

THE FEEDING ECOLOGY OF APES

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A thorough understanding of the feeding ecology of wild apes is helpful for their successful conservation, and a fairly large number of studies have been conducted on this topic. Using data from the literature, we suggest that food types probably affect natural ape distribution in particularly important ways. An understanding of ape feeding ecology can be used in the development of conservation strategies.

Feeding Ecology Methods Used in the Literature

Several methods are currently used for recording diets in the wild (Altmann, 1974; Lehner, 1996). Ideally feeding behavior would be recorded as grams of intake per unit time of each food type, whether plant part, insects, or vertebrate prey (Altmann, 1998). This is also the only method from which kilocalories consumed per unit time can be calculated. However, this would also ideally require that the researcher be able to sample feeding behavior at all times of day, and in considerable detail. This goal is rarely achieved due to problems of habituation, elusiveness, and visibility. Three alternative methods are therefore commonly employed.

The method most frequently used in primate studies is to report the percentage of feeding time spent feeding on a particular food item. If differences exist among items in bite sizes or in feeding rates, this method fails to estimate relative intakes accurately. Foraging or searching time is not generally included as feeding time. A few studies of primates have included limited information on grams of intake versus feeding time (Kurland and Gaulin, 1987), but only one study (Knott, 1999) has reported both feeding time and grams of intake for apes (specifically orangutans) continuously for over a year. Knott (1999) found some differences in the diet when described by these two methods but in most cases results were similar for the two methods. Altmann (1998), studying baboons, found similar results.

The third method used to describe primate diets has been used for the terrestrial apes living in dense vegetation—gorillas and bonobos (for example: Tutin et al., 1984, 1997, 1991; Remis, 1995, 1997; Badrian and Malenky, 1984; Badrian et al., 1981). Here visibility can be so poor, or the individuals so difficult to habituate, that researchers are forced to simply list plant species and plant parts consumed according to an informal context-specific index of relative frequency. This information is based on a combination of feeding remains, fecal analysis, and visual observations.

There has been no thorough evaluation of how these three methods compare to each other. Nevertheless, we assume that no matter which method is employed, the dominant food items do reveal themselves. Consequently, for the purposes of producing a condensed, manageable review, we have not weighted any method more or less, nor did we consider the fact that seasonal study durations and the number of observation hours varied among studies. We have taken the data at face value, calculating simple means for each ape species regardless of the data collection method used. To ameliorate

the simplifying or distorting effects of this assumption we have included ranges around each mean, to emphasize the wide variations possible, both across time and from one site to another.

RESULTS OF LITERATURE REVIEW

ASIAN APES

Gibbons

As a group, gibbons (*Hylobates* spp.) are normally considered to be ripe fruit specialists, and a survey of the literature confirms this, with two exceptions (Table 1). Not all gibbon species are represented in Table 1. Some species, for example *H. gabriellae* and *H. leucogenys*, do not seem to have dietary reports published.

Almost all of the studies included in Table 1 published results based on percentage of time spent feeding. Some reports gave only annual differences or habitat differences based on annual averages and these ranges are usually narrower than are monthly ranges. The widest ranges are generally due to exceptional diets in particular months, which probably do not represent diets that could be sustained for any length of time. These range characteristics hold true for all species of apes in this report.

Table 1 assigns the studies for which we found feeding data into four categories, based on dietary composition. These categories became apparent as a consistent pattern when we summarized the data for each species. In categories 1 and 2, the species in these studies were predominately frugivorous. Leaves appear to be likely fallback foods, consumed when fruit is not abundant, but systematic data on this question are scarce.

Regarding *H. concolor*, the only dietary study so far published is on individuals living at a medium to high altitude in mountains with a limited number of fruiting tree species. This species has a larger body size than other *Hylobates* species, except *H. syndactylus*, which perhaps facilitates a switch to a highly folivorous diet. The siamang (*H. syndactylus*) is the largest gibbon at 10-15 kg, and is consistently more folivorous than most other gibbons. Both of these species seem to have been able to make a fallback food (leaves) a major part of their permanent diet.

Orangutans

Orangutans (*Pongo* spp.) are also considered highly frugivorous, especially if seed eating is included under the umbrella of frugivory. However, we tend to think granivory or seed predation should be considered a separate feeding category. Unfortunately, most of the orangutan literature does not separate seed eating separate from fruit eating (Table 2), so it is difficult to thoroughly review seed eating by orangutans. Most of the studies summarized here reported their results as percentage of time spent feeding.

It is difficult to say whether there are significant differences between Borneo and Sumatra. More feeding information has been re-



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Table 1
Gibbon Diet

Species	% Fruit (Range)	% Flowers (Range)	% Leaves (Range)	% Prey (Range) n
Category 1	72 (38-100)	6 (0-24)	15 (0-62)	7 (0-25)
<i>H. hoolock</i>				3
<i>H. agilis</i>				2
<i>H. klossii</i>				1
<i>H. lar</i>				8
<i>H. pileatus</i>				1
Category 2	60 (56-62)	2 (0-4)	37 (32-44)	1 (0-2)
<i>H. moloch</i>				1
<i>H. muelleri</i>				2
Category 3	40 (6-59)	6 (0-32)	49 (24-70)	5
<i>H. syndactylus</i>				10
Category 4	21	7	11 + 61% leaf buds and shoots	1
<i>H. concolor</i>				

n = number of studies

Studies are assigned among four categories, from mainly frugivorous (1) to mainly folivorous (4).

References: Category 1—Ahsan, 1994; Alfred, 1992; Islam and Feeroz, 1992; Aldrich-Blake, 1980; MacKinnon and MacKinnon, 1980, 1978; Palombit, 1997; Raemaekers, 1978, 1979, 1995; Ellefson, 1974; Gittins, 1982; Whitten, 1982. Category 2—Robbins et al., 1991; Rodman, 1978. Category 3—Aldrich-Blake, 1980; Chivers, 1974, 1977; Chivers et al., 1975; Curtin and Chivers, 1978; MacKinnon and MacKinnon, 1980, 1978; Palombit, 1997; Raemaekers, 1978, 1979. Category 4—Lan, 1993.

Table 2
Orangutan Diet

Species	% Fruit (Range)	% Flowers (Range)	% Leaves (Range)	% Pith (Range)	% Bark and Misc. (Range)	% Prey (Range)
<i>P. pygmaeus</i>	62 (0-100)	4 (0-60)	19 (0-77)	1 (0-22)	14 (0-73)	2 (0-27)
<i>P. abelii</i> Sumatra	74 (22-98)	na	15 (7-42)	na	6 (0-16)	5 3 (0-40)

n = number of studies

References: *P. pygmaeus*—Hamilton and Galdikas, 1994; Galdikas and Teleki, 1981; Knott, 1998, 1999, 1996; Rodman, 1977, 1978, 1984, 1988; MacKinnon, 1974, 1977; Leighton, 1993; Wheatley, 1982; Suzuki, 1994. *P. abelii*—MacKinnon, 1974; Rijksen, 1978; Ungar, 1995.

ported from Borneo, and the Sumatran literature generally lumped flowers with fruit and pith with bark or leaves, so the categories are not entirely comparable. On both islands there can be drastic seasonal differences where, for example, the diet can consist of 73% bark for one month and 82% figs another month (Suzuki, 1994).

Southeast Asia is subject to dramatic shifts in food availability due to the periodic mast fruiting of certain trees, and this may affect all the animals living there as much as does habitat differences between the islands. Suzuki (1994) and Rodman (1977) found males ate more bark and females ate more flowers during one- or two-month

comparisons. However, over the course of 14 months, Knott (1998) did not find differences in the proportions of plant parts eaten by males and females. She also found that while bark (cambium) and leaves are important foods during times of extreme fruit scarcity, the orangutans lose weight when forced to rely heavily on bark.

Only three researchers differentiated between seed consumption versus pulp or whole fruit consumption (Knott, 1996; Leighton, 1993; Rodman, 1988), all working in Borneo. They found that seed eating constituted about 24% of the total feeding time in studies ranging from 6 months to one year, thus reducing pulp or whole fruit eating to about 38%, instead of 62%.

AFRICAN APES

Bonobos

The bonobo (*Pan paniscus*) is considered to be frugivorous but with a large terrestrial herbaceous vegetation (THV) component to the diet (Malenky and Stiles, 1991; Malenky and Wrangham, 1994). The feeding ecology data is a mixture of time spent feeding and estimates based on feeding remains and fecal analysis (Table 3). Some of the short-term studies have found the bonobo to be highly dependent on high-quality shoots, leaves, stems, and pith of THV, for several months at a time. However, when averaging with studies of longer duration (1+ years), bonobos prefer fruit when fruit is available (Wrangham et al., 1996).

As with all the apes, prey consumption as an annual average is quite low (prey includes vertebrates and invertebrates). There are reports of bonobos occasionally eating fish (Kano, 1979), as well as a variety of invertebrates and a few mammals like squirrels (Bermejo et al., 1994). It has been suggested that the bonobo is dietarily like a chimpanzee—partly occupying the lowland gorilla niche, in a forest that might be expected to be excellent gorilla habitat but where no gorillas are found (Wrangham and Peterson, 1997). Compared to their probably chimpanzee-like ancestor, their preferred food continues to be ripe fruit but they appear to have shifted to consuming higher levels of leaves, young shoots, and stem tips of higher quality THV than common chimpanzees eat (Wrangham et al., 1996).

Chimpanzees

Compared to supposedly frugivorous monkeys, the common chimpanzee (*Pan troglodytes*) has been shown to be a ripe fruit specialist (Wrangham et al., 1998). The data collected for chimpanzees is mostly in terms of the percentage of time spent feeding on different food items (plant parts or prey), but some of the data is in terms of the percentage of species eaten per plant part, based on feeding remains and fecal analysis. Compiling the results from 24 studies, either method seemed to give similar results, so they were all included in the same summary (Table 4).

The percentage of fruit in the diet is less than the value usually obtained from populations of chimpanzees living in a rain forest, like Kibale (Conklin-Brittain et al., 1998; Isabirye-Basuta, 1989; and Wrangham et al., 1996: average 78%), but the 64% value is similar to results from drier areas (McGrew et al., 1981; Wrangham, 1977; and van Lawick-Goodall, 1968: average 62%). Chimpanzees can live in slightly drier environments compared to bonobos and gorillas. When fruit becomes scarce, chimpanzee communities disperse to search for fruit as individuals or in small groups, thus maintaining their focus on fruit intake (Wrangham, in press), although THV consumption increases somewhat (Wrangham et al.,

1991) and dietary diversity increases more (Isabirye-Basuta, 1989) when fruit is scarce. The THV that chimpanzees eat is usually a moderately low-quality pith (the core of stems), rather than the high-quality young shoots and stem tips that the bonobos eat (Malenky and Stiles, 1991), which may explain why chimpanzees do not seem able to utilize THV as extensively as bonobos do. Bonobos and gorillas (Tutin et al., 1991) both switch to THV during times of fruit shortage. Once again, the percentage of animal prey in the diet is very low.

Gorillas

While mountain gorillas (*Gorilla gorilla berengei*) are generally exclusively folivorous, consuming almost no fruit, both eastern (*G.g. graueri*) and western (*G.g. gorilla*) lowland gorillas are much more frugivorous (Table 5). Most of these studies reported their findings based on feeding remains, fecal analysis, and some visual observations.

The mountain gorillas stand out as depending almost exclusively on terrestrial herbaceous vegetation (which also includes woody shrubs) compared to the lowland gorillas. The THV plant parts consumed are primarily pith (also referred to as stems, but it is usually the center core of stems) and can also include leaves or young shoots from the same plants. The lowland gorillas' fruit consumption appears similar or somewhat lower than that of other apes, while their tree leaf intake appears to be higher, though it is sometimes difficult from the literature to know whether "leaves" are of woody or herbaceous origin. Nevertheless, their consumption of THV is clearly greater than for chimpanzees and is more similar to bonobos. At times of low fruit abundance, the lowland gorillas can survive on THV for an extended period of time. Meanwhile, a chimpanzee in a similar situation continues searching for fruit and thus ranges farther (Tutin et al., 1991).

FEEDING SUMMARY

Seasonally there can be great diversity among apes in terms of plant parts eaten, or in terms of fall-back foods. However, increasing numbers of studies show that all ape species eat fruit when it is available and abundant; these fruits are therefore assumed to be their preferred food. In fact, all but the orangutans prefer ripe fruit; the orangutans will also focus on some ripe seeds during periods of fruit abundance (Knott, 1998, 1999).

An important question with respect to ape range distribution and therefore conservation is what they eat when fruits are not abundant, whether due to seasonality or habitat differences. Gibbons continue to search for fruit but to some extent fall back on leaves (more for some species than for others). Chimpanzees continue to eat ripe fruit but communities disperse to lessen the pressure on smaller fruiting patches, and they consume more terrestrial herbaceous vegetation (THV). Bonobos and gorillas also continue to eat fruit if available but increase their use of THV, usually more than chimpanzees. Gorillas can shift completely to THV. Orangutans present a more complicated picture. During times of extreme fruit shortage (generally immediately following a super-abundant mast fruiting, which occurs every 2-10 years) they switch to bark and leaves and they move very little (Knott, 1999). During the non-mast years (which are the majority), less dramatic fluctuations are seen in the fruit abundance and the orangutans move widely in search of fruit.

Table 3
Bonobo Diet

Species	% Fruit (Range)	% Flowers (Range)	% Leaves (Range)	% THV (Range)	% Bark and Misc. (Range)	% Prey (Range)
<i>Pan paniscus</i>	55 0 - 100	2 0 - 7	14 0 - 28	25 0 - 100	2 0 - 11	2 0 - 3

THV = terrestrial herbaceous vegetation (which can also include small woody shrubs)

Data summarized from 6 studies, representing two sites: Badrian and Malenky, 1984; Badrian et al., 1981; Hashimoto et al., 1998; Kano and Mulavwa, 1984; Uehara, 1990; Kano, 1992;

Table 4
Chimpanzee Diet

Species	% Fruit (Range)	% Seed (Range)	% Flowers (Range)	% Leaves (Range)	% THV (Range)	% Bark and Misc. (Range)	% Prey (Range)
<i>Pan troglodytes</i>	64 19 - 99	3 0 - 30	2 0 - 14	16 0 - 56	7 0 - 27	4 0 - 41	4 0 - 28

Data summarized from 24 studies at eleven sites: Conklin-Brittain et al., 1998; Galdikas and Teleki, 1981; Ghiglieri, 1984; van Lawick-Goodall, 1968; Hladik, 1977, 1973; Isabiry-Basuta, 1989; Kuroda, 1992; Kuroda et al., 1996; Matsumoto-Oda and Hayashi, 1999; McGrew et al., 1981; Newton-Fisher, 1999; Peters and O'Brien, 1981; Rodman, 1984; Sabater-Pi, 1979; Sugiyama and Koman, 1987; Tutin and Fernandez, 1993; Tutin et al., 1984, 1997, 1991; Wrangham, 1977, 1996; Yamagiwa et al., 1992.

Table 5
Gorilla Diet

Species	% Fruit (Range)	% Flowers (Range)	% Bark/Root (Range)	% THV (Range)	% Misc. (Range)	% Tree Leaf (Range)	% Prey (Range)
<i>G.g. beringei</i> Mountain	1 (0-2)	2 (0-3)	3 (0-6)	91 (85-96)	2 (0-5)		1 4 (0-1)
<i>G.g. gorilla</i> Western	48 (17-68)	1 (0-6)	6 (0-32)	17 (7-43)	2 (0-11)	21 (6-34)	1 14 (0-4)
<i>G.g. graueri</i> Eastern	23 (9-47)	2 (0-3)	15 (0-29)	19 (11-33)	1 (0-3)	41 (17-51)	0 5

n = number of studies

References: Mountain—Fossey, 1974; Fossey and Harcourt, 1977; Vedder, 1984; Watts, 1984. Western—Kuroda, 1992; Kuroda et al., 1996; Nishihara, 1995, 1992; Remis, 1995, 1997; Sabater Pi, 1966, 1977; Tutin et al., 1984, 1997, 1991; Tutin, 1996; Tutin and Fernandez, 1993; Williamson et al., 1990. Eastern—Goodall, 1977; Casimir, 1975; Yamagiwa et al., 1994, 1992, 1996.

CONSERVATION APPLICATIONS

An adequate food supply is critical for the survival of any population. The question is: what is the definition of a food item for a given animal? In the case of these largely vegetarian primates, we have thus far defined their foods on the basis of plant parts (fruit or leaves) or plant types (THV or arboreal). It may eventually become necessary to determine the critical individual plant species, but at this point we will stay with plant parts and types. There are then three issues of importance: how feeding ecology affects or determines animal distribution in the wild; what are the critical foods consumed during times of preferred food shortage (a.k.a. fall-back foods), which will often determine the carrying capacity of an area; and finally, what is the vulnerability of the apes and their foods over time. The vulnerability of the individuals themselves also refers to how long they can survive on their fall-back foods. Specifically, how much weight do they lose and how quickly during times of heavy fall-back food consumption?

Using gorillas as an example of a species well adapted to surviving on their fall-back food (THV), we looked at the modern distribution of gorillas (Figure 1) (Groves, 1970). The question is: why are there no gorillas yet known between the eastern and western populations? What is “wrong” with the territory between those two populations? If one assumes THV is critically important to the gorillas, which much evidence indicates, and that the type of THV that they eat requires high humidity, it is possible that north of the Zaire River is outside the wettest “funnel” of humidity going from the coast, eastward and narrowing to the Virunga Mountains? A close examination of the rainfall patterns over this area would answer this question. However, another related possibility is that the gorillas are, for some reason, dependent on areas that are considered to have been ancient rain forest refugia during the last ice age (18,000-12,000 years ago) (Figure 2) (Sayer et al., 1992), when Africa went through an arid period. The two distributions overlap. These ancient forest refugia have been estimated based on the concentrations of the greatest biological diversity within modern forests, which also coincide with topographically determined areas of high rainfall today and probably also 18000 years ago. This is a key to the puzzle of gorilla distribution. A vegetational comparison of the territo-

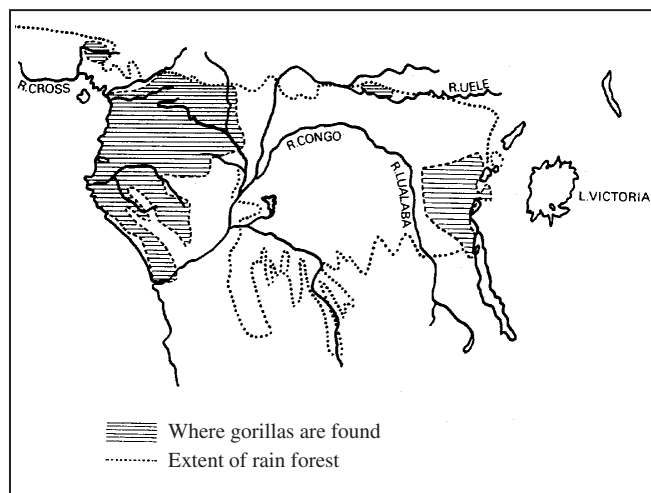


Figure 1. Gorilla distribution (Groves 1970).

ry between the two populations and a comparison to gorilla foods would help us understand what are the limitations to the gorillas' ability to distribute themselves within the rain forest.

Orangutans are an example of a species that, at first glance, is not very well adapted to surviving on its fall-back foods (bark and leaves); they appear to lose a great deal of weight when forced to rely heavily on them. It is possible that the fall-back food paradigm does not apply as well to orangutans as it does to the other apes. Given the inadequacy of their fall-back food, and the fact that they do not move in search of fruit during times of extreme fruit shortage, Knott (1999) suggested that one critical fall-back strategy is their reliance on their own body fat in addition to consuming low-quality fall-back foods. Their quantity of body fat is dependent on their ability to take full advantage of trees fruiting during the mast by eating as much as they can and storing body fat (Knott, 1999). Orangutans also cope with regular fluctuations in food availability by moving between habitats (Tilson et al., 1993; Leighton and Leighton, 1983). They may therefore not be as tied to their fall-back food as the gorillas seem to be, in terms of their distribution, but instead orangutans need territories large enough to successfully exploit fruiting seasons. Unfortunately the effects of human occupation and activities are increasingly influencing modern orangutan distribution. Nevertheless, based on recent maps (Yeager, 1999) it seems that they would naturally have a broad and general distribution throughout much of Sumatra and Borneo, in the absence of human interference.

CONCLUSIONS

The question of how food availability affects natural ape distribution should receive more attention in order to make progress in setting aside viable areas of land as preserves for these species. The deforestation that has already occurred complicates the process of studying natural ape distribution, so there is great urgency for this type of research. Additional details to the feeding ecology are also needed to understand ape distribution based on the critical key foods or fallback foods. The answers to these questions should clarify the carrying capacity of an area for a given primate species and the vulnerability of the food items over time.

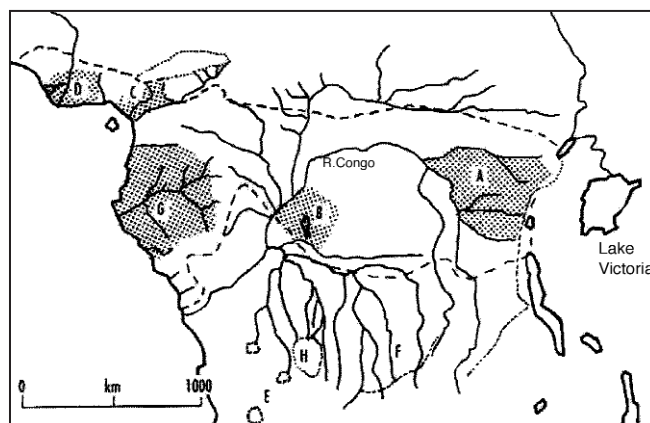


Figure 2. Forest refugia during arid, glacial periods in Central Africa (Sayer et al. 1992).

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