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Seasonal feeding on bark by gorillas: An unexpected keystone food?

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There are a number of reports in the literature of primates feeding on the bark of trees, but bark has only occasionally been considered as a major food to be studied in its own right (e.g., Waser, 1977; Beeson, 1987; Norris, 1988). All the great apes feed on bark at certain times, and clearly have preferences as to which species they choose (e.g., Schaller, 1963; Jones & Sabater Pi, 1971; Casimir, 1975; Nishida, 1976; Goodall, 1977; Rodman, 1977; Sabater Pi, 1977, 1979). Evidence has been presented that bark feeding by chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*) is a seasonal phenomenon related to scarcity of preferred fruits (Nishida, 1976; Rodman, 1977), and similar conclusions have been drawn from studies of blue monkeys (*Cercopithecus mitis*) living near plantations of exotic pines (Beeson, 1987; Maganga & Wright, 1992). Bark feeding is also well known in other mammals where, again, it often occurs seasonally (e.g., elephants, Wing & Buss, 1970; grey squirrels, Kenward & Parish, 1986).

Western lowland gorillas (*Gorilla g. gorilla*) were recently reported to eat bark during the dry season in Gabon (Rogers et al., 1988; Williamson, 1988; Tutin et al., 1991), but no detailed data were given. This paper presents information from the last two years of field study in 1990 and 1991, when bark from a single species of tree was an important seasonal food.

Feeding on bark by gorillas in the Lopé Reserve

Our study site, in Gabon (0°10'S, 11°35'E), shows a highly seasonal pattern of rainfall, with two rainy seasons (October-December and March-May), and a major and minor dry season (June-September and January-February). Fruit availability is at its lowest during the major dry season (Williamson, 1988; Tutin et al., 1991). Gorillas consume large quantities of fruit during most of the year, but become more folivorous at times when fruit is scarce. This can be visualised by looking at the amount of fibre and leaf fragments in faecal samples in comparison to the number of fruit species per faecal sample (Fig. 1).

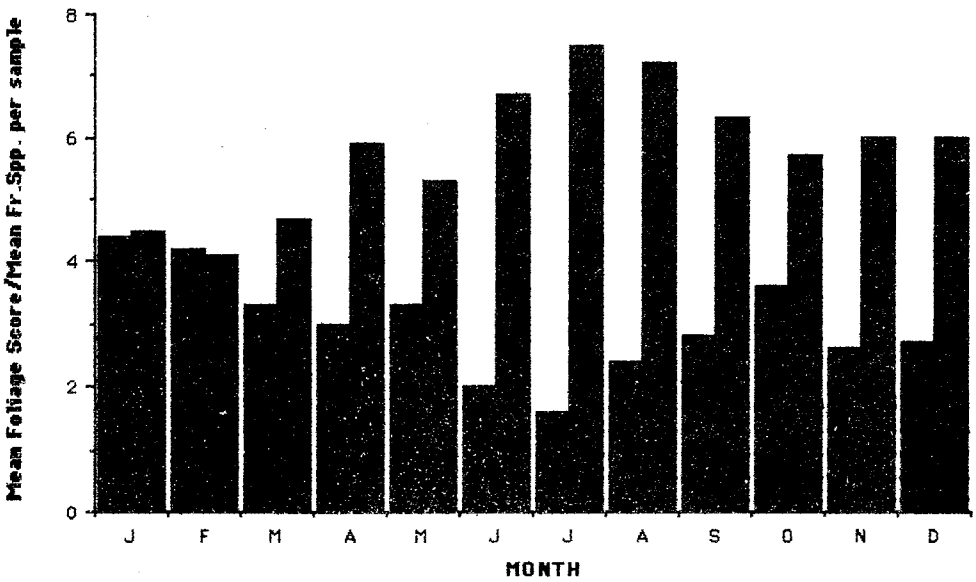

Fig. 1. The mean foliage score (hatched bars) for gorilla faeces collected over a 3-yr period (1987-89) plotted with the mean number of fruit species per faecal sample (solid bars) over the same period. The same y axis scale applies to both data sets. The foliage score is derived from an assessment of the volume of fibre and leaf fragments in relation to the total mass of the faecal sample, each on a scale of 1=rare to 4=abundant (data from Table 2 in Tutin et al., 1991).

In the major dry season of 1986, we first recorded a high incidence of feeding on the mature leaves and bark of *Milicia excelsa* (formerly *Chlorophora excelsa*), a large tree in the family Moraceae. Young leaves and galls on the leaves were also eaten, but most of the feeding was on the inner bark of the terminal branches and on mature leaves. Recent data have supported these findings, and show that gorilla contacts occurring in *Milicia* trees are clumped in the dry season months (χ^2=31.1; d.f.=1; p<.001), when 60% of total contacts may involve *Milicia* feeding (Fig. 2). When fruit is scarce outwith the dry season, i.e., in years when many species do not fruit, gorillas may feed on *Milicia* at other times of year as well, but apparently not to the same extent (Tutin et al., 1991).

How strong is the correlation between feeding on *Milicia* bark and scarcity of preferred succulent fruit? We tested the correlation between the numbers of *Milicia* trees fed in (determined from observation and gorilla trails) and the numbers of species of gorilla food plants bearing ripe fruit each month (Fig. 3). The correlation is significant and negative for both years (1990: r_s=-.64, p<.05; 1991: r_s=-.87, p<.001). There is, however, no obvious

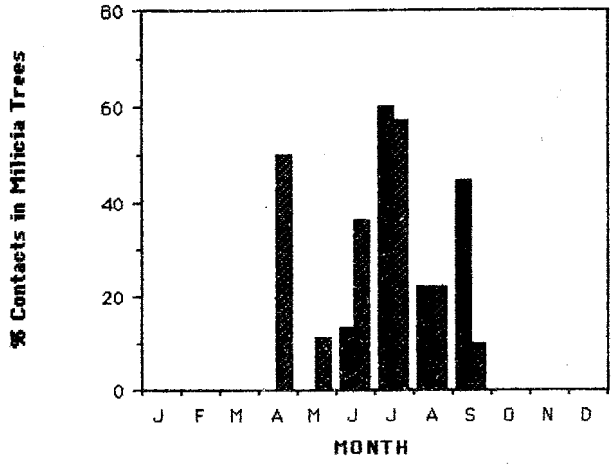

Fig. 2. The distribution of gorilla contacts in *Milicia* trees during 1990 and 1991, as a percentage of total contacts. Solid bars, 1990 data; hatched bars, 1991 data.

correlation between bark feeding and particular events in the phenology of *Milicia* trees themselves; more data need to be collected on this.

Nutritional value of *Milicia* bark

Gorillas strip off the inner bark with their teeth, and discard the outer bark, thus rejecting those parts with a high fibre (see ADF for outer bark, Table 1) and tannin content (Rogers et al., 1990), and eating the phloem and cambium which are the most nutritious. Inner bark is generally a source of soluble sugars and amino acids or protein, so we analysed it for these nutrients and for fibre content, including hemicellulose which may be a source of energy for apes (Wrangham et al., 1991). The results are summarised in Table 1.

Of the non-fruit dry season foods consumed by gorillas at Lopé, *Milicia* bark has a soluble sugar content in the middle of the range at 8%-10% dry weight; but we did not measure sugar in the sap itself, where it may be at much higher concentrations than those shown in Table 1. Given their preference for ripe, sweet, succulent fruit, it is very likely that gorillas eat *Milicia* bark because it is sweet, and sap would be exuded as the inner bark was stripped. Because *Milicia* is a large tree, and only the bark of the terminal branches is consumed, collecting samples to prove this is extremely difficult.

The crude protein content of *Milicia* bark is much lower than that of several species of leaves which gorillas eat during the dry season, but it is not negligible and is more than double the average level for important fruit foods

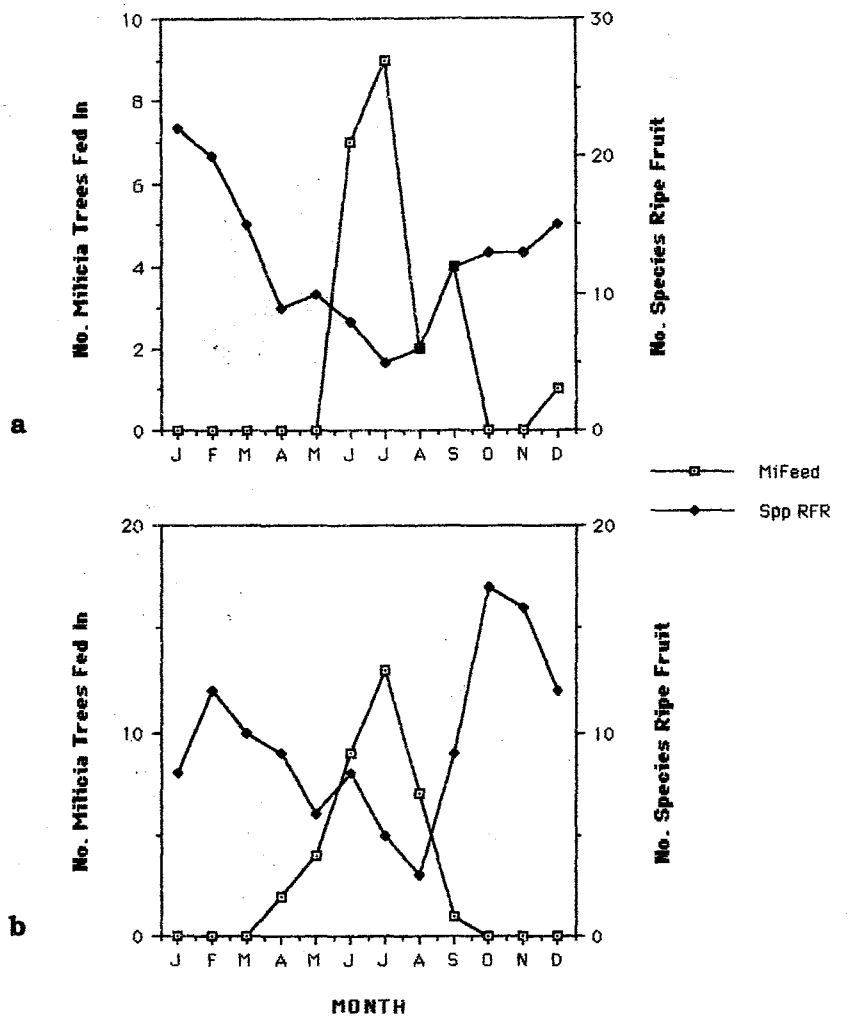

Fig. 3. The numbers of *Milicia* trees fed in each month (□) established through contacts with gorillas and from feeding remains on their trails, plotted with the numbers of species of gorilla foods with ripe fruit (◆) established from a monthly phenology circuit: a - 1990, b - 1991.

(Rogers et al., 1990). A more important point, though, is that gorillas usually eat *Milicia* leaves at the same time as they eat branch bark. In 1991, of 32 instances of bark feeding, 28 also involved feeding on leaves. Thus, they can obtain sugar and protein simultaneously and cut down on foraging costs (see Table 1 for crude protein content of *Milicia* leaves).

Table 1. Nutrient and fibre content of inner bark from *Milicia excelsa* (Moraceae) in different seasons, 1991.

	WSC	CP	NDF	ADF	HC
Dry season					
Tree 1	9.6	10.3	48.0	34.4	13.7
Tree 2	9.4	8.5	51.7	37.9	13.9
Non-dry season					
Tree 1	9.8	9.2	48.5	34.2	14.3
Tree 2	9.1	9.1	49.8	37.0	12.8
[Trees 88	8.5	12.1	n.d.	36.6	n.d.]
[Outer bark	3.7	7.0	n.d.	46.8	n.d.]
[Mature leaves	4.0	15.6	n.d.	23.3	n.d.]

Dry season, June-September; Non-dry season, October-May; WSC, water-soluble carbohydrate; CP, crude protein; NDF, neutral-detergent fibre; ADF, acid-detergent fibre; HC, hemicellulose; n.d., not done. Data for inner bark from trees 1 and 2 were collected in 1991, and can be compared with bark collected and pooled from three different trees in the 1988 dry season (Trees 88). The outer bark was from these same trees.

We have detected no obvious seasonal difference in the nutrient content of *Milicia* bark, although because of the difficulty of collecting samples we only have data from two trees (plus the pooled data from 1988, Table 1). Variations in sap composition and cambial activity must occur, however. What we can say is that our methods have not so far demonstrated variations that are sufficiently large to make *Milicia* bark particularly desirable in the dry season, and so to account for seasonal feeding patterns on specific nutritional grounds alone.

How important is *Milicia* bark for gorillas?

From the proportion of contacts with gorillas in the dry season that occur in *Milicia* trees (Fig. 2), it is clear that a considerable amount of time is spent on this particular feeding activity. All-day follows of gorillas show that they go from tree to tree, and may feed in several during a day. We do not have data on precise amounts of bark ingested because of observational difficulties, but 31% of gorilla faecal samples (n=235) collected in the 1986 dry season contained *Milicia* leaf fragments. Since gorillas seldom feed on leaves without also eating branch bark, this suggests a significant consumption of bark (which would not be specifically identifiable in faeces without microscopical examination).

We do not know why gorillas select *Milicia* from among many other species whose bark they might eat, except that members of the family Moraceae do seem to feature often in the bark feeding of apes (Rodman, 1977; Sabater Pi, 1977, 1979). *Milicia excelsa* is not a particularly common tree in our study site; it is not in the "top twenty" trees, and occurs at a density of 1/ha (>10 cm dbh) and 1/25 ha (>70 cm dbh)(White, pers. comm.; Williamson, 1988). Gorillas are certainly using it as a food more frequently than would be predicted from its density in the forest. Trees in leaf are always available, because their phenology is asynchronous (characteristic of other members of the family Moraceae, particularly figs). We suggest that the combination of moderately palatable and nutritious inner bark and leaves provides gorillas at Lopé with a dependable food source which they can fall back on at any time when fruit is scarce, and thus *Milicia excelsa* is a good example of a keystone food species (*sensu* Terborgh, 1986). However, these are foods of last resort, for gorillas prefer even unripe fruit pulp or seeds if they are available (Tutin et al., 1991). Our results support Nishida's (1976) suggestion that the bark of certain trees may have always been an emergency food for all hominoids.

Milicia as a commercially exploited timber species

Commercial logging has not generally been seen as a direct threat to ape food plants; rather it is the accompanying habitat destruction which is more serious. *Milicia*, however, is exploited for timber under its *nom pilote* of "Iroko", and, in Gabon, it is cut wherever encountered - at least in the Lopé Reserve (White, pers. comm.). In 1987, about 12000 m^3 were exported (Wilks, 1990), and iroko was seventh among those species exported at a level of more than 5000 m^3. This corresponds to about 3000 iroko trees.

If economic pressures grow in Gabon to increase the level of timber exploitation, it is likely that gorillas will lose one of their major dry season foods. One effect of this could be to force them into areas of secondary forest and disturbed habitats where their herbaceous foods are more common, but where they may be in greater conflict with humans.

Acknowledgments

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