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A Comparative Study of the Feeding Strategies of Two Sympatric Species of Leaf Monkeys: *Presbytis senex* and *Presbytis entellus*

C. M. HLADIK

Laboratoire d'Ecologie et Primatologie du CNRS, Muséum National d'Histoire Naturelle, Brunoy, France

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1. INTRODUCTION

Since the publication of our ecological work concerning the food choices and food availability for primates in Sri Lanka (Hladik and Hladik, 1972), we have obtained new results concerning the composition of the foods used by these primates, which allow a different type of interpretation of the relationship between feeding behaviour, and social and individual behaviour. The details about methods and interpretation of the analysis of the food samples will be published in a separate paper (Hladik *et al.*, in press), but we must refer to these recent results as a basis of objective comparison between the food choices of two sympatric species of *Presbytis*: the purple-faced langur, *P. senex* (Fig. 1) and the gray langur, *P. entellus* (Fig. 2).

The ecological data concerning these two species have been complemented with information from other primatologists. Ripley (1967, 1970) developed the theoretical aspects of territorial behaviour and social foraging strategy of the gray langur in the field station of Polonnaruwa (Sri Lanka): we utilized her data on ranging patterns to estimate the food available for the different groups of langurs. Rudran (1970, 1973) and G. Manley studied the ecology and reproductive behaviour of the purple-faced langur, in the same field station, in the semi-deciduous forest of Polonnaruwa; we have used their information to help calculate the amount of food available for each group of purple-faced langur (Hladik and Hladik, 1972). Most of this research was part of the Smithsonian Biological Program in Ceylon, Primate Survey, initiated by Drs. J. F. Eisenberg and S. Ripley.*

2. METHODS OF MEASURING FOOD CHOICES

2.1. Direct Observation v. Stomach Content

It might appear surprising that the most simple method of quantification of feeding behaviour, direct visual recording, has not been utilized by many investigators, except the author (Hladik and Hladik, 1969, 1972; Hladik and Charles-Dominique, 1971, 1974; Hladik, 1973, 1975)

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FIG. 1. A group of *Presbytis senex* at Polonnaruwa.



FIG. 2. *Presbytis entellus* feeding on the young leaves of a Palu tree, *Manilkara hexandra*, at Polonnaruwa.

and fairly recently Iwamoto (1975). The observation of one monkey during the whole day, and the continuous recording of the number of fruits and leaves eaten, are practicable only when the conditions of visibility are exceptional and when the monkeys tolerate the presence of an observer very close to the group. For this reason, the field stations chosen for such studies were carefully selected.

Records of the daily feeding activity of one monkey are necessarily inaccurate to some degree: even in the best field conditions, the animal chosen may be partly hidden in a tree for short periods. In such cases, we extrapolated from the feeding rates observed in the preceding or following minutes. In a few other cases, when the identification of one individual monkey among a group was very difficult, we had to shift to another individual in the same group (our observations only concerned the adults). These occasional shifts were not important in this study, since the feeding bouts were closely synchronized within each group.

When the feeding rates were too fast to allow note-taking, we used a

small tape recorder to describe the feeding bouts observed. The counts of leaves and fruits eaten were made afterwards. At any change of activity, a reference to the time was noted (± 0.5 min). Thus it is possible to refer to our notes to calculate the time spent feeding (see Section 2.2). In order to keep continuous day-records, the author was partly assisted by Annette Hladik and two students of the University of Sri Lanka: F. P. Amerasinghe and B. W. B. Van Cuylenberg.

The food samples were collected the day after (or a few days after) the period of feeding observation. One-hundred fruits or leaves were immediately weighed to obtain the average fresh weight estimates of the different samples eaten. The most difficult and probably the least accurate estimates concern the small leaf shoots and flushes and the small flower bunches that the leaf monkeys pick directly by mouth. After the period of field observation and collection of the food specimens, we reproduced 100 "picks" or "mouthfuls" and weighed the quantity obtained. From these data, the estimates of the fresh weight eaten may have a bias of 20 to 30% concerning the leaf shoots but the accuracy is better than $\pm 5\%$ for all the materials recorded as units, such as fruits and large leaves which form the main part of the total amount ingested.

Estimates of diet based on observation were checked against weighed contents of the first part of the stomach of some leaf monkeys which were shot [permit no. WL/P 91 (1) of the Department of Wild Life of Sri Lanka]. The relative proportions of leaves and fruits eaten were in good agreement with our direct recording, though we were unable to identify the different food species.

Some more reliable tests were made by the author on howler monkeys and capuchins of Barro Colorado Island (BCI) and in mainland Panama (Hladik and Hladik, 1969). One of the capuchins, accidentally introduced several months before, was shot from the group under direct observation. In its stomach content, the different food items could be clearly identified and the relative proportions of their fresh weight corresponded ($\pm 10\%$) to our quantitative estimates from direct observation.

The differences between the diets of different primate species are generally large enough to rely on the method of direct observation, in spite of its lack of accuracy. It seems that there is no alternative method of measuring feeding behaviour which allows interspecific comparison.

2.2. Time Spent Feeding

The most accurate data published on feeding behaviour concern the time spent feeding, measured by different methods (Clutton-Brock

1975a; Struhsaker, 1975). Unfortunately, the time spent feeding cannot be accepted as an estimate of the food intake, since feeding rate may differ considerably between food items. Tables I, II and III illustrate these variations in the feeding rates of *P. senex* and *P. entellus* on different food items of the Polonnaruwa forest. Our field notes from different days of continuous observation have been used to compare the percentages of feeding time and the percentages of food intake, from the method described in the preceding section.

In the example concerning *P. senex* (Table I), half of the feeding time was spent on the mature leaves of two species of trees. The proportion of leaves actually ingested is slightly higher in terms of fresh weight and represents 75.9% of the dry weight ingested. Conversely, the proportion of feeding time spent on the young leaves and shoots is higher than the proportion of food ingested.

The differences between the time spent feeding on particular foods by *P. senex* and food intake (fresh weight) are generally small, particularly if we compare seasonal variation in the two measures (Figs 3 and 5). These two graphs show a close correlation between the two measures, except for the details of small peaks probably due to the small size of the sample and the relative inaccuracy of the second method. The highest proportion of time spent feeding on young leaves and shoots (Fig. 3) and the largest amount of intake of mature leaves at the

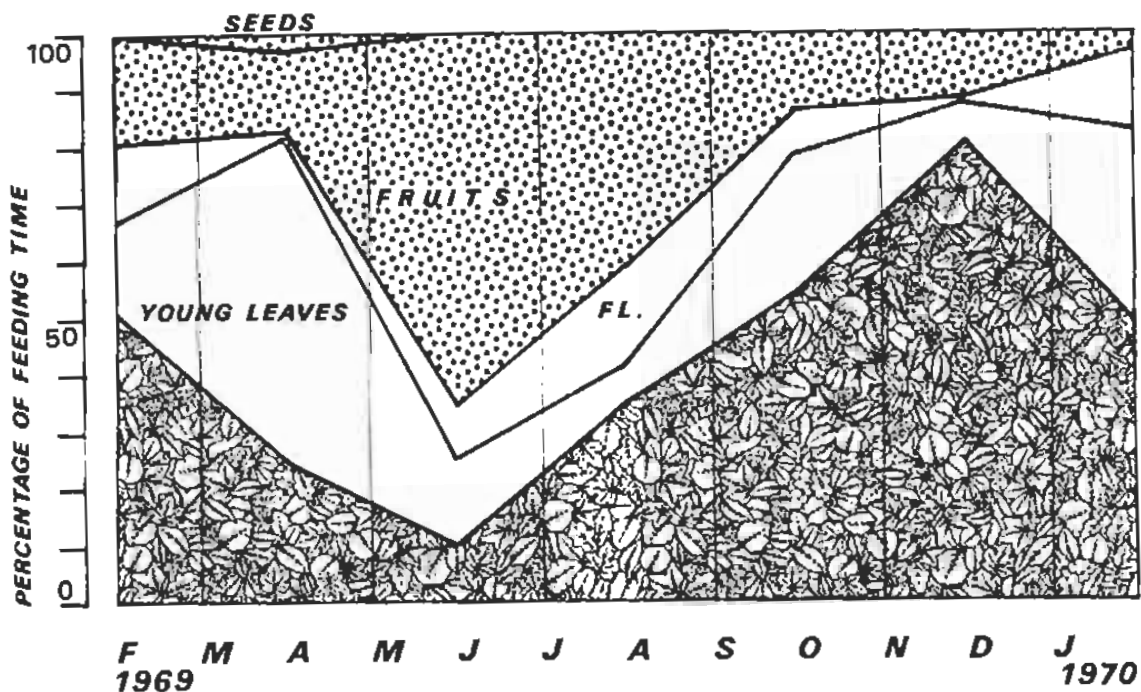


FIG. 3. Percentage of feeding time of *Presbytis senex*, on different food categories and throughout the year, after data of Rudran and Muckenhirn, in press. Food categories are (from bottom to top): mature leaves; young leaves and shoots; flowers; immatures and mature fruits; seeds.

TABLE I

Time spent feeding and food intake in Presbytis senex at Polonnaruwa (8th April 1969; from 6.32 to 18.30h)

Sample eaten	Time spent feeding		Amount ingested, fresh weight		Amount ingested, dry weight	
	(min)	(%)	(g)	(%)	(g)	(%)
Mature leaves of <i>Adina cordifolia</i>	57	30.0	165	30.0	56.0	29.8
Mature leaves of <i>Schleichera oleosa</i>	40	21.1	150	27.3	86.7	46.1
Young leaves and shoots of <i>Schleichera oleosa</i>	52	27.4	115	20.9	22.9	12.2
Young leaves of <i>Garcinia spicata</i>	27	14.2	70	12.7	7.1	3.8
Leaf flushes (and some flowers) of <i>Walsura piscidia</i>	9	4.7	30	5.5	9.0	4.8
Green fruits of <i>Adina cordifolia</i>	5	2.6	20	3.6	6.3	3.3

51.1% of the feeding time spent on leaves

57.3% of the fresh weight ingested from leaves

75.9% of the dry weight ingested from leaves

46.3% on young leaves and shoots

39.1% from young leaves and shoots

20.8% from young leaves and shoots

TABLE III

Time spent feeding and food intake in Presbytis entellus at Polonnaruwa (11th August 1969; from 5.40 to 18.00h)

Sample eaten	Time spent feeding (min)	Time spent feeding (%)	Amount ingested, fresh weight (g)	Amount ingested, fresh weight (%)	Amount ingested, dry weight (g)	Amount ingested, dry weight (%)	
Immature fruits of <i>Walsura piscidia</i> (with seeds)	53	19.4	425	29.1	46.8	16.1	25.7% of the dry weight ingested from fruits
Green fruits of <i>Elaeodendron glaucum</i>	9	3.3	35	2.4	10.3	3.6	
Green fruits of <i>Syzygium cumini</i>	20	7.3	70	4.8	17.4	6.0	
Flowers of <i>Cassia fistula</i>	26	9.5	170	11.6	26.5	9.1	
Flowers of <i>Cassia roxburghii</i>	5	1.8	10	0.7	3.1	1.1	
Flowers of <i>Tamarindus indica</i>	33	12.1	40	2.7	10.3	3.6	16.9% from flowers
Flowers of <i>Glennia unijuga</i>	6	2.2	10	0.7	4.1	1.4	
Flowers (and a few leaves) of <i>Tridax procumbens</i>	5	1.8	50	3.4	5.0	1.7	
Young leaves of <i>Ficus religiosa</i>	29	10.6	310	21.2	81.9	28.2	47.6% from young leaves
Young leaves of <i>Alangium salvifolium</i>	12	4.4	120	8.2	31.4	10.8	
Shoots of <i>Bridelia retusa</i>	9	3.3	25	1.7	4.6	1.6	
Young leaves of <i>Streblus asper</i>	39	14.3	65	4.5	11.0	3.8	
Young leaves of <i>Walsura piscidia</i>	5	1.8	30	2.1	9.2	3.2	
Leaves of <i>Cassia roxburghii</i>	5	1.8	40	2.7	11.4	3.9	9.8% from leaves
Other leaves not identified	17	6.2	±60	4.1	±17.1	5.9	

beginning of 1969 (Fig. 5) are easy to understand (see Table I) since large leaves require less time to be gathered and eaten than the small shoots. *Per contra*, the fruits generally eaten by *P. senex* are green and unripe small-sized objects (about 2 g, like the large leaves), thus ingested approximately at the same rate as the leaves.

In the examples concerning *P. entellus* (Tables II and III) there is an obvious lack of correlation between the time spent feeding on different categories of foodstuffs and the food intake, especially for leaves and fruits. In the data given as examples, the measures are accurate ($\pm 5\%$) for the food intake of large quantities and for the longest feeding times (each total time includes two or three feeding bouts, so the resulting accuracy is $\pm 3\%$ for more than 30 min). The gray langur spent 28.1% feeding time eating the large fruits of *Ficus benghalensis* that composed 77.3% of the total fresh weight ingested (Table II). All the other fruits eaten the same day account for 16.6% of the fresh weight ingested and 46.8% of the feeding time. The proportion of time spent feeding on flowers and leaf buds is ten times higher than the food intake.

The last example (Table III) shows that these relative proportions are not as different when the gray langur feeds on green unripe fruits which are more similar in size and texture to leaves. When feeding on young leaves of large size, the amount eaten is high per unit time (for *Ficus religiosa* young leaves, 21.2% of the fresh weight corresponding to 10.6% of feeding time). Conversely, for small leaves such as *Streblus asper*, the amount eaten is low per unit time.

For insect feeders like macaques and capuchins, time spent feeding is almost totally meaningless: a small amount of prey necessitates a very long foraging time and the definition of the feeding time is necessarily arbitrary (see discussion about chimpanzees, Hladik, this volume).

Detailed comparison of the diet or food choices of different species of primates cannot be achieved by measurement of time spent feeding on different food items. Nevertheless, measures of feeding time may be sufficiently accurate to compare different groups of population of the same species which are feeding on fairly similar items.

2.3. Size and Distribution of Observation Samples

Days of uninterrupted observation were spent alternatively on *P. senex*, *P. entellus* and *Macaca sinica*, at the Polonnaruwa field station. Each month, one week or more was spent in this study area, from March 1969 to February 1970.

The results concerning feeding behaviour of the Polonnaruwa

primates have been extracted from 5790 minutes of observation of *P. senex* and 7125 minutes concerning *P. entellus*. The distribution of these observations throughout the year is shown on Fig. 5: the days during which the observations have been carried on are marked with dots along the time axis.

The diets of both species of leaf monkeys were generally fairly constant from day-to-day since a limited number of food species were available at any one time. For this reason, the average diet for one season could be obtained from a small sample of data (about 2000 minutes of observation). The agreement of the general shape of the graph of the seasonal variations with the figure obtained from another sampling technique (Fig. 3) is an indirect evidence of the sufficient size of the observation sample.

2.4. Collection and Processing of the Food Samples

A large part of the time involved in this comparative study of the diets was devoted to collecting and preparing food samples for analysis. The resulting restriction of the time spent on direct observation cannot be avoided in a study aiming to attain complete information on the diets.

Collection of the food samples at Polonnaruwa was possible without climbing the trees, with the help of a tree-pruner mounted on a series of bamboo poles. Samples were kept in large polythene bags, to avoid desiccation before weighing the series of fruits or leaves as described in Section 2.1. Alcoholic and dry fixations were made from the different samples and stored for further analysis (see Appendix II).

One of the most important problems was to deal with shoots and young leaves in which size and composition vary rapidly during the flushing periods. To allow an accurate calculation of the food intake, the best method would have been to collect and weigh the samples corresponding to each day of observation, which would have required most time that was available. As a compromise, the leaf flush specimens were collected only when the differences were obvious (colour and size) and we utilized these average data for the entire period of observation.

We tested a few food specimens for the local variations in size and composition of the mature leaves and for differences between male and female specimens in dioecious trees. Variations in composition among different trees of a given species were small and would not have affected our estimates of food intake.

3. COMPARISON OF SELECTIVITY AND DIVERSITY IN THE LANGUR SPECIES

3.1. The Study Area

The field station of Polonnaruwa was chosen for its exceptional convenience for direct observation of the primates. The undergrowth of this forest has been cleared by the archaeologists to bring to light the ruins of a city of the twelfth century. In this "sacred area", where most of the observations on primates were carried out, the canopy is intact. The conditions of visibility are extremely good and it was possible to follow the different species of primates because they have been habituated to the presence of buddhist pilgrims for centuries.

The vegetation is typical of the dry zone of Sri Lanka (Mueller-Dombois, 1969): a semi-deciduous tropical forest with trees not exceeding 20–25 m in height. The annual rainfall is 1700 mm, but the dry season of June/July/August is generally very marked.

The frequency of the main tree species of the Polonnaruwa Field Station is shown in Table IV, from two plots of 10 ha (plot 2) and 5 ha (plot 3) which have been compared to the undisturbed forest nearby (Hladik and Hladik, 1972).

A large area covering 54.5 ha (2 km in length) was surveyed and mapped, using a large-scale aerial photograph. The canopy of each tree was measured after ground identification, to allow calculation of the total production in leaves and fruits after sampling the average production of each species from a square metre of canopy. Distributions of the two *Presbytis* species were recorded in the same area (Figs 7 and 8), thus making it possible to predict the availability of their food. Except for primates, mammalian fauna is fairly scarce at Polonnaruwa and there are no longer large predators.

3.2. Food Selection by *P. senex*

At Polonnaruwa, the social units of *P. senex* are generally "one-male groups" (Rudran, 1970, 1973) including three to five females and some juveniles. These groups are barely mobile in small territories of about 2–3 ha in which the food is obtained from the most common tree species.

The food ingested during one year includes an average (fresh weight) of 60% leaves, 12% flowers and 28% fruits. Among the leaves, about two-thirds (i.e. 40% of the total food ingested) were "mature leaves" but the distinction between young and "mature"

TABLE IV
Frequency of tree species at Polonnaruwa*

Tree species	Trees per hectare	
	plot 2	plot 3
<i>Alangium salvifolium</i> (Alangiaceae)	0	2.0
<i>Elaeodendron glaucum</i> (Celastraceae)	1.7	1.0
<i>Diospyros montana</i> (Ebenaceae)	0.4	1.0
<i>Bridelia retusa</i> (Euphorbiaceae)	0.4	0
<i>Drypetes sepiaria</i> (Euphorbiaceae)	10.6	1.4
<i>Garcinia spicata</i> (Guttiferae)	1.9	0.2
<i>Alseodaphne semicarpifolia</i> (Lauracae)	0.9	0.2
<i>Cassia fistula</i> (Leguminosae)	3.9	0.4
<i>Cassia roxburghii</i> (Leguminosae)	1.4	0.2
<i>Strychnos potatorum</i> (Loganiaceae)	2.8	0
<i>Aglaia roxburghiana</i> (Meliaceae)	0.2	1.4
<i>Chloroxylon swietenia</i> (Meliaceae)	0.2	0
<i>Walsura piscidia</i> (Meliaceae)	3.6	0
<i>Ficus amplissima</i> (Moraceae)	0.7	0.2
<i>Ficus benghalensis</i> (Moraceae)	0.1	0
<i>Ficus retusa</i> (Moraceae)	0.1	0.6
<i>Syzygium cumini</i> (Myrtaceae)	0.2	0.2
<i>Adina cordifolia</i> (Rubiaceae)	10.3	10.8
<i>Ixora arborea</i> (Rubiaceae)	1.1	0.6
<i>Glennia unijuga</i> (Sapindaceae)	2.2	0.2
<i>Lepisanthes tetraphylla</i> (Sapindaceae)	0.9	0.2
<i>Sapindus trifoliatus</i> (Sapindaceae)	1.4	0.4
<i>Schleichera oleosa</i> (Sapindaceae)	2.0	1.0
<i>Manilkara hexandra</i> (Sapotaceae)	0.7	0.2
<i>Sterculia foetida</i> (Sterculiaceae)	0.1	0
<i>Grewia polygama</i> (Tiliaceae)	1.8	2.8
<i>Holoptelea integrifolia</i> (Ulmaceae)	0.4	3.4
<i>Premna tomentosa</i> (Verbenaceae)	0.3	0
<i>Vitex pinnata</i> (Verbenaceae)	5.6	3.2

Variations between plots 2 and 3 show uneven distribution.

* The naming authorities of the plant species are those mentioned in Hladik and Hladik (1972).

leaves is not always obvious. Any leaf of maximum size was included as "mature", except when its texture was very soft. Since a similar criterion was used to qualify the food of the other langur species, a comparison is nevertheless meaningful.

Most of the food ingested by *P. senex* (more than 90%) was taken from 12 species of trees listed in Table V (in fact, *Ficus* includes seven species but all of them are not present in each group's territory). The first species in the list accounts for the main part of the food; *Adina*

TABLE V
Plant species eaten by Presbytis senex at Polonnaruwa

Species eaten	Percentage of total food intake accounted for
<i>Adina cordifolia</i> (Rubiaceae)	40
<i>Schleichera oleosa</i> (Sapindaceae)	70
<i>Drypetes sepiaria</i> (Euphorbiaceae)	
<i>Alangium salvifolium</i> (Alangiaceae)	>90
<i>Elaeodendron glaucum</i> (Celastraceae)	
<i>Grewia polygama</i> (Tiliaceae)	
<i>Syzygium cumini</i> (Myrtaceae)	
<i>Holoptelea integrifolia</i> (Ulmaceae)	
<i>Garcinia spicata</i> (Guttiferae)	
<i>Walsura piscidia</i> (Meliaceae)	
<i>Ficus spp.</i> (Moraceae)	
<i>Sapindus trifoliatus</i> (Sapindaceae)	

cordifolia, from which leaves, flowers and fruits are eaten, accounted for 41% of the animals' diet and, together with *Schleichera oleosa*, for 58% of the total. The top three food species accounted for around 70%.

This low dietetic diversity is similar to that observed by Oates (1974 and this volume) for *Colobus guereza*. Three food plants accounted for 69% of Oates' feeding observations. The main food species, *Celtis durandii*, which accounted for 46.8% of observations, can be compared to the *Adina* trees which gave the bulk of the food of *P. senex*. Shoots and young leaves account for 58% of feeding time in *Colobus guereza* though the proportion of intake is probably smaller. The strategy of this type of leaf monkey is to obtain the main part of its food from a very small number of common tree species, even if a large amount of mature leaves has to be ingested.

The proportions of shoots and young leaves could be more important in the diet of *Presbytis senex monticola*, the subspecies which inhabits the montane rain forest of Sri Lanka. After a small sample of observation (25 hours of contact; see Hladik and Hladik, 1972), we obtained an estimate of 75% young leaves, 16% coriaceous leaves and 10% flowers and fruits.

3.3. Food Selection by *P. entellus*

The gray langurs at Polonnaruwa are grouped in multimale units (Ripley, 1967, 1970) that comprise 20 to 30 animals. They occupy

territories of 10 to 15 ha. They are less arboreal than *P. senex* and move around frequently, collecting a wider variety of foodstuffs from tree species which are more widely dispersed.

The average yearly diet of gray langur includes 48% leaves, 7% flowers and 45% fruits. Less than half of the leaves (21% of the food intake) are "mature leaves". The diet is more diverse than that of the purple-faced langur. The types of fruits eaten by *P. entellus* are generally mature and fleshy while those eaten by *P. senex* tend to be fibrous and desiccated.

Many food tree species are eaten by both langurs at Polonnaruwa though they do not account for the same proportion in the diet of the two species. Larger numbers of foods are utilized by *P. entellus*: 23 tree species make up 90% of its total food intake (Table VI). Ten species

TABLE VI

Plant species eaten by Presbytis entellus at Polonnaruwa

Species eaten	Percentage of total food intake accounted for
<i>Walsura piscidia</i> (Meliaceae)	30
<i>Drypetes sepiaria</i> (Euphorbiaceae)	
<i>Schleichera oleosa</i> (Sapindaceae)	
<i>Adina cordifolia</i> (Rubiaceae)	50
<i>Ficus benghalensis</i> (Moraceae)	
<i>Strychnos potatorum</i> (Loganiaceae)	70
<i>Mimosa pudica</i> (Leguminosae)	
<i>Cassia fistula</i> (Leguminosae)	
<i>Cassia roxburghii</i> (Leguminosae)	
<i>Streblus asper</i> (Moraceae)	
<i>Elaeodendron glaucum</i> (Celastraceae)	> 90
<i>Sapindus trifoliatus</i> (Sapindaceae)	
<i>Holoptelea integrifolia</i> (Ulmaceae)	
<i>Ficus religiosa</i> (Moraceae)	
<i>Ficus amplissima</i> (Moraceae)	
<i>Ficus retusa</i> (Moraceae)	
<i>Grewia polygama</i> (Tiliaceae)	
<i>Sterculia foetida</i> (Sterculiaceae)	
<i>Tamarindus indica</i> (Leguminosae)	
<i>Vitex pinnata</i> (Verbenaceae)	
<i>Lepisanthes tetraphylla</i> (Sapindaceae)	
<i>Glennia unijuga</i> (Sapindaceae)	
<i>Bridelia retusa</i> (Euphorbiaceae)	

account for 70% (versus three species only accounting for the same proportion in the diet of *P. senex*) and there is no predominant food species. The young leaves of *Adina cordifolia* are occasionally eaten but they form only a small part of the total food intake.

A comparison of the "dietograms" of the two species (Fig. 4) shows a difference in the relative proportions of leaves and fruits as well as differences in particular types of food. Both species eat small amounts of earth, like many other folivorous primates (Oates, 1974; Pollock,

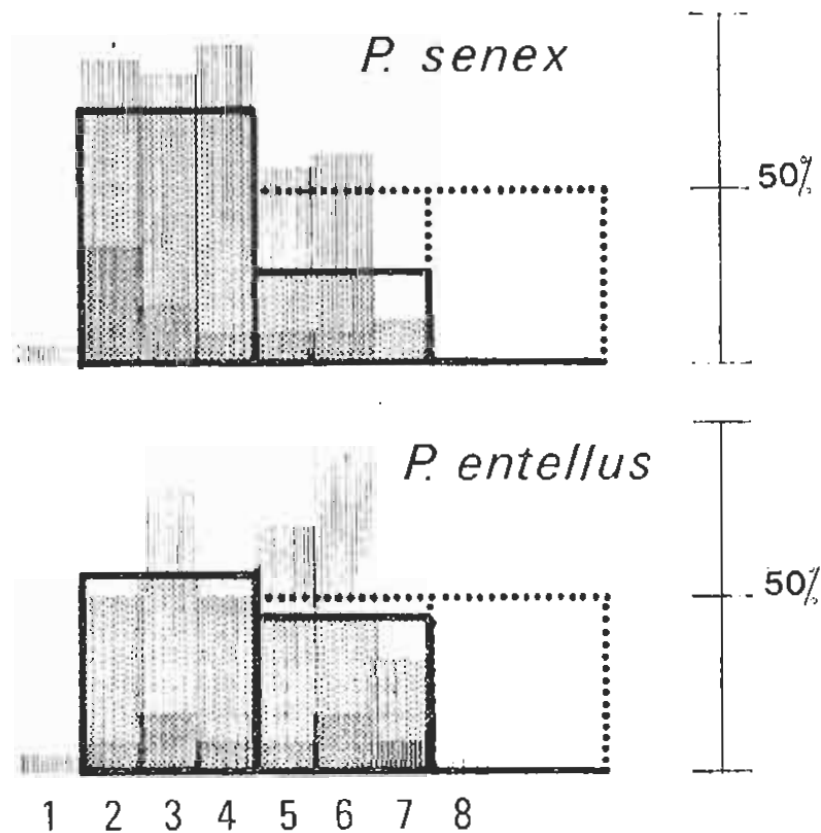


FIG. 4. Comparison of the "dietograms" of *Presbytis senex* and *P. entellus*. Variation of daily food intake is shown in columns as follows: (1) earth, (2) mature leaves and bark, (3) young leaves, (4) flowers, (5) immature fruits, (6) mature fruits, (7) seeds, (8) insects. The grey rectangles show the average proportion for the whole year.

1975b; Hladik, 1973) without any need for mineral intake (see Section 6.3, and Hladik and Gueguen, 1974). *P. entellus* may eat large amounts of fruits (up to 80–90%) while *P. senex* never eats more than 50% and generally selects coriaceous fruits. *P. entellus* never utilizes more than 50% mature leaves, while *P. senex* can eat up to 80% mature leaves over periods of several days. Both langur species do not select insects intentionally though *P. entellus* may ingest rather more animal matter than *P. senex* when feeding on *Ficus* fruits.

The red colobus, *Colobus badius*, observed in the Gombe National Park by Clutton-Brock (1974a, 1975a) may be ecologically similar to

the gray langur there is no dominant species in the diet and nine species accounted for 70% of Clutton Brock's feeding records. A very similar dietary diversity was found by Struhsaker (1975). In both studies, a large amount of shoots and young leaves was eaten by the red colobus. Furthermore, the groups of red colobus are multimale social units utilizing medium-sized territories, just like the groups of gray langurs. The species may differ in the selection of higher feeding levels by the red colobus (Clutton-Brock, 1973) and eventually more humid habitats, though *Colobus badius temmincki* can survive in very dry conditions (Gatinot, 1975).

4. SEASONAL VARIATIONS IN FOOD CHOICES

The daily records of food intake of *P. senex* and *P. entellus* did not show any marked differences in food choices between consecutive days. The diet of *P. entellus*, with around ten to 12 food species being eaten each day, varied slightly more from day-to-day than that of *P. senex*. The sample is not sufficient to study these short-term variations but we can assume that the diet of each species is very stable over successive periods of two to three days.

Availability of particular food species changes throughout the year (Hladik and Hladik, 1972) as does progressively the diet of both *Presbytis* species (Fig. 5). On these graphs, data concerning the food intake of both species have been grouped together for each period of two months and one period of three months, to make samples of about 2000 minutes corresponding to each season.

During the winter monsoon (February–March) *P. senex* feeds on a very high proportion of leaves (95%) including a high amount of young leaves and shoots. *P. entellus* at this time also eats many shoots, especially those of *Walsura piscidia* and *Drypetes sepiaria*, and a smaller amount of mature leaves. In the dry season that follows (May–June), the amount of leaves eaten by both langurs decreases because fruits are available, mainly those of *Drypetes sepiaria* and different *Ficus*; but *P. senex* utilizes less fruits than *P. entellus*, and mainly unripe fruits such as *Elaeodendron glaucum*. During the major dry season (July–September) a large amount of flowers, mainly those of *Adina cordifolia*, is eaten by *P. senex*, while *P. entellus* still utilizes many fruits such as *Schleichera oleosa* and *Walsura piscidia*. Many shoots and young leaves are available during the next monsoon (October–November), on which *P. entellus* takes the major part of its food, while *P. senex* eats a lesser amount mixed with *Adina* mature leaves. In December to January, the rain being uninterrupted, leaves increase in proportion in the diet of *P. entellus* as

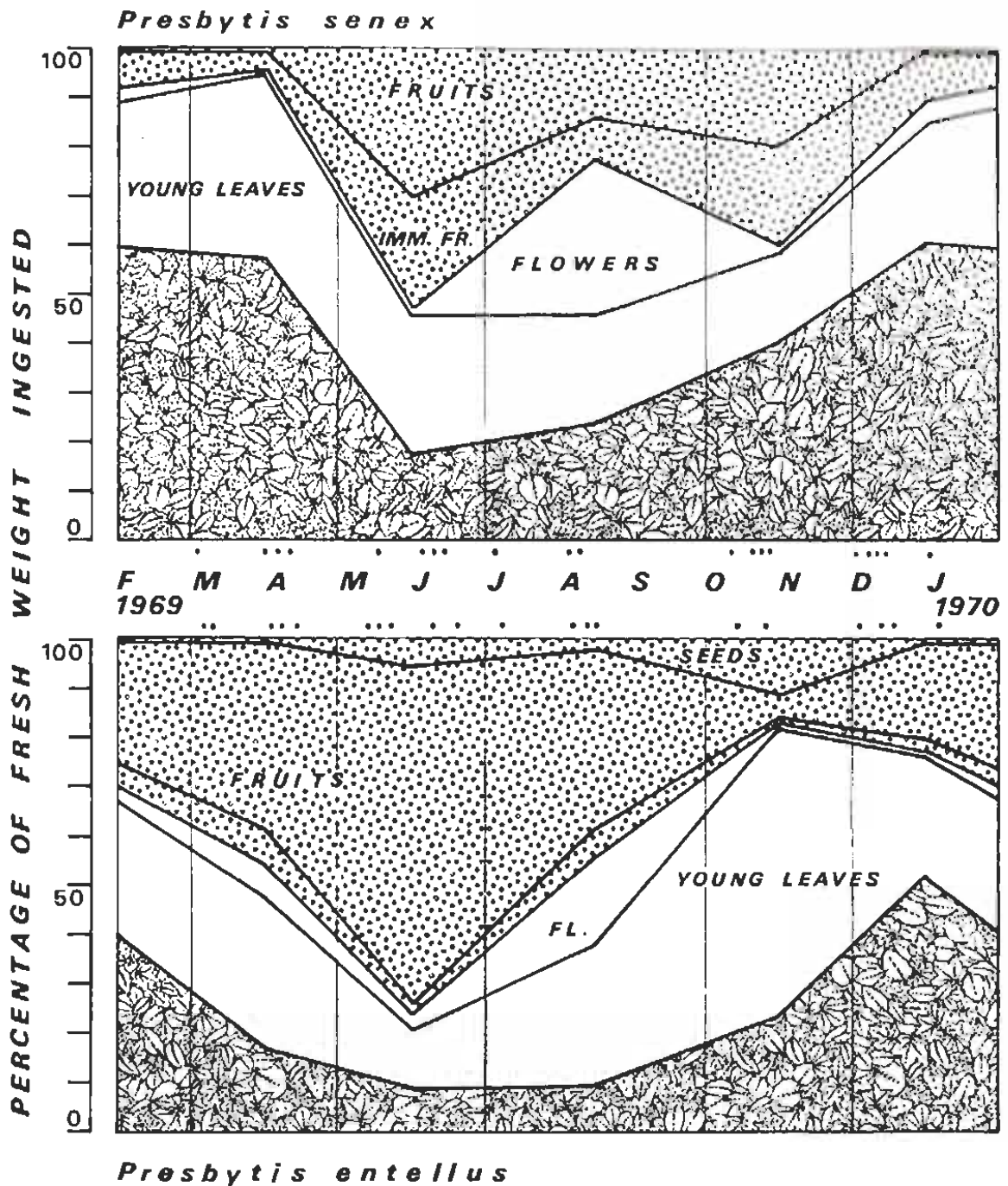


FIG. 5. Percentage of the fresh weight ingested of different food categories, throughout the year, by the two langur species of Polonnaruwa. Food categories are (from bottom to top): mature leaves; young leaves and shoots; flowers; immature fruits; mature fruits; seeds (small amounts of bark and stems have been included in the "mature leaves" category).

shoots become less available; but leaves are also utilized in larger amount at this time by *P. senex*.

In spite of the important variations of the availability in shoots, young leaves, fruits, etc. each of the *Presbytis* species maintains its own tendency, shown by a typical choice. Marked seasonal variations follow the seasonal cycle in both diets; but the dietetic differences remain approximately constant: at any time of year, *P. senex* eats more leaves and *P. entellus* more shoots and fruits.

5. THE SUPPLYING AREA AND ITS RELATION TO FEEDING BEHAVIOUR

5.1. Ranging Behaviour: Definition of the Supplying Area

The inventory of the food resources available for each group of langurs of Polonnaruwa necessitates a clear definition of what is actually available for the different groups in the overlapping parts of their home ranges (Fig. 6). For example, group A has the exclusive utilization of all the resources in the core area and in the rest of area 1. In area 2 where A and B's ranges overlap, an equivalent amount of the food is available for each group. The supplying area of group A thus includes half of area 2 and one-third of area 3 where the ranges of group A, B and C overlap. The limits of the "supplying area" (dashed lines on Fig. 6) are fictitious but are useful in calculating the quantity of food available for each group in an homogeneous environment.

5.2. Distribution of Food Resources for *P. senex*

The supplying area of each group of purple-faced langur observed at Polonnaruwa was measured according to data collected by G. Manley

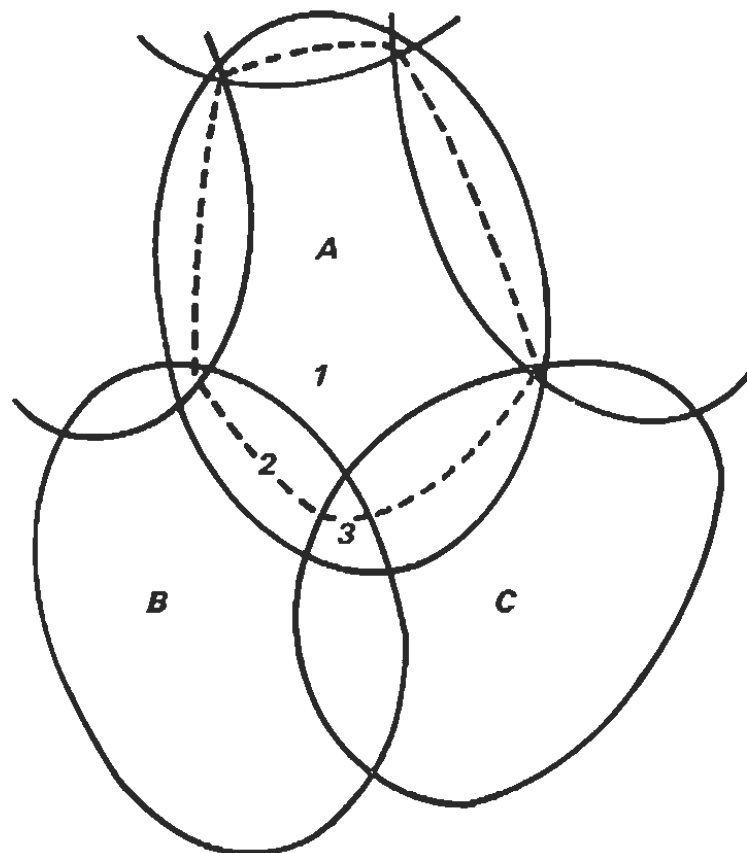


FIG. 6. Diagram showing the home ranges of groups A, B and C (solid line) and the supplying area of group A (dashed line).

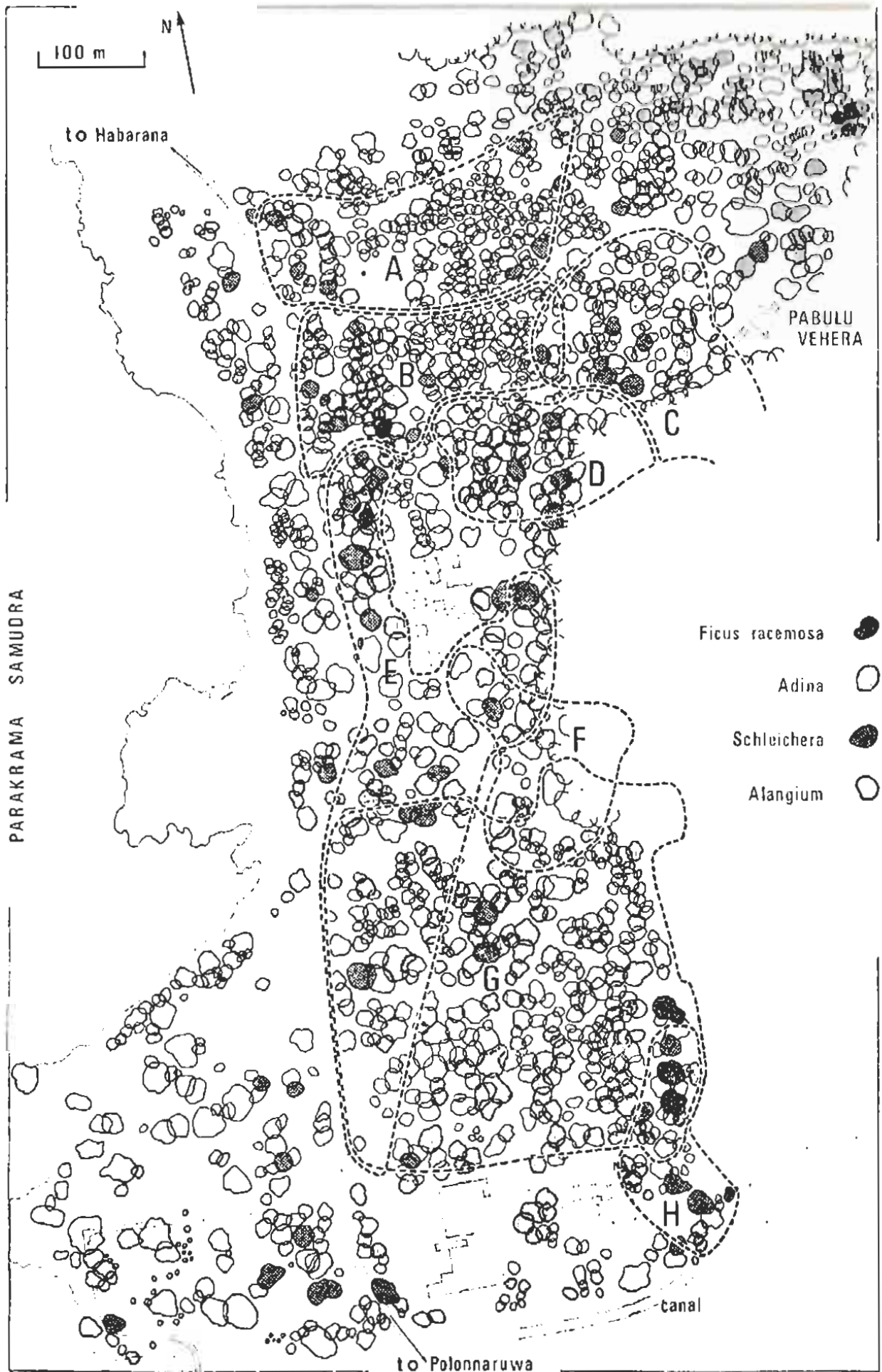


FIG. 7. Distribution of the main food-producing trees in the home ranges of the groups of *Presbytis senex*, at Polonnaruwa.

(pers. comm.) and Rudran (1970 and pers. comm.) (see Fig. 7). In each of the supplying areas, the total production of food (i.e. of food species actually selected by *P. senex*) was calculated (see Hladik and Hladik, 1972) and the main results are presented in Table VII. Taking into account the number of monkeys in each of the groups, we obtained the average production of food per monkey and per year in the different groups. A purple-faced langur ingests about 400 kg (fresh weight) per year (1006 g of food were found in the first part of the stomach of a specimen of 7600 g shot in the evening, but very important variations between days were observed). Thus the potential food supply is more than ten times what is actually eaten, and the variations between different groups are small.

TABLE VII

Total food in kg (fresh weight) available per year for one monkey in the different groups of Presbytis senex at Polonnaruwa

Groups	<i>Adina cordifolia</i>		<i>Schleichera oleosa</i>		Other trees leaves
	leaves	flowers	shoots	fruits	
A	1300	60	240	65	1100
B	3500	160	380	105	2200
C	2100	100	420	115	2200
D	4700	215	350	100	2000
E	3500	160	510	160	2000
F	1000	50	200	55	2800
G	6500	300	300	85	5800
H	600	30	130	35	1000

After Hladik and Hladik, 1972.

Eating one-tenth of the food production might be the maximum permissible for a folivore utilizing an important amount of young leaves without endangering the food plant population (C. M. Hladik, 1977). In the supplying area of group H, which is reduced by the pressure of the dominant neighbouring group (Fig. 7), the food available per individual is effectively less than 2000 kg per year. In this particular area, some *Alangium salvifolium* trees were dying because their young leaves were too frequently plucked by the purple-faced langurs. This case can probably be considered as a density limit, since group H will necessarily disappear when too many trees are destroyed.

In each of the supplying areas of groups A to G, there are more than 500 m² of total canopy of *Adina cordifolia*, the main food source. The relative abundance and even distribution of the trees utilized by *Presbytis senex* appears clearly on Fig. 7 and Table IV. It allows each

group to obtain an equivalent share in a small supplying area. The distribution of the food resources cannot be estimated by a single recording of the number of trees in different plots. Dittus (1974) discussed the different mathematical interpretations of distribution in plots and concludes that a visual estimate is a necessary starting point. The average distance between two trees of a given species, and its variability, might be a useful measure of species distribution; but to measure production it is also necessary to take differences of canopy size into account.

5.3. Distribution of Food Resources for *P. entellus*

Using data supplied by Ripley (1970 and pers. comm.) and N. Muckenhirn (pers. comm.), we measured the supplying areas of the different groups of gray langurs. Our measures of production and calculation of the average quantity of food available for each group allowed us to make comparisons between groups (Hladik and Hladik, 1972—see Table VIII).

The different tree species utilized by the gray langur (Fig. 8) are less evenly distributed than those used by the purple-faced langur. The average distance between the trees of a given food species of the gray langur is greater and varies widely: for example, the mean distance between *Ficus* trees is more than 100 m. Large home ranges allow access to these species with scattered distribution. In many cases, the supplying area of the different troops contains similar amounts of important food species: for example, an average of one female *Drypetes sepiaria* (producing fruits) and one-and-a-half male *Drypetes sepiaria* (producing only leaf shoots) is available for each monkey of different troops. Other types of food-producing trees differ in abundance between groups (Table VIII) but other tree species compensate for what is missing. An average of 500 kg of fruits per individual per year is available from the

TABLE VIII

Annual mean production available for one individual in the different groups of Presbytis entellus, for some of the commonest food species at Polonnaruwa*

	<i>Walsura piscidia</i> shoots	<i>Drypetes sepiaria</i> shoots	<i>Drypetes sepiaria</i> fruits	<i>Ficus</i> spp. fruits	<i>Schleichera oleosa</i> fruits
North group	40	180	23.5	62.5	30
Central group	20	135	20	262	115
South group	(few)	>50	>10	197	40

* In kg fresh weight.

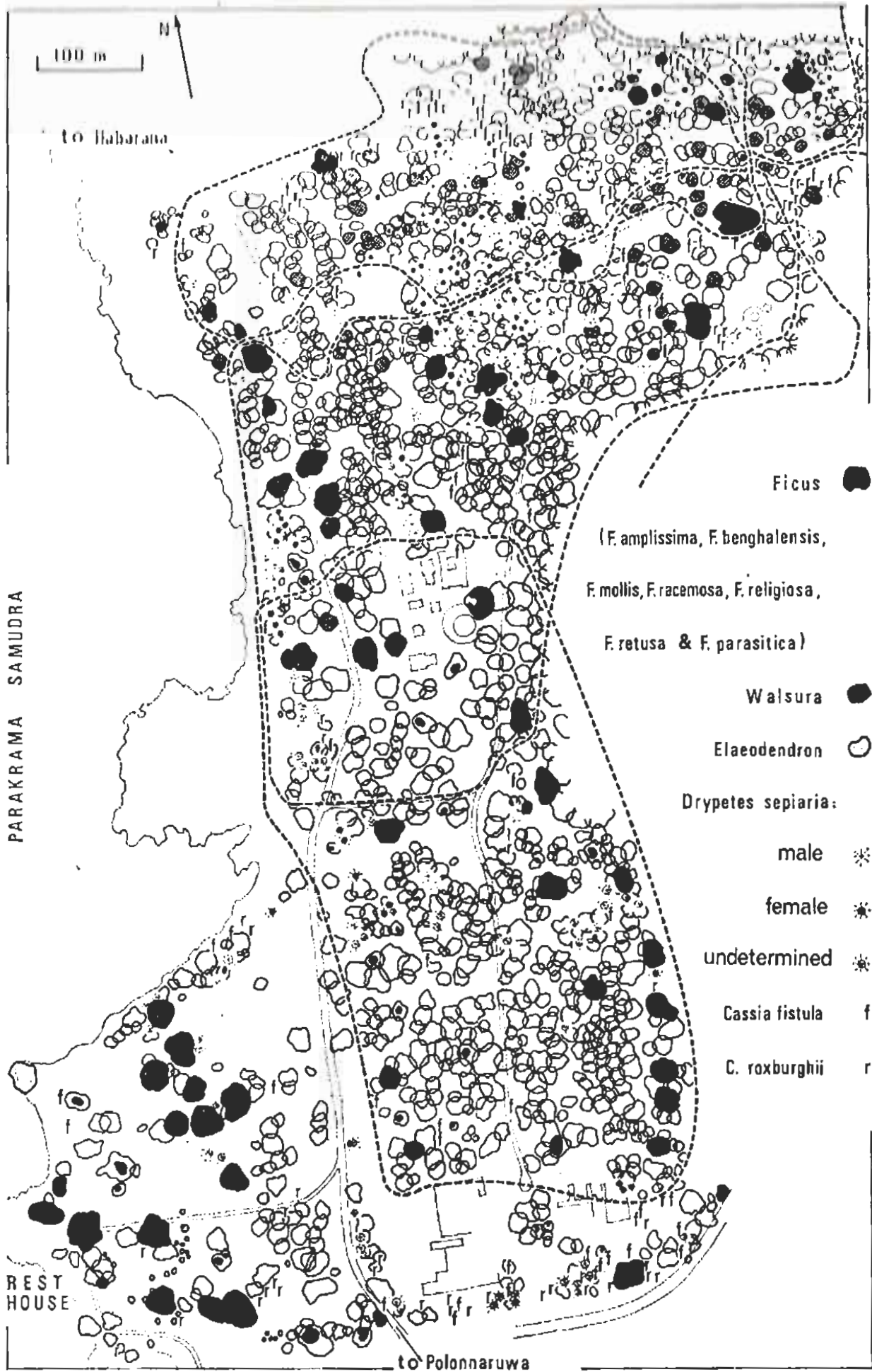


FIG. 8. Distribution of some important food trees in the home ranges of the groups of *Presbytis entellus*, at Polonnaruwa.

ten first species of the list (Table VI) and about half of these fruits are actually eaten.

Both langur species show approximately similar population densities (about two animals per hectare), with biomasses of 10 to 15 kg per ha in maximum density locations. The success of each of the langur species is due to a different strategy of adaptation in the same environment, the large groups of gray langurs dealing with a larger set of scattered food species.

6. COMPOSITION OF THE FOOD SUPPLY

6.1. Composition of the Food Samples

The food samples collected at Polonnaruwa were analysed to allow comparisons of the diets of the primates of Sri Lanka and other primate species (Hladik *et al.*, 1971a; Charles-Dominique and Hladik, 1971; Hladik, 1973, 1975). The results have been compiled out of a set of 1800 analyses (Hladik *et al.*, in press) including several samples of each species of Polonnaruwa collected in different seasons and different places.

For many frugivorous species of primates the leaves, especially young leaves and shoots, are necessary to increase the protein content of the diet (C. M. Hladik, 1977) and plant species with the highest protein contents (such as Leguminosae) are usually selected. By contrast, protein content is less likely to determine food choices in *Presbytis* species whose staple food (leaves) is protein rich. In fact, some samples have a very low protein content though they are selected preferentially by *P. senex*. Food samples selected by *P. entellus* are generally richer in primary compounds, especially in soluble glucids.

6.2. Comparison of the Intake of Protein, Lipids and Glucids

The average composition of the foods ingested was calculated for different periods of the year, using the composition of the different food samples and their proportion in the diet during different seasons (see Section 4).

There is marked seasonal variation in dietary composition (Fig. 9) and the two *Presbytis* species show different characteristics. The dietary pattern of *P. senex* shows less seasonal variation than that of *P. entellus*. The protein intake of *P. senex* is low and approximately constant at 11.5% of the dry weight. *P. entellus*, in contrast, shows the highest average of protein intake for the whole year, but has a rate as low as 10%, reaching 16% during the rainy season when leaf buds and leaf

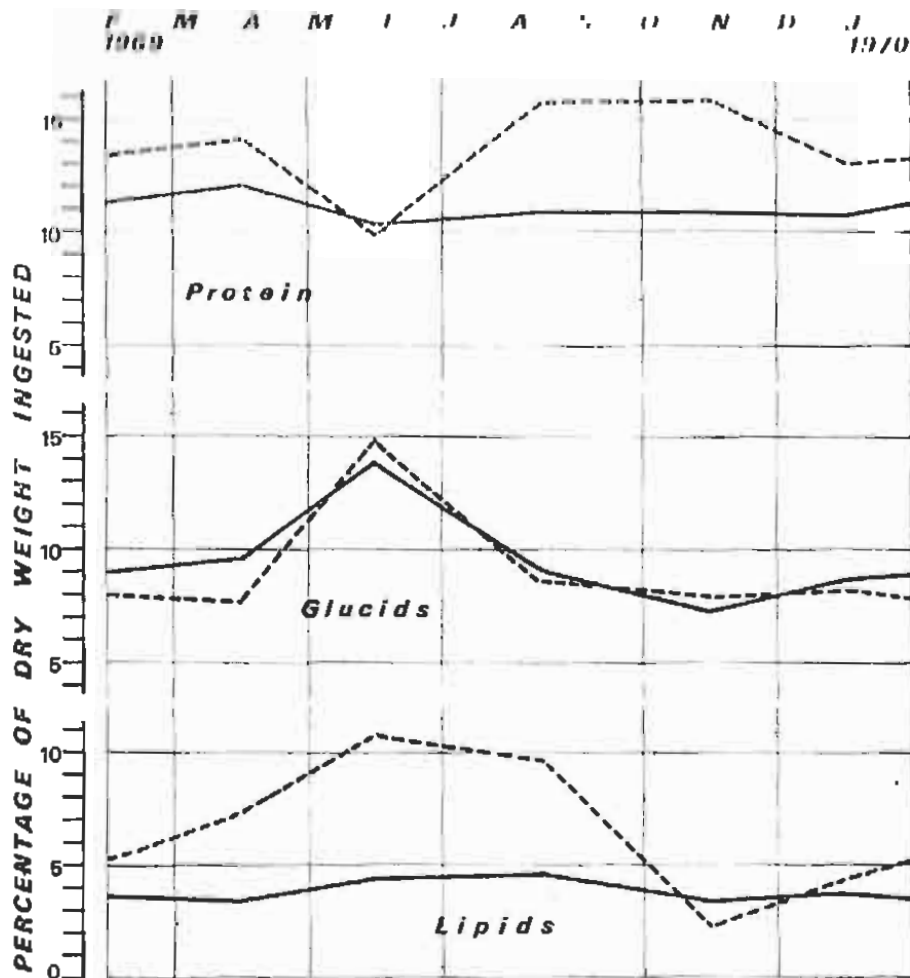


FIG. 9. Seasonal variation in the content of the diet of *Presbytis senex* (solid line) and *Presbytis entellus* (dashed line).

flushing are eaten in large quantity. The same applies to the rates of lipid intake: these vary little and lie around 4% for *P. senex*, while in *P. entellus* they vary from 3 to 11% of the dry weight of the total diet and are generally considerably higher. The amounts of soluble glucids (the results of the analysis, after a short hydrolysis, show approximately the amount of glucids actually assimilable; see Hladik *et al.*, in press) are more similar for the two species and follow seasonal variation in the flowers and fruits available.

As a result, *P. entellus* obtains much more energy from its environment but has to spend more energy than *P. senex* in finding scattered food resources over a wider range. The less mobile system of *P. senex* minimizes energy expenditure but allows a relatively low nutritional gain with little variation throughout the year.

6.3. Mineral Intake and Geophagy of the Leaf Monkeys

Seasonal variation in the intake of some minerals was also found (Fig. 10) but, at any time, rates of intake are generally higher than the minimum requirements for both langur species.

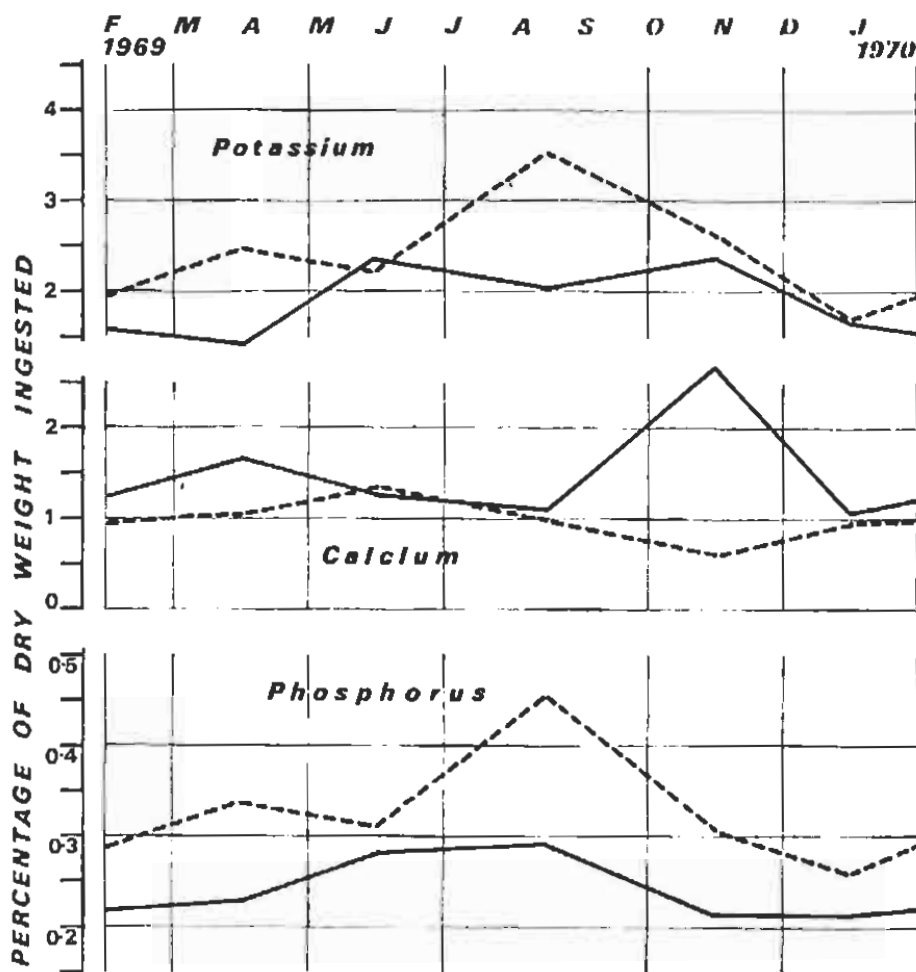


FIG. 10. Seasonal variation of mineral content in the diet of *Presbytis senex* (solid line) and *Presbytis entellus* (dashed line).

Many leaf-eating primates eat small amounts of earth (Ripley, 1970; Hladik and Hladik, 1972; Hladik, 1973; Oates, 1974; Pollock, 1975b). This behaviour (geophagy) has no apparent connection with the mineral nutrition, as might have been expected (Hladik and Gueguen, 1974). If we compare the results of the analysis of a piece of termite mound collected by S. Ripley at Polonnaruwa to the composition of different food samples eaten at the same time by the gray langur (Table IX), the amounts of minerals in the earth sample are very small, with the exception of iron which is not necessary at such a high rate (the iron of leaves and fruits covers all physiological requirements). Sodium and zinc, the only elements that might be low in the diet, are present in the earth sample but in smaller quantities than in many common foods. Several samples of earth eaten by African primates have also been found to contain low mineral levels when compared with leaves.

One possibility is that the small quantities of clay which are eaten by folivorous primates may act as an adsorbant of the tannins and compensate for their inhibitory effect on protein absorption as demonstrated by Feeny (1969). Alternatively, they may have a similar

TABLE IX

Comparison of minerals* in earth and in some foods eaten by *Presbytis entellus* at Polonnaruwa

	P	Ca	Mg	K	Na	Fe	Zn	Mn	Cu
Earth from a termite mound (sample 1 from S. Ripley)	257	565	1290	773	148	25 000	59	970	22
<i>Walsura piscidia</i>									
young leaves	2580	2290	1540	32 060	87	73.5	47	79.5	8.9
mature leaves	1250	10 250	2400	18 000	87.5	105	185	200	4.5
<i>Drypetes sepia</i>									
young leaves	1600	9900	3700	22 100	930	143	35	183	6.5
mature leaves	2000	10 000	4200	27 000	840	155	24	178	3
<i>Schleichera oleosa</i>									
mature leaves	1900	23 000	1850	7500	285	—	28.5	32.5	10
<i>Ficus amplissima</i>									
fruits	1810	9630	3400	21 970	240	78	21	10	8.2

* By dry weight p.p.m.

physiochemical effect on the other secondary compounds which are frequently found in small quantities in leaves.

6.4. Intake of Secondary Compounds by the Langurs

Secondary compounds or allelochemicals (Whittaker and Feeny, 1971), such as alkaloids, tannins, saponins, glucosides etc. are generally considered as toxic or repellent for insects and vertebrate plant-eaters. They may represent antipredator devices produced by the plants. Strong evidence of the advantage to the plant of such toxic compounds in seeds has been presented by Janzen (1970). The occurrence of the allelochemicals in large quantity in leaves is not so common (A. Hladik, 1977). A variety of secondary compounds is present in the leaves of many species but their concentration is generally low.

Tests for alkaloids were made on a series of dried herbarium samples of the plants eaten by the langurs at Polonnaruwa (Hladik *et al.*, in press). Only three species (out of a set of 41 species) have strongly positive reaction with Mayer's and Dragendorff's reagents and these positive results may eventually be due to a partial decomposition of the protein during hydrolysis. Further investigation was carried out on *Strychnos potatorum* (Fig. 11) whose unripe fruits are eaten by the gray

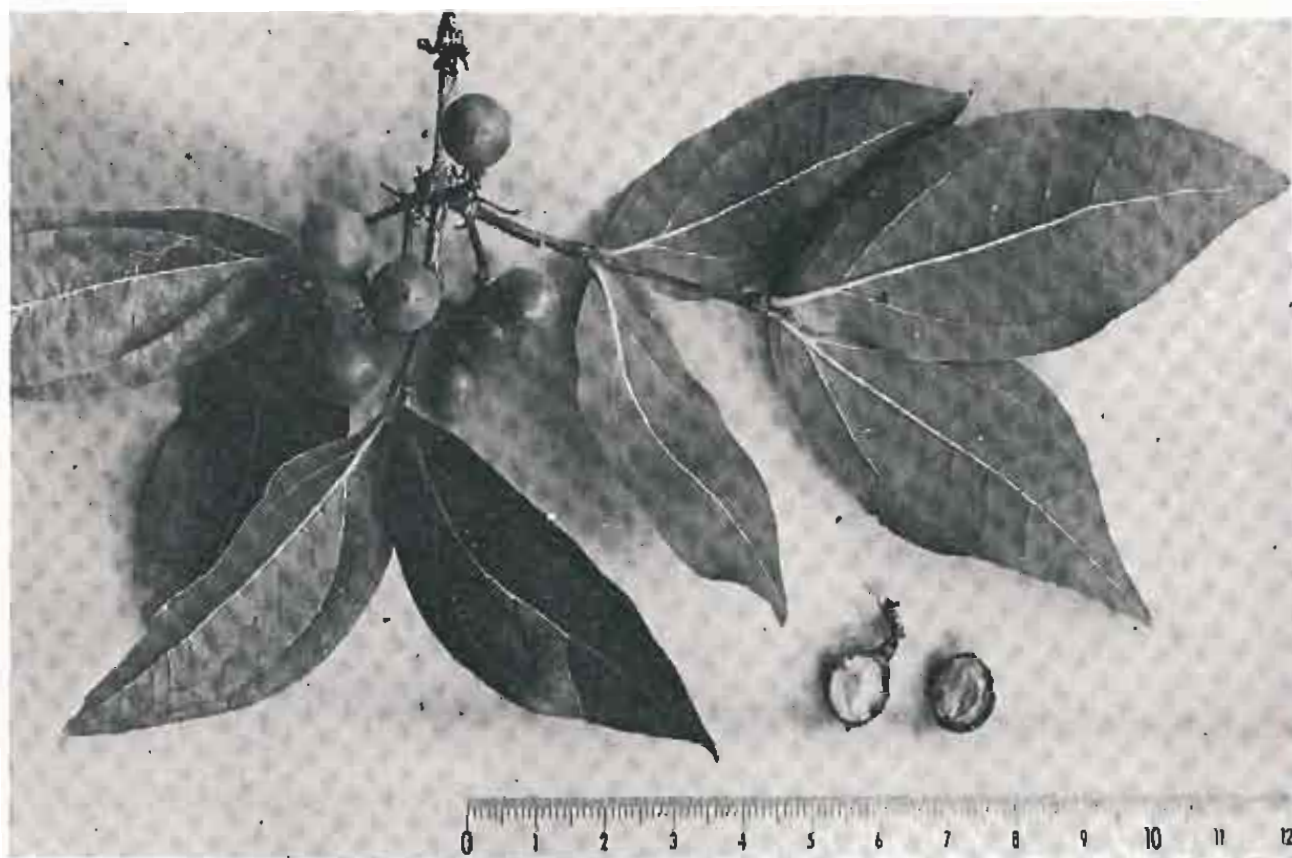


FIG. 11. *Strychnos potatorum* fruits (eaten by *Presbytis entellus*) and leaves (the only part selected by the macaques). Rule in cm.

langur in large quantities and whose leaves are frequently eaten by *Macaca sinica*. We found a large amount of alkaloid (neither strychnin nor brucin) in the fruit but no alkaloid in the leaves (the positive reactions of the screening tests were due to the protein for which the macaques eat the leaves).

It is not surprising that some toxic compounds can be eaten by the langurs since, in contrast to frugivorous species such as macaques, the bacterial flora of their stomach will decompose such products before intestinal absorption (Kuhn, 1964; Moir, 1968). As a protective device against primate leaf-predator, the secondary substances of plants would not be very efficient.

Another type of chemical protection may be more efficient: the small amounts of nutrients in *Adina cordifolia* and some other common tree species (Hladik *et al.*, 1976) would encourage leaf eaters to select the foliage of species with higher nutrient levels. To feed on these low-level nutrients necessitates the highest physiological and ecological specialization of an animal adapted to a low level of energy input and output (such as *P. senex*).

7. DISCUSSION: PHYSIOLOGY AND FEEDING BEHAVIOUR

Physiological and behavioural adaptations of mammals have evolved to meet the requirements of different ecological niches. The result is a tendency to maintain a particular kind of diet but to vary this in accordance with seasonal cycles of food availability (see Section 4).

The behavioural regulation of the *milieu interne* is the prime cause of feeding behaviour (Garcia *et al.*, 1974) but it involves two distinct processes: firstly, a long-term effect via conditioning operating through the beneficial effects of food ingestion and absorption and, secondly, through taste stimulation. Each of these two processes may have a different importance for different species, as shown for the primates of Central America (Hladik *et al.*, 1971a): the long-term effect plays the major role for species which are partly folivorous such as *Alouatta palliata*, while immediate taste stimulation is more developed in frugivorous species such as *Ateles geoffroyi* and *Cebus capucinus* that must be strongly motivated to gather dispersed foods of high nutrient content.

Among the two *Presbytis* species of Polonnaruwa, the long-term effect of the same type of food may be very similar, since the digestive systems of both species are quite similar (with only small variations of the cell populations along the mucosa of the small gut; Amerasinghe

et al., 1971). Thus the differences in food choice may be explained by a difference of intensity of the immediate taste response.

Similar differences in the feeding strategies of *Colobus guereza* (see Section 3.2) and *Colobus badius* (see Section 3.3) suggest that the evolution of social structure as described by Oates (1974 and present volume), Struhsaker (1975) and Clutton-Brock (1973, 1974a, 1975a) is associated with the evolution of the intensity of the response to taste stimulation. The difference in feeding behaviour between siamang and gibbon (Chivers, 1973 and this volume) and between gorilla (Casimir, 1975) and chimpanzee (Hladik, 1973 and this volume) also needs to be examined, in terms of sensory physiology, according to the composition of the food selected in natural conditions.

8. SUMMARY

1. Direct observation of the feeding behaviour of two sympatric species of leaf monkeys (*Presbytis senex* and *P. entellus*) was carried out in the semi-deciduous forest of Polonnaruwa, Sri Lanka.

2. The food ingested by these two species was estimated from the weights of samples collected in the field. There are important differences between the proportions of the different categories of food ingested and the proportions of time spent feeding on the same types of food.

3. All tree species were surveyed and mapped in an area of 54.5 ha covering the home ranges of different groups of langurs which were observed. The food produced by each of these trees during one year was also calculated.

Presbytis senex obtained 70% of its food from three tree species only. The food ingested included (by wet weight) 60% leaves, 12% flowers, 28% fruits.

Presbytis entellus obtained 70% of its food from ten tree species. The food ingested included (by wet weight) 48% leaves, 7% flowers, 45% fruits.

4. Seasonal variations in the food choices were marked in both langur species but similar differences between them were present throughout the year.

5. Comparison of the supplying areas of the different groups showed that food resources were distributed similarly between them, with a different model of habitat utilization concerning each species.

6. The composition of the foods ingested varied between the two species. The food of *P. senex* was lower in nutrient contents than that of *P. entellus* but varied less throughout the year.

Geophagy frequently observed among langurs and other folivorous primates does not appear to be associated with the selection of deficient minerals.

Secondary compounds play a small role in the feeding ecology of langur species. Food choice is mainly determined by the distribution of primary compounds with taste stimuli playing a different role in relation to different feeding strategies.

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