Chapter 7 Food as a Selective Force in Primates

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PRIMATES MUST EAT to survive; the acquisition of food resources is thus among one of the most significant selective pressures affecting their biology. The necessity of finding food to meet nutritional requirements must be balanced with avoiding predation and securing mates, and thereby influences primate physiology, ecology, activity, movement, and social relationships. All animals, including primates, should typically avoid expending energy through unnecessary travel, and should eat the most nutritious foods available to them. In a classic study of baboons (*Papio cynocephalus*), Altmann found that the closer an individual's foraging approached the optimal amounts of protein and energy (Pyke 1984), the higher its fitness (Altmann 1991; Altmann et al. 1993; Altmann 1998). Because of the importance of food as a selective pressure for so many aspects of primate biology, it is not surprising that primate feeding ecology has received considerable attention in the literature over the past 25 years (Clutton-Brock 1977; Milton 1980; Cant & Temerin 1984; Rodman & Cant 1984; Hohmann et al. 2006).

Here we examine the feeding problems primates encounter and the strategies they employ to satisfy their nutritional needs. We also consider the consequences of adopting specific strategies. Our goal is to evaluate what is known about primate diets and to stimulate research on primate foraging strategies by identifying new ways to interpret diet and feeding data. We start by reviewing primate nutritional requirements, diets, and digestive strategies. We then address three central problems in the study of primate feeding biology: how do foraging strategies influence primates with respect to their (1) ecology and distribution, (2) movement and ranging patterns, and (3) behavior and social organization. For each problem, we present basic information and an illustrative example. We conclude with a summary of how feeding and foraging biology impacts the conservation potential of a species.

Primate Nutrition and Diet

Like all animals, primates require a full complement of carbohydrates, protein, lipids, vitamins, and minerals for growth, development, survival, and reproduction. Obtaining an adequate balance of these nutrients, while minimizing the ingestion of toxins, is challenging. For field biologists, understanding the precise requirements of different primates is difficult because it requires experimental studies that include manipulation and deprivation of key nutrients. Studies of this nature are often impractical and unethical. Nonetheless, the US National Research Council has assembled the requirements of 31 different nutrients, primarily based on experimental studies of rhesus macaques (*Macaca mulatta*), baboons (*Papio* spp.), squirrel monkeys (*Saimiri* spp.), and humans (NRC 1998).

Energy

Energy requirements are determined by three key factors: the energetic costs of baseline functions (basal metabolic rate, or BMR), the costs of activity, and the costs of specific life stage reproduction and lactation for females and growth for juveniles. These requirements are typically met by ingesting a combination of lipids and carbohydrates. The energy needs for sustaining basic metabolism and bodily function were historically estimated by Kleiber's equation, which states that the energy needed to maintain BMR is a function of body weight (BW), specifically $BW^{0.75}$ (Kleiber 1961). This general relationship means that larger animals need to consume less energy per kilogram of body mass than smaller animals. Some specific data are available for primates (Ross 1992; Genoud 2002). The Kleiber equation has been substantially revised over the past few decades to include data from more species (McNab 1988, 2002; Nagy 1994). For free-ranging mammals, the equation to estimate energy needed to maintain life during normal activities, field metabolic rate (FMR), is expressed in kilojoules as $4.63\ BW^{0.762}$ (Nagy & Milton 1979; Nagy 1994). Neither FMR nor BMR is constant for particular species. For example, in callitrichines, sleeping reduces BMR by 30% (Thompson et al. 1994; Genoud et al. 1997). Ambient temperature also significantly affects FMR and BMR estimates, particularly for cheirogaleid primates that hibernate or go into torpor (Schülke & Ostner 2007); metabolic rates during torpor were 86% of those not in torpor (Schmid et al. 2000). Numerous studies have attempted to estimate the energy requirements of primate activities (Madame Berthe's mouse lemurs, *Microcebus berthae*, Schmid et al. 2000; golden lion tamarins, *Leontopithecus rosalia*, Miller et al. 2006; mantled howlers, *Alouatta palliata*, Milton 1998; Nagy & Milton 1979; colobines, DaSilva 1994; Wasserman & Chapman 2003; brown capuchins, *Cebus apella*, Janson 1988; chimpanzees, *Pan troglodytes*, N'guessan et al. 2009). For example, Pontzer and Wrangham (2002) estimated the locomotor energy costs of chimpanzees and found that they spent much more energy on terrestrial than arboreal travel. Interestingly, orangutans (*Pongo* spp.) have an extremely low rate of energy use, which may be an evolutionary response to food shortages (Pontzer et al. 2010), which are seasonally common (Knott 1998).

Pregnancy and milk production incur additional costs for female primates, while juveniles need to meet the energy requirements of growth. Pregnant females require about 17% to 32% more energy than nonreproducing females (Robbins 1993). These increased energy requirements can influence female foraging strategies, since females that are sized similarly to males will need to eat higher-quality food than males, or increase their intake per kilogram of body mass. The energy cost incurred by primate females compared to males depends on the degree of sexual dimorphism. Where male body size exceeds female body size by 60% or more, male energy costs on an absolute basis are greater than those for females (Key & Ross 1999), and this may reduce the need for diet-based sexual segregation among primates (Kamilar & Pokempner 2008). Juvenile primates are likely the most susceptible to nutritional stress because their small body size coupled with the increased energy needed for growth means that they require more energy per kilogram of metabolic body mass than adults of both sexes. For example, captive juvenile gorillas (*Gorilla gorilla*) can accumulate as much as 19 kg of body mass per year, so that by age 10 they may reach 120 kg (Leigh & Shea 1996; Bedyaev 2002). This will require juveniles to consume more energy per kilogram of body mass than adults (Rothman et al. 2008b). Provisioned juvenile baboons grow faster and reach sexual maturity earlier than do unprovisioned baboons (Altmann & Alberts 2005), indicating that resource availability strongly affects the growth rate of juveniles.

Protein

Many studies have focused on the importance of protein in primate diets, suggesting that protein is an important criterion for food selection (Milton 1979; Oates et al. 1990; Chapman & Chapman 2002; Chapman et al. 2002a). However, primates generally have slow growth rates, produce dilute milk, and reach their full size later than other mammals, suggesting that they may not have high protein requirements and may consume more protein than needed (Oftedal 1992). Like energy requirements, protein requirements are dependent on life stages, and immature animals require the most protein per unit of metabolic body mass. The protein requirements of primates depend on protein quality and available energy. Most primates require less than three grams of protein per kilogram of metabolic body weight per day, or 6% to 8% of the dietary dry matter (NRC 2003). However, the quality of protein must be assessed. For example, tannins (Robbins et al. 1987), fiber-bound nitrogen (Conklin-Brittain et al. 1999; Rothman et al. 2008a), and amino acid imbalances can all affect the digestibility of protein. In general, the quality of protein is rarely estimated in primate diets (Rothman et al. 2008a), and very few studies have examined the amino acid profiles of foods eaten by primates (but see Milton & Dintzis 1981; Curtis 2004).

Vitamins and Minerals

Very little is known about vitamin and mineral requirements of wild primates, although recent work highlights their significance. Minerals are particularly important for juvenile growth, and deficiencies may have permanent consequences for growth and lifetime fitness. Calcium and phosphorous make up 70% of the mineral matter in animals, and are predominant in bones and teeth in a 2:1 ratio. They are necessary for growth, and a deficiency in either element markedly affects bone development and can cause rickets, osteomalacia, and osteoporosis (Robbins 1993). Since plants do not typically concentrate sodium and the soils of many tropical regions are poor in that element, tropical herbivores often have difficulty obtaining the sodium they need. Symptoms of sodium deficiency include softening of bones, reduced growth, blindness, and reproductive impairment. Sodium is the only mineral that elicits a particular hunger and drive for acquisition. Guerezas (*Colobus guereza*) visit underground caves and increase their travel distances to exploit high-sodium resources (Oates 1978; Fashing et al. 2007; Harris & Chapman 2007), and mountain gorillas eat decaying wood that contains high levels of sodium (fig. 7.1; Rothman et al. 2006). Rode and colleagues (2003) demonstrated that the sodium content of foods eaten by primates was extremely low; no single food met the guidelines set by the National Research Council (NRC 2003), and sodium intake from the typical plant diet fell well below suggested requirements throughout the year (Rode et al. 2003; Rode et al. 2006). However, infrequently eaten foods can provide important mineral sources. Gums from selected tree species, eaten infrequently by chimpanzees (Ushida et al. 2006) and by saddleback (*Saguinus fuscicollis*) and mustached (*Saguinus mystax*) tamarins (Smith 2000), are a rich source of calcium and sodium. Seemingly nutrient-deficient bark and wood can also provide needed micronutrients that are absent in frequently eaten foods (Rode et al. 2003; Rothman et al. 2006; Stephens et al. 2006; Reynolds et al. 2009), and for colobus monkeys, flowers provided a source of copper, a mineral typically deficient in the diets of monkeys (Rode et al. 2003, 2006). As more information about the mineral contents of primate diets becomes available, we will be in a better position to understand their nutritional needs and how food ultimately influences primate biomass and diversity.

Primate Foods

Over the past 65 million years, primates have adopted several strategies to solve problems associated with feeding (Fleagle & Gilbert 2006). The adoption of these different strategies means that the same food can yield different benefits to each species that feeds on it, but some general patterns do emerge. Extant primates have evolved specializations to consume fruit, seeds, leaves, insects, gums, or most often a mixture of these dietary items. Each food source exhibits significant structural and chemical differences which influence primate foraging strategies and feeding adaptations. In tropical forests, most tree species produce fleshy fruits thought to have coevolved to be eaten and dispersed by frugivores. Primates constitute 25% to 40% of the frugivore biomass in these forests, likely making them an essential part of this coevolutionary process (Chapman 1995). Many fruits contain sugars, encouraging primates to eat them and disperse their seeds. This relationship does not require fruits to be nutritionally balanced, and frugivorous primates typically supplement their diet with young leaves or insects, which provide protein (Janson & Chapman 1999). While there is debate regarding how such coevolutionary relationships develop, in many cases fruiting species are thought

Fig. 7.1. Alternative means of obtaining salts through foraging: (A) a red colobus monkey eating soil and (B) mountain gorillas eating decaying wood. Photos courtesy of Jessica Rothman.

to have coevolved with specific dispersers and to be consumed by them (Howe & Smallwood 1982; Herrera 1985; Fischer & Chapman 1993). In such cases, fruits may contain secondary compounds that are toxic to some species but not others. For instance, the chemicals that make red peppers spicy to humans and other mammals do not apparently affect birds (Janson & Chapman 1999). Secondary compounds may have important consequences for primate feeding behavior. For example, the fruits of *Strychnos mitis* are laden with compounds that are toxic to some mammals; they include phenolics, terpenes, flavonol glycosides, and various alkaloids (Thepenier et al. 1990). Some cercopithecines, however, appear to have evolved means to deal with these compounds. Thus, *Strychnos mitis* fruits in Kibale are readily eaten by redtail monkeys (*Cercopithecus ascanius*, Lambert 2001) and blue monkeys (*Cercopithecus mitis*, Rudran 1978) but are ignored by chimpanzees (Lambert 1997; although different *Strychnos* species are eaten by chimpanzees at Gombe: Goodall 1986).

Unlike fruits, seeds are typically mechanically protected with hard protective structures designed to stop primates getting to the nutritious embryo inside. As a result, only a handful of primates have evolved the dental and morphological skull features needed to break seeds (e.g., *Cacajao* spp. and *Lophocebus* spp., Kinzey 1992; Lambert et al. 2004). For these primates, seeds can be an important part of their diet. For example, the average monthly seed consumption by white-faced sakis (*Pithecia pithecia*) was 63.2% ± 32.7% (Norconk & Conklin-Brittain 2004; fig. 7.2).

Leaves provide the photosynthetic energy used for plant growth and reproduction. Thus, it is not to a plant's advantage to have its leaves eaten. Fiber, including hemicellulose and cellulose, is a polymer of sugar molecules, but without the help of microbes, primates cannot digest the structural components that may form a large portion of leaves. Only a few species (e.g., *Colobus, Procolobus, Indri,* and *Alouatta*) with a large capacity for hindgut or foregut fermentation can rely on a diet comprised mostly of leaves (Milton 1981b; Lambert 1998). Folivores typically choose specific leaf species and leaf parts (Glander 1982; Chapman

Fig. 7.2. A relatively small number of primate species have evolved the specializations to support a diet based heavily on seeds, but white-faced sakis (*Pithecia pithecia*) are one example. Here an adult male at Brownsberg Nature Park, Suriname, feeds on the seeds of *Garcinia madruno* of the Clusiaceae family. Photo courtesy of Marilyn A. Norconk.

Fig, 7.3, Individuals of many primate species—such as this young male white-faced capuchin monkey in Lomas Barbudal, Costa Rica—spend considerable time eating insects on a seasonal basis. Photo courtesy of Susan Perry.

& Chapman 2002). Young leaves are most often selected, as they usually have smaller concentrations of fiber than mature leaves (Milton 1979; Chapman & Chapman 2002). Eastern red colobus monkeys (*Procolobus rufomitratus*) commonly eat only leaf tips or petioles (Chapman & Chapman 2002).

Insectivory is practiced by many primates (fig. 7.3). Insects are typically high in protein and energy and are easy to digest, with the exception of their chitinous skeleton (Moir 1994; Barker et al. 1998). Some primates are well-adapted insectivores. For example, the northern lesser galago (*Galago senegalensis*) and western fat-tailed dwarf lemur (*Cheirogaleus medius*) masticate insects to a small size, which probably improves chitin digestion (Sheine & Kay 1979). The potto (*Perodicticus potto*) uses chitinolytic enzymes to digest insects (Cornelius et al. 1976), and a gene for chitinase has apparently been conserved in a variety of primates (Gianfrancesco & Musumeci 2004). Insects can be poisonous, but some nocturnal strepsirrhines may have evolved mechanisms to deal with their secondary compounds because they specialize on noxious prey (Charles-Dominique 1977).

Lastly, only a few species specialize on gums, but gummivory is prominent among strepsirrhines and callitrichines (Nash 1994). These species typically supplement their diets with insects, fruits, and young leaves. Patas monkeys (*Erythrocebus patas*) feed extensively on *Acacia* gums, which is unusual because patas monkeys are large-bodied in comparison to typical gummivores like callitrichines (Isbell 1998). Gums are nutritionally different from saps because gums require fermentation while saps do not (Nash 1994). Few primates possess diets containing large portions of sap, but slow loris diets (*Nycticebus coucang*) contain 35% phloem sap and 32% floral nectar (Weins et al. 2006).

This description of primate foods might lead one to assume that species consistently specialize on particular foods. However, there can be extreme variation in the types of foods eaten among populations of the same species. For example, Butynski (1990) studied four groups of blue monkeys at the same site and found that the amount of time feeding on fruit ranged from 22% to 35% among groups. Fruit intake of blue monkeys among populations in East and South Africa ranged from 26% to 91%, and leaf intake varied from 3% to 47 % (Chapman et al. 2002b). Another population of blue monkeys relies on bamboo (*Arundinaria alpina*) for 60% of its foraging time (Twinomugisha et al. 2006). Such variability makes it extremely difficult to identify the components of a diet that lead to selection, because one population will experience one selective regime while other populations, which may interbreed with the first, will experience different selection pressures. In addition, there can be marked spatial and temporal variation in the same food item. In the Kibale National Park, Uganda, young leaves of the same tree species varied in protein content from 22% to 47% (Chapman et al. 2003), and the fat content of a single species of ripe fruit varied seasonally from 0.3% to 30% (Worman & Chapman 2005). Consequently, few generalizations can be made about the nutritional contents of foods, and classifying feeding strategies broadly (e.g., folivory, frugivory) may not be a reliable indicator of a diet's nutritional quality (Danish et al. 2006; Rothman et al. 2007).

Primate Digestive Strategies

It is often assumed that different primate species obtain similar nutritional benefits from the same food item (Cords 1986; Chapman 1988; Isbell 1991), but nutritional gains are best interpreted and understood in light of species adaptations. For example, leaves are considered low-quality "fibrous" food sources because they often contain high amounts of structural carbohydrates. Depending on their digestive anatomy and physiology, however, primates can gain substantial amounts of energy from leaves (Milton et al. 1980; Milton & McBee 1983). As a result, the nutritional value of a particular food item is often species-specific. Here we first explore the potential for significant variation in digestive strategies among species eating the same foods by considering a single digestive process: variation in food transit time. Second, we evaluate the digestive mechanisms that primates use to consume the secondary compounds in plants.

Food Transit Time

The time it takes food to clear the digestive tract is critical to evaluate primates' foraging strategies, since longer transit times are typically associated with a greater ability to digest structural carbohydrates via fermentation (Chivers & Hladik 1980; Milton 1981b; Kay & Davies 1994; Canton et al. 1999; Lambert 2002). In contrast, faster transit times are usually associated with an increase in the total amount of food that can be processed. Thus, easily digestible nutrients (e.g., simple sugars) are more accessible, and indigestible material like seeds and chitin is expelled faster (Lambert 2002).

In a classic study, Milton (1981b) compared the digestive ecology between two sympatric monkeys in Panama, the primarily frugivorous Geoffroy's spider monkey (*Ateles geoffroyi*) and the folivorous mantled howler monkey. Milton found that howler monkeys had much longer transit times than spider monkeys, and suggested that digestive constraints forced both monkeys to consume particular foods (Milton 1981b; 1993). Although both monkeys ate both fruit and leaves, the diet foundation of howler monkeys was leaves, and that of spider monkeys was fruit. Howler monkeys ate ripe fruit when it was available, but their diet was never completely fruit because their long transit time prevented them from consuming it in sufficient quantities. Conversely, spider monkeys with short transit times were committed to a frugivorous foraging strategy because they could not gain enough energy from a leaf-dominated diet since they required fermentation time. These seminal ideas on the differences in digestive ecology inspired subsequent investigations into primate digestive ecology.

Lambert (1998) documented large variations in transit time in similarly sized frugivorous primates, which imply a diversity of digestive strategies. Primarily frugivorous brown capuchins (3.5 kg) have transit times of 3.5 hr, while similarly sized frugivorous crowned mona monkeys (*Cercopithecus pogonias*, 3.75 kg) and redtail monkeys (3.6 kg) have transit times of 16.6 and 19.7 hr respectively. The slower transit times of crowned mona and redtail monkeys imply that guenons have a greater ability to gain nutrients from food items that contain structural carbohydrates, like fibrous leaves and fruits, than do capuchins. Although primates with specialized guts and longer transit times have the ability to digest fibrous foods, this does not mean they will select those foods; primates will typically prefer foods that have the most easily gained nutrients, like simple carbohydrates. In periods of preferred-food scarcity, primates that have adaptations to deal with structural carbohydrates may be better equipped to deal with food shortages than those with less flexible digestive tracts (Lambert 2007; Marshall & Wrangham 2007). The ability to digest fibrous foods has important implications for the conservation of frugivores, because animals faced with a low supply of their preferred foods often need to eat more fibrous foods like leaves instead of fruit.

Plant Secondary Compounds

Primate species can vary in their ability to obtain nutrients from plants containing toxins. Many plants contain one or more defensive compounds, including phenols, tannins, terpenes, alkaloids, cyanogenic glycosides, protease inhibitors, lectins, nonprotein amino acids, cardiac glycocides, and oxalates (Glander 1982; Seigler 1991; McNab 2002; Foley & Moore 2005). These include some well-known compounds such as strychnine, caffeine, cocaine, nicotine, and cyanide.

A classic and still very useful distinction of plant chemical defense concerns whether defenses are qualitative or quantitative (Feeny 1976). Qualitative defenses are typically found in small amounts in the plant and typically represent less than 2% of the dry weight. They usually interfere with a metabolic process and are often toxic, unless the species has evolved a detoxification mechanism that is specific to the defensive compound in question. One example of a qualitative defense is cyanide. For most primates cyanide is lethal at small doses, but the bamboo eaten by golden bamboo lemurs (*Hapalemur aureus*) contains about 10 times the amount of cyanide that would be lethal to humans (Glander et al. 1989; Ballhorn et al. 2009). It remains unclear what mechanism these lemurs or other bamboo-eating primates use to detoxify the bamboo (Glander et al. 1989; Twinomugisha et al. 2006).

A quantitative defense is typically present in substantial amounts and has properties that reduce the digestibility of cell constituents such as tannins. Tannins are common in tropical plants and can render protein inaccessible to animals (Mole & Waterman 1985; Robbins et al. 1987). Several studies have demonstrated that tannins affect primate foraging behaviors (Oates et al. 1977; McKey et al. 1981; Wrangham & Waterman 1981; Glander 1982; Marks et al. 1988), but others have ambiguous results (Barton et al. 1993; Chapman & Chapman 2002). This may be due in part to some primates having adaptations to deal with tannins. These include proline-rich salivary proteins, which have a higher than average affinity for binding with tannins and allow for uptake of plant protein in the presence of tannins (Mole et al. 1990) and microbes in the fore or hind-gut, which are able to degrade these toxic compounds (Foley & Moore 2005; Frey et al. 2006). Alternatively, methodological problems may have hindered our ability to measure the tannins accurately (Foley et al. 2005; Rautio et al. 2007; Rothman et al. 2009).

Evidence suggests that environmental conditions can influence the frequency in occurrence of some of these compounds, or the amount present in particular food items. For example, some areas of the Amazon have white, sandy, poor soils while other areas have soils that are high in organic content (Emmons 1984). Kinzey and Gentry (1979) contrasted the diet of two species of titi monkeys (*Callicebus* spp.): white-collared titi monkeys (*Callicebus torquatus*) are found living in habitats with poor white-sand soils, while dusky titis (*Callicebus moloch*) occur in forests that grow on soils rich in organic content. Kinzey and Gentry speculated that the monkeys' diets differed because plants growing on poor soils protected their leaves with quantitative defenses (see also McKey et al. 1978 for a similar example). This intriguing speculation requires further study.

There is good evidence that some species respond behaviorally to the presence of secondary compounds, varying their consumption of foods with different plant toxins. With the exception of weasel lemurs (*Lepilemur mustelinus*), most species in one lemur community selected foods with high levels of protein (Ganzhorn 1988, 1989). Indris (*Indri indri*) and eastern woolly lemurs (*Avahi laniger*) ate leaves with high levels of tannins but avoided alkaloids, while *Hapalemur* avoided both. In contrast, brown lemurs (*Eulemur fulvus*) and greater dwarf lemurs (*Cheirogaleus major*) tolerated tannins and alkaloids while weasel lemurs ate leaves high in alkaloids. Such food selection suggests that different species have evolved different physiological mechanisms to cope with these compounds.

The action of plant toxins is complex, and it is clear that we are only beginning to understand the physiological strategies that different species employ to deal with these compounds (Foley & Moore 2005; Rothman et al. 2009). Primates can either detoxify the compounds, bind substances to them to make them inoperable, or tolerate them. Each of these strategies will be a function of a species' abilities and will influence the value of a food item. For example, detoxifying a compound can have a significant cost. Thomas et al. (1988) demonstrated that meadow voles (*Microtus pennsylvanicus*) increase their metabolic rate by 14% to 24% when fed phenolic compounds. Comparable data for primates are not yet available.

Three Important Questions in Primate Foraging Ecology

Food as a Selective Force Influencing Primate Ecology and Distributions

How food resources influence the ecology and distribution of primates has been a central question of primate research since the first field studies began, and a critical problem involves temporal and spatial changes in food availability. Many researchers have documented seasonal variation in the food supply (Beeson 1989; van Schaik et al. 1993; DaSilva 1994; Remis 1997; Conklin-Brittain et al. 1998; Poulsen & Clark 2004), but food availability and distribution changes more rapidly than that. The availability of plant reproductive and vegetative parts is irregular, and it induces short-term changes in abundance and scarcity of food for consumers (Gautier-Hion 1980; van Schaik et al. 1993). Monitoring these phenological changes is often time-consuming because the fruiting and leafing patterns of food trees must be examined at least on a monthly basis. In addition, it is often not known at the beginning of a study which foods are being eaten. Primates respond to these phenological changes in a complex fashion that may involve increased travel, reliance on less nutritious foods, decreased activity, or lower reproductive and juvenile survival rates (Peres 1994; Brugiere et al. 2002).

Seasonal and monthly phenological differences are critical; however, there are also marked interannual changes in food availability (Tutin et al. 1997; Chapman et al. 2005a). Over 12 years, temporal variability in fruit availability in Kibale National Park, Uganda, was pronounced, with the proportion of trees per month with ripe fruit varying between 0.14% and 15.93% (Chapman et al. 2005b). Primates respond to this variation across years, making characterization of a primate population's diet for purposes of comparative studies difficult, unless studies encompass many years of the same population. For example, the fruits of *Bursera simaruba* were available for every dry season during a six-year study of Geoffroy's spider monkeys in Santa Rosa National Park, Costa Rica (Chapman et al. 1995), but it was only in the last year of the study that they fed heavily on this fruit. Because the fruit occurred at a very high density, a logical conclusion to be drawn from a study of just that year would have been that fruit density was higher in the dry season than in the wet season. However, since spider monkeys ignored this fruit in the previous five years of the study and instead fed on rarer foods (Chapman 1987), it seems likely that the opposite is true, and that in most dry seasons they relied on rare foods that were more profitable. In the last year, when other resources were unavailable, they fed on *B. simaruba.*

The phenology and availability of specific foods are important for particular primate species, and these foods have often been called keystone species. Keystone species are defined as those species that have a large and disproportionate impact on the community relative to their abundance such that their removal would be devastating to the entire animal community (Power et al. 1996). To determine community-wide importance, factors to consider include (1) temporal redundancy, (2) degree of consumer specificity, (3) reliability, and (4) abundance (Peres 2000). The term "keystone species" should not be used when referring to a food source that is important only to a single primate species; it must apply to a community of organisms. The importance of this concept for conservation is readily apparent: if a manager could identify keystone species in an ecosystem and conserve them, it would likely ensure the integrity of the whole community. Implementing this strategy is nonetheless difficult (Peres 2000).

Figs have been frequently hypothesized as examples of keystone plant resources in tropical forests (Terborgh 1986; Power et al. 1996), and recently textbooks have presented figs as a clear case to illustrate the keystone species concept (Bush 2000). This proposal remains to be critically examined, as few data exist demonstrating their importance to a community of species. This is worrisome because the conservation of figs has been advocated in management strategies (Primack 2006). Two studies have provided detailed analyses to determine whether figs serve as keystone species for primates. Gautier-Hion and Michaloud's (1989) study in Gabon showed that figs were infrequently eaten by most primates and other mammals, occurred at very low densities, and had unpredictable fruiting patterns. They concluded that fig fruits could not sustain most populations of frugivorous species during periods of low fruit availability, and thus were not keystone species. Similarly, a 12-year study in Kibale National Park, Uganda, determined patterns of fruit scarcity and the spatial and temporal availability of figs. Temporal variability in fruit resource availability was high; the proportion of trees (> 10 cm diameter at breast height) per month with ripe fruit varied from 0.14% to 15.93% (Chapman et al. 2005b). If figs served as keystone species for the frugivore community (or fallback foods; see below) over these 12 years, they would have had to be available during months when few other trees were fruiting. Less than 1% of the monitored fig trees fruited in the 34 months when fruit was scarce during the 149 months of the study. Figs failed to fruit in 17 of the 34 fruit-poor months, and more than 1% of the fig trees fruited during 11 of those 34 months. Accordingly, figs may provide fruit during some periods of food scarcity, but the number of trees is probably inadequate and the fruiting phenology is too inconsistent to sustain all of the frugivorous primate community in Kibale. This example demonstrates that the role of figs as keystone species (or as fallback foods) is likely scale-dependent. During periods of fruit scarcity, figs can best be exploited by highly mobile species with large home ranges who possess the ability to track fruiting figs. In Kibale, only gray-checked mangabeys (*Lophocebus albigena*) and chimpanzees have large enough home ranges to monitor widely dispersed fruiting fig trees (Chapman et al. 2005b). For species with small feeding ranges, like redtail monkeys (Chapman et al. 2005b), figs are unlikely to be important resources during periods of fruit scarcity. Because figs could only be keystone species for 2 of the 13 primate species in Kibale, they cannot be considered keystone species for the whole community. It is our view that figs have never been demonstrated to be a keystone resource for any primate community.

Even if figs are not a keystone resource, they may be an important food source for some primates at some periods of time. The importance of figs in tropical forests is substantiated by the large number of primates and other vertebrate frugivores that eat them (Shanahan et al. 2001). If figs are important foods and are being commercially harvested by humans, this would be a concern for primate communities. We present Bolivia as an example of what may be a general trend in timber harvesting. In Bolivia, the volume of *Ficus* timber harvested has increased by at least 65% since 1999 and the export value of *Ficus* products was approximately $US 1.4 million, which represented 13% of Bolivia's total revenue from exported timber products (CFB 2006; Felton et al. unpublished manuscript). Given that the commercial harvest of *Ficus* timber is increasing dramatically as more profitable timbers have already been removed, the value of figs to different primate communities should be assessed. If figs prove to be a generally important food resource, then pressure could be placed on the timber industry to decrease the rates of their extraction.

Food as a Selective Force Influencing Movement

An important theoretical challenge in primatology and a pressing issue in primate conservation is to understand how primates are distributed with respect to the temporal and spatial variation of food resources. All primates, regardless of their diet, confront the problem of gaining sufficient food to satisfy their nutritional requirements, and the solution involves selecting an optimal diet and travel routes (Charnov 1976; Pyke 1984; Stephens & Krebs 1986; Grether et al. 1992; Altmann 1998). The temporal and spatial availability of ripe fruits and young leaves of high quality varies considerably (van Schaik et al. 1993; Worman & Chapman 2005), and faced with this variation, animals must move across their landscape and adjust their diet.

In the past decade a great deal has been learned about the travel routes of primates (see also chapter 27, this volume). While it is clear that primates follow different strategies, in general they aim to minimize search costs relative to resource gain. Accordingly, it is interesting to consider whether primates move to the nearest available resource

(Garber 1988; Janson 1998) or plan their travel routes in the most efficient way to maximize the gains of future resources (Noser & Byrne 2006; Janson 2007). Milton (1980) noted that mantled howler monkeys oriented their travel patterns towards "pivotal" trees, which were food sources visited repeatedly until depleted; these trees were used as bases, but the monkeys then moved to nearby areas where they could feed on leaves and monitor many other fruit trees. Instead of monitoring the phenological states of thousands of tropical trees, a simple routine may provide the best means to exploit available resources (Di Fiore & Suarez 2007). Sympatric white-bellied spider monkeys (*Ateles belzebuth*) and Poeppig's woolly monkeys (*Lagothrix poeppigii*) traveled the same routes for several years, using topographical features of the landscape such as ridge tops (Di Fiore & Suarez 2007). For gray-cheeked mangabeys living in forests whose phenological patterns are difficult to predict (Chapman et al. 1999; Chapman et al. 2005a), individuals rely on detailed and sophisticated knowledge of the fruiting states and locations of their fruit trees (Janmaat et al. 2006a). Furthermore, mangabeys appear to use weather as a cue to locate fruit resources when they become ripe (Janmaat et al. 2006b). Understanding how primates move within their habitats and the methods they use to evaluate their space provides important insights into primate cognition (Chapman et al. 1999; Barton 2000; Janson 2007; chapter 27, this volume) and useful data for conservation managers.

Food as a Selective Force Influencing Behavior and Social Organization

Theoretically, differing combinations of levels and types of feeding competition should lead to variation in social structure and social bonding (Wrangham 1980; van Schaik 1989; Sterck et al. 1997; chapter 9, this volume). The nature of food resources determines the level and type of feeding competition. Scramble competition involves the common depletion of food resources while contest competition, including aggression, displacement, and avoidance, involves direct contests over food and can occur within and between groups (Nicholson 1933; Janson & van Schaik 1988). Animals must compete for access to resources when they are (1) limited in availability, (2) patchy and depletable, (3) variable in quality, or (4) able to be monopolized (Janson & van Schaik 1988; van Schaik 1989; Isbell 1991; Saj et al. 2007). When both within- and between-group contest competition are absent and only scramble competition is present, or when there is no competition for food and food resources are not monopolizable (Snaith & Chapman 2007), females are not expected to engage in agonistic interactions over food. This in turn should be associated with an absence of linear dominance hierarchies and infrequent coalitions (Sterck et al. 1997). These patterns should co-occur with female dispersal because coalition partners are not required in feeding competition. Female agonistic relationships are predicted to be rare, as are affiliative behaviors among females.

When food resources are limited, patchy, depletable, and monopolizable, contest competition will occur. Under these circumstances it will become advantageous for females to remain with kin on whom they rely as allies for cooperative defense of resources, either within or between groups (Sterck et al. 1997). Accordingly, female dispersal should not occur, as a female who attempted to transfer would lose access to allies. Contest competition between groups should only lead to a system in which female dominance relationships are egalitarian and individualistic, and where coalitions are rare. The presence of within-group contest competition (and its absence between groups) should lead to a nepotistic system in which females form linear and despotic dominance relationships, coalitions with kin, and mutualistic coalitions with other females to acquire and maintain their dominance rank, as the latter will be associated with priority of access to limited food resources.

Initially folivores were generally considered not to be food-limited. This idea stemmed from the assumption that leaves are superabundant in forest habitats. However, many studies have recently demonstrated that folivorous primates are very selective in what they eat, typically preferring young leaves of just a few species (Chapman & Chapman 2002; Koenig & Borries 2006). These observations suggest that leaf-eating primates may have different competitive regimes than previously thought. For example, several recent studies have found that eastern red colobus monkeys are food-limited and experience within-group scramble competition for food resources (Snaith & Chapman 2005, 2007, 2008). Large groups occupied larger home ranges than small groups, and group size was related to depletion of feeding patches. In addition, individuals in large groups suffered reduced foraging efficiency, assayed by long travel distances, more time spent feeding, less frequent feeding at preferred food sites, and more frequent feeding in small trees. Monkeys in large groups also experienced a concomitant reduction in female reproductive success. These results suggest that within-group competition occurs in red colobus monkeys. The behavioral consequences of this competition are currently under investigation.

Socioecological models rely on an understanding of the size, density, and distribution of food resources and how these variables influence a primate's ability to monopolize them (Wrangham 1980; Chapman et al. 1995; Isbell & Young 2002). However, the best way to measure these characteristics of food resources is not clear. There are two contrasting approaches. Isbell and colleagues have suggested that the behavior of the forager should be used to assess food distribution, because it is not the patchiness of the resource itself that is important, but whether the resource can be monopolized or usurped (Isbell et al. 1998; Isbell & Young 2002). This method suffers from measurement challenges for some species (e.g., how to measure such behaviors for primates feeding in dense canopy cover) and from the fact that usurpation of feeding sites may depend on a suite of non-food variables (e.g., stability of the dominance hierarchy). In cases where a resource can be monopolized, if it is abundant it may not induce competition. Other studies have attempted to quantify a direct measure of the characteristics of food resources (Chapman et al. 1995; Koenig 2000; Koenig & Borries 2006), but this approach also has limitations. What should one consider a food item? Most studies opt for an arbitrary inclusion of foods based on a set percentage of foraging effort (e.g., the top 5 or 10 of most frequently eaten foods), but typically there is no rationale presented for the percentage chosen or how it is calculated, and using different cutoff points can produce different outcomes (C.A. Chapman unpublished data). It is also not clear whether the animals respond similarly to all food items in the list of included foods. For example, if one food source is particularly preferred or provides needed nutrients, it may be more influential than another food source in determining competition and social organization. Several studies indicate that there is a strong tendency for primates to eat leaves at the end of the day, often just prior to entering the sleeping site (e.g., Chapman & Chapman 1991). Leaves can be high in fiber and difficult to digest. By choosing to feed on leaves just prior to resting at night, animals may reduce the distance travelled with a full stomach of leaves and not miss feeding opportunities on more profitable food items, as predicted by central place foraging (Orians & Pearson 1979). It is not clear whether the trees providing such leaf resources should be included in the resources that determine competitive regimes. It seems likely important to consider the "value" of particular items and how that influences the nature of the competitive regime.

One potential means of defining resource importance could be to use a geometric analysis of feeding and nutrition (Simpson & Raubenheimer 1995, 1999; Behmer & Joern 2008; Raubenheimer et al. 2009). Researchers could define functional optima (e.g., intake targets) for a specific period in which social behaviors are evaluated (e.g., a day), including a specified food, such as the leaves eaten by monkeys at the end of the day. Subsequently, if a food item is of questionable importance, the optima can be redefined excluding that specific item and the outcome can be reevaluated. Both the inclusion and exclusion of this item can be presented. The value of food items that are rarely selected but provide particularly important resources also requires consideration, but how they influence competitive regimes is largely unknown. For example, when species select particular food items such as decaying wood or soils to obtain salts (fig. 7.1; Rode et al. 2003; Rothman et al. 2006), the nature of the competitive regimes has not been quantified.

Food and the Conservation Potential of a Species

Current threats to primate populations have increased our need to understand these complex animals, their nutrient requirements, and how food resources act as a selective force. According to the Food and Agricultural Organization's Global Forest Resources Assessment (FAO 2005), forest lost between 2000 and 2005 was about 7.3 million hectares per year or approximately 200 km^2 of forest per day. Between 1990 and 2005, forest cover in Africa decreased by 21 million hectares (FAO 2005; Chapman et al. 2006). An understanding of the importance of specific food resources (i.e., how foods meet nutritional needs), dietary flexibility in primates, the importance of fallback foods, and nutritional requirements for different species will provide information vital for conservation planning. For example, foods that provide critical nutrients or are important fallback foods should not be cut in selective logging operations or, more realistically, harvested trees can be directionally felled away from species that bear these critical foods. This could potentially reduce the decline of some primate species caused by selective logging.

To address the issue of whether food influences the conservation potential of a species, it is important to consider whether primates are food-limited. The question of whether primate populations are limited by food resource availability has been evaluated previously (Janson and Chapman 1999). In considering the importance of minerals (see also Rode et al. 2003, 2006), food species diversity, food productivity, and food quality, a general conclusion is that many primates face food shortages—either seasonally, in the case of frugivores, or in terms of the rarity of high-quality leaves for folivores. There are, of course, exceptions to these generalizations. For example, extensive chimpanzee predation affects the eastern red colobus population size at Ngogo in Kibale National Park (Mitani et al. 2000; Lwanga 2006; Teelen 2007). Disease can also be an important limiting factor and can clearly cause short-term reductions in population size (Collias & Southwick 1952; Work et al. 1957; Milton 1996; Nunn & Altizer 2006), likely below carrying capacity. For instance, yellow fever accounted for a 50% decline in the mantled howler monkey population on Barro Colorado Island, Panama, between 1933 and 1951 (Collias & Southwick 1952).

To use nutritional ecology data in conservation efforts, one could study the nutritional needs of each endangered species, but that would be time consuming and often the required information would only become available years after action was needed. As discussed previously, in many primates there is considerable variation between the diets of different populations in the types of foods eaten, making it difficult to define their nutritional needs. Thus, there have been few direct tests of general hypotheses proposed to account for this variation. Notable exceptions are studies of folivorous primates. Milton (1979) proposed that the protein-to-fiber ratio was a good predictor of leaf choice. By measuring overall mature-leaf acceptability as the ratio of protein to fiber, several subsequent studies have found positive correlations between colobine biomass and this index of leaf quality at local (Chapman & Chapman 2002; Chapman et al. 2002a, 2004; Ganzhorn 2002) and regional scales (Waterman et al. 1988; Oates et al. 1990; fig. 7.4). Milton (1979; 1998) and Milton and colleagues (1980) proposed a physiological explanation for the importance of protein-to-fiber ratios in regulating population densities.

The protein/fiber ratio appears to be a useful predictor of the biomass of folivorous primates and a useful conservation tool. With this knowledge one can define critical food resources. Unfortunately, however, it is unclear what is driving this relationship. Most primates require about 4% to 7% protein for growth and maintenance, and 8% to 10% protein for reproduction if the protein is of high quality (Oftedal 1992; NRC 2003). At some sites where this relationship has been examined, the mean mature-leaf protein of the abundant trees is about 17% dry matter (Chapman et al. 2002a), and so it would seem that protein is not limiting (Oftedal 1992). Therefore it is unclear whether high amounts of protein are unavailable for digestion because they are bound to fiber (Rothman et al. 2008a) or tannins (Robbins et al. 1987), or if the amino acids within the leaf protein are imbalanced. Alternatively, other factors may be driving this relationship, such as energy. In a recent study, Harris et al. (2010) found that guerezas regularly excrete ketones in their urine, an indication that they could be using excess-protein foods as energy (fig. 7.5). Unraveling the mechanisms behind the protein-to-fiber model is an important priority for future studies of folivorous primates.

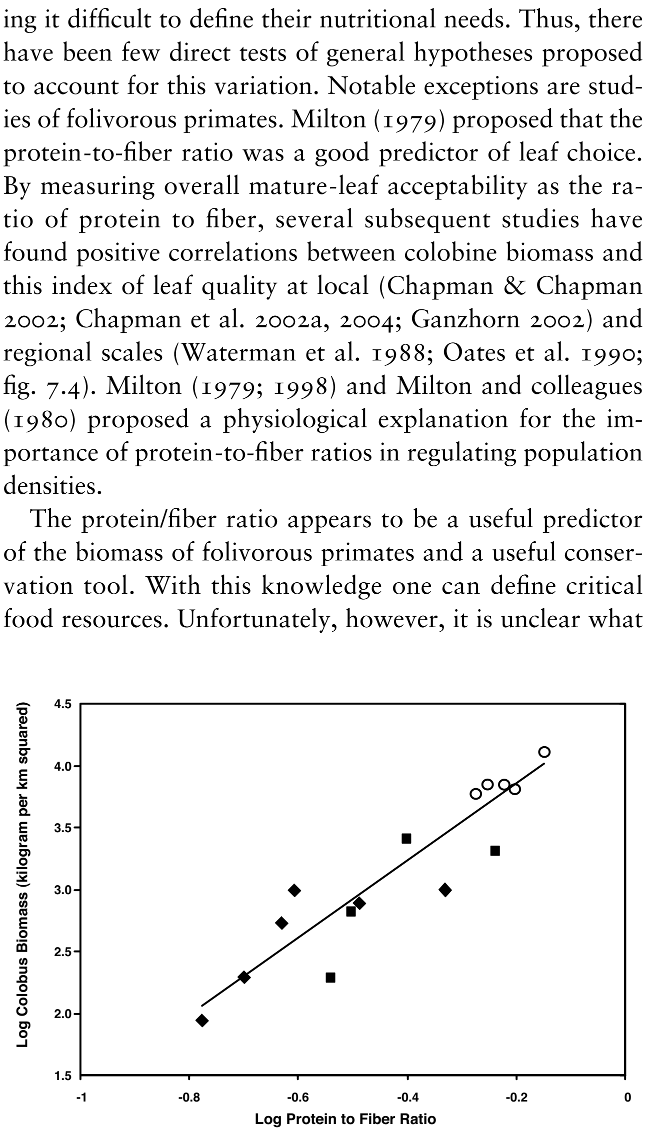

Fig. 7.4. The relationship between mature leaf chemistry and colobine biomass at rainforest sites in Africa and Asia. Chemical values are weighted by mean percentages of dry mass, standardized to the species basal area to account for different proportions of the flora being sampled at each site. The weighted values were calculated from $\sum(P_i + X_i)/ \sum P_i$, where P_i is the proportion of the basal area contributed by species *i* and X_i is the chemical measure for species *i*. This figure is standardized to 100%. Diamonds denote sites around the world (Oates et al. 1990; Fashing et al. 2007), squares denote forest sites within Kibale National Park, Uganda (Chapman et al. 2002a), and open circles denote the forest fragments (Chapman et al. 2007).

Geometric analysis of feeding and nutrition promises to identify targeted nutrients in foraging strategies and to yield generalizations about primate feeding behavior (Felton et al. 2009; Raubenheimer et al. 2009). This modeling technique allows identification of the intake targets of a species, and it could help in evaluating how animals direct their foraging efforts. With this information, one can make reasonable hypotheses that trees providing high levels of particular nutrients will be the most critical for specific species. Efforts can then be made to protect those types of plants or to restore them in a degraded habitat (Chapman and Chapman 2002; Felton et al. 2009).

In addition to studies concerning the protein-fiber ratio for folivores, there are three key concepts that need further consideration when evaluating how food resources act as selection pressures to influence a species conservation potential: ideal free distribution, ecological sinks, and fallback foods.

Ideal Free Distribution

Evaluating the variation in primate density as a function of habitat disturbance (an index of habitat quality) should be considered in terms of population distribution theory. If individuals or groups are free to select among habitats, then their distribution should represent an ideal free distribution (Fretwell & Lucas 1969; Fretwell 1972), with the density of animals being proportional to the resources available in the area. There is evidence that this is often not the case. These situations have not been adequately investigated, particularly in primates. A Web of Science search conducted on January 13, 2011, using the term "ideal free distribution primates" yielded 86 papers, but only three had to do with

Fig. 7.5. A young guereza feeds on the young leaves of *Celtis durandii* (note the small, unripe fruit also evident). *C. durandii* is one of the major dietary items of this colobine species, and its young leaves have one of the highest protein-to-fiber ratios that have been documented at Kibale National Park, Uganda. Photo courtesy of Colin A. Chapman.

nonhuman primate behavior. If, in contrast, the term "primates" was dropped from the search, 1,471 papers were listed. Work by Olupot (2000) illustrates the value of considering ideal free distributions for primate conservation. This study found that gray-cheeked mangabey males in unlogged forest in Kibale National Park, Uganda, were significantly heavier than males in logged forests. The mangabeys in the logged forest had almost 30 years to recover from the logging and reach their population equilibrium. Thus, this result is not easily understood, particularly since males frequently move among groups (Olupot & Waser 2005; Janmaat et al. 2009). According to the expectations of an ideal free distribution, the animals should distribute their density in proportion to food availability and should have equal body mass. It may be that this situation represents instead an ideal despotic distribution (Fretwell & Lucas 1969; Fretwell 1972), where mangabeys in the better habitat exclude other mangabeys from entering. Movement patterns of male mangabeys, however, do not support this idea (Olupot & Waser 2005, Chapman unpublished data). The fact that there is a discrepancy between what theory would predict and what was observed in this study of gray-cheeked mangabeys clearly illustrates the need to evaluate the natural history of primates in situations like this to determine the missing pieces of information needed to understand such situations.

Ecological Sinks

Source-sink patterns occur when populations occupying low-quality habitats ("sinks"), where mortality rates exceed reproductive output, are sustained by immigration from populations inhabiting nearby high-quality habitats ("sources"), where reproductive output exceeds mortality and a surplus of individuals are produced. Identifying sources and sinks is difficult because it requires long-term demographic data from diverse habitats with different food resources, as well as data on dispersal patterns. Thus, the source-sink framework has rarely received explicit consideration in studies of primates, despite its usefulness for understanding population dynamics and identifying populations of high conservation priority (i.e., sources). Pulliam (1988) and Holt (1985) first formalized the theory of source-sink dynamics and highlighted the importance of explicitly considering habitat-specific demographic trends and dispersal patterns when assessing habitat quality and interpreting species' foraging adaptations (Holt 1992; Dias & Blondel 1996; Kawecki & Holt 2002). The theory of source-sink dynamics has since become a robust paradigm in the field of ecology for understanding population dynamics, selective pressures, and adaptations. Siex and Struhsaker (1999) suggested that the population dynamics of Kirk's red colobus (*Procolobus kirkii*) populations in Zanzibar represented a source-sink dynamic. If a study is conducted in a sink habitat, it is difficult to understand how food resources influence anatomical or behavioral adaptations because the observed patterns are not in response to the selective pressures that have favored them. This highlights the need to study a species in a variety of settings to obtain the information needed to construct informed management plans.

Fallback Foods

Building on a wealth of ecological information on diets and optimal foraging theory (Altmann 1998; MacArthur & Pianka 1966), there has recently been interest in the ecological and evolutionary significance of fallback foods (Conklin-Brittain et al. 1998; Wrangham et al. 1998; Lambert et al. 2004; Hemingway & Bynum 2005; Lambert 2007; Marshall & Wrangham 2007). Fallback foods are those used when preferred food items are not available, and as such are negatively correlated with the availability of the latter (Lambert 2007, 2009; Marshall & Wrangham 2007; Marshall et al. 2009). Because they help sustain populations during periods of food scarcity, fallback foods are ecologically significant components of primate diets. Information about them is also necessary to evaluate the ability of a species to respond to anthropogenic habitat disturbance.

Variation in fallback foods will have important consequences for primates, who rely on them. It seems likely that for species with flexible diets the nature of fallback foods will be highly variable. For example, when fruit was scarce, Geoffroy's spider monkeys at Santa Rosa National Park, Costa Rica, fed on young leaves during 86.3% of their feeding time in one month. In another food-poor month, however, they fed on the dry fruits of *Bursera simaruba* during 68.2% of the time (Chapman 1987; C. Chapman unpublished data). These different fallback foods will place very different selection pressures on spider monkey anatomy and social behavior. Evaluating changes in anatomy and behavior due to variation in fallback foods will require additional information about how other populations of spider monkeys respond to times of food scarcity, but such data are currently lacking.

Most primates live across a range of interconnected forest types or habitats. As a consequence they are not likely to rely on specific food items as fallback foods, but instead will exploit classes of foods with certain traits— for example, large fruits with thick exocarps, or plants with high levels of specific secondary compounds. Thus it is not surprising that cercopithecines have adapted to deal with secondary compounds or structural properties, such as hardness, rather than to specific types of foods such as fruits or leaves (Wrangham et al. 1998; Lambert et al. 1999; Balcomb & Chapman 2003; Lambert 2007). From a conservation perspective, the ability of a species to be flexible regarding the types and diversity of fallback foods will greatly increase its ability to tolerate habitat destruction and the potential removal of preferred foods.

Summary and Conclusions

Primates face the difficult challenge of obtaining a nutritious diet in an energetically efficient manner while avoiding plant toxins. To meet this challenge, different primate species have evolved a diversity of strategies and adaptations to satisfy their nutritional requirements. Foraging strategies affect virtually every aspect of primate biology, including their (1) ecology and distribution, (2) movement and ranging patterns, and (3) behavior and social organization. Most primates are endangered due to extensive deforestation and high hunting pressure, and an understanding of primate foraging strategies and their diversity is necessary to construct informed conservation management plans.

It is clear that food resources act as strong selective forces along several dimensions, including *physiology, ecology, behavior, and social organization*. We suggest that a way forward in primate foraging ecology must involve a shift in perspectives on food and primate biology. New methods in nutritional ecology, in addition to still untapped classic methods, are available to primatologists though they remain largely underused (e.g., Rothman et al. 2009). Geometric analyses, new methods in nutritional assays, and the application of ideal-free and sink-source models will be useful in interpreting not only what primates consume but why they consume it. In particular, investigations into the nutritional composition of the specific food items primates eat (e.g., a specific food item from a particular individual tree of a particular species), instead of types of foods (e.g., fruits) or single samples of food items, will shed light on how food acts as a selective pressure.

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