ecology of gibbons and leaf monkeys suggests that different classes of food exert distinct influences on primate populations on ecological time scales as well. Through long-term monitoring of the dietary intake of both species and of temporal variation in the availability of plant food resources, we operationally defined preferred and fallback foods for both primate species (Marshall, 2004; Marshall and Leighton, 2006). In addition, we assessed the population density of each species in each of seven distinct tropical forest types at GPNP and assessed the density of all foods in each of these habitats (Marshall, 2004, 2009; Marshall et al., 2009b). We found that habitat-specific population density for both species was unrelated to total food abundance (Fig. 3A,B). Furthermore, we found that leaf monkey density was highly correlated with measures of preferred food abundance during high fruit periods (Fig. 3D,F), while gibbon density was not (Fig. 3C,E). In contrast, habitat-specific gibbon abundance was closely related to the availability of figs, their primary fallback food (Fig. 3G), while the availability of fallback foods did not explain any variation in leaf monkey density across the seven forest types (Fig. 3H). These results clearly confirm that different classes of food have distinct effects on primate populations; all foods are not created equal. These analyses also suggest that the same class of foods may have divergent effects, depending on which primate species is using them. We consider a potential explanation for this pattern in the next section.

Is there a link between fallback foods and life history?

As noted earlier, our long-term work suggests that gibbon populations are limited by the availability of their most important (i.e., most frequently eaten) fallback food, while the abundance of leaf monkeys is determined by preferred food abundance during high fruit periods. We suggest that this difference may be the result of different selection pressures and life history adaptations in the two species.

Both gibbons and leaf monkeys exhibit the general life history traits characteristic of most primates; they are relatively long lived and reproduce slowly compared to other mammals (Harvey and Clutton-Brock, 1985; Charnov and Berrigan, 1993). However, gibbon life histories are substantially slower than leaf monkey life histories, despite the fact that these species are similar in size. Mitani (1990) calculated a mean interbirth interval (IBI) of 3.2 years for *Hylobates albibarbis* at GPNP and acknowledged that this was most likely an underestimate. He also reported extremely high infant and juvenile survivorship, with cumulative mortality to 6 years of age of only 18% (Mitani, 1990). Comparable data on the IBI and mortality of wild *Presbytis rubicunda* populations are not available. Asian colobine species for which such data are available (e.g., *Presbytis entellus*) are subject to high rates of infanticide (which increase infant mortality and decrease IBI), making them inappropriate comparisons. Harcourt and Schwartz (2001:7) suggest that 1.4 years is a “biologically reasonable” value for the IBI of *Presbytis*. Observations of several female leaf monkeys at GPNP with two offspring whose appearances suggested that they were less than 2 years apart in age indicate that this is a plausible estimate (AJM, personal observation). This suggests that leaf monkeys reproduce more than twice as often as gibbons. Mortality

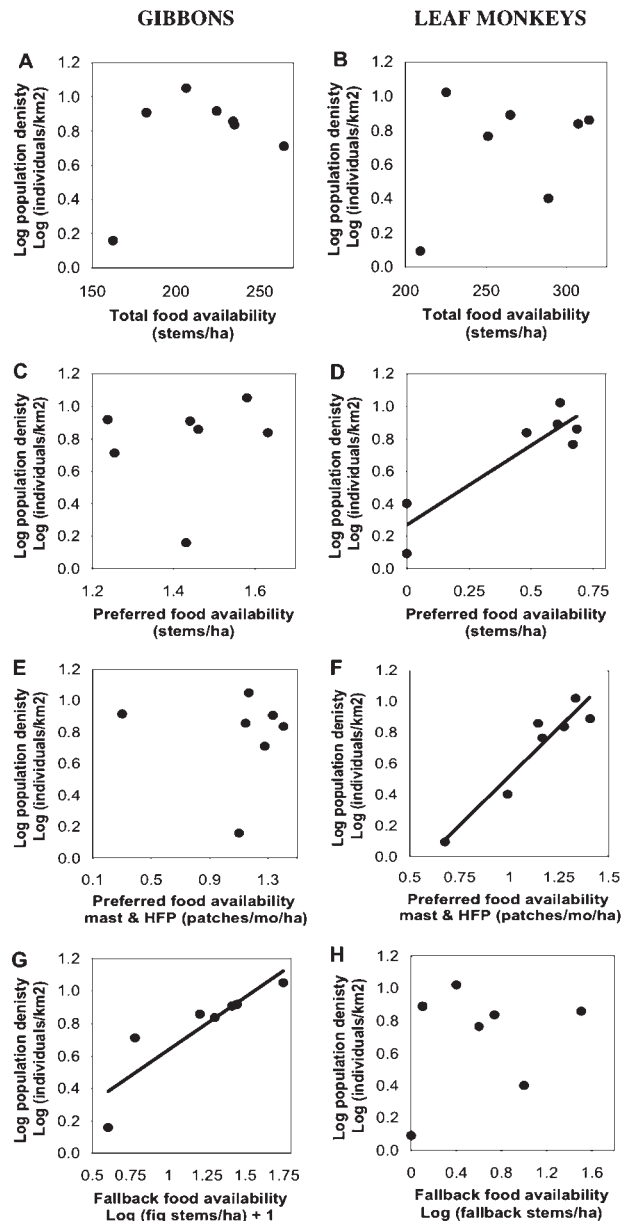


Fig. 3. Population density of gibbons and leaf monkeys in seven forest types at GPNP plotted against various measures of food availability. Population density is not correlated with total food availability (total food stems per hectare, measured in 10 ha of plots placed in each forest type) for gibbons (A, $r^2 = 0.19$, $P = 0.32$) or leaf monkeys (B, $r^2 = 0.11$, $P = 0.32$). Leaf monkey population density is highly correlated with the stem density of preferred food resources (D, $r^2 = 0.83$, $P = 0.004$), whereas gibbon population density is not (C, $r^2 = 0.02$, $P = 0.74$). Leaf monkey population density is similarly highly correlated with the total number of patches of preferred food available per month per hectare during periods of fruit abundance [masts and high fruit periods, see Marshall (2004) and Marshall and Leighton (2006); F, $r^2 = 0.90$, $P = 0.001$], whereas this measure has no predictive power for gibbon density (E, $r^2 = 0.006$, $P = 0.86$). Gibbon population densities are highly correlated with the abundance of figs (stems per hectare), their most important fallback food (G, $r^2 = 0.78$, $P = 0.008$); leaf monkey abundance is unrelated to the stem density of their fallback foods (H, $r^2 = 0.06$, $P = 0.60$). Lines are OLS regression lines, provided only for significant relationships.

data are unavailable for leaf monkeys, but their shorter IBIs suggest decreased investment in each offspring and consequently higher mortality relative to gibbons. This difference is in accordance with some comparisons between primate species showing that ape life histories are generally slower than monkey life histories (Schultz, 1968; [Smith, 1989](#)), although we note that there is considerable variation in life history strategies both within and between primate taxa ([Kappeler and Heymann, 1996](#); [Lee and Kappeler, 2003](#)).

It is reasonable to hypothesize that differences between the life history strategies of these two species explain why they are limited by distinct environmental factors. When compared with leaf monkeys, gibbons have relatively risk-averse life history strategies (i.e., low IBI, high infant and juvenile survivorship), suggesting that there has been strong selection in this species on traits that promote survivorship. Consumption of fallback foods permits individuals to survive through critical periods of resource scarcity. Thus, fallback foods limit gibbon populations through their effects on female condition during periods of low-food availability, which in turn affect birth rates (see [Marshall and Leighton, 2006](#)). In contrast, leaf monkey populations appear to be limited by the amount of preferred food that is available during periods of high resource availability. Such high-quality foods provide the necessary energy for reproduction. Although reproductive rate did not vary among leaf monkey females in different habitats ([Marshall, 2004](#)), high-quality habitats supported a higher number of reproductive females and therefore more offspring were produced there than in low-quality habitats. In short, the species with relatively slow life history is limited by foods that ensure survivorship, while the species with relatively rapid life history is limited by foods that enable reproduction. Whether this hypothesized link between life history and the nature of resource limitation holds more broadly across primates remains to be seen.

Do fallback foods always limit carrying capacity?

Although there is broad general support for the idea that food is a key determinant of habitat quality for primates, we still have a limited understanding of the mechanisms by which food limits primate population density. Classical ecological theory (e.g., [Wiens, 1977](#)) and some recent empirical results suggest that fallback foods may be particularly important as they provide sustenance during periods of low food availability when competition for food is most intense. As [Cant \(1980, p 542\)](#) explains, “food may be sufficiently abundant for long periods of time when resource limitation, if present, may operate in very subtle ways. When on rare occasions resources decrease dramatically, monkeys do indeed fall out of trees dead from hunger ... reducing population density ...” Empirical studies from a range of species support this view, suggesting that fallback foods serve as the key limitation on primate population density ([Foster, 1982](#); [Milton, 1982](#); [Davies, 1994](#); [Nakagawa et al., 1996](#); [Tutin et al., 1997](#); [Marshall and Leighton, 2006](#); [Marshall et al., 2009a](#)).

Although substantial evidence suggests that fallback foods are of paramount importance, several studies have suggested that preferred foods are the primary determinants of population density for some species ([Altmann et al., 1985](#); [Djojosedharmo and van Schaik, 1992](#);

[Balcomb et al., 2000](#); [Stevenson, 2001](#); [Marshall, 2004](#)). Other studies suggest that alternative components of food availability or quality—such as total or mean food availability, the abundance of important food resources, or protein to fiber ratios—primarily determine population density ([Mather, 1992](#); [Decker, 1994](#); [Chapman and Chapman, 1999](#); [Wasserman and Chapman, 2003](#); [Hanya et al., 2004](#)). Unfortunately, many of these results are difficult to interpret, as few studies explicitly and independently examine the effects of various food categories, and even fewer conduct multivariate tests that would allow us to conclusively determine which class of foods is the key factor that limits primate population density. Therefore, although identifying the fundamental ecological factors that limit populations remains a central goal of primate ecology, we still lack information on precisely how resources affect most primate populations. In particular, we cannot yet conclusively ascertain the extent to which fallback foods play a uniquely important role in determining habitat quality for primates. Despite this uncertainty, it is worthwhile to consider cases in which fallback foods are more or less likely to limit population density. Here, we mention three.

First, and most obviously, if factors other than food availability—such as predation, infanticide, disease, or social stress—limit population density, then the availability of fallback foods will have little effect on carrying capacity. Interestingly, alternatives to food as a limiting factor on primate density are often invoked in cases where fallback foods are assumed to be superabundant, and therefore by definition could not be limiting factors. Such arguments are frequently made about colobine species that can fall back on mature leaves. For example, [Yeager and colleagues \(Yeager and Kirkpatrick, 1998; Yeager and Kool, 2000\)](#) argue that Asian colobines are not food-limited since their fallback foods are leaves of tree species that appear to be superabundant in the forests that they inhabit. Instead, they argue that social stress may be the primary factor determining population density in these taxa ([Yeager and Kirkpatrick, 1998; Yeager and Kool, 2000](#)). Many others have also noted the apparent unimportance of food competition for colobines, but these discussions typically address ecological factors constraining group size, and as such, are not directly relevant to discussion of factors limiting population density. However, the assumption that feeding competition is a generally weak force for folivores is pervasive (e.g., [Wrangham, 1980](#); [Isbell, 1991](#); [Janson and Goldsmith, 1995](#); [Sterck et al., 1997](#)) and continues to inspire hypotheses about alternative ecological forces that might affect colobine populations (e.g., infanticide: [Isbell, 1991](#); [Janson and Goldsmith, 1995](#); [Crockett and Janson, 2000](#); [Steenbeek and van Schaik, 2001](#)).

Although many of these hypotheses are intriguing, they are generally based on the untested assumption that food is not a limiting resource for leaf-eating monkeys, rather than an empirical demonstration that fallback foods are superabundant and that other forces limit population density. With recent evidence that at least some folivores experience competition for food resources ([Koenig, 2000](#); [Snaith and Chapman, 2005, 2007](#)) and the knowledge that colobine species are generally highly selective in the leaves that they consume ([Oates et al., 1980](#); [Milton, 1981b](#); [Waterman et al., 1988](#)), the assumption that food is not limiting for these primates requires careful examination. To convincingly demonstrate that factors other than food availability limit a

primate species' population density, it must be shown that nonfood factors hold populations at a density below the level that would be imposed by food availability (as opposed to these factors simply being sources of mortality). Such a demonstration would be complicated by that fact that we lack a sufficiently clear understanding of how food limits population density to predict carrying capacity from first principles. An alternative test of the hypothesis that factors other than food limit population density would be a comparison of the population density of a species living in a range of contiguous habitats of varying quality. If food were the limiting resource for a primate species occupying several different forest types, then population densities would be expected to vary in direct proportion to the availability of relevant food resources. In contrast, if other factors (e.g., social stress and infanticide risk), which are unlikely to vary widely across habitats, primarily limit population density, then little variation in group sizes would be predicted.

Second, as noted earlier, fallback foods may be expected to be particularly important in setting carrying capacity for primate taxa with relatively slow, risk averse life histories that place a premium on survivorship, particularly of offspring. In contrast, species with relatively fast life histories and high-reproductive rates that enable them to more closely track fluctuations in resource availability may be expected to be limited by nonfallback food resources (e.g., preferred foods and important foods).

Third, it is unlikely that fallback foods serve as the primary factor limiting population density for species whose fallback foods are of such low quality that they do not provide sufficient energy to support physiological maintenance for extended periods. In such species, in the absence of higher quality food resources, individuals (and by implication, populations) would be unable to sustain themselves. A comparison of the two orangutan species illustrates this point. During periods of fruit scarcity, Bornean orangutans rely heavily (although far from exclusively) on the inner cambium from a fairly limited set of rainforest trees (Leighton, 1993; Knott, 1998), whereas Sumatran orangutans fallback on relatively high-quality foods, such as figs (van Schaik, 2004; Wich et al., 2006a). The fallback foods used by Bornean orangutans appear to be insufficient to maintain basic functions of physiological maintenance; during low-fruit periods, they mobilize fat reserves and appear to be susceptible to high rates of infection (Knott, 1998). In contrast, Sumatran orangutans seem to be much less severely affected by the periods of fruit scarcity that they experience, and unlike Bornean orangutans, they appear not to experience periods of extreme negative energy balance (Wich et al., 2006b). The population density of Sumatran orangutans is closely correlated with the stem density of figs (Wich et al., 2004a), implying that figs, a high-quality fallback food, may importantly limit their population density. However, this relationship does not appear to hold generally for Bornean orangutans (Marshall et al., 2006, 2007, 2009a), presumably due both to the lower stem densities of figs on Borneo and the fact that periods of fruit scarcity on Borneo are more extreme and tend to be of longer duration (Marshall et al., 2009a; Morrogh-Bernard et al., 2009). As noted earlier for gibbons and leaf monkeys, differences in the ecology and degree of environmental variability experienced by Sumatran and Bornean orangutans may underline apparent differences between the life histories of these two taxa (van Schaik et al., 2009).

Are lianas particularly important as fallback foods?

Figs are an important food resource for primates across the tropics; they are generally available year round, providing food when other resources are scarce (Janzen, 1979; Leighton and Leighton, 1983; Terborgh, 1986; Lambert and Marshall, 1991; Conklin and Wrangham, 1994; O'Brien et al., 1998). Several primatologists have reported that some lianas (woody climbing vines) play a similar ecological role at a number of sites in Africa and Asia (Leighton and Leighton, 1983; Davies, 1991; Moscovice et al., 2007; Takenoshita et al., 2008), suggesting that this plant growth form might be a particularly important source of fallback foods for primates more generally. The broad question of whether lianas are disproportionately important as fallback foods across the primate order will require a comparative analysis of more detailed phenology and primate feeding data sets than are available in the published literature (see above). Here, we simply consider whether lianas, as a broad category of plants incorporating a wide range of taxa, serve as important fallback foods for gibbons and leaf monkeys at GPNP.

At GPNP, liana fruit production does not follow the predominant pattern of reproductive behavior observed among trees (Cannon et al., 2007a,b). In fact, only one liana taxon, *Willughbeia* spp. (Apocynaceae), significantly limits its reproduction to community-wide mast fruit events, and this taxon does so only weakly (Cannon et al., 2007b). Lianas that produce fruits consumed by gibbons and leaf monkeys follow a similar pattern to that observed among all lianas. Fruit production by these lianas is very weakly correlated with tree fruit availability, a pattern also observed in figs at GPNP (Fig. 4A,B). At present, we cannot assess whether or not liana taxa might have evolved reproductive strategies that are distinct from trees, although it is plausible to hypothesize that lianas have been selected to fruit outside of periods of generally high fruit production, possibly due to their inability to compete with trees for vertebrate dispersers.

Lianas are important food resources for both gibbons and leaf monkeys during certain periods. Lianas comprise roughly 15% of all independent feeding observations for each species, although the importance of lianas varies substantially over time (range, 0–24% for gibbons, 0–40% for leaf monkeys; Marshall, 2004; Fig. 5). The observation that lianas are important food resources that are available during periods of resource scarcity suggests that they may, as a group, serve as fallback foods for gibbons and leaf monkeys. We did not find support for this general hypothesis at GPNP: the total importance of all lianas in the diet was not negatively correlated with the abundance of preferred food resources for either primate taxon. Nevertheless, a substantial number of particular liana taxa do serve as fallback foods for each species (e.g., some Annonaceae lianas, *Agelea* (Connaraceae), *Phytocrene* (Icacinaceae), and *Zizyphus* (Rhamnaceae) for gibbons; *Agelea*, *Gnetum* (Gnetaceae), and *Uncaria* (Rubiaceae) for leaf monkeys).

Does an understanding of fallback foods contribute to primate conservation?

We end with three points that address how the concept of fallback foods might be usefully applied to primate

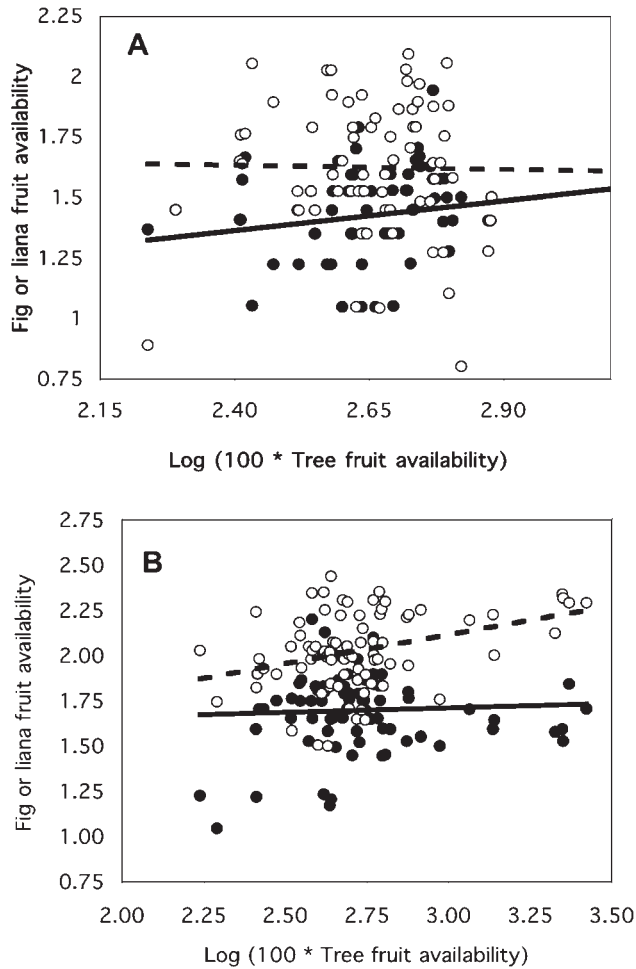


Fig. 4. Fig and liana fruit availability compared to tree fruit availability for gibbons and leaf monkeys at GPNP. The availability of figs and liana fruits are essentially unrelated to availability of fruit from trees for both gibbons (A) and leaf monkeys (B). Closed circles indicate fig [log (fig patches per hectare) + 2] and open circles indicate liana [log (liana patches per hectare) + 2] fruit availability versus tree fruit availability in each of 69 months between January 1986 and September 1991 at GPNP. Fruit availability was assessed in 126 phenology plots placed across the seven forest types that these species inhabit. Fruit production by figs is uncorrelated with tree fruit availability and fruit production by lianas is weakly correlated with tree fruit availability (A: figs: Spearman's $\rho = 0.12$, $P = 0.30$, lianas: $\rho = 0.28$, $P = 0.02$; B: figs: $\rho = 0.06$, $P = 0.61$, lianas: $\rho = 0.27$, $P = 0.01$). OLS regression lines are included for visualization purposes only (solid lines for figs, dashed lines for lianas); because months are nonindependent, regression analyses are inappropriate.

conservation efforts. First, an understanding of the ecological importance of fallback foods could improve the management and conservation of primate populations living in timber concessions. Since fallback foods are frequently the primary determinant of primate carrying capacity, special attention should be taken to spare fallback foods during selective logging operations. Some reduced impact silvicultural regimes entail the cutting of all liana stems prior to logging to reduce collateral damage when trees are felled (Meijaard et al., 2005). As many lianas serve as fallback foods, this practice may have a severe and unintended consequence on primate

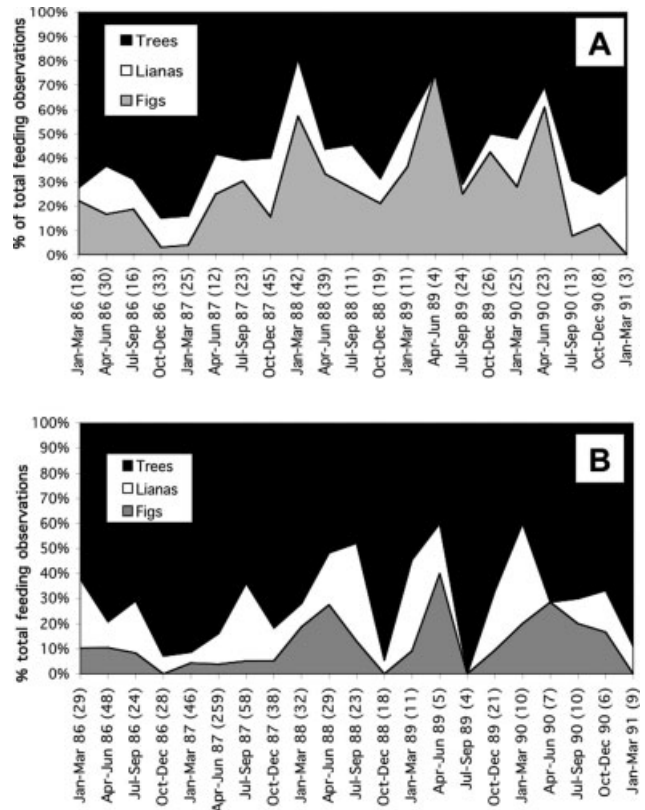


Fig. 5. Changes in dietary composition for gibbons and leaf monkeys at GPNP. Dietary composition over time by plant growth form for gibbons (A) and leaf monkeys (B) at GPNP. Figure is based on independent feeding observations recorded on censuses between January 1986 and March 1991 ($N_{\text{GIBBONS}} = 450$, $N_{\text{LEAF MONKEYS}} = 715$). Data are lumped into 3-month periods to reduce the effects of sampling error associated with small sample sizes. Parentheses indicate the number of independent feeding observations during each period.

populations (Schnitzer and Bongers, 2002). In addition, foresters attempting to manage timber concessions to maximize conservation benefit should make efforts to avoid the felling of timber trees that serve as hosts for large strangling figs, which serve as fallback foods for many vertebrate taxa (Leighton and Leighton, 1983; Johns, 1986).

Second, when degraded lands are being reforested or rehabilitated to increase their value for primate conservation, fallback food resources should be carefully considered as potential species to be planted. Often managers assume that the planting of preferred fruit trees is the best way to increase the carrying capacity of a forest block (Meijaard et al., 2005). However, if fallback foods, not preferred foods, are the primary determinant of population density, population size might be maximized by planting trees or lianas that provide food during periods of low overall food availability. Planting of such taxa may provide the added benefit of reducing the pressure on primate populations living near human settlements to raid crops during fruit poor times, which would reduce the potential for conflict among human and non-human primates (Naughton-Treves et al., 1998).

Third, the logic underlying the importance of fallback foods can be applied equally well to fallback habitats.

Many primate species, especially larger-bodied species with extensive home ranges, occupy a range of distinct habitat types. Often certain habitats are disproportionately used during periods of overall fruit scarcity, serving, in effect, as fallback habitats (Fleming and Partridge, 1984; Kano and Mulavwa, 1984; Watts, 1998; Curran and Leighton, 2000; Furuichi et al., 2001; Cannon et al., 2007a). Such habitats are crucially important in maintaining populations. A well-protected, large tract of normally preferred habitat may not be able to sustain a population if fallback habitats used during occasional periods of food shortage are not also protected. This implies that a habitat may be crucially important for the conservation of a species, even though the species may rarely inhabit it. In other words, just as occupancy of a habitat does not always imply suitability (e.g., due to source-sink dynamics, Marshall, 2009), lack of occupancy during certain periods does not necessarily imply that a particular habitat is not important for conservation.

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