

An Experiment on the Relation Between the Feeding Speed and the Caloric Intake Through Leaf Eating in Japanese Monkeys

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ABSTRACT. In order to know the bioenergetic effect of leaf eating in Japanese monkeys experiments were conducted on caged animals. Two monkeys from the Koshima troop were fed with leaves in a cage shortly after their capture. The monkeys were tested to determine in what duration they could fulfill their daily energy requirements by solely leaf eating or by solely wheat eating. Twelve hours of feeding solely on leaves did not fulfill the monkeys' maximum daily intake, whereas 4 hr of feeding solely on wheat satisfied their daily energy requirements. The ratio of the daily intake to the daily energy consumption was 90% for leaf eating and 120% for wheat eating. It is difficult for Japanese monkeys to fulfill their daily energy requirements by leaf eating only. Thus, the combination of fruits (nuts) and leaves must be necessary for their energy intake. These facts are to be considered in the studies of feeding activity, food abundance, or the home range size.

INTRODUCTION

Recently, the feeding activity of primates has been studied (CHALMERS, 1968; RICHARD, 1970; CLUTTON-BROCK, 1974; STRUHSAKER, 1975; YOTSUMOTO, 1976), and bioenergetic studies of primates have developed (IWAMOTO, 1974, 1975; COELHO, 1974; COELHO, BRAMBLETT, & QUICK, 1976).

IWAMOTO (1974) conducted intensive studies on the food intake of Japanese monkeys, and stressed the importance of their leaf eating. In winter, Japanese monkeys feed mostly on leaves, while they feed on a variety of foods, mainly fruit in autumn. The major objective of the present study is to know the bioenergetic effect of leaf eating in Japanese monkeys.

It is very difficult to obtain feeding activity data which are not affected by various external factors under natural conditions. The feeding potential which is not affected by external factors is of much interest. The feeding potential includes feeding rhythm, feeding speed under conditions where external variable are minimized and also includes digestion speed. Monkeys were fed only with leaves shortly after their capture from the wild in order to clarify their feeding potentials. Then the feeding activity on leaves was compared with the feeding activity on wheat.

MATERIAL AND METHODS

Two Japanese monkeys (*Macaca fuscata*) that escaped from Koshima Islet and damaged crops on farmland were captured in May and June 1976. The experimental subjects were *Hato* (an 8 years old male weighing 5.9 kg), and *Shii* (a 13 years old

female weighing 6.8 kg). The experiments of feeding monkeys with natural food were conducted shortly after the capture, in June 1976.

Experiment 1

An experiment to estimate feeding speed on natural food and the amount of daily food intake was conducted in June 1976 and designed as follows. As the amount of daily intake is affected by the feeding speed, experimental changes in feeding duration in a day may affect the feeding speed and the amount of daily food intake. If the start of feeding is delayed, the monkeys will try to compensate for the shortened feeding duration, and will increase their feeding speed. In this experiment, the time of the start of feeding is varied, while the time of the end of feeding is fixed. Thus, the relationship between the maximum amount of daily food intake and the changes in feeding duration was obtained. This amount was assumed to be the daily food intake when monkeys were permitted to feed freely for a whole day.

Leaves of *Ficus erecta* var. *Sieboldi king* (Japanese name, hosobainubiwa) were chosen to represent the leaf food items. The leaves of *Ficus erecta* are one of the staple foods in the wild Koshima troop. Although the variety used is not as abundant as the original species in Koshima Islet, it is also favoured by monkeys. The leaves of this variety were chosen because there was not much difference in the preference between the leaf stocks, though the original species showed many differences.

The time of the start of feeding was varied, while the end of feeding was fixed at 17:00. The two monkeys were caged in two adjoining cages (1.4 m × 1.4 m × 2.0 m) and subjected to alternate 10 min feeding and 10 min non-feeding sessions during a whole day's feeding duration.

Leaves given to the monkeys were placed on a table in front of the cages and were easily taken by the monkeys. A few (one to four) leaves were placed on the table at a time, and after they were taken by the monkeys new leaves were added to the table again, and the procedure was repeated during a session. Leaves left on the table at the end of a session were removed and the amount of leaves eaten for a session was thus obtained. The remaining fragments of leaves on the floor of the cage were gathered and weighed at the end of the whole day's feeding duration.

Fresh leaves were collected two times a day, once in the morning and again in the afternoon and kept in nylon bags and placed in a cooled box. Monkeys were permitted to drink water freely.

Experiment 2

The same procedure as in Experiment 1 was conducted using wheat as a food item in November and December 1976. Wheat was given to the monkeys using the same procedure as in Experiment 1, but the wheat was poured 5 g at a time into saucers in the cages, and the wheat grains left in the saucers at the end of a feeding session were not removed, and were passed to the next feeding session. The last 5 g which were not completely consumed within a feeding session were counted as a whole 5 g in the next session.

Experiment 3

In order to estimate the digestibility of leaves by Japanese monkeys, 7 hr (10:00–

17:00) of feeding each day were conducted for 12 days in April 1977. Feeding was conducted using the two stable food plants of wild monkeys, *Ficus erecta* (Japanese name, inubiwa) and *Callicarpa japonica* (Japanese name, ohmurasakishikibu). The leaves of *Ficus erecta* were fed upon at the beginning of the daily sessions. When feeding speed declined about 2 hr later, *Callicarpa japonica* were given and continued to be given to the end of the daily sessions. Body weights of the subject monkeys were checked at 9:00 before cleaning the cages. Faeces were gathered at 9:00 and 17:00 at the end of the daily experiment. Considering the effect of long time separation on the intestinal bacteria of the caged monkeys fresh faeces of wild monkeys were diluted in water and were given to the caged monkeys as drinking water two times before the start of the experiment. Grasses, as well as wheat and soybeans, were fed to the monkeys for one week preceding the experiment.

Experiment 4

The same procedure as in Experiment 3 was conducted using wheat. Seven hours for feeding (10:00–17:00) each day were conducted for six days in June 1977.

Experiment 5

The caloric values of given leaves, wheat and faeces after the respective feedings were measured using an automatic adiabatic bomb calorimeter (SHIMAZU CA-2).

RESULTS AND DISCUSSIONS

Activity Patterns of Feeding, Measurements of Feeding Speed, and Food Intake

Feeding activities were studied by changing the duration of feeding per day (Experiment 1). The activity patterns of feeding on leaves of *Ficus erecta* are shown (Fig. 1). The activity patterns of both monkeys in the same day experiments are shown on the same graphs. When the feeding duration of a day was long, the feeding rate was high in the early morning and then dropped for 4–5 hr, and a high level of feeding resumed in the afternoon. This pattern is considered to be typical as a feeding potential for Japanese monkeys feeding on leaves. When the feeding duration for a day was shortened, the initial feeding rate increased extremely without much decline later as observed in the cases of longer feeding duration.

A tendency towards synchronization was observed in the activity patterns of the two monkeys in the same day experiments. This is partly because the two monkeys were in adjoining cages and were affected by each other, and partly because they were fed with leaves of the same stocks. The cases where the feeding patterns of the two monkeys differed much (the graph in the middle of the upper row of Fig. 1) does not necessarily indicate the refutation of the typical pattern, but might be the result of extraneous factors. Individually the two monkeys showed the typical feeding pattern mentioned above for leaf eating. This activity pattern: intensive feeding in the early morning which then declines and a high feeding rate in the afternoon also occurs as a troop feeding pattern in the wild observed during the winter when monkeys mainly depend on leaves (KUROKI, 1976; YOTSUMOTO, 1976). Similar kinds of patterns might be expected in the troop feeding pattern of other species (e.g., CLUTTON-BROCK, 1974).

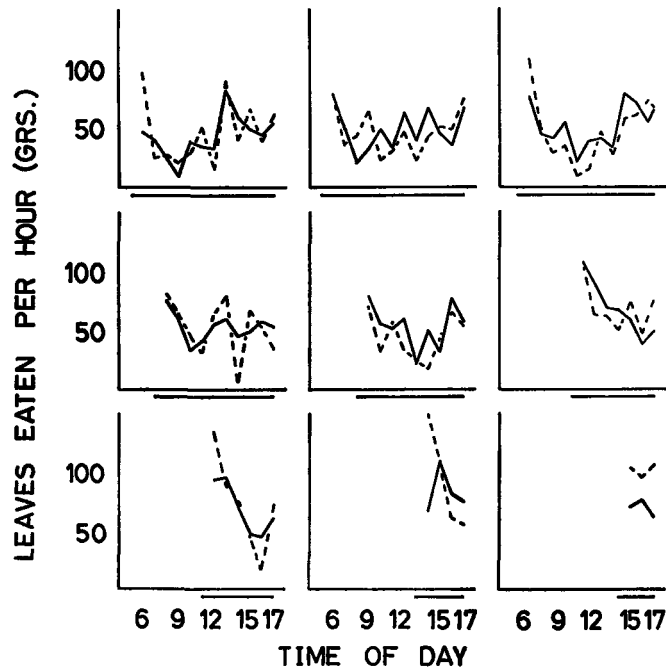


Fig. 1. The feeding activity upon leaves of *Ficus erecta* var. *Sieboldi king*. The activities of the two monkeys are shown on the same graphs. The straight lines indicate Hato's activity and the dotted lines indicate Shii's activity. The line below each graph indicates the feeding duration.

When the total food intake for a day is plotted on a graph as the function of feeding duration, the curve, which might be obtained (but is not shown on the graph) by connecting these dots, may exhibit feeding at a maximum speed (Fig. 2). The dots on the graph indicate that the total food intake increased rapidly with an increase in feeding duration, but did not reach a plateau within the experimental duration, 12 hr. The feeding rate declined, but continued to increase for the feeding duration over 7 hr.

An average cumulative food intake for 7 hr was obtained in Experiment 3. Seven hours of feeding were conducted for 12 days and the data of eight consecutive days, each with a relatively stable food intake total, were selected. The total amounts of feeding in 7 hr are nearly equal in both Experiments 1 and 3. The cumulative feeding curve for 7 hr is equal to or rather higher than the dots in Figure 2 for a much shorter feeding duration, though these dots should exhibit maximum speed of feeding according to the design of Experiment 1. Though this seems a little contradictory, this rather indicates that the monkeys fed at a maximum speed in the relatively short feeding duration of 7 hr. A twelve hour cumulative curve was figured using four cases of 12 hr of feeding and two cases of 11.5 hr of feeding; the 11.5 hr data were converted to 12 hr data by doubling the feeding amount of the last 30 min (Fig. 2). Comparing the two cumulative curves, the most remarkable difference is that the 7 hr curve shows a rapid increase in food intake for the initial 3 hr without a decline in the feeding rate which follows. Comparing feeding amounts in both

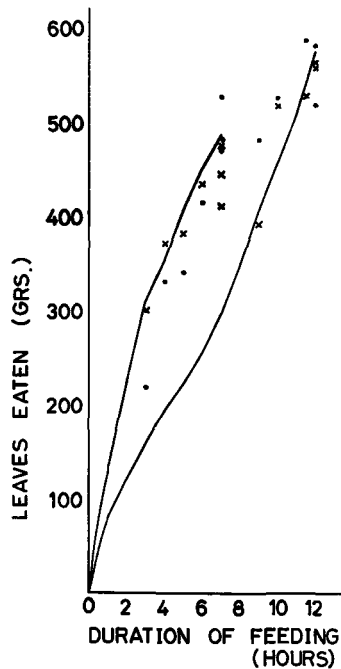


Fig. 2. The changes in the daily intake of leaves plotted against the changes in the feeding duration. The symbols ● and × indicate the daily food intake by *Hato* and *Shii*, respectively. The straight lines indicate the hourly cumulative amount of leaves fed for 7 and 12 hr feeding durations. The data for 7 hr feeding were obtained in Experiment 3. The data for 12 hr feeding were obtained in Experiment 1 and are a mixture of the data of 12 hr feeding and 11 hr and 30 min feeding, where the feeding amount of the last 30 min was doubled.

Experiment 1 and Experiment 3 for the same 7 hr feeding duration, the difference is in the food plants given: *Ficus erecta* var. *Sieboldi king* in Experiment 1 and the mixture of *Ficus erecta* and *Callicarpa japonica* in Experiment 3. The average intake for 7 hr of feeding in Experiment 3 was 488 g and was not much different from the amount in Experiment 1, 469 g. This suggests that the observed intake is a fairly common one as a feeding potential for Japanese monkeys feeding on leaves of staple food plants.

In order to obtain some comparative data with leaf eating, in Experiment 2 only wheat was given to the monkeys using a similar procedure as in Experiment 1. The feeding pattern on wheat shows a high feeding level at the beginning of feeding and a gradual decline with the lapse of time (Fig. 3). The changes in the total amount of feeding for a day plotted against the changes in feeding duration are shown on the graph in Figure 4. Only 3 hr of feeding was enough for the monkeys to feed the maximum amount for a day, and an extension of the feeding duration in a day did not increase the total food intake. The short duration of feeding on wheat to reach a plateau for food intake after 4 hr is in sharp contrast with the case of leaf eating where even after 12 hr of feeding, a plateau was not reached, though a decline in the feeding rate was observed. This indicates that a long duration is necessary for

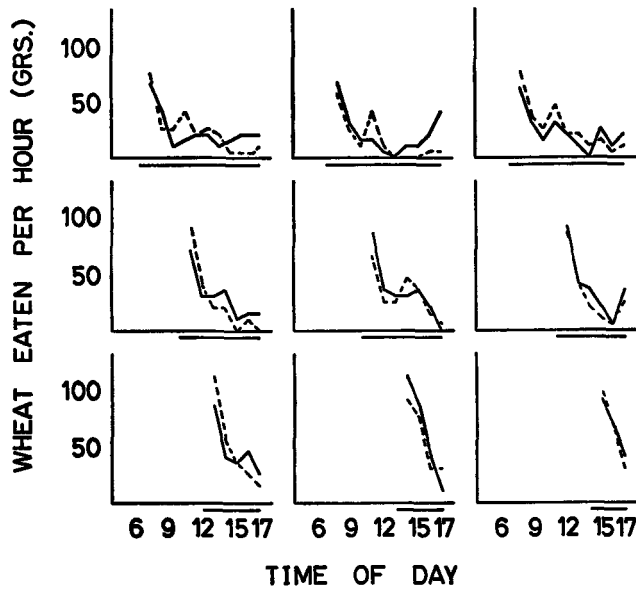


Fig. 3. The feeding activity when wheat was fed. The activities of the two monkeys were shown in the same graphs. The straight lines indicate *Hato*'s activity and the dotted lines indicate *Shii*'s.

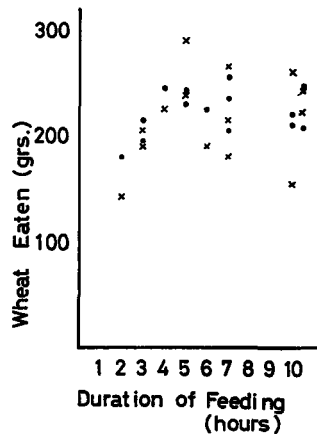


Fig. 4. The changes in the daily intake of wheat against the changes in the feeding duration. ● : Food intake by *Hato*; × : Food intake by *Shii*.

monkeys to feed on leaves and that they can feed upon only a small amount of leaves at a time. This suggests that a long duration is necessary for the digestion of leaves or for their passage through the intestine.

In order to calculate the daily energy intake, the energy intake rate for leaves and wheat were studied (Experiments 3, 4, & 6). Seven hour feedings on solely leaves and solely wheat were conducted for 12 and 6 days respectively and the relatively stable feeding data of 8 and 5 days respectively were used for calculation. Faeces were

Table 1. Measurement of the digestibility

A. Leaves	Food intake (wet weight, g)		Faeces (dry weight, g)		
	<i>Hato</i>	<i>Shii</i>		<i>Hato</i>	<i>Shii</i>
4/18	272.3	196.2			
4/19	417.2	432.8	4/19 E., 4/20 M.	27.9	18.1
4/20	404.1	254.1	4/20 E., 4/21 M.	33.0	26.3
4/21	568.2	439.1	4/21 E., 4/22 M.	34.2	24.2
4/22	480.0	495.2	4/22 E., 4/23 M.	45.8	34.5
4/23	566.2	455.9	4/23 E., 4/24 M.	43.7	31.6
4/24	559.5	513.0	4/24 E., 4/25 M.	41.5	30.5
4/25	547.4	474.6	4/25 E., 4/26 M.	46.8	45.5
4/26	505.8	416.6	4/26 E., 4/27 M.	45.1	33.2
4/27	214.5	423.6	4/27 E., 4/28 M.	40.8	46.0
4/28	421.8	555.0	4/28 E., 4/29 M.	39.8	42.3
4/29	590.2	585.8	4/29 E., 4/30 M.	48.1	48.4
Sum	3,885.4	3,919.7	Sum	351.6	312.0
(4/22-4/29)			(4/22 E.-4/30 M.)		
Dry weight	1,014.0	1,023.0			
Caloric value	4,563	4,603		1,863	1,652
Caloric value/day	570	575		233	207
Digestibility = 1 - Faeces (D.W.) / Food intake (D.W.)					
Ratio of energy intake = 1 - Caloric value of faeces / Caloric value of food intake					
	Digestibility		Ratio of energy intake		
<i>Hato</i>	0.653		0.591		
<i>Shii</i>	0.695		0.640		
Average	0.674		0.61		
B. Wheat	Food intake (dry weight, g)		Faeces (dry weight, g)		
	<i>Hato</i>	<i>Shii</i>		<i>Hato</i>	<i>Shii</i>
6/6	113.1	172.3	6/6 E., 6/7 M.	23.7	22.2
6/7	133.3	150.4	6/7 E., 6/8 M.	17.9	13.4
6/8	138.8	175.3	6/8 E., 6/9 M.	29.7	40.2
6/9	164.5	203.0	6/9 E., 6/10 M.	15.6	24.9
6/10	172.1	175.7	6/10 E., 6/11 M.	17.7	26.3
6/11	169.7	161.9	6/11 E., 6/12 M.	18.8	23.5
Sum	778.4	866.3	Sum	99.7	128.3
(6/7-6/11)			(6/7 E. - 6/12 M.)		
Caloric value	3,191.4	3,551.8	Caloric value	458.6	590.1
Calorie/day	638	710		91	118
	Digestibility		Ratio of energy intake		
<i>Hato</i>	0.87		0.856		
<i>Shii</i>	0.85		0.833		
Average	0.86		0.84		

The caloric values of leaves and faeces after leaf eating were 4.5 and 5.3 cal/g (D.W.), respectively. The caloric values of wheat and faeces after wheat eating were 4.1 and 4.6 cal./g (D.W.), respectively. The symbols E. and M. indicate faeces collected in the evening and in the morning, respectively.

gathered at 9:00 and 17:00 every day, and dried and weighed (Table 1). The ratios of dry to wet weight of leaves and wheat were 26 and 90.5%, respectively. The caloric values of leaves and faeces after leaf eating were 4.5 and 5.3 cal/g (Experiment 5). The caloric values of wheat and faeces after wheat eating were 4.1 and 4.6 cal/g. From these data, energy intake rates for leaves and wheat were calculated to be 0.61 and 0.84. These values are a little lower than the rate calculated from the weight loss of food through digestion, 0.67 for leaves and 0.86 for wheat. Though the food intake

Table 2. The daily energy intake (DEI) and the daily energy consumption (DEC)

Monkeys	DEI		BMR		DEC		DEI/DEC		
	Leaves	Wheat	1976	1977	1976	1977	Leaves (I)	Wheat (II)	I/II
<i>Hato</i>	396	537	260	271	424	441	0.93	1.22	0.76
<i>Shii</i>		596	284	296	463	482	0.85	1.24	0.68

The body weights of *Hato* and *Shii* were 5.9 and 6.8 kg in June 1976 and 6.3 and 7.2 kg in June 1977, respectively. BMR stands for basal metabolic rate.

through leaf eating did not reach a plateau within 12 hr (Fig. 2), it is reasonable to consider the amount eaten in a 12 hr feeding as a standard daily amount, since 12 hr is roughly equal day time length. The daily food intakes of the two subject monkeys were not much different and were computed together to average 555 g for 12 hr of leaf eating (Experiment 1). Experiment 2, which measured the daily intake of wheat, was conducted in November and December 1976, and the average temperature was 10°C at the time. It is necessary to adjust basal metabolic rate to this temperature (TOKURA et al., 1975). Thus, it is much better to use wheat feeding data for June 1977 (Experiment 4). Furthermore, it has been already confirmed that 4 hr of wheat feeding (7 hr in Experiment 4) is enough to satisfy the food intake for one day (Fig. 4). The average dry weights of wheat eaten were 156 and 173 g for *Hato* and *Shii*, respectively. From these data, daily energy intakes are calculated to be 396 ($555 \times 0.26 \times 4.5 \times 0.61$) cal for leaf eating and 537 ($156 \times 4.1 \times 0.84$) and 596 ($173 \times 4.1 \times 0.84$) cal for wheat eating by *Hato* and *Shii*, respectively (Table 2).

Daily energy consumption was also calculated. The basal metabolic rate (BMR) was calculated according to the equation, $BMR = 79.5 W^{2/3}$ (IWAMOTO, 1974). The body weights of the subject monkeys, *Hato* and *Shii*, were 5.9 and 6.8 kg in June 1976 and 6.3 and 7.2 kg in June 1977. Thus, the BMRs of *Hato* and *Shii* were 260 and 284, respectively in June 1976 and 271 and 296 in June 1977. Since activity data were not gathered in the present study, the activity data of caged Formosan monkeys (*Macaca cyclopis*) (KAWAI & MITO, 1973) were adopted for a rough calculation. This data indicate non-movement for 22 hr and 53 min and movement for 1 hr and 8 min. Non-movement and movement are regarded as sitting and walking for the calculation. The ratios of the energy consumed in sitting or walking to the BMR are 1.52 and 3.80 (IWAMOTO, 1974). Then, daily energy consumption (DEC) of *Hato* and *Shii* are estimated to be 424 and 463, respectively in June 1976 and 441 and 482 in June 1977 (Table 2). Thus, the ratio of daily energy intake to DEC was 0.85–0.93 for leaf eating and 1.2 for wheat eating. Furthermore, energy intake by leaf eating provided only 69–76% of that by wheat eating. In summary, Japanese monkeys cannot gain enough energy for daily energy consumption by leaf only which provides 69–76% of that obtained by wheat eating, though they feed on leaves all day long.

The changes in body weight due to leaf eating were checked in Experiment 3. The body weight changes of the two monkeys are plotted on the same graph (Fig. 5). Only leaves were given from April 17 until April 30. In the first 2–3 days, but especially on the first day, of feeding on leaves the monkey's feeding levels dropped, and then



Fig. 5. The changes of body weights. The body weights of the two monkeys are shown on the graph. Solely leaves were fed from April 18 until April 29. Solely wheat was fed from June 6 until June 11.

recovered and constant levels were observed. During this decline in feeding, body weights also decreased rapidly and these low weights were maintained in spite of the recovery in feeding activities. Though further decreases in body weights were not observed for the short period of this experiment, body weights did not show any signs of recovery for six days after the change to an adequate diet of soybeans, wheat, and leaves. In the experiment where only wheat was given for six days (June 6–June 11, 1977), body weights did not change. These experiments also suggest that leaf eating alone did not supply adequate energy.

Despite their energy requirements and the low caloric value of leaves, one characteristic of leaf eating in Japanese monkeys is slow feeding. The author considers that the slow feeding is a result of slow digestion or the slow passage of food through the intestine. Japanese monkeys must be unable to digest too much food at a time. This is the reason for the occurrence of the feeding activity pattern on leaves in this experiment; especially high feeding activity was observed in the early morning after having digested most of the food in the previous day, and the high activity was followed by the low activity and the middle level feeding activity resumed and continued in the afternoon. As the subject monkeys in the experiments could intake a high caloric value in a relatively short duration in wheat eating, the activity pattern of feeding in wheat eating differed much from that in leaf eating. Thus, the activity pattern of feeding differs depending on different food items. Free-ranging Japanese monkeys have similar kinds of feeding pattern in winter to those in the present leaf eating experiment (YOTSUMOTO, 1976), though the activity pattern differed much in summer and autumn when fruits or nuts are abundant. When we compare with the data in other species, CLUTTON-BROCK (1974) showed similar feeding patterns in red colobus, the leaf eater, to those leaf eating in the present experiments. Though, STRUHSACKER (1975) showed a little different activity rhythm of feeding in the same species from that of CLUTTON-BROCK, but the important points are that the feeding activity hold a high score in the time budget, and that feeding peaks were observed in the late afternoon and in the early morning. These facts indicate that consuming a large quantity of leaves is a hard work even for the red colobus which has rumen-like digestive organ. Though the Japanese monkeys showed a relatively low feeding duration following the morning feeding peak in the present experiments, the red colobus did not show such a

decline (STRUHSAKER, 1975). This is the difference in adaptation between the mixed food (leaves and fruits) eater and the leaf eater.

IWAMOTO (1974) conducted a bioenergetic study among Japanese monkeys of the Koshima troop and stated that "monkeys fed mainly on the leaves of *M. thunbergii*, *F. erecta*, and *D. teijsmanni*.... Monkeys living in a warm-temperature zone, such as Koshima Islet, depend largely in winter on the ever-green broad leaves for their nourishment. There seems to be an unlimited quantity of these trees for the present Koshima population." OGINO (1973) tried to compare the production of leaves of food plants and energy requirements of the Koshima troop, and roughly calculated that the production of food plants is 1.2—4 times that of energy requirements of the troop. These ideas seem to be too simplistic for two reasons; the one is that monkeys cannot eat as much quantity of leaves as their energetic requirement through leaf eating alone, the other is that only a small portion of the potential food which is produced by the forest for a year is edible to the monkeys. The former reason is clear from the result presented in this paper; the abundance of food plants with low caloric values does not fulfill the monkeys' energy requirements and that food plants with high caloric values which are easily digestible are important. Thus, the combination of leaves, nuts, and berries is necessary in the diet of Japanese monkeys, this fact is especially important when we consider factors which determine the home range size. The latter reason became clear in conducting present experiments. In the experiments to determine the quantity of leaves eaten, we tried to make monkeys feed upon a large quantity of leaves, and selected two species, *F. erecta* and *C. japonica* and one variation of the former, *F. erecta* var. *Sieboldi king*. In the intensive feeding solely on leaves, the feeding activity changed greatly depending on different trees of the same species. For example, leaves of the above selected species were given, and monkeys began to feed at first, but sometimes stopped feeding completely in 30 min or in 1.5 hr. When leaves of the same species, but of a different tree, were given, the monkeys began to feed again. As for *F. erecta*, monkeys preferred small leaves which were gathered in a shaded area, and rejected hard ones from a sunny area. As the feeding activity on *F. erecta* so much differed depending on individual trees, we mainly gave *F. erecta* var. *Sieboldi king* on which monkeys showed more consistent feeding. Monkeys still showed a preference for sun-hardened leaves of the latter. As for *C. japonica*, monkeys preferred slightly hard leaves from a sunny area, though they showed fairly consistent feeding. Likewise, only a small portion of the staple foods must be edible to monkeys in the wild. This fact must be paid much attention in considering food abundance.

When we consider home range size and food abundance in Japanese monkeys, their features are completely different from those of tropical species. COELHO, BRAMBLETT, and QUICK (1976) stated that one species of fruit among the staple food is 170 times more abundant in the quasi-rain forest of Guatemala than the estimated potential Cebidae (howler and spider monkeys) population supported by this one species, and that nutritional inadequacy is not a population limiting factor. When we consider Japanese monkeys, and take account both of the results in this paper and of OGINO's rough calculation, food is not as abundant as COELHO states for Cebidae in the case of Japanese monkeys.

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