

14 • Resources and primate community structure

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INTRODUCTION

The concept of carrying capacity is fundamental in determining a species' density and biomass, which enter into the equations used in ecological theory to predict species diversity and community structure (MacArthur, 1972). Therefore, you might think that a great deal was known about how to determine the carrying capacity of species in nature; however, this is not the case. In the vast majority of species, if the carrying capacity is measured at all, it is estimated as the population density of individuals associated with a zero growth rate (Dennis & Taper, 1994). The more fundamental question of what resources determine that population level is often left unanswered.

Debate has raged over the past two decades as to the extent or even existence of resource limitation in primate populations. Early observations (Struhsaker, 1969) suggested that many fruit-eating primates faced an overabundance of resources in the trees that they used. Later study quantitatively confirmed that some trees produced more fruit than a group of monkeys could consume in one sitting (Janson, 1988*b*), but also showed that many trees did not produce enough fruit to satiate even a single animal. In one of the few attempts to relate primate population densities to resources directly, Coehlo *et al.* (1976) compared the biomass and consumption rates of howler and spider monkeys in Guatemala to the availability of the major food resources that they used. They found that over an annual cycle total food production vastly exceeded the requirements of the population density in that site. However, in Peru, Janson (1984) found that the productivity per unit area of food species used by capuchin monkeys varied enough so that in the dry season insufficient fruit was produced to sustain the population. At that time, these

fruit-eating monkeys were seen to switch to alternate plant products. In the same study site, Goldizen *et al.* (1988) showed that fruit-eating tamarins of both sexes lost weight during the dry season. The general scarcity of fruit during the dry season in Peru and the convergence of many primate species on a few resources then (Terborgh, 1983) led to the concept of keystone resources: a relatively few plant species that are predictably available during periods of food scarcity and may serve to sustain primate populations at these critical times (Terborgh, 1986).

At the level of the entire community, Janson & Emmons (1990) found that the estimated metabolic requirements of frugivorous mammals at Cocha Cashu, Peru, was only 20% less than the total annual production of fleshy fruits. At least for this system, it appears reasonable to argue that the major resources consumed by fruit-eating primates indeed limit their population density. However, this argument does not work either for seed consuming or leaf-consuming primates. The same study showed that the production of seeds in all fruit types exceeded by a factor of 20 the metabolic needs of seed consuming mammals in the community. Similarly, it is clear that in no forest study site do folivorous mammals consume more than a small fraction of the biomass of leaves available on a steady basis (Hairston *et al.*, 1960). Either the density of leaf-eaters is controlled by factors other than food, or they must be exceedingly selective about what they consider to be "food". Such selectivity can also occur among 'omnivorous' primates (Altmann, 1998), and it aggravates the problem of estimating the potential carrying capacity of a habitat for any given primate species (see Appendix 14.1).

Given the difficulty of estimating the limiting resources for individual primate species or ensembles at a single site, it is hardly surprising that few analyses have focused on

how resources limit primate biomass. Most of the broad comparative surveys of primate community structure have dealt with species diversity (Bourlière, 1985; Reed & Fleagle, 1995; Kay *et al.*, 1997; Peres & Janson, chapter 3, this volume). Although it is well documented that the population density of a primate species varies inversely with its body mass (Robinson & Ramirez, 1982; Fa & Purvis, 1997), the resource basis for these correlations is not understood beyond the speculative inference that energy flow is independent of body mass in mammals (Brown, 1995). Only for folivores do there exist a few studies that have analyzed ecological factors correlated with biomass (Oates *et al.*, 1990; Ganzhorn, 1992; Peres, 1997*b*). The purpose of this chapter is to review what is known about resources used by primates, discuss methods to measure the abundance or quality of these resources, and describe the relationships between primate diversity or biomass and resources across study sites within and between continents. We do not tackle more detailed questions of primate community structure such as the mechanisms of niche separation among primate species (Ganzhorn, 1988) or between primate species and other animals (see Emmons, chapter 10, this volume).

PRIMATE DIETS AND THEIR NUTRITIONAL CHARACTERISTICS

Primate diets typically are divided into three major resource categories: insects, fruit, and leaves (Kay, 1984). However, these categories do not describe the full range of foods commonly used by primates. For instance, many primate species use flowers extensively for a short period each year (Janson *et al.*, 1981), although flowers do not comprise the majority of the diet of any known primate. A further problem is that the three major food categories often contain several quite distinct types of foods. For instance, species that feed on insects will also consume small vertebrates, so this category is more accurately labeled faunivores. Similarly, primates that eat fruit pulp or seeds are both called frugivorous, but the nutritional content, density, and temporal availability of these two components of fruits are very distinct (van Roosmalen, 1984). Finally, there are at least two distinct leaf digestion strategies shown by mammals: slow but relatively complete fermentation of foods in the forestomach vs. relatively rapid extraction of soluble nutrients with minimal

fermentation in the mid- or hind-gut (e.g., cows vs. horses, colobines vs. lemurs or howler monkeys). Even within a single community of primates, there can be many distinct constraints on eating leaves with major implications for resource availability and foraging strategies (Ganzhorn, 1989). We shall now discuss these dietary categories in more detail.

Insects and other animals

Eating animal prey generally requires little in the way of digestive specializations, as the body composition of most animals is fairly similar and the consumer can obtain nearly all essential nutrients from its prey (Moir, 1994). Thus the digestive systems of faunivores tend to be rather simple and comparable between species (Chivers & Hladik, 1980). Nevertheless, there are a few major differences between insects and other animals as food items. First, there is the chitinous exoskeleton of adult insects and other arthropods. It is hard to chew into pieces, compared to the soft muscle tissues of vertebrate prey. Primarily insectivorous primates fracture the chitin with very high-crowned molars (Strait, 1997). Chitin also is hard to digest. Many frugivore-insectivore primates appear to avoid ingesting chitin (Janson & Boinski, 1992) and the chitinous parts of their insect diet pass nearly unaltered through their digestive systems. However, more dedicated insectivores do appear to break down some of the chitin they ingest (Kay & Sheine, 1979). Second, many insects (but few warm-blooded vertebrates, see Dumbacher *et al.*, 1992) are toxic or distasteful. Some nocturnal prosimian primates appear to specialize on such noxious prey (Charles-Dominique, 1977), whereas diurnal monkeys have developed a variety of behavioral mechanisms to get around stinging hairs and other defenses of insect prey (Janson & Boinski, 1992). Third, there may be nutritional differences between insects and vertebrates, although existing composition data show no consistent contrasts (Leung, 1968). Many primate species that depend on insects for protein seem eager to consume vertebrate prey on occasion, and some even focus their foraging efforts largely on vertebrate prey seasonally (Terborgh, 1983; Fedigan, 1990).

Absolute insect availability may be similar for both small and large primates within a given site. The size of insects ingested does not appear to be limited by primate body size, at least within the range of 300–3000 g in the

New World (Terborgh, 1983). Thus, larger primates should not have a markedly greater pool of insects available to them than do smaller species (one possible exception being the nests of social insects that are too tough for small primates to tear apart). Yet, larger primate species must satisfy a larger metabolic demand. Thus, as primate species become larger, they should and do spend more time foraging for insects (Charles-Dominique, 1977; Terborgh, 1983), and the fraction of the diet that is composed of insects declines (Hladik & Hladik, 1969).

Fruits

Because fruit pulp serves the apparent evolutionary purpose of attracting seed dispersers, it generally presents far fewer problems for primates to find and catch than do insects, and pulp is easier to ingest and digest than are leaves. However, plants also have been selected to provide fruits that cause dispersers to leave the tree; otherwise dispersal is not effected (Herrera, 1982). One mechanism to guarantee that dispersers eventually leave a tree crown is to make fruit pulp an incomplete diet (Janzen, 1983). Most fruit pulps are high in sugars but low in fats and proteins. Although some fruit pulps are high in particular minerals (such as potassium in bananas), it seems unlikely that primates would actively seek out such fruits as there is little evidence for taste receptors for minerals other than sodium (Hladik & Simmen, 1997; but see O'Brien *et al.*, 1998). Because of the nutritional deficiencies of fruit as a diet, every predominantly fruit-eating primate species must complement its diet with either insects or leaves or both. The constraints on ranging behavior set by these alternative resources may have important effects on primate social ecology (Janson, 1988a).

Fruit-eating primates have to cope with other problems as well. First, fruits are often chemically defended against insect or mammalian herbivores before the pulp and seed mature, and some continue to be defended even when the pulp is ripe (Cipollini & Levey, 1997). Second, plants have evolved a variety of ways to restrict dispersal of their fruits to a fraction of all of the potential fruit-eating animals in the forest: particular fruit presentations (Denslow & Moermond, 1982), morphologies (Janson, 1983), ripening schedules (McKey, 1975), and taste or defensive chemicals (Janzen, 1983). For instance, the chemicals that make red peppers spicy to humans and other mammals are

apparently not perceived by birds; conversely at least one taste compound in fruits, methyl anthranilate, is palatable to mammals but so noxious to birds that it is used as a commercial bird repellent on fruits, grains, and lawns (Mason *et al.*, 1989). Because of some combination of fruit size, protection, taste, toxicity, inaccessibility, or slow ripening rate, primates will use only a fraction of the many hundreds of fruit species in a forest.

Fruit-eating primates have to solve the challenge of locating ripe fruit crops that are often sparsely distributed in tropical forests. Searching for rare fruit trees is likely to be inefficient because detection distances for fruit crops are probably short (Janson & Di Bitetti, 1997). Instead, many primates appear to remember the locations of fruit crops over periods of days or weeks, returning at relatively predictable intervals to the same tree crown and moving in relatively straight lines from one resource to the next (Garber, 1989; Janson, 1998). Spatial memory can increase foraging efficiency up to 300% relative to random searching (Janson, 1998). Thus, the use of spatial memory may substantially increase primate biomass in a forest.

Seeds

Although often lumped under the category of fruit, the seeds consumed by primates should be considered a distinct category for several reasons. First, unlike fruit pulp, the seed must contain complete nutrition for the growing seedlings. Thus, seeds typically are higher in fats, proteins, and minerals (especially phosphorus, a potentially limiting nutrient for vegetarian animals, see below) compared to fruit pulp. Although the nutritional needs of growing plants and primates are not likely to be identical, some primates appear capable of surviving on seeds alone for extended periods (Ayres, 1989; Norconk *et al.*, 1997), whereas no primate species is known to feed strictly on fruit pulp. Second, plants typically defend their seeds either with hard shells or noxious chemicals, making it time-consuming or dangerous for a primate to eat the seeds. However, there may be limits to the kinds and concentration of toxic chemicals that a plant can put into its seeds (Orians & Janzen, 1974). Third, seeds are often available over much longer time spans than is ripe fruit pulp in the same tree crowns. Not only do seeds typically mature somewhat earlier than fruit pulp ripens within a fruit, but heavily defended seeds may remain available on

the forest floor long after they are dispersed and serve as primate food sources for an extended period (e.g., palm seeds: Terborgh, 1983). Altogether, seeds present characteristics somewhat intermediate between those of fruit pulp and leaves. Like fruits, seeds are produced in large clumps and have relatively high energy concentrations, but like leaves, seeds often contain toxins as well as scarce mineral nutrients, and they may be available over longer time spans than ripe fruit pulp.

Flowers

Little attention has been paid to flowers as a primate resource (but see Terborgh & Stern, 1987). Generally, primates eat only a few flower species out of hundreds or thousands of plant species in a community (Janson *et al.*, 1981; Overdorff, 1992). Although flowers rarely comprise more than 10% of a primate's annual diet, they can provide over 70% of the feeding time in a given month (Janson *et al.*, 1981). Flowers appear to be fall-back resources for primates, used when little else is available, because nectar is usually dilute compared to fruit pulp and produced in minute quantities per flower per day (Terborgh and Stern, 1987). Because flowers are generally frail compared to fruits, primates need no specializations to eat them. At least in Peru, flower-feeding is seen in primate species from the smallest to largest in a given community, including gummivores, frugivore-insectivores, frugivore-folivores, and folivores (Janson *et al.*, 1981 and unpubl. data). However, even primate species of similar size may differ substantially in how they feed on flowers of a given species and hence their effects on floral survival and pollination (Overdorff, 1992).

Leaves

Eating and digesting leaves undoubtedly present the biggest dietary challenges to primates. It is not that leaves are a 'low-quality' resource in absolute terms. On a per-weight basis, leaves are often richer in protein than other primate vegetal resources (Milton, 1980; Waterman, 1984; Barton *et al.*, 1993), and the potential energy density is very high as the major component of leaves, cellulose, is nothing more than a polymer of sugar molecules. However, plants have evolved a dazzling array of defensive chemicals to protect their leaves from herbivores. Cellulose is the

first line of defense. Despite its similarity to starch, this ubiquitous structural compound of plants is configured in such a way that no vertebrate can digest it without the help of protozoans or bacterial symbionts. How then do primates choose and cope with ingesting and digesting leaves? I will present here only a brief outline of this issue, which is covered in much greater detail in a recent review by Lambert (1998).

The simplest strategy to use leaves is to avoid the problem of cellulose digestion altogether. Many fruit-eating primates obtain protein from leaves by selecting low-fiber parts of plants, which are processed in the gut relatively quickly to extract soluble carbohydrates and proteins; little emphasis is placed on digestion of cellulose. Although this method of eating leaves seems to provide only slightly more digestive challenge than eating fruit, two difficulties remain. First, finding these leaves may require almost as much searching as looking for sparsely distributed insects because many tropical evergreen trees produce tender young leaves at low, relatively even rates (Sterck, 1995). In seasonally dry areas of the tropics, trees may put out young leaves synchronously in a single seasonal flush that may attract primates that otherwise eat few leaves (Terborgh & van Schaik, 1987), but this food source is available only briefly. Second, even young growing leaves are chemically defended, usually with small, often highly toxic compounds such as cyanide, alkaloids, and terpenes (Coley & Barone, 1996). Either the primate must restrict its leaf intake to poorly defended species or parts (such as petioles), or it must possess the ability to detoxify these poisons. In sum, high-quality vegetation presents a more sparsely distributed and chemically better-defended resource than do fruits, although certainly more abundant and easier to capture than insects. For fruit-eating primates that depend on leaves for protein, fitness and population density may be limited by ability to find and extract protein rather than energy (Whiten *et al.*, 1991).

There are two major methods of microbial digestion of cellulose in vertebrates, forestomach and caeco-colic fermentation (Lambert, 1998). In either type, fiber is exposed to complex communities of microbes in the primate's gut for relatively long periods of 8–24 hours. Forestomach (often known as "foregut") fermentation requires anatomical specializations of the stomach and complex relationships between the microbes and their host, which appear to arise relatively rarely in evolution. In extant primates,

stomach-based fermentation has arisen only once, in the ancestors of the colobines.

Forestomach fermentation has advantages and costs. The advantages are (1) that any microbes that wash out of the stomach are digested in the intestines, thus reclaiming their precious proteins, and (2) it may help to detoxify plant defensive chemicals (Parra, 1978; Janzen, 1979; Langer, 1986), as well as break apart phytin. Phytin is one of the major chemical 'storage' compounds for phosphorous, a mineral that is often limiting to large herbivores (T. Pope, pers. comm.). The major costs of forestomach fermentation include (1) holding the fiber for long periods in the uppermost part of the digestive tract, thereby hindering further ingestion while it is fermenting, (2) the loss of the easily absorbed parts of leaf cell contents, which are taken up and used by the microbes in the stomach rather than being absorbed by the primate host directly through its intestine, and (3) the need to regulate stomach acidity, as excess acidity can disrupt the microbial community and even lead to host death. To reduce the cost of fiber 'storage' in the stomach, primate forestomach fermenters that use both low- and high-fiber parts in the diet may have the capacity to 'shunt' non-fibrous foods past the fermenting chambers of the stomach to the acid-enzymatic hindstomach, where digestion is faster (Cork, 1994). To prevent excess acid accumulation, foregut fermenters must avoid ingesting large amounts of acid fruit pulp or a diet too high in fiber (Lambert, 1998). Because of these constraints forestomach fermenters should choose relatively high-nitrogen plant matter of low or moderate fiber content with near-neutral pH. Thus, primate forestomach fermenters are selective browsers on leaves and seeds.

Fermentation in the mid-gut (caecum and right colon) or hind-gut (descending colon) is much more widespread than forestomach fermentation. Indeed, some fermentation in the caecum or colon probably occurs inevitably even in omnivorous species that ingest leaves as a source of protein. Fermentation can be enhanced by enlarging the caecum or colon, because cellulose-rich material remains exposed longer to microbial action. Such caeco-colic (previously referred to simply as "hindgut") fermentation has evolved at least four times in the primates, once in each of the major primate radiations (Lambert, 1998).

Caeco-colic fermentation of cellulose has its own distinct advantages and costs. Its advantages include (1) that

it does not hinder further ingestion of food if the upper parts of the digestive tract are empty, and (2) any easily-absorbed cell contents are taken up directly by the host before being exposed to microbial symbionts. Thus, when foliage is low in nitrogen and fiber-rich (dead grass, for instance), a caeco-colic fermenter can survive by pushing large amounts of material through the gut and extracting only the easily-obtained fraction while ignoring fermentation as a major option; this is the digestive strategy of horses. The costs of caeco-colic fermentation include (1) the loss in feces of the symbiotic microbes (and their proteins), (2) exposure to plant defensive chemicals in the gut before the microbes have a chance to detoxify them (Waterman *et al.*, 1988), and (3) little breakdown of phosphorous-rich phytin, thus limiting the absorption of phosphorous from foliage to between 44–65% of that achievable by forestomach fermenters (T. Pope, pers. comm.). To reduce the cost of lost microbial proteins, caeco-colic fermenters can (and do) ingest their feces and have evolved intra-colonic separation mechanisms to retain the microbes and shunt them back to the fermentation chamber (Björnhag, 1994). Their inability to avoid exposure to plant toxins in the fore- and mid-gut may account for the often extreme food selectivity of some caeco-colic fermenting primates (Glander, 1982). However, it is not clear whether forestomach and caeco-colic fermenters differ systematically in their ability to detoxify plant defensive chemistry (Foley & McArthur, 1994).

For either strategy of microbial fermentation to be effective, two requirements must be met. First, leaves must be shredded into fine particles to expose as much surface area of cellulose to microbial action as possible (Kay & Hylander, 1978). Second, fermentation takes time, so that gut passage must be relatively slow compared to insect- or fruit-eaters. A comparison of leaf- versus fruit-eating primates shows that the passage time in folivores is much slower than in fruit-eating species of comparable body size (Milton, 1984; but see Lambert, 1998). Longer gut retention times effectively limit the maximum daily rates of nutrient extraction by leaf-eating primates, which in turn affects their energetics and social behavior (e.g., Janson & Goldsmith, 1995). The lower the metabolic needs of a folivore relative to its gut capacity, the lower the quality of leaves it can afford to eat (Cork, 1994). Because mass-specific metabolic rates tend to decline with larger body mass, whereas relative gut capacity stays roughly constant, larger

herbivores usually can survive on lower-quality foliage (Cork, 1994). All primate folivores of less than 15 kg ingest more easily-digested non-foliage items (immature fruits, seeds, gums) as well as leaves, perhaps because they are too small to rely completely on a leaf diet regardless of digestive strategy (Cork, 1994). Primate species that succeed in fermenting cellulose can achieve very high densities and biomass compared to non-fermenting fruit- or insect-eating species (see below).

How do the two distinct fermenting strategies compare? The answer may depend on body size. Theoretical studies suggest that forestomach fermentation is preferable in larger herbivores, while caeco-colic fermentation is best for small species, but neither strategy may be clearly superior within the 5–15 kg mass range of most arboreal folivores (Parra, 1978; C. M. Hladik, 1978; Illius & Gordon, 1992). Caeco-colic fermentation may be more flexible, with the primate having considerable control over the length of time material ferments in the gut, as well as over the fraction of material that is shunted past the fermenting chamber (Lambert, 1998). Published data on digestive efficiency suggest that fore-stomach fermenting colobine monkeys are nearly twice as efficient at digesting cell-wall contents as are the caeco-colic fermenting howler monkey (Kay & Davies, 1994; Milton, 1998); however, the diets used in different studies were not standardized, and more controlled comparisons are desirable.

Gums

This category usually combines both true gums, which consist of branched carbohydrate polymers (as well as soluble sugars; Hladik & Chivers, 1994), and sap, which may be little more than a solution of soluble sugars and proteins being transported by the plant from roots to leaves or vice versa. These two classes of foods should be distinguished, however. Despite the lack of cellulose and cell walls, true gums may not be much easier to digest than are leaves (Hladik & Chivers, 1994). Recent studies have shown that different gum-eating prosimians and callitrichines differ in their ability to digest the complex carbohydrates in gums (Nash, 1986; Power & Oftedal, 1996), at least in part through caecal fermentation. In contrast, sap-eating primates are quite small (including the smallest anthropoid, the pygmy marmoset) and most necessarily have short gut passage times (but see Power, 1996). Such a digestive

strategy works well for dissolved nutrients such as occur in plant phloem contents.

Why are primates such generalized feeders?

Dietary specialists are uncommon in primates. Because of the dearth of protein in fruit pulp, all fruit-eating primate species complement their diet with proteins (and probably minerals) from either animals or leaves (Kay, 1984). Depending on their body size, primates species vary in the degree to which energy vs. proteins limit their foraging effort. For instance, Terborgh (1983) showed that the percentage of the activity budget devoted to obtaining fruit was essentially constant across a tenfold range of primate body masses in Peru, whereas the time devoted to searching for insects increased markedly with increasing body size. For the largest study species, the brown capuchin monkey (*Cebus apella*), foraging for dispersed insects occupied two to three times as many hours per day as did feeding on fruit. In this species, it can be shown that energetic returns from insect searching are negative – that is to say a brown capuchin would starve to death if all it could eat was insects (Janson, 1985). The relative superabundance of fruit at most times compared to the scarcity of insects implies that, at least in this case, fruit feeding usually subsidizes energetically the search for protein. For fruit-eating species larger than brown capuchin monkeys, it is difficult to meet protein needs by using insects alone, so these larger species include or depend entirely upon leaves as a protein source (see also Kay, 1984). Because they do not require the energy from cellulose in the leaves, these omnivores can afford to choose only high-protein, low-fiber leaves, thus minimizing problems of digestion. Even so, however, these frugivore-folivore species typically ingest leaves at the end of their foraging day, a time when they can fill up their gut with relatively indigestible material without inhibiting the digestion or intake of less fibrous fruit or insect material (Chapman & Chapman, 1991; but see Ganzhorn & Wright, 1994). Many Old World monkeys (*Cercopithecus*) appear to use slow passage time and fermentation of fiber as a digestive strategy despite little obvious enlargement of the mid- or hind-gut (Lambert, 1998).

Primate faunivores and folivores can be dietary specialists. Nearly all specialized faunivorous primates are small-bodied. Their short digestion times force them to use easily absorbed foods such as insects or nectar, while their low

total metabolic demands allow them to specialize on these scarce high-quality foods. By contrast, folivores tend to be large bodied (Kay, 1984). Their large body size and long gut-passage times permit them to ferment relatively common but complex vegetation, while their high absolute metabolic demands preclude their being specialized on relatively scarce insect resources. Even if they eat only leaves, however, leaf-eating primates typically use vegetative parts of many dozens to hundreds of plant species in a single area. Given that most tropical trees are evergreen, why do leaf eating primates not specialize on just the few types of leaves that provide the highest protein-fiber ratio? Because most tropical trees species occur at low densities, a primate that favored only a few tree species in its diet might be forced to travel long distances to obtain a stomach full of food. In addition, for caeco-colic fermenters, there is no easy way to avoid the toxins in leaves, so that excessive consumption of one or a few plant species might overload the capacity of the digestive system and liver to detoxify the plant defensive chemicals encountered (Milton, 1979; Glander, 1982). Forestomach fermenters may be less hindered in this regard, and at least some colobine monkeys are quite specialized in their choice of leaves (*Colobus guereza*: Oates, 1977). Studies that contrast folivores that vary in their degree of specialization can reveal interesting dietary strategies (Struhsaker & Oates, 1975).

Summary: primate dietary niches

Primates have diversified into a broad array of dietary types that span most of the dietary specializations among mammals in general (Chivers *et al.*, 1984). Body size is a major correlate of primate diets (Kay, 1984). The smallest species (50–500 g) tend to be restricted to foods of relatively high digestibility – insects, small vertebrates, saps and gums. Species of intermediate size (500–5000 g) tend to rely largely on fruit or seeds, but obtain their protein needs from insects (species up to ca. 3000 g) or leaves (species above 3000 g). The largest species (>5000 g) are capable of fermenting sufficient fiber to obtain at least part of their energy requirements from leaves in addition to fruits, or they may rely entirely on leaves for brief periods (species up to ca. 10 000 g) or prolonged periods (species above 10 000 g). These generalizations are by no means absolute, as there are relatively small-bodied species that are entirely folivorous (*Lepilemur mustelinus* at 650 g) and

large species that are extremely frugivorous (chimpanzees, *Pan troglodytes*, at 45 000 g).

Within dietary types, there can be finer-scale differences as well. The major ecological differences that distinguish primate faunivores are the methods used to find prey or to hunt them. Such differentiation is well illustrated by Terborgh's (1983) study of five insectivorous-frugivorous primates in Manu National Park, Peru or Charles-Dominique's (1977) study of prosimians in Africa. In both studies, species differed in the height in the forest and in the size of substrates they moved on while searching for insects. In Peru, the major difference among primate species was in the toughness of substrates manipulated to extract insect prey, from open-leaf gleaning by smaller species to ripping apart palm fronds and tree trunks by the largest (Terborgh, 1983). However, some species have developed behaviors to cope with the defenses of caterpillars (squirrel monkeys: Janson & Boinski, 1992), and others even appear to specialize on slow-moving distasteful insects (slender lorises: Charles-Dominique, 1977).

Niche differences among fruit-eating species are less obvious. There is a positive correlation between body size and mean fruit size used among New World monkeys (Janson, unpubl. data), but even very small species such as tamarins may ingest the pulp of some of the larger fruits (Terborgh, 1983). In Africa and Asia, where most of the frugivorous primates belong to a single genus (either *Cercocebus* or *Macaca*), body-size-related differences in fruit use are much less pronounced. Many of the differences in fruit use among primate species in both areas show up as preferences for species with distinct phenological patterns – sudden-ripening, large-crowned figs vs. slowly-ripening, small-crowned understory plants (e.g., Terborgh, 1983). Chemical differences among preferred fruits may exist, but have not been studied systematically (see Appendix 14.1). Oddly, differences in overall fruit species use were far less than in insect-foraging techniques among the Peruvian primates in Terborgh's (1983) study, even though fruit comprised a majority of the energy intake for all of them. However, recent ecological theory argues that species may overlap broadly on common resources but diverge in their use of rare but fitness-enhancing ones (Robinson & Wilson, 1998).

What major differences in leaf choice are predicted from the three types of digestive strategies (non-fermenting, forestomach, and caeco-colic fermentation)? Because fiber

(cellulose) always presents a cost of retaining relatively slowly-digestible bulk relative to rapidly-absorbed soluble proteins and carbohydrates, nearly all primates that eat leaves strongly prefer leaves with high protein-to-fiber ratios (Cork, 1994). Non-fermenting primates should be restricted to leaves with low absolute fiber levels. Small-bodied caeco-colic fermenters are likely to be relatively specialized feeders on relatively rare high-protein, low-fiber plant parts. They may evolve to deal physiologically with large amounts of particular plant toxins (Glander *et al.*, 1989), with different primate species specializing on different kinds of plant defensive chemicals (Ganzhorn, 1989). Most large-bodied caeco-colic primates are capable of surviving on leaves of a broad range of protein/fiber ratios, but may need to avoid ingesting large amounts of the secondary chemicals of any one plant species (Milton, 1979; Glander, 1982). They can add fruit to the diet opportunistically as availability dictates. Forestomach fermenters should generally browse only relatively high protein, low- to medium-fiber leaves and seeds, while avoiding most ripe fruit pulp to prevent acidosis (Kay & Davies, 1994). They can become fairly specialized (Oates, 1977) because of the ability of the forestomach microbes to detoxify plant defensive chemicals at the first stages of digestion. When two or more species of colobines coexist, their diets may differ in leaf maturity and degree of specialization on few vs. many food species (Struhsaker & Oates, 1975).

PATTERNS OF RESOURCE AVAILABILITY IN PRIMATE HABITATS

A brief sketch of tropical forests

There is no such thing as a 'typical' tropical forest, which can include relatively short-stature deciduous woodlands with only 500 mm of rainfall per year and evergreen forests with 60 meter tall emergent trees in areas of more than 2500 mm rainfall. Although the bewildering diversity of plants associated with tropical forests is typical of unflooded forests, in some areas (permanently-flooded oxbow lakes, swamps, tidal river edges), species diversity is typically low, and virtually mono-specific stands of palms or fig trees occur both in New and Old World tropical sites. Even areas of relatively similar physical and climatic characteristics can produce forests dominated by

quite distinct plant families with unique biological traits, depending on their evolutionary and biogeographic history. The myth that tropical forest is a single biome is only one of many; we shall briefly review some others.

Of all the misconceptions common about tropical forests, the most enduring is that they lack definite seasons. It is true that average temperatures are high (above 20 °C) and seasonal temperature variation is slight in the tropics. However, most tropical forests on continents have distinct rainy and dry periods severe enough to limit plant production, and predictable enough to produce repeatable seasonal patterns of plant reproduction and leaf loss (e.g., Fig. 14.1). Rainfall patterns are driven by total solar radiation received per unit land area, and are therefore affected both by latitude and the inclination of the earth's axis relative to the plane of the earth's orbit (MacArthur, 1972). Areas more than 5 degrees from the equator typically possess a single dry season of 1–3 months alternating with a longer rainy season per year (Terborgh, 1992). However, this pattern also occurs closer to the equator near the east-

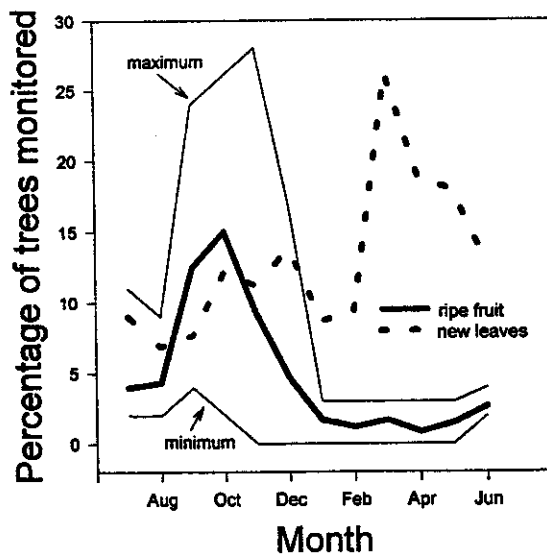


Fig. 14.1. Curves of monthly phenological changes in new leaves and ripe fruit in a sample of 58 Malaysian rainforest trees (data from Whitmore, 1975). Data are averaged across six years for both categories of foods, and the range of values per month is shown for ripe fruits. Although the seasonal pattern of fruit and leaf production is quite predictable, there are notably 'good' and 'bad' years for total amount of fruit produced.

ern edges of Africa and South America (Whitmore, 1975). Within 5 degrees of the equator near continental edges, one can find two brief dry seasons alternating with two longer rainy seasons per year (Martin, 1991, pp. 52–53). Alternatively, rainfall patterns are virtually aseasonal in a few equatorial sites far from the ocean in Africa and South America, and, oddly, also in the Indonesian islands (Whitmore, 1990, p. 11; Terborgh, 1992, p. 180). Such even rainfall can be associated with highly unpredictable fruit production (e.g., at Lomako in Democratic Republic of Congo: Malenky, 1990). However, the overall prevalence of seasonal food production in tropical forests means that most primate species need to be flexible enough to shift dietary preferences rapidly as preferred foods dwindle or increase.

A more subtle aspect of seasonality in tropical areas is variation between years. Some plants fruit only every other year. Others store nutrients for reproduction over several years before producing a large burst of flowering and fruiting, known as mast crops. Yet even among those species that attempt to reproduce every year, fruiting failure is common in many years due to between-year climatic variation. Sometimes this variation is global in extent (such as in El Niño years), albeit with different effects on different parts of the world. Such large-scale patterns can produce reproductive failure in a large percentage of the plant species in a tropical site, even leading to starvation among the fruit- and seed-eating animals (Foster, 1982). Even at a more local scale, however, the reproductive output of a given plant species can vary many-fold from year to year (Chapman *et al.*, in review), so that the composition of available fruit resources is never the same two years in a row. Far from being a constant aseasonal source of food, tropical forests vary markedly in food production both seasonally within years and on average across years. Again, primates need to be flexible in their foraging to cope with such variation.

Another prevailing myth about tropical forests, spawned by their lushness and species diversity, is that they are areas of extraordinary fertility. Soil fertility varies a great deal, from high-fertility sites near volcanoes or young mountain ranges like the Andes to old, weathered soils dating back to the pre-Cambrian era, 600 million years ago. Often the fertility of a tropical area can be surmised by looking at the color of the rivers that lead from it (Janzen, 1974). Fertile soils produce muddy runoff leading to

so-called 'white-water' rivers. By contrast, the low productivity on infertile soils leads to clear runoff that is often tinged dark brown by leaching from tannin-rich leaves, thus producing 'black-water' rivers. What nutrients are present in most tropical sites are not stored in the soil (unlike many temperate areas), but are sequestered in the living mass of plant tissue. Thus, when tropical forests are cleared, the nutrients are released rapidly to the soil and wash away, producing sites that can sustain agricultural crops for a few years at most. The soils under some diverse forests in Brazil are so nutrient-poor that they cannot sustain a single crop of corn after clearing (Lathwell & Grove, 1986). Although poorly documented, soil fertility is thought to be an important determinant of resource availability for primates (Peres, 1997b).

A final widespread view of the tropics, even among biologists, is that they are more 'stable' in evolutionary time than temperate forests. This perspective is not entirely false – something like tropical forest has been present for over 80 million years in areas we now consider tropical. What is now apparent, however, is that many areas in today's temperate zone were once at least subtropical when world climate was much warmer than it is today, and that much of the expanse of rainforest we know today (at least before recent human destruction) was much drier woodland or savanna during recent glacial maxima (Whitmore & Prance, 1987). Thus, the extent and continuity of tropical forests have changed markedly over the past 20 million years. More recent changes brought about by human occupation, including the frequent use of fire, may have radically altered the balance of continuous forest vs. savanna woodland in tropical Africa (see Tutin & White, chapter 13, this volume). One consequence of long-term changes is that the potential pool of primate species available to colonize a given forest is not the same between different regions even on the same continent, with obvious effects on primate community diversity, species composition and perhaps biomass (see Peres & Janson, chapter 13 and Struhsaker, chapter 17, this volume).

Because of variation in total amount and seasonality of rainfall, soil types, and history, tropical forests vary considerably across space and time in resource availability for primates. We shall now explore these availability patterns in more detail.

Insects

In virtually all tropical sites sampled, insects show strong seasonal variation in apparent abundance (Smythe, 1982; Kato *et al.*, 1995). Because many insect sampling methods require movement of the insects, some of the seasonal pattern may be due to inactivity as insects respond to drought or cold (however, see Wolda & Wright, 1992). Peak abundance is usually correlated with periods of new leaf flush at the end of the dry season in seasonally dry forests, or the onset of warmer weather in the subtropics (Coley & Barone, 1996). Because most methods of insect sampling have little control over the area sampled, it is not usually possible to compare the abundance of insects absolutely across different study sites. Anecdotal data suggest that insects are scarce in low-productivity areas of highly-weathered soils (Coley & Barone, 1996).

Fruits

Differences in fruit production between distinct communities are not well-documented, but some broad patterns have been suggested. Janzen's classic article (1974) noted that white-water river drainages were characterized by high fleshy fruit production, high animal densities, lots of mosquitoes, and relatively thin, short-lived leaves, with black water rivers typically being the opposite. His interpretation of this pattern was that in black-water rivers, low nutrient availability favored slow growing, chemically heavily defended plants, thus compounding the effect of low productivity in limiting the abundance of animals. As part of the same pattern, plants in black-water rivers should tend to produce fewer fleshy fruits than in white-water systems, thereby favoring seed predators over seed dispersers.

Plants characteristic of different successional stages may also produce different amounts of fruit. Early successional plants typically produce large quantities of fruit relative to their size, probably because they are selected for rapid growth, early maturation and prolific reproduction in a relatively energy rich environment (Levey, 1990). In later stages of succession, plants suffer more competition for light and so must produce fewer and larger-seeded fruits (Janzen, 1969; Foster & Janson, 1985).

Because fruit may be a major energy source sustaining primate populations (Janson & Emmons, 1990), the density

of fruit eating primates may be limited by the lowest seasonal level of fruit availability (Terborgh, 1983; Janson, 1984). In nearly all sites known, fruit production changes seasonally, although much between-year variation of phenological patterns is noted in virtually all long-term studies (Fig. 14.1; Whitmore, 1975; Terborgh *et al.*, 1986; Tutin & Fernandez, 1993; van Schaik, 1986; Chapman *et al.*, in review). Typically, fruit production peaks in the late dry season or early rainy season. This pattern has been explained by several hypotheses based on optimal reproductive patterns in plants (review in van Schaik *et al.*, 1993).

Leaf quantity

As noted above, a leaf is not a leaf is not a leaf. Thus, measuring differences in leaf production may be meaningless in comparison to differences in leaf quality. Therefore we shall review as distinct topics the ecological factors that affect total leaf production vs. leaf quality. Often data are reported only on net primary production, the sum of all new plant parts produced per area, but leaves typically form the major part of the total. It is generally acknowledged that the high productivity and diversity of tropical forests depends on high levels of annual rainfall (Richards, 1996). However, recent analyses suggest that primary productivity actually declines above 2500 mm of rain per year (Fig. 14.2, redrawn after Kay *et al.*, 1997), either because of nutrient leaching or low effective levels of solar irradiance due to dense cloud cover (cf. van Schaik *et al.*, 1993). Maximum primary productivity probably occurs in areas that receive between 2000 and 2500 mm of rainfall, dropping off more than 50% below 2000 mm and less so (by ca. 15%) above 2500 mm. The vast majority of primate study sites occur in areas with 1000–3000 mm of rainfall (see Table 14.1 and other chapters in this volume).

Because of the relatively slight effect of rainfall on average productivity within the moist tropics, much site-to-site variation in leaf production may be due to other causes. In fact, traditional analyses of tropical forest productivity do not even mention rainfall, but instead emphasize the importance of soil type (Lathwell & Grove, 1986; Vitousek & Sanford, 1986). Weathered, old soils do not readily retain cations (calcium, potassium, magnesium) and most of the phosphorus has been lost to leaching or is chemically bound and unavailable to plants (see Schlesinger,

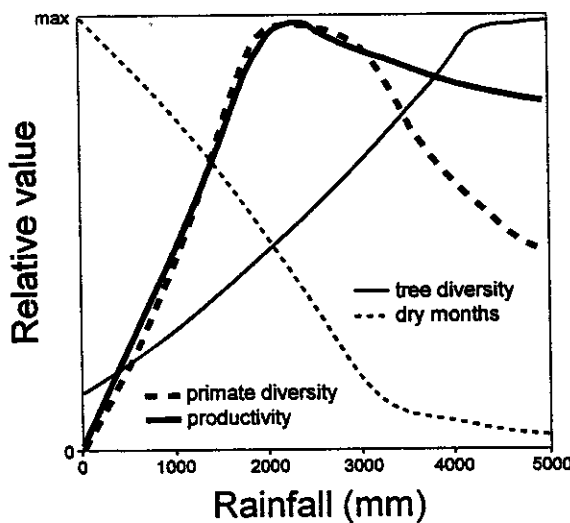


Fig. 14.2. Curves relating plant primary productivity, tree species diversity, number of dry months and primate species diversity to total annual rainfall in neotropical forests (based on Kay *et al.*, 1997). The relative value axis ranges from 0 to the maximum value appropriate to each curve; see Kay *et al.* (1997) for methods and definitions.

1997). Such low-nutrient soils cover over 70% of the tropics (Vitousek & Sanford, 1986) and have relatively low annual carbon fixation rates (Lathwell & Grove, 1986). Although soil weathering is affected by rainfall and temperature (Drever, 1994), it also depends on recency of origin, as weathering is a time-dependent process (Schlesinger, 1997). Geologically active areas in the tropics (Central America, areas close to Andes mountains, east Africa, Indonesia) have young soils that are usually productive despite high rainfall (Whitmore, 1990, pp. 138). Other sites (Guianan Shield) have old weathered soils despite average rainfall. Some south-east Asian sites are in regions of high volcanic activity and thus should have relatively young and productive soils (Burnham, 1975), but they receive so much rainfall that productivity may be low because of low solar irradiance.

Leaf quality

All mammalian folivores have to solve the problem of digesting fiber, and they do so in the same essential way, by fermentation (Cork, 1994). Thus, it is fairly easy to

develop criteria of leaf digestibility that apply to folivores anywhere (Milton, 1979; Oates *et al.*, 1990; Ganzhorn, 1992; Barton *et al.*, 1993). In contrast, how folivores deal with plant defensive compounds can be quite varied (Ganzhorn, 1989). One species, the golden bamboo lemur (*Hapalemur aureus*), daily ingests enough cyanide to kill an adult human (Glander *et al.*, 1989), while other lemur species in the same forest specialize on leaves rich in alkaloids or tannins (Ganzhorn, 1989). If each folivorous primate species were restricted to using a distinctive set of plant species because of such chemical specialization, estimating food abundance (and hence population density) for a species would require a detailed understanding of both the consumer's detoxification abilities and the chemical makeup of all plant species in a given site. However, at present there is little direct evidence that secondary compounds limit leaf choice among primate folivores in general (Milton, 1998). Furthermore, at least in Africa and Madagascar, it appears that site-to-site differences in leaf digestibility (protein to fiber ratios) are adequate to predict differences in folivore biomass (Oates *et al.*, 1990; Ganzhorn, 1992), suggesting that chemical specialization does not override the digestibility problem in setting limits to total folivore densities. This significant effect between sites of leaf digestibility on folivore biomass does not preclude the possibility that leaf-eating primate species diverge ecologically within sites based on detoxification ability, because the digestibility of plant species with distinct chemical profiles may vary in parallel between sites.

Are there habitat predictors of community-wide leaf digestibility? Allocation theory in the literature on plant defensive chemistry (Coley *et al.*, 1985) suggests that when plants can easily replace leafy tissue by growth, they should invest relatively little in chemical defense because toxins are often costly to produce (Zangerl *et al.*, 1997). Thus, areas of high nutrient soils should produce both relatively large amounts of leaves per year and leaves of relatively high quality. In fact, the availability of mineral nutrients in tropical soils generally correlates well with nutrient availability in the plants growing on them (Vitousek & Sanford, 1986). Peres (1997b) found that the densities of howler monkeys were much higher in floodplain soils than unflooded upland areas, and the former are known to contain higher concentrations of nutrients than the latter in Amazonian white-water river systems (but not

Table 14.1. Estimates of primate biomass per km², primate community richness and rainfall at selected sites

Site	Total biomass	Frugivore biomass	Folivore biomass	No. of species of frugivores	No. of species of folivores	Rainfall	Source
<i>Asia</i>							
Kutai Nature Reserve, Borneo	335	273	82	7	3	2177	1
Kuala Lompat, Malaysia	933	596	337	6	2	2120	2
Ketambe, Sumatra	837	702	135	6	1	3000	3
Polonnaruwa, Sri Lanka	2480	300	2180	3	2	1670	4
Sepilok, Sabah	268	184	82.5	6	2	3000	5
<i>Africa</i>							
Kibale National Park, Uganda	2759	682	2077	11	2	1570	6
Kibale National Park, Uganda	1954	754	1200	11	2	1490	7
Tai, Cote d'Ivoire	802	244	558	9	3	1800	8
Tiwai Island, Sierra Leone	1379	785.5	599.5	11	3	2708	9
Douala-Edea, Cameroon	409	198	217	7	1	4000	10
Lopé Reserve, Gabon	318.6	227.9	90.7	8	1	1506	11
Budongo Forest Reserve, Uganda	545	261.5	283.5	5	1	1495	12
Ituri Forest, Zaire	709.6	401.9	307.7	12	3	1802	13
<i>South/Central America</i>							
Manu National Park, Peru	636	456	180	11	1	2080	14
Urucu River, Amazonas, Brazil	381	344	37	13	1	3256	15
Barro Colorado Island, Panama	445	29	416	5	1	2730	16
Raleighvallen, Suriname	251	157	94	8	1	3000	17
La Macarena, Columbia	497.55	411.3	86.25	7	1	2600	18
Santa Rosa, Costa Rica	327	180.7	145.8	3	1	1527	19
Los Tuxtlas, Mexico	171.3	10.3	161	2	1	4900	20
<i>Madagascar</i>							
Morondava N5, Madagascar	685	247	438	7	2	950	21
Morondava CS7, Madagascar	583	357	226	7	2	950	21
Ampijoroa, Madagascar	771	444	327	7	3	1250	21
Ankarana, Madagascar	346	165	181	10	1	1900	21
Analamazaotra, Madagascar	375	208	167	11	3	1700	21
Ranomafana, Madagascar	290	249	41	12	3	2600	21

- Note: 1. Rodman, 1978; Rodman pers. comm.; Waser, 1987.
 2. Terborgh & van Schaik, 1987; Raemaekers & Chivers, 1980.
 3. Terborgh & van Schaik, 1987.
 4. Eisenberg *et al.* 1972, Dittus, 1975, Oates *et al.*, 1990.
 5. Oates *et al.*, 1990, Davies *et al.*, 1988.
 6. Struhsaker, 1975, 1978, 1981, Struhsaker & Leland 1979; Weisenseel *et al.*, 1993, Chapman & Wrangham, 1993, Chapman, unpublished data.
 7. Butynski, 1990 (Ngogo only).
 8. Terborgh & van Schaik, 1987; Galat & Galar-Luong, 1985, with *Pan* added from Boulière, 1985.
 9. Oates *et al.*, 1990 (mid-point in range used).
 10. Oates *et al.*, 1990.

in black-water ones: Furch & Klinge, 1989). However, Oates *et al.* (1990) found leaves of high protein/fiber ratios and a high biomass of folivorous primate on very infertile soils in Sierra Leone, apparently because of the prevalence of nitrogen-fixing leguminous trees in the forest (see also Harrison, 1986).

The effect of rainfall on leaf digestibility may be complex. If leaf digestibility parallels total primary productivity, both should reach a maximum between 2000 mm and 2500 mm of rainfall (Fig. 14.2, Kay *et al.*, 1997). However, lower amounts of rainfall are almost always associated with stronger patterns of seasonality in rainfall as well, with areas of less than 2000 mm of rain often having a distinct dry season of three or more months, leading to at least some canopy trees shedding their leaves (Richards, 1996, pp. 167–8). Because deciduousness necessarily limits leaf life span, plants in seasonally dry forests invest less in defensive chemicals for their short-lived leaves than do plants in ever-wet areas with long leaf life spans (up to 14 years: Coley & Barone, 1996). Thus, the effect of seasonality may mean that leaf digestibility increases, rather than decreases, as rainfall drops below 2000 mm.

Leaf quality may also vary over very short spatial and temporal scales. For instance, leaves that receive more light may have substantially higher levels of digestible carbohydrates, proteins, and tannins than shaded leaves on the same tree or species (Ganzhorn, 1995). Likewise, leaves accumulate carbohydrate during the day when they photosynthesize, so that leaves sampled at the end of the day are of significantly higher quality than those sampled in the early morning (Ganzhorn & Wright, 1994). Unless leaves are sampled at a standard time of day and tree

position, measures of leaf quality may be unreliable and difficult to compare across species or sites.

Leaf quality may also vary between plant families (see Gupta & Chivers, chapter 2, this volume). In particular, legumes (the bean family) frequently have nitrogen-fixing bacteria associated with their roots, thereby allowing them to produce foliage of relatively high nitrogen content (as well as a high concentration of nitrogen-containing defensive compounds, such as alkaloids). Although nitrogen does not appear to be limiting to productivity in most tropical soils (Vitousek, 1984), the relative abundance of legumes in a forest may determine the productivity for leaf-eating primates (Davies, 1994). In addition to leaf quality, different plant families are distinguished by particular sets of defensive chemicals that may favor particular consumers adapted to cope with these defenses (Ehrlich & Raven, 1964; Ganzhorn, 1989; Jaenike, 1990). Folivore species compositions may respond to dominance by different plant families in different regions.

Finally, leaf quality is expected to decrease in older successional stages of a forest (Coley & Barone, 1996). Because leaf life spans are short (average of 6 months) in tropical trees of early successional stages, they should be less defended chemically than those of mature forest species. In fact, leaves of early successional tree species sustain over four times more damage per leaf than do leaves of mature forest species (48 vs. 11%: Coley & Barone, 1996). Thus, areas that differ in disturbance history may well differ in mean leaf digestibility despite similar rainfall and seasonality (Ganzhorn, 1995).

Altogether, leaf quality for primates appears to be indexed well by the ratio of protein/fiber or protein/(fiber

Notes to Table 14.1 (*cont.*)

11. White, 1994 (mean of 5 neighboring sites).
12. Plumptre *et al.*, 1994; Plumptre & Reynolds, 1995 (density – unlogged forest only); Harvey *et al.*, 1987 (weights assuming 50/50 sex ratio and 1/2 group immature weighing 1/2 adult); Egging, 1947 (rainfall).
13. Thomas, 1991 (density); Hart, 1985 (rainfall).
14. Terborgh, 1983 and Symington, 1988 for *Ateles belzebuth*; Harvey *et al.* 1987 (weights).
15. Peres, 1993.
16. Glanz, 1982; Eisenberg & Thorington, 1973.
17. Mittermeier & van Roosmalen, 1981 (body weights adjusted).
18. Stevenson, 1996 (assuming 1/2 group immature weighing 1/2 adult).
19. Chapman, 1988; Chapman, 1990b, Glander *et al.*, 1991; Chapman, unpublished.
20. Estrada & Coates-Estrada 1985.
21. Ganzhorn, 1992.

+ tannins) despite some specializations among folivorous species for particular classes of plant defensive compounds. These simple indexes of leaf quality increase in more fertile soils, younger successional stages of forest, more seasonally deciduous forests, sunnier locations within a tree crown, at the end of the day, and in selected plant families such as the legumes. These diverse factors make it difficult to predict accurately the leaf quality of a given area from general climatic or latitudinal measures, or how a given primate species will choose leaves within a site.

Covariation in productivity among dietary items

Should the productivity of different diet categories covary among communities? Janzen's (1974) and Coley *et al.*'s (1985) arguments suggest the answer should be yes: high-nutrient soils should favor plants that have relatively high growth rates, which should lead to higher leaf turnover (i.e., more flush leaves), and less heavily-defended leaves. All these characters should increase leaf quality, thereby benefitting folivorous monkeys. Insect production should also flourish, which will favor insectivorous primates. Higher fertility should also allow more fruit production, which will support more dedicated frugivores and may encourage greater investment in fleshy fruits as opposed to the mechanically well-defended, non-fleshy species such as Lecythidaceae and Dipterocarpaceae typically found in low-nutrient, low-production areas of the tropics (Janzen, 1974; see also Ganzhorn *et al.*, chapter 4, this volume). Leaf quality and fruit production may also parallel each other across stages of succession, both being highest in early succession, albeit for different reasons (see above). Even though rainfall and primary productivity are broadly correlated (except in the wettest sites: Kay *et al.*, 1997), rainfall may affect fruit and leaf availability to primates in different ways. Fruit-eating species should benefit from higher overall productivity as rainfall increases, but folivore biomass may peak in seasonally dry areas with modest total productivity because these would contain short-lived leaves of high digestibility. Existing data are not sufficient to test whether some resource categories increase more than others as a function of site-related differences in total productivity, given that insect abundance is rarely measured on a per-area basis, and few studies break down primary productivity into its components (Kay *et al.*, 1997). To facilitate future comparisons of resource production

among primate communities, we briefly review below (Appendix 14.1) methods for sampling distinct resource types, along with some suggestions for improving comparability of results across studies.

Distinct resources often vary in parallel across the tropical seasons. Many primate ecological studies have measured the availability over an annual cycle of at least two dietary components (insects and fruits, fruits and flush leaves). Peaks of fruit and insect abundance often overlap or coincide markedly (Terborgh *et al.*, 1986), and the peak of flush leaf production usually occurs only shortly before the peak of ripe fruit production in seasonally dry forests (Terborgh & van Schaik, 1987). However, in the moist and wet forests which comprise most of the tropics, there is little or no correlation between fruit and new leaf production (Terborgh & van Schaik, 1987). Initial comparisons suggested that South America might differ from Old World sites in having greater synchrony between fruit and new leaf production patterns, so that frugivore-folivores might suffer a real dearth of resources in the early dry season (Terborgh & van Schaik, 1987). However, this conclusion was based on data from only one Neotropical study site, and more recent data on other study areas in South America show no or even a negative correlation between the availability of fruit and new leaves (Peres, 1993; Chapman, unpubl. data).

WHAT RESOURCES LIMIT PRIMATE DENSITIES?

There are three major candidate explanations for what determines differences in primate densities across undisturbed sites: (1) total or seasonally low plant productivity; (2) resource diversity; (3) mineral availability. We will deal with these in reverse order, as the evidence for the latter two is limited at present.

Minerals

The evidence that any mineral nutrient may limit primate densities is largely anecdotal. Primates occasionally ingest substances not generally considered as food, such as dirt, and seem to go out of their way to obtain certain foods that would seem to offer few advantages over other dietary items in terms of either energy or protein yield. Leaf eating colobine monkeys have been observed to prefer to eat

water plants that contain relatively high levels of sodium (Oates, 1977). Many primates, as well as other herbivorous mammals, congregate at "salt licks" in the New World, where they eat layers of dirt rich in sodium (Emmons & Stark, 1979). However, many primates and other herbivores consume clay-like soils even when these do not contain high concentrations of sodium or other ions (Mahaney *et al.*, 1995). It has been suggested that soil consumption may aid in digesting leaves with high tannin content by precipitating the tannins (Hladik & Chivers, 1994; Struhsaker *et al.*, 1997) or that the clay content in the soil may help to stop diarrhea (Mahaney *et al.*, 1995).

For many large herbivores, phosphorus is a limiting nutrient (Freeland & Choquenot, 1990) because bones require a ratio of calcium to phosphorus between 1:1 and 1:2, whereas most leaf material contains ratios of 5:1 or greater, both for crop plants (Lloyd *et al.*, 1978) and tropical forest species (Vitousek & Sanford, 1986; Theresa Pope, pers. comm.). Furthermore, on highly weathered or acidic tropical soils, absolute phosphorus availability is extremely low (Vitousek & Sanford, 1986; Schlesinger, 1997). High ratios of calcium to phosphorus are detrimental even if phosphorus levels are absolutely high because excess calcium prevents the absorption of phosphorus. Phosphorus limitation might help to explain the striking differences in folivore biomass between African and New World rainforests (cf. Terborgh & van Schaik, 1987), as forestomach fermenters can access from 50–110% more phosphorus in leaf tissue than can caeco-colic fermenters (see above). At least one colobine primate, the proboscis monkey, prefers leaves with higher phosphorus concentrations (Yeager *et al.*, 1997).

Fruit-eating animals may be limited by other minerals, most of which are scarce in fruits. The nearly universal popularity of figs as a major fruit resource in the tropics might be linked to the fact that they have higher absolute concentrations of calcium than do other types of fruits in the same forests (O'Brien *et al.*, 1998). However, fig trees are also often immense and tremendously productive trees, so many animals may prefer them simply because they offer a vast abundance of food in one place (Terborgh, 1986). Calcium availability clearly does not explain the apparent love of anthropoid primates for domesticated bananas, as they contain less than one quarter of the calcium of figs and have the lowest levels of calcium of any domesticated fruit (from data in Watt & Merrill, 1975).

Food species diversity

Ecological theory has predicted that the diversity of consumers should relate to the diversity of resources they can use. As most primates depend largely on plants, plant species diversity should be a simple predictor of primate diversity and perhaps biomass (if only because the more consumer species can coexist in an area, the greater the total density of animals if they do not compete strongly for resources). The relationship of food plant diversity to primate species diversity, however, is complex (Ganzhorn *et al.*, 1997; Kay *et al.*, 1997). Although both increase in parallel with rainfall up to 2500 mm, plant species diversity increases slowly or not at all above this level, whereas primate species diversity actually declines (Fig. 14.2). Ganzhorn *et al.* (1997) attribute this decline to the rarefaction problem – as plant species diversity increases, the density of each species necessarily declines if total stem density is roughly constant. Thus, at very high plant diversities, consumers may have difficulty locating or foraging efficiently on the plants they need to survive. In this explanation, it is not clear why each consumer species does not simply expand its diet, as expected from foraging theory when preferred resource density is low (Stephens & Krebs, 1986).

Quantitative field comparisons of primate biomass and the biomass of their foods are rare. Gautier-Hion (1983) proposed that the higher consumption of fruit by *Lophocebus albigena* and *Colobus guereza* in Makokou relative to Kibale, and the generally more frugivorous diet of the entire community at Makokou, were a result of the fact that fruit is available in greater quantities and there are more fruiting species in central Africa than east Africa. At Makokou, 95 species (> 5 cm DBH) were identified in a 0.4 ha plot (A. Hladik, 1978), while at Kibale, Struhsaker (1975) describes only approximately 34 species in a 1 ha sampling area. Yet, the primate community richness is similar at these two sites and the biomass of primates is higher at Kibale than Makokou (Waser, 1987). In a 3-year study of red colobus monkeys (*Procolobus badius*), Chapman & Chapman (in review) assessed red colobus density and diet and quantified the diversity of their food trees at six sites in Kibale National Park, Uganda and found that higher-density populations tended to be those with richer diets.

Productivity

At the level of single species, authors have sometimes been successful in explaining variation in primate population density using ecological measures. For instance, Mather (1992) found a nearly perfect ($r = 0.99$) correlation across sites in south-east Asia between the biomass of gibbons (including siamangs) and the proportion of trees that were gibbon food trees. Using ecological variables related to food production, Dunbar (1992) was able to explain the limits to the distribution of gelada baboons, in effect predicting where gelada density reached zero. Such single-species analyses are worth attempting for other primates.

At the level of entire communities, direct evidence relating productivity to primate community structure is scarce because most methods of measuring food production only estimate relative, not absolute, abundances (see above). Comparisons between sites, even when the method used is similar (phenological surveys, plant structure indices, or fruit traps), show little relationship between primate biomass or species diversity and measured food abundance (Chapman & Onderdonk, unpubl. data). Fruit traps could provide comparable absolute measures of fruit production between sites, but the criteria for what is potential primate food and the methods used to interpret the fruit biomass captured have varied between studies (Terborgh, 1983; Janson, 1984; Chapman *et al.*, 1994; see Appendix 14.1). Therefore, researchers have often looked for simple surrogates for resource productivity that can be used in predictive models of primate species richness or biomass (Coe, 1984; Oates *et al.*, 1990; Davies, 1994; Reed & Fleagle, 1995).

The most widespread such substitute for resource productivity is rainfall. At some level there is an obvious relationship between the amount of rain an area receives and primate community structure (e.g., desert primate communities are impoverished and have a relatively low biomass when compared to rainforest communities). Positive correlations between rainfall and primate species diversity are strong within each major primate radiation except Asia (Reed & Fleagle, 1995; but see Gupta & Chivers, chapter 2, this volume). Nonetheless, plant productivity does not increase indefinitely with rainfall (Fig. 14.2), reaching a peak in the New World tropics between 2000 and 2500 mm. Above this level, both plant productivity and primate species diversity in the New World decline

(Kay *et al.*, 1997; see also Peres & Janson, chapter 3, this volume). Similar declines seem to be present in Madagascar and south-east Asia, and may hold true in Africa (Kay *et al.*, 1997). A possible reason for the relatively low primate diversity found in south-east Asia compared to other areas could be the very high levels of rainfall (see Gupta & Chivers, this volume).

Further support for the effect of productivity on primate species diversity comes from comparison of communities on distinct soil types in Amazonia. The impoverished soils of upland terra firme forest support fewer primate species than those of more productive terra firme forests near rivers (see Peres, chapter 15, this volume). Although the most productive chronically-flooded alluvial forests have fewer species than either type of terra firme forest, this low diversity may be caused simply by the direct effect of flooding on insect availability, as most of the species that are absent from flooded forest are small-bodied forms that rely on insects for protein (Peres, 1997a). Thus, primate species diversity in general appears to track total forest productivity. Does the same trend hold for primate biomass?

Because so few studies of primate communities have measured local primary production, most studies on primate biomass use correlates of productivity such as rainfall. Attempts to relate rainfall to primate biomass have revealed somewhat surprising results. Contrary to the common view that primate biomass should increase with total productivity and hence with annual rainfall, Peres (1997b) discovered a negative relationship among sites between the biomass of *Alouatta* populations and rainfall. Similarly, Ganzhorn (1992) documented that the biomass of folivorous lemur species was negatively related to the annual rainfall of the area, and Gupta & Chivers (this volume) find a similar negative trend of total primate biomass with rainfall in south-east Asia. In an effort to test the generality of these patterns, we present here an analysis of primate community biomass and rainfall from well-studied primate communities across the tropics (Chapman & Onderdonk, unpublished). Our first clear result, consistent with the observations of previous studies (Terborgh & van Schaik, 1987) is that present-day primate biomass is significantly greater in regions with forestomach fermenters (Africa and Asia) than where only caeco-colic fermenters occur (New World and Madagascar). These regional differences parallel the difference in cell-wall

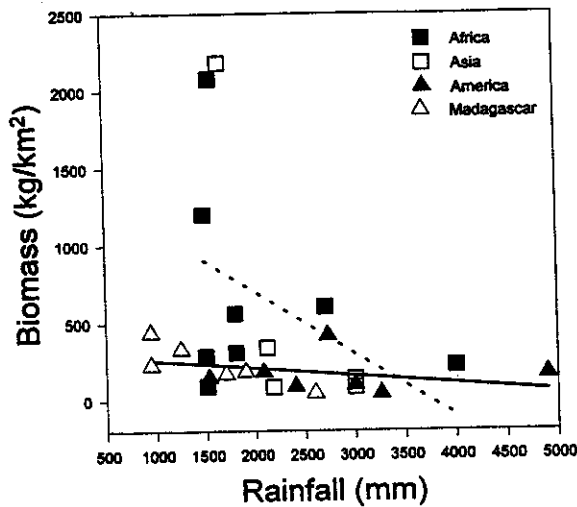


Fig. 14.3. Regression of folivore biomass on rainfall across study sites (data from Table 14.1). Regressions are separated by forestomach (Africa and Asia: dotted line) vs. caeco-colic (South America and Madagascar: solid line) fermenters because of the large mean difference in absolute biomass maintained by folivores of these two types. In an analysis of covariance, forestomach fermenters have higher mean biomass than caeco-colic fermenters ($F(1,22) = 4.95$, $P = 0.039$), and the biomass of both types decreases with increasing rainfall ($F(1,22) = 3.97$, one-tailed $P = 0.030$). The difference in the slopes between digestive types is not significant ($F(1,22) = 2.44$, $P = 0.132$).

digestive efficiency between howlers and colobine monkeys (Milton, 1998). Once these large-scale differences are accounted for, the biomass of folivores decreases with increasing rainfall (Fig. 14.3) and frugivores show similar, but not statistically significant, trends (Fig. 14.4). The parallel decline of primate biomass (Fig. 14.3) and primary production with rainfall above 2500 mm (Fig. 14.2) might suggest that primate biomass is broadly limited by productivity.

The inferential link between primate biomass and productivity is at best weak, however. First, rainfall explains only a small part of the variation in primate biomass in our regressions (0.1–23%) and in primary production in moist New World sites (< 10%: Kay *et al.*, 1997). Second, nearby sites of similar rainfall and seasonality can differ markedly in primate biomass, such as the neighboring forest communities of Kanyawara and Ngogo (2759 kg/km² vs. 1954 kg/km², 1660 mm vs. 1490 mm rainfall) in Kibale

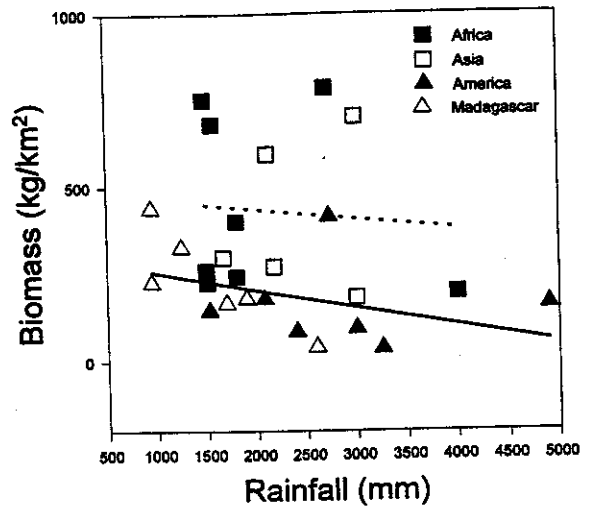


Fig. 14.4. Regression of frugivore biomass on rainfall across study sites. Data are separated by region as in Fig. 14.1. In an analysis of covariance, the effect of region is significant, but that of rainfall is not (respectively, $F(1,22) = 7.25$, $P = 0.013$; $F(1,22) = 1.84$, one-tailed $P = 0.094$). Although the difference in the slopes of the rainfall effect between areas is not significant ($P = 0.64$), the regression for America and Madagascar alone is significant ($F(1,11) = 4.3453$, $P = 0.03$, one-tailed), whereas that for Africa and Asia is not ($F(1,11) = 0.09$, $P = 0.38$, one-tailed).

National Park, Uganda (Chapman, unpubl. data). Almost surely, some of the remaining variation in both primary productivity and primate biomass among sites is related to soil fertility. In fact, Peres (chapter 15, this volume) found that primate biomass increases markedly with expected soil fertility among sites of similar rainfall in Amazonia. How primate biomass relates to productivity will remain a puzzle until we possess much better measures of primary production for many sites with known primate densities.

Food quality

Food quality is an important determinant of food choice for dedicated as well as opportunistic folivores (Milton, 1979; Barton & Whiten, 1994). Do differences in leaf digestibility between communities contribute substantially to explaining variation in primate biomass? Researchers have met with considerable success predicting leaf-eating primate biomass using indices of leaf quality alone. Studies of colobines (Waterman *et al.*, 1988; Oates *et al.*, 1990)

and folivorous lemurs (Ganzhorn, 1992) have found a significant positive correlation between the biomass of folivorous primates and the simplest index of leaf digestibility, the ratio of protein/fiber or protein/(fiber + tannins). Leaf quality differences explained 90% of the variation in colobine biomass and 76% of the variation in folivorous lemur biomass. Such strong relationships are surprising, given the simplicity of this leaf quality index, the difficulty of determining primate biomass, and the number of alternative explanations available to explain primate biomass (Freeland, 1977; Cant, 1980; Terborgh & van Schaik, 1987). Less clear results are found in southern Asia, where the protein/fiber ratio of dominant plant families varies nearly 20-fold among sites, but does not correlate well with primate biomass for the region as a whole (Gupta & Chivers, chapter 2, this volume).

Another way to test the importance of leaf digestibility to primate biomass uses the observation that plants invest less in structural toughness and chemical defense of short-lived leaves in deciduous forests than in leaves that will last for several years as in everwet forests (Janzen, 1975; Coley & Barone, 1996). Thus, leaves in more seasonal environments should have higher digestibility. This relationship allows a direct test of the importance of leaf quality vs. leaf production in determining folivore biomass. The total primary production of more deciduous tropical forests (at 1000–2000 mm of rainfall) is generally less than those of moist or wet forests with more than 2000 mm of rain (Fig. 14.2), but the leaf quality in deciduous forests is expected to be greater. If folivore biomass depends primarily on total primary production, it should be lower in more deciduous forests than in moister forests; the opposite pattern should hold if leaf quality is more important to folivore biomass.

Existing data support the importance of leaf quality. In Madagascar, the biomass of folivorous lemurs (Ganzhorn, 1992) increases with increasing seasonality, as does that of howler monkeys in the New World (Peres, 1997b). Our regressions show the same trend. We separated sites with less than 2000 mm as seasonal/more deciduous from those with more than 2000 mm of rainfall. As expected from the leaf quality hypothesis, folivore biomasses tended to be higher in the former than in the latter ($t = -1.86$, $P = 0.077$), after accounting for digestive strategy. No such difference is apparent for frugivorous species in a comparable analysis ($t = -0.01$, $P = 0.99$), which reinforces the

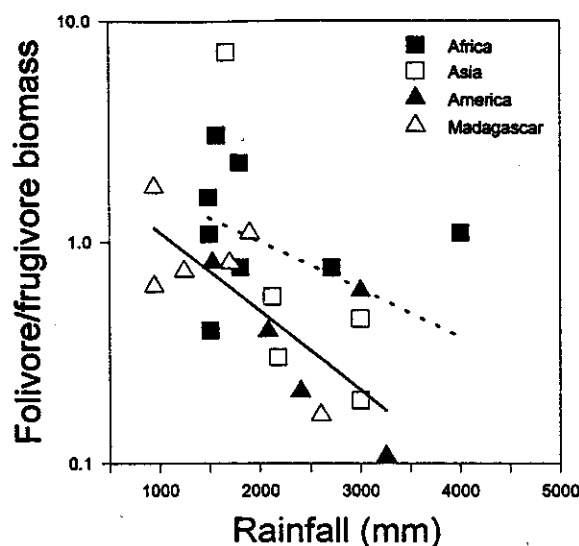


Fig. 14.5. Regression of the ratio of folivore to frugivore biomass on rainfall across study sites. Data are separated as in previous figures. Data for Barro Colorado Island (Panama) and Los Tuxtlas (Mexico) are removed because these had strongly deviant values of this ratio within the America/Madagascar data set (the two sites were, respectively, 2.1 and 2.4 standard deviations from the overall mean). Both sites are actual or habitat islands and so may not represent the equilibrium tendency among tropical forests in general (see also Kay *et al.*, 1997). The effect of rainfall on $\log(\text{folivore/frugivore biomass})$ is highly significant ($F(1,22) = 5.02$, $P = 0.018$, one-tailed), but neither the slope nor the intercept of the regression differs between areas.

inference that the result for folivores is not due to overall productivity. Furthermore, the fraction of total primate biomass that consists of folivores declines linearly from the driest sites in our sample toward the wettest (Fig. 14.5). It appears that leaf quality really is more important than total leaf production in explaining folivore biomass, although presumably the critical variable is really the total production of high-quality leaves.

CONCLUSIONS

Despite the initial appearance of superabundant food for primates in tropical forest, many studies support the idea that primates do face food shortages, either seasonally in the case of frugivores, or in terms of sparse or ephemeral

high-quality leaves for folivores. Although food abundance has been related directly to the population density of few primate species (Janson, 1984), general measures or correlates of habitat productivity have been successful in explaining some of the between-site variation in primate species richness and biomass. Because folivorous primates often comprise a major fraction of the total biomass of a primate community (Fig. 14.5), nearly three-quarters of the variation in total primate biomass derives from variation in folivore biomass in our data. Therefore, explaining variation in total community biomass of primates largely is an exercise in explaining variation in folivore biomass. The somewhat surprising conclusion from our review of the literature and our own data is that folivore biomass actually declines with increasing rainfall, and may decline even in areas of greater primary productivity. The success of a simple index of average leaf quality in predicting between-site variation in folivore biomass suggests either that leaf quality is more important than leaf quantity, or that this index of leaf quality is a more precise reflection of habitat productivity than is rainfall. Perhaps the constraints of being arboreal folivores of modest body size place leaf quality above leaf quantity in affecting their population density.

To distinguish among these hypotheses will require far more complete data on various measures of food production than are currently available. We emphasize in Appendix 14.1 that the major common methods of estimating fruit and insect availability do not currently allow consistent comparisons of absolute production between study sites. Phenological methods should ideally be complemented with litterfall (fruit, seed, leaf) traps and vice versa to provide more informed and objective absolute measures of fruit and leaf production. Insect samples based on known areas or volumes of vegetation, although tedious, are the only method likely to provide absolute density data that can be compared between sites. Leaf quality may vary across short distances and time spans, so care must be taken to sample leaves in the same location in the tree and time of day that the primates actually ingest them.

Many interesting questions about the determinants of primate diversity and biomass remain to be investigated. First, are these aspects of community structure determined more by the total annual or the minimum seasonal availability of foods. Resolving this question will have to await better data on absolute food production for a variety

of sites. Second, is the niche partitioning of leaves according to toxin chemistry, as found in lemurs, more general to folivores, at least where more than one species coexist? Although comparisons of general foraging ecology of coexisting colobines do exist, focused studies of comparative leaf chemistry of their food choices appear still to be lacking. Third, do forestomach fermenters have any real advantage over caeco-colic fermenters in terms of energy extraction per unit of time or ability to handle plant defensive compounds? What really is the basis for the more than two-fold difference in folivore biomass between areas with forestomach- and those with only caeco-colic-fermenting primate species (Fig. 14.3)? Why does this difference in biomass appear both in folivorous species and in frugivore-folivores in the same regions (Fig. 14.4)? Fourth, does disturbance history affect the quality of an existing habitat differently for folivores vs. frugivores (see Ganzhorn, 1995)? This last question is of special concern as more and more primate habitats become disturbed by human activity.

APPENDIX 14.1: METHODS AND CAUTIONS FOR SAMPLING THE ABUNDANCE OF PRIMATE DIETARY RESOURCES

Few quantitative data exist to support the claim that primate populations are limited by the availability of food resources. Few studies provide data on the densities of every primate species in a community and have simultaneously collected data on the food available to those species. The study of primate resources is greatly hindered by methodological difficulties that reduce the reliability and comparability of results across study sites.

The first methodological difficulty is answering the seemingly simple question of: "what is primate food"? Tropical rainforests are famously species-rich in plants, with up to 200 plant species in a 25 by 25 m plot in Africa (Hall, 1977; Hall & Swaine, 1981), and over 1000 woody species in an area of a few square kilometers (Croat, 1978). Only a fraction of this diversity is consumed by any one primate species, but knowing exactly which plants are potential foods is difficult. Typical lists of plant foods for a single primate species vary from 60 to over 200 species, and often these lists grow even after several years of study.

Some food items may be so low on a primate species' preference list that they would be eaten only during periods of severe food scarcity (cf. Stephens & Krebs, 1986). During five years of observation of a spider monkey (*Ateles geoffroyi*) community in Santa Rosa National Park, Costa Rica (Chapman, 1990a), animals were rarely seen to eat the fruits of *Bursera simaruba*; however in the sixth year, the community fed on this fruit extensively during a month when little else was available. Furthermore, even the fraction of the diet that is fruit vs. other components can vary greatly over time (Terborgh, 1983; Chapman & Chapman, 1990), making it difficult to assess the potential diet of a species. For example, MacKinnon (1974, 1977) studied the diet of orangutans (*Pongo pygmaeus*) in Sumatra. In one month the orangutans were primarily frugivorous, spending 90% of their feeding time eating fruit and only 5% eating leaves, and 5% eating insects. In another month this population was primarily folivorous, spending 75% of their time eating leaves, 15% eating bark, and only 10% eating fruit. Similar variation can be found in spider monkeys, that are typically considered ripe fruit specialists (Klein & Klein, 1977). Chapman (1988) described that in one month the spider monkey community in Santa Rosa National Park, Costa Rica, ate only fruit (100% of their feeding time); however, in another month they ate primarily leaves (86%) and little fruit (14%), and in yet another month, insects were a common component of their diet (30%). Only long-term study can reveal a reasonably complete profile of the foods used by one or more primate species.

Without complete food lists, methods of estimating food availability must make some assumptions about what to consider food. At one extreme, some studies assume that any fleshy fruit is a potential food for a fruit-eating primate, even when the study species has not been observed to eat that fruit (Terborgh, 1983). This assumption is partly justified by the fact that there is much overlap in the fruit part of the diets of co-existing primate species (Terborgh, 1983), and the fact that primates eat many species of fruit that apparently have evolved to be dispersed by other animals (Janson, 1983). However, this premise is clearly only an approximation; it is often made for convenience when fruit traps are used to measure fruit production, as it is much easier to assign the half-decomposed remains of a fruit to broad categories (fleshy, dry, winged) than to particular species (but see below). At the other extreme, many observational studies consider as food only

the species which the study animals have been seen to eat in the study site. Because behavioral and ecological data are often collected at the same time, it usually happens that new food species are being added to the diet during a study; the availability of these resources can only be monitored after they are known to be eaten. An intermediate solution for a primate species that has been studied in several sites is to include as possible foods all the species known to be consumed by that primate in any area; any of these foods that occur in a given study site should then be monitored and measured. Even if you know which foods you need to measure, assessing their production for an entire primate community requires many distinct methods, as most primate communities are diverse, including species that use very different types of resources, as well as many that eat a mixed diet of fruit and either insects or leaves. We now review what is known about variation in the different major classes of primate resources and how they affect primate community structure.

Insects

Insects make up a large proportion of animal biomass in tropical habitats (Fittkau & Kline, 1973) and are very diverse even in single localities. For example, Stork (1991) used insecticide fogging to sample the arboreal arthropod fauna in 10 individual Bornean rainforest trees and altogether found 23874 individuals of at least 3000 species. Despite the abundance and richness of arboreal insects, rarely has insect availability been estimated in conjunction with studies of primates. The likely reason is that the great diversity of insects, their various specialized microhabitats and seasonal changes in abundances make rigorously quantifying their abundance a difficult task. The problem would be less daunting for a specialized insect-eater, but primates often search for insects in many distinct places and ways (see above). Thus, they almost certainly consume many dozens to hundreds of insect species, the availability of which to the primate may depend on more than just the absolute abundance of the insect. Humans might mimic the foraging style of primates to estimate their foraging success, but most primates forage in the forest canopy, a difficult task for a researcher to replicate.

Several means have been employed to quantify insect abundance ranging from traditional sweep samples, to sticky boards, to fogging of entire trees (Southwood,

1978). Hladik *et al.* (1980) used a combination of methods to quantify seasonal changes in the insects available to the prosimian community of Morondava, Madagascar. An ultraviolet lamp was used to attract flying insects, and the biomass of insects coming to the light during two hours at the beginning of each night was measured. To estimate the seasonal abundance of caterpillars, feces were collected from litter traps. Sampling regimes must be designed to accommodate the fact that invertebrate distributions are not homogenous. For example, Hladik *et al.* (1980) found that invertebrate abundance was twice as great in dense vegetation neighboring a temporary pond than in dryer areas. In any case, such indirect methods can only index relative abundance of insects. Such an index may be adequate for estimating seasonal trends in insect availability (Janzen, 1973), but they are not likely to be useful to compare absolute abundances between different areas even within the same general study site. Even as a measure of seasonal availability, indirect methods may be biased toward a few insect orders (e.g., nocturnal lepidoptera for ultraviolet lamps). These may not be the taxa used by primates nor is their abundance necessarily correlated with the kinds found in primate diets. To increase comparability of insect abundance across study sites, effort should be directed toward direct censuses of the actual prey used by primates whenever this technique is feasible (e.g. searching a known number of leaves by hand or visually: Terborgh *et al.*, 1986).

Fruit

Fruit resources have primarily been quantified using either phenology methods or fruit traps (Blake *et al.*, 1990; Hutto, 1990; Janson & Emmons, 1990; Chapman *et al.*, 1994). Phenology transects (or quadrats) involve the establishment of areas in which trees are routinely monitored for the presence of fruit. Typically a subset of all trees within the sampling area is selected for monitoring; a standard that is often used is to monitor all trees >10 cm DBH (Diameter at Breast Height) on a monthly basis. By selecting trees above a specific size, one is making the assumptions that trees smaller than the size criteria used are incapable of producing fruit that are useful to primates; this assumption may often be correct for large-bodied canopy species, but is clearly false for small-bodied understory species (Terborgh, 1983). Instead of using a criterion that is based on size, researchers can monitor only those species

known to be eaten by particular primates. The problem with this alternative is that new food species often appear as a study progresses.

Various means are used to assess the size of fruit crops on individual trees. However, there are few guidelines available to indicate which procedures are most appropriate in different situations (Peters *et al.*, 1988; Chapman *et al.*, 1992). In some instances no estimate of crop size is made and ripe fruit availability is indexed simply as the number of trees bearing fruit during a given sampling period. This method suffers in that it ignores large differences in production of fruit between individual large and small trees. For many species, determining if the fruit on the tree is ripe is not difficult, because ripening is often associated with a color change, fruits ripen over a short period, and ripe fruits often fall to the forest floor soon after the time when frugivores start eating them (but they may be delayed longer in falling, see Zhang & Wang, 1995). However, for some species, it is difficult or impossible to distinguish ripe from unripe fruit based on a visual assessment through binoculars. For example, *Monodora myristica* bears large (16 cm diameter) green fruit that exhibit no visual signs of ripening. Although its fruits may remain on the tree at full size for up to 3 months, when chimpanzees (*Pan troglodytes*) and baboons (*Papio anubis*) view these fruits as being ripe, they often remove an entire fruit crop in a few days (Balcomb, pers. comm).

Other researchers have assumed that larger trees will produce more fruit than smaller trees and have used a variety of indices of tree size to weight the value of a fruiting tree (e.g., DBH—Leighton & Leighton, 1982; Peters *et al.*, 1988; Chapman, 1990b; crown volume—Symington, 1988). Using such indices assumes that the relationship between tree size and fruit production is the same for a variety of species, which is likely inappropriate. Other researchers have attempted to visually assess fruit crop size and assign a relative rank to crop size. Chapman *et al.* (1992) compared the accuracy and precision of three methods of estimating fruit abundance on tropical trees: tree diameter (DBH), crown volume, and visual estimation. DBH was the most consistently accurate method and exhibited low levels of inter-observer variability. Generally, crown volume was neither precise nor accurate. The visual estimation method was accurate for trees with very large fruits, but inter-observer variability was high and this method required a large time investment per tree.

Although DBH is simple and accurate to measure, the relationship between DBH and fruit production is not known either within or between species. It is very unlikely to be perfectly proportional even within species. DBH is a linear function of tree size, whereas fruit production within a species should scale with the area or volume of the tree crown, which are respectively quadratic or cubic measures of tree size. For instance, a tree of 100 cm DBH is only twice as big in linear dimension as a tree of 50 cm DBH, but the difference in fruit production between them is likely to be in the range of fourfold to eightfold. Between plant species, additional problems creep in. Different life-history adaptations or habitat light regimes may lead to very different patterns of allocation to fruit production among species of similar DBH. It appears that sunlit canopy and emergent trees are much more productive per unit of leaf area than are severely shaded understory trees and shrubs (cf. Levey, 1990; Ganzhorn, 1995). Because of these problems, summing or averaging DBHs is unlikely to be a reliable way of gauging mean production. If the regression between $\log(\text{fruit production})$ and $\log(\text{DBH})$ is linear, then the most reliable gauge of mean fruit production is first to calculate the mean of the $\log(\text{DBH})$ of the sampled trees, and then use the regression equation to estimate the mean $\log(\text{fruit production})$.

Counting trees is relatively easy, detecting ripe fruit is generally not too difficult, but quantifying biomass is difficult. Although it might be possible to count all the fruit in a tree, doing so would be tedious and prone to many inaccuracies. Therefore, nearly all phenology methods use an index of fruit biomass which depends on a number of assumptions. Typically, the fruit in a tree will be scored on a relative scale from 0 (no fruit) to a small integer (often 3 or 4) which represents 'many' (e.g., Koenig *et al.*, 1997). Usually, these scores are species-specific, so a 'many' score means different amounts of fruit for different tree species. The scaling of fruit abundance between 0 and 'many' is not necessarily linear and is usually not specified in detail. An alternative semi-quantitative index is to note the \log_{10} of the estimated number of fruits in the tree: 0 for 1–9, 1 for 10–99, 2 for 100–999, etc. Although estimating the order of magnitude of number of fruits is more time-consuming than a 0-to-3 scale, it is not very much more so, and at least provides a rough idea of absolute fruit numbers. Pulp mass per fruit can be determined by dissection of individual fruits (Janson, 1985).

In contrast to phenology transects, fruit traps are used to estimate fruit production directly. Fruit traps are simply baskets that are placed, usually at regular intervals, somewhat away from existing trails to catch falling fruit. Because one can weigh the fruits that fall into traps, this method has the benefit of providing information directly related to biomass. However, fruit traps measure fruit fall, not fruit production. Terborgh (1983) points out a number of biases inherent in the fruit trap method. Fruit fall is potentially underestimated during periods of fruit scarcity when frugivores consume a greater proportion of the available fruit than during period of fruit abundance. Fruit traps are biased against catching more preferred fruits that are removed by frugivores and do not fall into the traps in the same proportion as less preferred fruits. Fruit traps also may contain a large number of fruits that are aborted by their parent trees. Finally, this method is likely biased against plant species that produce fruits that ripen slowly over a long period, since it is probable that a greater proportion of the fruits of slow ripening species are eaten and therefore do not fall into the traps. All these biases can be markedly reduced by counting not fruits that fall into traps, but rather mature seeds, and then estimating the equivalent biomass of pulp produced by the observed catch of seeds per species, based on detailed measurement of the components of freshly-collected ripe fruits (Janson, 1984; Janson & Emmons, 1990). With this procedure, the removal of fruit by frugivores does not affect the estimated production as long as seeds are not destroyed in the animals' digestive systems – a trap will catch the seed either below the tree that produced it or after it is deposited by the frugivore. Likewise, aborted fruits are not counted as they do not produce mature seeds. There is still the problem that seeds typically fall into traps up to a month after the fruits are available on the tree (Zhang & Wang, 1995), so that ideally production of pulp for each species should be allocated seasonally according to independent phenological estimates of relative ripe fruit availability for that species (see Janson, 1984).

In a review of studies using fruit traps to quantify habitat-wide fruit availability, Chapman *et al.* (1994) point out that fruit traps typically sample only a very small proportion of a focal species home range (on average 0.004% of the area used by the study animal). The fact that fruit traps cover only a small proportion of the total area of interest can lead to biases. If traps are placed under rare tree

species, which produce many fruits (e.g., *Ficus* sp.) or large fruits (e.g., *Monodora myristica*), fruit traps may overestimate habitat-wide fruit abundance. Such biases are exaggerated by non-random fruit trap placement, so traps should be located either randomly or at fixed intervals with a random starting point to reduce the possibility of sampling only more productive trees. Another potential criticism of fruit traps is that rodents or other frugivores could systematically remove fruit or seeds from the traps. However, data collected by Goldizen *et al.* (1988) and Chapman *et al.* (1994), suggest that this is not typically a large problem.

Although sympatric primate species overlap broadly in their use of fruit (Terborgh, 1983), not all fruits are of similar quality and not all primates have similar abilities to handle the various secondary compounds found in fruits. For example, whereas tannins are avoided by many primates (Oates *et al.*, 1977, 1980; Waterman *et al.*, 1980; Glander, 1982; Leighton, 1993) this does not appear to be the case with gorillas (*Gorilla gorilla*, Calvert, 1985; Rogers *et al.*, 1990) or spider monkeys (Howe & Vande Kerkhove, 1981). Similarly, the fruits of *Strychnos mitis* are readily eaten by redtail monkeys (*Cercopithecus ascanius*, Lambert, 1997) and blue monkeys (*C. mitis*, Rudran, 1978), while they are steadfastly ignored by chimpanzees (Lambert, 1997). This particular genus of tropical tree is laden with compounds that are toxic to mammals: the fruit pulp, root, bark and leaves of this genus are reported to contain high levels of phenolics, terpenes, flavonol glycosides, and various alkaloids (Thepenier *et al.*, 1990). Thus, an accurate assessment of fruit availability should take into account any specialization in fruit consumption for each primate species. Fruit or seed traps allow the researcher to assess production of all fruiting species (identified using seed reference collections), subsets of which can be used afterwards to produce quantitative measures of resource availability tailored for a particular study species (Janson, 1984).

Leaves

When quantifying the availability of leaf resources, one faces many of the same issues considered when dealing with fruit. Correspondingly, researchers have used the same sorts of methods to assess leaf availability: transects (Oates, 1977) or leaf-fall traps (Proctor, 1980), with the

same range of problems and biases as for fruit. In addition, however, the quality of leaves is probably far more important a confounding issue than it is for fruits (see above). If the fraction of leaf material in a forest that is edible varies considerably from site to site or season to season, then measures of gross production may have little value.

Although the variety of possible plant defensive chemicals is vast, as is the list of chemical techniques needed to detect them, some fairly simple measures of leaf chemistry appear to be important predictors of food quality across primate species (Barton *et al.*, 1993). The ratio of protein to fiber or to fiber-plus-tannin has been shown to predict diet choice in both folivores (Milton, 1979; Oates *et al.*, 1990) and in frugivore-folivores (Whiten *et al.*, 1990). It is odd that this index works at all given the diversity and toxicity of many plant defensive chemicals, but several factors may help to explain this seeming paradox. First, generalized mammals may have the ability to detoxify at least small quantities of many kinds of plant defensive chemicals, so that these do not represent an absolute barrier to ingestion. Second, the cost of detoxifying a given plant defensive chemical may be offset by high protein content, so that primates may eat a nutritious plant leaf despite high defensive chemical content. Third, primates prefer to eat expanding leaves that typically possess low fiber content, and may also be limited in the concentration or kinds of secondary chemicals they possess (Orians & Janzen, 1974; Coley and Barone, 1996). Although different leaf-eating lemurs in Madagascar may specialize on the use of distinct plant defensive chemicals (Ganzhorn, 1988), it is not known to what extent this is true of other folivorous primates.

Despite the seeming simplicity of the protein/fiber ratio as a measure of leaf quality, some possible problems must be kept in mind. As noted above, leaf chemistry can vary markedly in a single tree across space (sunlit vs. shaded branches, Ganzhorn, 1995) and time (morning vs. evening, Ganzhorn & Wright, 1994). Greater comparability of leaf quality may be achieved in future surveys across study sites by standardizing the place and time of leaf collection (for instance, always collect leaves at midday from branches exposed to sunlight). Researchers interested in understanding leaf selection by individual primates should take care to sample the leaves at the same location and time of day that the animals actually ate them.

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Primate Communities

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