# Feeding Behavior and Diet of the Japanese Monkey (Macaca fuscata yakui) on Yakushima Island, Japan

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ABSTRACT. Feeding behavior in a troop of one subspecies of the Japanese monkey, the Yakuzaru (*Macaca fuscata yakui*), was observed for 407 hr on Yakushima Island between March and December 1976, after a three-month preliminary survey in 1975. The troop dwells in a mature warm temperate forest at a density of over 30 animals/km<sup>2</sup>. The 5-min scanning technique was employed from August to December 1976, to detect the quantitative features of feeding behavior. The members of this troop fed on 76 plant species: on the leaves of 26, the fruits of 45, and other parts of 12 species. The Yakuzaru is essentially frugivorous. The pattern of food selection is discussed in relation to fruit production. The animals fed much more on the leaves of deciduous than of evergreen woody plants. "Selection ratio" the percentage of time spent feeding on each species to the percentage abundance of each species in the sample strip, was calculated in order to evaluate food selection from the plant community. In addition, the food habits of this subspecies were compared with that of six other populations in various habitats in Japan, by computing the similarity index for the woody plant community, all woody plant food species, and all major woody plant food species.

#### **INTRODUCTION**

The study of feeding behavior is essential to understand a species' ecological adaptation to the environment, and it is also an important factor to be considered when examining the relationship between ecology and sociological problems (troop size, inter- and intra-troop relations, and social changes). In recent years, many quantitative studies on the food habits of primate species have been carried out by various methods (CLUTTON-BROCK, 1977). Bioenergetic or nutritional analysis of feeding behavior, moreover, have been performed for some primate species: *Macaca fuscata* (IWAMOTO, 1974), *Theropithecus gelada* (IWAMOTO, 1979), *Presbytis senex* (HLADIK, 1977), and *Gorilla gorilla* (CASIMIR, 1975). The parting and joining of members of a social group might be related both to the condition of vegetation and to the amount and distribution of food supply in many primate species: *Pan troglodytes* (SUZUKI, 1969), *Cercopithecus mitis* (ALDRICH-BLAKE, 1970), *Cercocebus galeritus* (GROVES, ANDREWS, & HORNE, 1974), *Cercopithecus ascanius* (HADDOW, 1963), *Ateles belzebuth* (KLEIN, 1974), and *Papio cynocephalus* (ALDRICH-BLAKE et al., 1971). Though many studies have been done on species living in the tropical or subtropical forest, there are few reports about species living in the temperate forest.

Japanese monkeys (*Macaca fuscata*), the primate with the northernmost distribution, dwell in a wide environmental cline, from Yakushima Island (30°N, 131°E) to Shimokita Peninsula (41°N, 141°E). Many sociological and ecological studies have been performed in the various regions of Japan. Many reports on various populations contain a food species list, but these reports have been qualitative and descriptive. In recent years, a few quantitative studies of feeding behavior have been carried out by fecal analysis (KOGANEZAWA, 1975), or by focal animal sampling (IWAMOTO, 1974). Yakuzaru, *Macaca fuscata yakui*, occurs only on Yakushima Island, the southernmost distribution of Japanese monkeys. It is a subspecies which differs from *Macaca fuscata fuscata* both morphologically and genetically (IWAMOTO, 1964; IKEDA & WATANABE, 1966; SHOTAKE, OHKURA, & NOZAWA, 1975). KAWAMURA and ITANI (1952) noted that both the home range and size of a natural troop of the Yakuzaru might be smaller than that of Japanese monkeys living on the Japanese Main Islands. Since then, there were few reports on this subspecies.

I studied the ecology and social structure of a natural troop of *Macaca fuscata yakui* to detect the variations in ecology and social structure between the two subspecies of Japanese macaques from the view-point of speciation on an island. This paper focuses on the food habits of the Yakuzaru (*Macaca fuscata yakui*), and attempts (1) to describe the seasonal variation in feeding pattern and food species, (2) to examine the quantitative and qualitative characteristics of the animal's food selection strategy, comparing the quantitative structure of feeding behavior to that of plant environment as food resource, and (3) to compare the diet of the populations of *Macaca fuscata* from various regions in Japan.

## STUDY AREA AND MATERIALS

The Yakuzaru (*Macaca fuscata yakui*) is found only on Yakushima, an island which lies 60 km south of Kyushu Island in the Pacific Ocean ( $30^{\circ}N$ ,  $131^{\circ}E$ ), covers 500 km<sup>2</sup> and at its highest point, Mt. Miyanoura, is 1,935 m above sea level (Fig. 1). Mean annual temperature is  $20^{\circ}C$  (range  $11-30^{\circ}C$ ) and mean annual rainfall is about 3,000 mm in the lowland. In August and September, the island is hit by several severe typhoons which cause some damage to the forest. Yakushima is covered with a diverse and well-developed forest, which changes with altitude from a warm temperate to a cool temperate forest. Its highest part is covered with grassland (mainly *Pseudosasa owatarii*) with patches of dwarf trees (*Rhododendron yakushimensis* and *Pieris japonica*).

The Yakuzaru inhabits almost all of Yakushima, but its ecological density may vary with different forest zones. The main study area was located in the northwestern part of the island

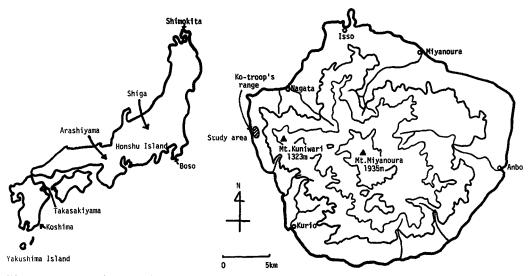


Fig. 1. Location of Yakushima Island and the study area.

on the western slope of Mt. Kuniwari (Fig. 1). Many little valleys cut this steep slope which is covered with a mature warm temperate forest. There is one road going from Nagata to Kurio along which no one lives and from which it is convenient to observe the monkeys. At least 17 troops have a continuous distribution in this area and the population density is over 30 animals/km<sup>2</sup> (MARUHASHI, 1977). In the middle of this study area, the main study troop, Ko-troop, ranged over an area of approximately 80 ha. In August 1976, it consisted of 47 animals: 3 adult males, 9 young adult males, 18 adult females, 11 juveniles, and 6 babies (MARUHASHI, 1977, in detail).

## **METHODS**

The feeding behavior of one wild troop of the Yakuzaru (Ko-troop) living in the lowland forest was observed between March and December 1976, after a three-month preliminary survey in 1975.

The best way to overcome a number of usual difficulties of observing animals in their natural habitat is to habituate them to the observer. Habituation enables one to study the ecology and social structure of a species by long-term observation and individual identification.

At the beginning of the study, the members of Ko-troop were very shy and often moved away immediately on encountering me. The more I grew accustomed to the terrain of the study area and the group movement, the longer was the time of direct observation per day. Consequently, the troop became used to my presence and its movement and behavior were no longer disturbed. On October 30, 1976 a young adult female tolerated my grooming her. This may imply complete habituation.

During the study period when habituation was taking place, the food species and plant parts eaten were recorded randomly whenever the animals were seen feeding on something. Between August and December 1976, data on feeding behavior was collected systematically by the scanning method (ALTMANN, 1974). The recording method used was to note at 5-min intervals the food species and plant parts eaten by all animals seen feeding. In each 5-min scan, I included both those feeding animals immediately visible and those which came into my range of vision while I moved around the troop (CLUTTON-BROCK, 1975). When the recorded animals fed on another food species or part in the same scanning unit, these samples were also added to the data, but these cases were rare. Scanning was recorded every 5 min at any time when the animals were directly observed. At quarter-hourly intervals, moreover, the activity of all visible animals was also recorded (MARUHASHI, in prep.).

I was usually able to identify the plant species and parts eaten through binoculars on the spot. The following typology of parts of food plants was adopted: (1) fruit: all juicy fruits, nuts, and seeds, (2) leaf: all new and mature leaves, (3) stem: all stems and twigs, (4) other plant parts: all flowers, bark, roots, broad buds, and petioles, (5) fungi: all fungi, (6) invertebrate animals: all insects, spiders, and so on, and (7) others: all unidentified plant parts and soil.

Ko-troop was directly observed for 41 hr in 1975 and 366 hr in 1976, for a total of 407 hr in this survey. During the last five months, Ko-troop was directly observed for 243 hr ( $\overline{X}$  = 49 hr per month) and a total number of 3,349 feeding records ( $\overline{X}$  = 670 animals per month) were recorded. Feeding records were analyzed by summing the total number of records for each food species or plant parts and expressing these as percentages of the total number of feeding records collected. These proportions were regarded as estimates of the proportion of time which the animals spent feeding on each food species or parts. Feeding records were pooled per half month or month.

Almost all plant species which are found in the home range of Ko-troop were identified. In order to survey quantitative and qualitative features of the forest, moreover, species, tree height, and diameter at breast height of all woody plants over 2 m in height were recorded in a sample strip (815 m in length and 5 m in breadth, 4,075 m<sup>2</sup>). The linear sample strip was located in the middle of the home range and varied in altitude from 50 m to 350 m above sea level so as to encompass both types of forest, in valleys and on ridges.

## RESULTS

#### FEEDING PATTERN AND TECHNIQUE

The daily pattern of Japanese monkeys consists mainly of three types of activities: traveling, feeding, and resting. Ko-troop traveled an average of 1.8 km (range 0.5–3.7 km) from dawn to sunset and spent about a fourth of its total activity time in feeding (MARUHASHI, 1977).

Ko-troop did not always move as an integrated compact group. Small groups which were constant neither in number nor in membership sometimes separated from it and moved independently. After spending the night apart, subgroups would reunite. Ko-troop did not divide into more than two subgroups. This parting and joining of subgroups was also observed in other troops of Yakuzaru.

When a large tree of a major food species with a sparse distribution in their home range (*Ficus wightiana, Cornus brachypoda, Ficus microcarpa*, and *Diospyros japonica*) had a good fruit crop, almost all of Ko-troop's members were scattered in its branches to feed on fruit in one feeding bout. On arriving at a feeding tree, there was a good deal of commotion for a few minutes while animals adjusted inter-individual distances between each other so as to feed calmly, emitted many "coo" sound and contact calls (A-1 or A-2, in ITANI, 1963), and moved up and down. This is called feeding call behavior. In some cases, the leader male emitted "ga-ga-ga" sounds (C-1, in ITANI, 1963) with tree shaking during this commotion. Afterwards, feeding was calmly carried on for about a half hour. While light individuals fed on fruit on terminal fruiting branches, heavy ones fed on boughs, bending or snapping the fruiting twigs. While sitting on the branches, the animals fed on grass and/or herbs, fallen nuts, fallen fruit, or invertebrate animals. It appeared that feeding on the ground comprised about  $10\frac{10}{0}$  of their feeding time.

#### HABITAT UTILIZATION

Ko-troop ranged in three types of forest: coastal forest, road-side secondary forest, and mature warm temperate forest. Coastal forest grows at altitudes less than 60 m above sea level and reaches 6 m in height. It mainly consists of *Raphiolepis umbellata*, *Litsea japonica*, *Quercus phillyraeoides*, and *Cinnamomum daphnoides*. The second type occurs in an area which was disturbed by road construction ten years ago. Some species characteristic of this forest type are *Lindera citriodora*, *Clerodendrum trichotomum*, *Mallotus japonica*, *Aralia erata*, and *Trema orientalis*. *Miscanthus sinensis*, *Rubus* spp., and many herb and/or grass species grow at the road side, and the forest edge is covered with bush trees: *Callicarpa* 

japonica, Debregeasia edulis, and Villebrunea frutescens. The last forest type, laurel-leaved forest, is more xeric in the study area than in other areas of Yakushima (TAGAWA, 1979b). The canopy of the last type reaches about 8–15 m and the scarce undergrowth allows close observation of the monkeys.

Within the range of Ko-troop, 231 plant species (96 families) were identified in my plant collecting. This flora list was comprised of 123 woody plant species, 74 herb and grass species, 28 fern species, and 6 orchid and others. Specimens from almost all woody plants were collected. Since Yakuzaru seldom feeds on ferns and orchids, the specimens of woody plants were sufficient to analyze the animals' food selection. HATSUSHIMA (1972) identified 1,205 species (154 families) including 275 woody plant species in all of Yakushima.

The animals spent much more time feeding on some species than on others. This was evidently not the result of differences in the abundance of the various tree species since comparison of the number of records of animals seen feeding on each tree species with the abundance of the tree species in the sample strip showed that the two measures were poorly correlated. The ratio of the percentage of time spent feeding on each species to the percentage abundance of each species in the sample strip gives an estimate of the extent to which the Yakuzaru selected the different tree species to feed on (Table 1). Calculation of this "selection ratio" for different species found at a high density were seldom selected: *Shefflera octophylla, Symplocos plunifolia,* and *Distylium racemosum,* while several tree species occurring at a low density had a high selection ratio: *Ficus wightiana* (45.3), *Diospyros japonica* (7.4), *Ficus erecta* (3.6), and *Rhus succedanea* (3.5).

Ko-troop utilized one third of the total plant species in its home range as food (Table 2). They rarely fed on ferns, herbs, and/or grasses, which were not important food sources, except the two Gramineae species, *Miscanthus sinensis* and *Digitaria timorensis*. One half of 123 woody plant species identified in the Ko-troop range were fed on and 21 of these were major food species. It is notable that in the road-side secondary forest four of the eight food tree species were major food plants. The fact that one of six species in the coastal forest was selected as a food species indicates that Ko-troop seldom traveled to this type of forest. The high tree species in the mature warm temperate forest comprised an average of 53.6% of the diet (range 31.1-73.4%) and those in the secondary forest, 8.3% of the diet (range 0.3-17.5%) (Table 3). All six species of Moraceae in the home range were utilized as food and these species were the most important taxon in Ko-troop's diet, comprising 18.2% of the diet. Species of Fagaceae were long-term food source species, because the animals fed on the immature albumen of nuts, as well as on fallen mature nuts.

#### DIET BETWEEN MARCH AND JULY

The five months between March and July 1976 can be divided into three periods: (1) spring: March and April, (2) early summer: May and June, and (3) summer: July. In the spring period a total number of 484 animal feeding records were recorded by random sampling to analyze the diet quantitatively, but in the early summer and summer periods the size and distribution of the samples was not large enough to do so.

The spring diet consisted mainly of both fallen nuts and new leaves. Nuts of *Pasania edulis* and *Quercus phillyraeoides* which had fallen in the previous year comprised 24.4% of the diet. The animals very often fed on the new leaves of *Lindera citriodora* and on the flower buds of *Ficus erecta*. These two species were major food species which strongly influenced group

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			T 16-	vines over		<b>D</b>	Selec-
	Succion nome	East la same	Life			Percentage	tion
	Species name	Family name	form	15 cm/na	30 cm/ha	abundance	ratio
	High trees	_	_		_		
1	Pasania edulis**	Fagaceae	E	108	5	15.1	0.33
2	Shefflera octophylla*	Araliaceae	E	98	7	13.7	
3	Daphniphylum teijsmannii*	Euphorbiaceae	Е	64	12	8.9	0.056
4	Ardisia sieboldii**	Myrcinaceae	E	56		7. <b>9</b>	0.75
5	Symplocos plunifolia	Symplocaceae	E	54	2	7.5	
6	Distylium racemosum	Hamamelidaceae	E	42	12	5.8	
7	Actinodaphne longifolia**	Lauraceae	E	34	10	4.8	1.3
8	Myrsine seguinii*	Myrsinaceae	Е	22		3.1	0.45
9	Myrica rubra**	Myricaceae	E	22	7	3.1	_
10	Rhus succedanea**	Anacardiaceae	D	22		3.1	3.5
11	Ternstroemia gymnanthera*	Theacea	Е	20	10	2.7	0.037
12	Machilus thunbergii*	Lauraceae	E	12	12	1.7	
13	Melia azedarach	Meliaceae	D	12	10	1.7	
14	Quercus salisina	Fagaceae	E	10		1.4	
15	Castanopsis cuspidata*	Fagaceae	E	10	5	1.4	0.14
16	Vaccinium bracteatum*	Ericaceae	E	10		1.4	1.0
17	Quercus phillyraeoides**	Fagaceae	E	7	5	1.0	
18	Ficus erecta**	Moraceae	D	7		1.0	3.6
19	Raphiolepis umbellata	Rosaceae	E	5		0.68	
20	Elaeocarpus sylvestris	Elaeocarpaceae	E	5	2	0.68	
21	Premna japonica	Vervenaceae	D	5		0.68	
22	Evodia glauca	Rutaceae	D	5		0.68	
23	Elaeocarpus japonicus*	Elaeocarpaceae	Е	5		0.68	1.0
24	Acer capillipes	Aceraceae	D	5	2	0.68	
25	Ilex integra*	Aquifoliaceae	Ē	2	_	0.34	1.5
26	Diospyros japonica**	Ebenaceae	$\overline{\mathbf{D}}$	2		0.34	7.4
27	Ficus wightiana	Moraceae	Ē	2		0.34	45,3
28	Glochidion obovatum*	Euphorbiaceae	Ē	2	1	0.34	
-•			-	648	100		
	<b>T</b>						
•	Low trees		F				
29	Camellia japonica*	Theaceae	E	32		4.5	
30	Rhododendron tashiroi	Ericaceae	E	25		3.4	
31	Cleyera japonica*	Theaceae	E	5		0.68	
32	Eurya japonica*	Theaceae	E	2		0.34	
33	Illicium religiosma	Magnoliaceae	Е	2		0.34	
				66	100		
				714	100		
	Woody vines						
34	Anodendron affine*	Apocynaceae	Е	100		27.0	
35	Lonicera spp.	Caprifoliaceae	D	61		16.4	
36	Psychotria serpens*	Rubiaceae	Е	54		14.6	
37	Morinda umbellata*	Rubiaceae	Ε	51		13.7	
38	Ampelopsis leeoides*	Vitaceae	D	32		8.6	
39	Actinidia rufa**	Actinidiaceae	D	22		5.9	
40	Smilax china*	Liliaceae	D	20		5.4	
41	Piper kadzura**	Piperaceae	Е	17		4.6	
42	Ficus spp.*	Moraceae	E	10		2.7	
43	Ampelopsis brevipedunculata*	Vitaceae	D	2		0.5	
44	Paederia scandens**	Rubiaceae	D	2		0.5	
				371			
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Table 1. The abundance of woody species and selection ratio in the range of Ko-troop.

The sample strip  $(5 \text{ m} \times 815 \text{ m}, 4,075 \text{ m}^2)$  was located from 50 to 350 m above sea level. Analysis was carried out only on the trees over D. B. H. (diameter at breast height) 15 cm which reach the upper layer of the warm temperate forest and on the woody vines over 1 cm in diameter. The woody species were divided into three types: high trees forming the first layer of the forest, low trees forming the second layer, and woody vines. The selection ratio (the percentage of time spent feeding on each species to the percentage abundance of each species in the sample strip) was calculated only for the high trees. \*\*: Major food species; \*: food species; E: evergreen; D: deciduous.

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	Pla	nt sp	becies	3	Fo	od sj	pecie	s	Ma	ijor i	food	species
Distribution type	Ī	II	III	Total	ī	II	III	Total	Î	II	111	Total
Woody plant	43	56	24	123	20	26	13	59	7	9	5	21
Woody tree	33	47	17	97	15	22	10	47	5	8	4	17
Mature warm temperate forest	24	43	9	76	12	20	6	38	4	7	2	13
High tree	11	25	3	39	7	13	2	22	3	6	1	10
Bush and low tree	13	18	6	37	5	7	4	16	1	1	1	3
Secondary forest	5	2	8	15	3	1	4	8	1	1	2	4
Coastal forest	4	2	0	6	0	1	0	1	0	0	0	0
Woody vine	10	9	7	26	5	4	3	12	2	1	1	4
Herb and/or grass				74				13				2
Fern				28				2				0
Orchid and others				6				2				0
				231				76				23

Table 2. Distribution of plant species, food species, and major food species, by forest type and life form, in the range of Ko-troop.

Distribution type of woody plants is divided into three categories: I: elements of the subtropical forest; II: elements of the warm temperate forest; III: elements of the warm and cool temperate forest.

Table 3. Percentage of time spent feeding on each type of food species, by both forest type and vegetation form.

	August	September	October	November	December	Average
Mature warm temperate forest						
High tree species	54.6 72.8	73.4 69.3	31.1	35.1 39.1	45.7 61.7	53.6 (%)
Low tree species	0.2 0.6	3.1 3.1	1.9	7.1 2.2	0.6 2.4	2.4
Road-side secondary forest	17.5 3.0	2.7 0.3	13.8	10.4 6.5	12.5 8.1	8.3
Coastal forest	0 0	0 0	- 0	0 2.2	2.4 0	0.5
Woody vines	19.0 13.3	10.6 16.5	19.9	31.7 25.4	24.3 9.8	18.9
Bush trees	2.9 1.1	0.7 0.3	- 1.6	5.6 10.1	9.8 15.6	5.3
Grass and/or herb	2.0 4.1	4.4 0.9	25.5	7.1 12.7	3.0 1.4	6.8

movement. Regardless of species, the diet consisted of fruit and nuts: 38%, leaves: 40%, others: 16%, and invertebrate animals: 6%. They fed on new leaves of the deciduous trees and/or vines three times more than on evergreen ones. Only two animals were seen feeding on leaf blades of the species of fern, *Dicranopteris linearis* and *Dryopteris varia*.

In the early summer, Myrica rubra (fruit) and Ficus wightiana (fruit) were the major food species. Ficus wightiana had its first fruit season in early summer in 1976. The animals frequently fed on stems of Miscanthus sinensis and on berries of Rubus grayanus and Rubus rosaefolius. The cambium of Machilus thunbergii was eaten by a few animals.

In the summer, Ko-troop very often fed on fruit of both *Ficus erecta* and *Lindera citriodora*. The seed of *Mallotus japonica* came to be a major food species towards the end of July, while the utilization of *Lindera citriodora* was gradually reduced. Besides these two species, they fed on leaves of *Paederia scandens*, fruit of *Ampelopsis brevipedunculata*, and seed of *Euscaphis japonica*.

DIET AND SEASONAL VARIATION BETWEEN AUGUST AND DECEMBER

The animals of Ko-troop living in the lowland forest of Yakushima were observed feeding on 76 species of plants (37 families) between March and December, excluding the winter (Appendix 1). The food species list contains several species on which Japanese monkeys have not previously been observed feeding, such as, *Morinda umbellata*, *Taxillus yadoriki*, and *Ardisia sieboldii*.

The feeding records collected between August and December 1976 are analyzed from various aspects.

One interesting aspect of the Yakuzaru's diet is the proportion of the time which they spent feeding on the various plant parts, regardless of species (Table 4). The average composition of parts eaten consists of fruit: 76.2%, leaves: 17.6%, other plant parts: 2.2%, fungi: 1.1%, invertebrate animals: 2.7%, and others (soil and unidentified species and parts): 0.2%. The diet consists almost entirely of leaves and fruits. The sum of the two parts comprised  $\bar{X} = 93.8\%$  (range 89.8-96.8%).

The animals often fed on immature unripe fruit and ate only a part of the fruit of some species. For example, the albumen of the immature fruit of *Pasania edulis, Ardisia sieboldii,* and *Actinodaphne longifolia,* the sarcocarpa of the immature fruit of *Actinidia rufa,* and the immature seed of the fruit of *Rhus succedanea.* 

The animals fed on the leaves of deciduous trees five times as frequently as on those of evergreen trees (Table 5). When they fed on the tender leaves of deciduous trees, they ate all of the leaf. When feeding on leaves of evergreen trees (*Daphniphyllum teijsmannii*, *Ficus wightiana*, etc.), they usually ate only the blade, leaving the main nerve and petiole. In some cases, they fed on a nearby leaf as "dessert" after eating insects. In the case of *Ficus wightiana*, only when young leaves were newly unfolded immediately after defoliation in the second half of December, especially, were they eaten (17.6%). Bark eating was not observed except for two animals who ate *Glochidion obovatum* and *Zanthoxylum ailanthoides*.

As well as feeding on fruit and foliage, the animals fed on fungi, insects, spiders, and soil.

				Other plant		Invertebra	te
	Fruit	Leaf	Stem	part	Fungi	animals	Others
August	79.9	14.2	2.2	0	0.2	3.1	0.4
-	78.8	13.1	2.8	0.2	0.4	4.3	0.4
September	82.9	9.9	1.1	1.0	1.7	3.4	0
-	84.2	5.6	0.6	0	6.2	2.5	0.9
October			_				
	82.8	11.0	0	0	0.3	5.9	0
November	82.8	14.2	0.4	0.4	1.1	1.1	0
	73.2	23.6	1.4	0	0	1.8	0
December	69.4	24.9	3.9	0.9	0	0.9	0
	51.9	42.4	3.4	1.3	0	1.0	0
Average	76.2	17.6	1.8	0.4	1.1	2.7	0.2

Table 4. Percentage of time spent feeding on plant parts, irrespective of species, in each half-month sample period.

Table 5.	Distribution	of	the	food	species	by	plant	parts	eaten.
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Typology of the plant part	No. of species	No. of animals	Frequency (%)
Leaf Evergreen trees	10	91	2.7
Deciduous trees	10	419	12.5
Grass and/or herb	6	24	0.7
Fruit Nut	2	168	5.0
Fig	5	609	18.2
Juicy fruit	28	1080	32.3
Seed	7	536	16.0
Achene	1	1	0.0
Weed ear	2	204	6.1
Stem	4	35	1.1
Twig	1	21	0.6
Flower	3	5	0.2
Root	1	1	0.0
Bark	2	2	0.1
Broad bud	1	1	0.0
Other food items	—	152	4.5

In the second half of September they fed on fungi when these were available (Table 4). Common insects such as grasshoppers, beetles, ants, cicadae, and so on and spiders were often eaten, though it is difficult to identify accurately the species of insects and spiders. The members of Ko-troop were especially fond of an insect which makes galls on the leaves of *Distylium racemosum*, a plant species of which no other part was observed eaten otherwise. They were sometimes observed feeding on larvae, stripping or breaking down the bark of the dead trunk. Only three animals were seen feeding on soil.

They were seen to drink water from a small stream. The following is the only case observed when an animal waded into a stream and foraged for food:

August 16. The alpha-male of Ko-troop, named *Nashi*, walked about in a stream and fed on the nuts which had sunk to the bottom of the stream (about 30 cm in depth). And some animals were observed to search to the bottom with their forelimbs from the stream-side stones and feed on nuts.

There were considerable differences between half-month periods in the diet of the Yakuzaru (Table 6). Most major food species varied greatly in the percentage of feeding observations which they comprised in each half-month sample period. However, *Ficus wightiana* showed relatively little variation and was among the top five species in every half-month sample period except for two cases. *Paederia scandens* is another species which regularly constituted one of the important food species, and like *Ficus wightiana*, may be considered a staple source of food for the Yakuzaru. Although important in the total percentage of observations, species like *Rhus succedanea* or *Digitaria timorensis*, cannot be considered staple food species through the intensive study period. Figure 2 reveals the half-monthly variation in utilization of 15 major food species. The utilization of most of these species was closely related to their seasonal availability of fruit. The fruiting season of each species lasted about two months.

Half-monthly overlaps in diet can be expressed more precisely by computing overlapping percentages. Each half-month was compared with every other half-month from August through December 1976, except the first half of October. The overlapping percentages in diet for any and all food species were calculated in the two half-months concerned (STRUHSAKER, 1975). Diet overlap in the 36 half-monthly pair combinations was extremely variable (Table 7). The range of diet overlap was 5.0-72.3% and the mean was 27.6%. High overlapping percentages in some half-monthly pair combinations probably reflect the similar dietary preference by the Yakuzaru. The figures in each row decrease almost constantly from left to right. It may indicate the clear seasonal change in the dietary preference. The exceptionally high percentages of the first half of August with the first half of November, 29.3%, and with the second half of October, 33.4%, reflect the utilization of the harvest of *Ficus wightiana*.

The diversity of the Yakuzaru's diet in each half-month is shown in Table 5. The following formula was used to compute indices of diversity for food species, regardless of parts eaten:

$$H = -\sum p_i \log_e p_i$$
 (Shannon-Wiener formula),

where  $p_i$  equals the proportion of observation for each species. Both in the first half of August and in the second half of September, the food species indices dropped,  $\bar{X} = 1.90$ , because they fed on one species concentratedly. At those times, *Ficus wightiana* constituted 43.4% of the diet and *Rhus succedanea*, 44.7%, respectively. These figures were about twice the mean percentage of the top food species of the other seven half-month sample periods  $(\bar{X} = 24.3\%)$ . The other seven indices are fairly regular,  $\bar{X} = 2.50$ , range 2.34–2.70. The index for the spring is 2.37.

Latin name	Total (%)	August		September	)er	October	r	November	ber	December	)er
Ficus wightiand	15.4	43.4**	11.8*	7.5*	5.3*		18.5**	17.2**	1.1	2.4	17.6**
Rhus succedanea	10.7	•6.0	26.8**	28.0**	44.7**	I	0.2	0	0	0.3	0
Paederia scandens	7.6	10.2**	10.1*	6.8*	5.3*		7.2*	5.2*	11.2**	6.5*	4.1*
Digitaria timorensis	6.0	0	0	0	0	1	23.8**	5.6*	8.7*	2.1	1.0
Ardisia sieboldii	5.9	0	0	0	0	ł	5.6*	14.2**	6.6*	24.3**	7.8*
Pasania edulis	4.9	0.4	15.0**	10.2**	16.5**	ļ	1.3	0	0	0	0
Piper kadzura	4.7	0	0	0	0	1	5.0*	18.7**	12.0**	11.3**	1.4
Cornus brachypoda	3.9	8.8*	13.7**	9.6*	0	1	0	0	0	0	0
Actinodaphne longifolia	3.8	0	0	0	0	ļ	0	0	2.9*	13.1**	25.4**
Ficus erecta	3.6	10.8**	0	0	0.3	I	2.8*	4.5*	2.5	6.5*	3.4*
Clerodendrum trichotomum	3.3	0	0.4	0	0	ļ	11.0**	6.0*	4.0*	2.7*	1.4
Diospyros japonica	2.8	0	0	0	0		3.1*	3.7*	23.2**	0	0
Actinidia rufa	2.7	0.4	0.2	0.3	7.7**		6.6*	6.3*	1.4	0	0
Callicarpa japonica	2.5	1.8*	0.2	0	0		0.3	0.7	4.3*	<b>*</b> 6.8	10.2**
Myrsine seguinii	1.4	0	0	0	0	I	0.8	0	4.0*	5.3*	4.4*
Eurya japonica	1.4	0	0.2	3.1*	3.1*	I	1.7*	4.9*	0.4	0.6	0
Ficus microcarpa	1.3	0.2	0.9	13.0**	0	1	0	0	0	0	0
Vitis flexuosa	1.1	6.9*	1.5*	0	0		0	0	0	0	0
Miscanthus sinensis	1.1	2.0*	2.4*	2.0	0.6*	1	0.3	0.4	1.4	0.6	0
Morinda umbellata	1.1	0	0	0	0		0	1.5	0.7	5.6*	4.1*
Villebrunea frutescens	1.0	0.2	0	0.7	0.3	1	0.6	3.0	2.9*	0.9	2.4
Mallotus japonica	0.8	6.2*	0	0	0	]	0	0	0	0	0
Ampelopsis leeoides	0.7	0.7	1.1	3.4*	0.6*	1	0.3	0	0	0	0
Lindera citriodora	0.7	0.2	0	0	0	ļ	0	0	0	3.3*	3.4*
Elaeocarpus japonicus	0.7	0	1.3	0	2.8*	۱	1.3	0	0	0	0
Daphniphyllum teijsmannii	0.6	0	0	0	0		0	0	0	0	6.4*
Aralia erata	0.6	0	2.4*	2.7*	0		•	0	0	0	0
llex integra	0.5	0	1.5*	3.4*	0		0	0	0	0	0
Youngia denticulata	0.5	0	1.5	0.3	0	ļ	0.9	0.4	0	0	0
Euscaphis japonica	0.4	0.9*	1.7*	0.3	0	I	0	0	0	0	0
Hydrangea angustipetala	0.4	0	0.9	0	0	]	0.3	0.7	2.2	0	0.3
Ficus pumila	0.4	0.0	0.4	0	2.2*		0.2	0	0	0.3	0
Eurva emarcinata	04	c	<	<	<		c	-	<i>c c</i>	74	C

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Table 6. (con	ontinued)										
Maesa tenera	0.4	0.2	0	0	0		0.2	0.4	0.7	0	2.7
Psychotria rubra	0.3	0	0	0	0		0	0.4	1.1	0	2.0
Castanopsis cuspidata	0.2	0	0.2	1.4	0	1	0	0	0	0.3	0
Debregeasia edulis	0.1	0.7	0	0	0	ł	0.2	0.4	0	0	0
Bidens biternata	0.1	0	0	0	0	I	0	0.4	1.4	0	0
Clevra iaponica	0.1	0	0	0	0	I	0	1.5	0	0	0
Glochidion obovatum	0.1	0.2	0.2	0	0	I	0	0.4	0	0	0
Psychotria serpens	0.1	0	0	0	0	ļ	0	0	0	0.6	0.3
Damnacanthus indicus	0.1	0	0	0	0	ŀ	0.2	0.4	0	0	0.3
Spolobolus indicus	0.1	0	0	0	0	1	0.5	0	0.4	0	0
Ficus stipulata	0.1	0	0	0	0.3	j	0	0	0	0	0
Parthenocissus tricuspidata	0.1	0	0	0	0	I	0.3	0	0	•	0
Cinnamomum camphora	0.1	0	0	0	0	1	0.3	0	0	0	0
Dianella ensifolia	0.0	0	0.2	0	0	I	0	0	0	0	0
llex goshiensis	0.0	0	0.2	0	0	I	0	0	0	0	0
Zanthoxylum ailanthoides	0.0	0	0.2	0	0	I	0	0	0	0	0
Farfugium japonicum	0.0	0	0	0	0	1	0	0	0	0.3	0
Crepidiastrum lanceolatum	0.0	0	0	0	0	I	0	0	0.4	0	0
Camellia japonica	0.0	0	0	0	0	Ι	0	0	0.7	0	0
Ternstroemia gymnanthera	0.0	0	0	0	0	ł	0.2	0	0	0	0
Anodendron affine	0.0	0	0	0	0.3	I	0	0	0	0	0
Polygonum chinense	0.0	0	0	0.3	0	I	0	•	0	0	0
Aeginetia indica	0.0	0	0	0.3	0	I	0	0	0	0	0
Buddleja venenifera	0.0	0.2	0	0	0		0	•	0	0	0
Vaccinium bracteatum	0.1	0	0	0	0	1	0	0	1.2	0	0
Rubus grayanus	0.0	0	0	0	0.3		•	0	0	0	0
Dioscorea japonica	0.0	0	0	0	0	I	0	•	0	0.3	0
Lysimachia sikokiana	0.0	0	0	0	0		0	0	0	0	0.3
Unidentified species		0.2	0.4	1.4	0	ł	0	0.7	0	0.6	0
Fungi		0.2	0.4	1.7	6.2	Ι	0.3	1.1	0	0	0
Invertebrate animals		3.1	4.3	3.4	2.5	I	5.9	1.1	1.8	0.9	1.0
Number of animals seen		452	467	293	322		639	267	276	337	295
feeding per half-month											
							11 0	03 0		03 0	с С

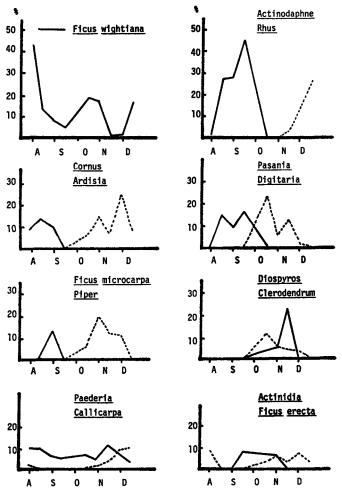


Fig. 2. Time spent feeding on 15 major food species in different half-month periods. The figures show the percentages of feeding records in which the animals were eating any part of each species.

THE QUANTITATIVE STRUCTURE OF THE YAKUZARU'S DIET

The animals appeared to choose various food species in each month by a common strategy. Though the amount of time which they spent feeding on different foods varied seasonally, it usually related to change in food availability.

The number of food plants comprising the diet of each half-month was  $\bar{X} = 23.1$  species (range 15-30 species) and  $\bar{X} = 25.3$  species parts (range 16-33 species parts) (Table 8). These figures show that there were few species from which more than one part of the plant was utilized during the same sample period.

The amount of time which they spent feeding on different food species, irrespective of parts eaten, was cumulated according to its importance rank. Each cumulative curve shows a fairly similar form. The sum of the percentages of the top three food species comprised  $\bar{X} = 54.7\%$  (range 46.4-68.9%); that of the top five and ten food species,  $\bar{X} = 69.7\%$  (range 61.7-80.1%), and  $\bar{X} = 86.7\%$  (range 79.8-91.9%), respectively (Table 8). The re-

	August	Septe	mber	Octo	ber	Nove	mber	Decer	mber
August	42.0	30.3	17.1		33.4	29.3	17.9	12.7	10.4
		72.3	57.7	—	28.2	19.3	13.0	8.2	5.3
September			58.0		22.1	17.4	12.2	9.9	5.8
					24.6	22.9	11.4	8.5	5.0
October									
						60.8	42.4	26.8	18.4
November							50.8	47.0	25.4
								46.5	25.5
December									54.9

Table 7. Percentage overlap in food habits of *Macaca fuscata yakui* for specific food items, from August to December 1976.

N = 36; range 5.0-72.3%;  $\bar{X} = 27.6\%$ . % overlap =  $100 - \sum_{i,j} \frac{|X_{ij} - Y_{ij}|}{2}$ .

	Augu	ıst	Septe	mber	Octo	ber	Nove	mber	Dece	mber	Average
Number of food species	22	25	19	15		30	26	27	24	20	23.1
-	(33	3)	(25	5)	(3	0)	(32	2)	(29	)	(30.2)
Number of parts eaten	24	25	22	16	_`	33	28	29	26	25	25.3
	(36	5)	(29	))	(3)	3)	(36	5)	(37	)	(34.2)
% of the top 3 food species	64.4	55.5	51.2	68.9		53.3	50.1	46.4	48.7	53.2	54.7
	(52	2.6)	(56	5.5)	(5)	3.3)	(39	).1)	(44	.9)	(49.3)
% of the top 5 food species	80.1	76.4	68.3	79.5		67.1	62.4	61.7	64.1	67.4	69.7
	(70	).5)	(68	3.6)	(6	7.1)	(56	5.4)	(61	.0)	(64.7)
% of the top 10 food species	91.9	85.9	87.7	88.8	`	85.3	86.3	79.8	87.5	86.8	86.7
	(80	5.4)	(83	3.6)	(8	5.3)	(79	9.0)	(84	.3)	(83.7)
% of the first species	43.4	26.8	28.0	44.7	·····	23.8	18.7	23.2	24.3	25.4	28.7
	(27	7.3)	(36	5.7)	(2)	3.8)	(15	5.3)	(18	.8)	(24.4)
Number of animals seen	452	467	293	322	`	639	268	276	337	295	372
feeding	(91	l <b>9</b> )	(61	5)	(6)	39)	(54	4)	(63	2)	(670)

Upper figures in each row indicate the character of the diet for each half-month and lower figures in parentheses indicate the character of the diet for each month.

maining portion consists of both other food plant species and of other food items (fungi, invertebrate animals, and others). A similar analysis was obtained by pooling the feeding records per month. The diet of a month consisted of  $\bar{X} = 30.2$  species (range 25-33 species). The sum of the top three food species comprised  $\bar{X} = 49.3 \%$  (range 39.1-56.5%). That of the top five comprised  $\bar{X} = 64.7 \%$  (range 56.4-70.5%) and that of the top ten comprised  $\bar{X} = 83.7 \%$  (range 79.0-86.4%) (Table 8). And as in the case of half-month sample periods, each monthly diet has a similar quantitative structure of food selection.

In spring, the sum of the percentages of the top three food species comprised 50.4% of the diet. That of the top five and ten comprised respectively 62.4% and 77.2%. These figures reveal that the diet of the spring had much the same quantitative structure as the other months of the intensive study period. Thirty food species and 35 species parts were utilized in the spring.

#### MAJOR, COMMON, AND RARE FOODS

Considering the quantitative structure of the Yakuzaru's diet, plant food species can be divided into three categories: major, common, and rare food species. Major food species are the top three food species in each half-month sample period. These species occupy approximately one half of the diet. The animals of the troop fed on them synchronously in a feeding bout of daily activity. The group movement is related strongly to foraging for these species.

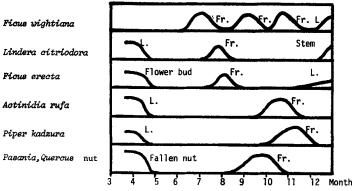


Fig. 3. Schema of seasonal variation in utilization of the parts of six major food species.

Common food species are the seven species from the fourth through the tenth rank. These species occupy approximately one third of the diet. There is neither strong synchronism of foraging for them nor a close relationship between the species and group movement. Rare food species are the plant food species below the tenth rank. These occupy approximately one tenth of the diet. The animals eat these species opportunistically.

During the intensive study period, the diet of the troop consisted of 61 identified plant food species: 15 major, 14 common, and 32 rare food species. The major plant food species were the following 15 species: Ficus wightiana, Rhus succedanea, Paederia scandens, Digitaria timorensis, Ardisia sieboldii, Pasania edulis, Piper kadzura, Cornus brachypoda, Actinodaphne longifolia, Ficus erecta, Clerodendrum trichotomum, Diospyros japonica, Actinidia rufa, Callicarpa japonica, and Ficus microcarpa (See Table 6). These comprised 79.1% of the total observations (N = 3,349 feeding records) and both major and common ones together comprised 90.2%. Between March and July, the major food species were Morus australis, Lindera citriodora, Myrica rubra, Ficus wightiana, Mallotus japonica, Rubus grayanus, and Rubus rosaefolius.

Almost all of the major and common food species were utilized during a particular part of a particular season of the year. But different parts of the same species were utilized in different seasons. The following species were of this kind: *Ficus wightiana*, *Ficus erecta*, *Lindera citriodora*, *Actinidia rufa*, *Piper kadzura*, *Pasania edulis* (nuts), and *Quercus phillyraeoides* (nuts) (Fig. 3).

Fifteen trees of *Ficus wightiana* were observed to have animals feed in them, the utilization of which comprised 15.4% of the total feeding records between August and December 1976. The animals fed concentratedly on figs of one big tree in each fruit season. One tree comprised 63% of the feeding records of this species in the second fruit season and another, 78% in the third. The latter tree was also often utilized during a two-week period as one of the major foods in the early summer. Its selection ratio is by far the highest of all food species. *Ficus erecta* and *Lindera citriodora* are deciduous sun tree species of which the road-side secondary forest consists. These have three utilization peaks, though the part eaten in each season was different. The woody vines, *Actinidia rufa* and *Piper kadzura*, have two peaks. The former is deciduous and the latter is evergreen. The animals fed on the immature albumen of the nuts in September and on fallen nuts in the spring (of both *Pasania edulis* and *Quercus phillyraeoides*). The sum of the percentages of these seven species comprised 32.0% of the diet of the intensive study period.

The annual variation in the Yakuzaru's diet is strongly related to fluctuations in the

ripening of woody tree species which form the first layer of the mature laurel-leaved forest. The following is an example:

In autumn, 1975, *Quercus phillyraeoides* had a large crop of nuts. Consequently, the animals fed intensively on the albumen of the immature fruit. In 1976, however, since this species bore few fruit, Ko-troop seldom moved to the ridge in the southeast corner of the range where many large trees of this species grow.

### DISCUSSION

The composition of the diet of wild primate populations can be assessed from feeding observations or an analysis of stomach or fecal samples (CLUTTON-BROCK, 1977). In this study, a scanning method (ALTMANN, 1974) was used to collect feeding records, because of the advantage that it is easily replicable. It provides an estimate of the proportion of time which animals spend feeding on each food species or plant parts. However, it has to be taken into consideration that it will not give a good estimate of the amount of different foods ingested since feeding rate and observability vary between foods, as HLADIK (1977) pointed out. Though the scanning method has some limitations, it has been adopted in many field studies (e.g., SUSSMAN, 1977; DUNBAR, 1977; CLUTTON-BROCK, 1975).

An inspection of the size and distribution of samples shows that this method guarantees the credibility of comparison and analysis between samples. The relation between the number of animals seen feeding and the number of plant food species eaten in each month is a curve which rises quickly and then levels off (Fig. 4). Thus the diversity in the diet is probably represented adequately, despite the small sample size in the early morning, which was due to time spent in searching for the troop.

The diet of the Yakuzaru (Macaca fuscata yakui) is essentially fruits. However, they

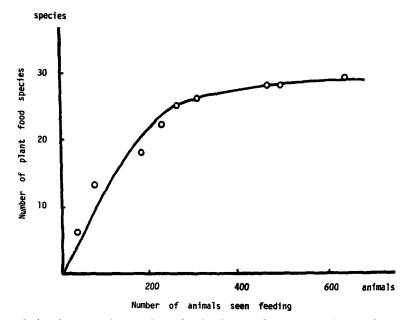


Fig. 4. The relation between the number of animals seen feeding and the number of plant food species eaten for each month. In this figure, only the case of October is described. The other four months' graphs are quite similar to this.

also fed on many diverse food items, including other parts of plants, fungi, ferns, invertebrate animals, and soil. The following is an outline of the seasonal changes in the Yakuzaru's diet: In spring, they fed mainly on new leaves of deciduous woody plants and fallen nuts of Fagaceae. Between May and December, fruits and seeds comprise most of their diet. A survey in 1978 revealed that in winter they fed on fruit of *Ardisia sieboldii* and fallen nuts which comprised a fairly large part of the diet (MARUHASHI, in prep.). The nut production of *Pasania edulis*, Fagaceae, which occurs at a high density in Ko-troop's range, leaves many fallen nuts on the ground. These nuts are one of the major food items when fruit is rare, from January to April. The species composition of their diet changed from one season to another corresponding to the fluctuations in fruit production by each species. They fed on the fruit of 18 of 23 major woody plant food species. Fruits occupy, at least, some part of the Yakuzaru's diet in any season of the year and nearly 80% of the diet from summer to autumn, especially. These two facts support the conclusion that the Yakuzaru is essentially frugivorous.

The animals fed much more on the leaves of deciduous than of evergreen woody plants. This may be due not only to the fact that they preferred the tender leaves of the former to the tough cuticle-covered leaves of the latter, but also to some nutritional factors or toxic secondary compounds which might influence their preference (FREELAND & JANZEN, 1974). However, a nutritional analysis of the feeding behavior of *Macaca fuscata* has not yet been done and therefore, this remains as a problem for the future. *Daphniphyllum teijsmannii* was almost the only evergreen woody plant species of which the mature leaves were eaten. Besides this species, they fed a little on mature leaves of a few other evergreen species. In the case of *Ficus wightiana*, they fed only on newly unfolded leaves which appear immediately after defoliation in December. STRUHSAKER (1975) found that red colobus monkeys prefer new leaves to mature ones of *Celtis durandii* because of the greater nutritional content of the former. It might be supposed that the same is true of *Ficus wightiana*.

The feeding behavior of Ko-troop is closely related to the pattern of fruit production by each species. TAGAWA (1979a) found three patterns of fruit production for evergreen tree species of the warm temperate forest: (1) irregular, (2) all-or-nothing, and (3) regular. Moreover, one third of the trees which were found in his study area were not observed producing fruit (TAGAWA, 1979a). In Ko-troop's range, species of the first type are Quercus phylliraeoides and Castanopsis cuspidata, of the second, Machilus thunbergii, and of the third, Pasania edulis, Ardisia sieboldii, and Ficus wightiana. Both the deciduous sun trees characteristic of the road-side secondary forest and the woody vines growing thick on the crown of the forest are of type (3) fruit production. Fairly stable production in woody vines, deciduous sun trees, and the evergreen tree species of type (3) is the foundation of the Yakuzaru's diet. These three kinds of plants make up one half of the multi-utilized food species in several seasons of a year belong to these three type. As the fruit of many evergreen tree species takes a long time to ripen, the animals can feed on the immature fruits. Fluctuations in the total amount of fruit production in a year are compensated for by the utilization of foliage of deciduous trees. In addition to this basic diet, the animals feed on the fruit of type (1) and (2) species when they are available. The diversity within Ko-troop's range of  $0.8 \text{ km}^2$  of the forest assures a stable quantity and quality for their diet (Shannon-Wiener Diversity Index = 2.22, calculated from Table 1).

The variations and common features in the diet of Japanese monkeys (Macaca fuscata)

Population	Shimokita	Shiga	Boso	Arashiyama	Takasakiyama	Koshima	Yakushima
Yakushima	8.8	6.2	28.6	21.1	33.3	53.3	
	5.8	5.4	19.7	17.4	16.8	37.6	
	4.0	3.5	11.3	11.4	14.9	19.6	
Koshima	9.6	8.0	40.2	31.3	49.3		
	2.2	5.9	25.6	20.5	33.3		
	0.0	4.3	26.7	13.6	21.4		
Takasakiyama	33.1	32.7	61.8	58.9			
	7.3	21.7	42.1	48.3			
	3.6	15.9	44.7	50.7			
Arashiyama	41.8	40.3	60.1				
-	12.4	24.7	43.1				
	6.9	39.4	45.6				
Boso	43.5	43.2					
	21.8	25.9					
	16.9	30.3					
Shiga	66.0						
-	35.0						
	26.7						
Shimokita							

Table 9. Similarity index of the diet among seven populations in Japan.

The comprehensive data of the Yakuzaru's diet is added to UEHARA (1977). The upper row is the index calculated for all woody plant species, the middle, all woody food species, and the lower, for the major and common woody food species only. These locations are arranged from south to north in Japan (See Fig. 1). N = 21;  $\bar{X}l = 36.7\%$ ;  $\bar{X}2 = 22.5\%$ ;  $\bar{X}3 = 12.9\%$ . Similarity index =  $2C/(A + B) \times 100\%$ .

are reexamined, in the light of UEHARA's (1977) data (Table 9). UEHARA (1977) stated that the six populations of Japanese monkeys on the Japanese Main Islands are divided into three groups: (1) Koshima; (2) Takasakiyama, Arashiyama, and Boso; and (3) Shiga and Shimokita (See Fig. 1). The first group dwells in the southern warm temperate forest near the coast, the second, in the warm temperate forest, and the third, in the cool temperate forest. The diet of Ko-troop living in the lowland forest of Yakushima occupies the fourth position in the food habits of Japanese monkeys. Though the flora of Yakushima is considerably similar to that of Koshima (S.I. = 53.9%), the dietary similarity (S.I. = 19.6%) between troops in the two locales is not great. This may imply pre-cultural differences in the food habits between the two locales (KAWAI, 1965). The similarity index between Yakushima and Shiga/Shimokita groups is very low and these two populations also live in quite different habitats. UEHARA (1975) concluded that the woody plant food species of type II are the most important for Japanese monkeys' food habits and those of type I are insignificant as major foods. For Ko-troop's diet, however, one half of the woody plant food species belong to type I, the subtropical forest elements, and these species comprised quantitatively one third of their diet.

The Yakuzaru dwells in the richest habitat in the range of Japanese monkeys. The population density of the intensive study area in the lowland forest of Yakushima is three times more than that of the Boso area (a little over 10 animals/km<sup>2</sup>, IWANO, pers. comm.) and nearly ten times more than that of the Shiga area (4-5 animals/km<sup>2</sup>, SUZUKI et al., 1975). The home range of a troop in the main islands is much larger than that of Yakushima. For example, three troops in the Shiga area range over 3, 6, and 2.5 km<sup>2</sup>, respectively (SUZUKI et al., 1975). Since diversity of each vegetation type decreases towards the north, on Honshu Island, a troop secures a diverse diet which guarantees a staple quantity and quality of food by ranging over a large area which includes several mosaic vegetation types. Acknowledgements. I wish to thank Drs. M. KAWAI, Y. SUGIYAMA, and A. SUZUKI who critically read this paper and Ms. E. PERNOTTO who corrected preliminary drafts of this paper. I also wish to thank Drs. S. SAKO and H. TAGAWA for identifying my plant collections. The SHIZUMI HIDAKA and KOTOKI KINO families who live in Nagata village, Yakushima Island, provided hospitality, invaluable help, and friendship throughout the study.

	Species name	Family name	Japanese name	Part eaten	Life form
1	Dicranopteris linearis	Gleicheniaceae	Koshida	L	F
2	Rumohra sristata	Aspidiaceae	Hosobakanawarabi	L	F
3	Spolobolus indicus	Gramineae	Nezuminoo	Fr	G
4	Digitaria timorensis	Gramineae	Komehishiba	Fr**	G
5	Miscanthus sinensis	Gramineae	Susuki	St**, L, Fr, R	G
6	Dianella ensifolia	Liliaceae	Kikyoran	Fr	н
7	Smilax china	Liliaceae	Sarutoriibara	St, Fr	DV
8	Dioscorea japonica	Dioscoreaceae	Yamanoimo	Se, Bb	DV
9	Piper kadzura	Piperaceae	Futokazura	Fr**, L*	EV
10	Myrica rubra	Myricaceae	Yamamomo	Fr**	EH
11	Quercus phillyraeoides	Fagaceae	Ubamegashi	Fr**, Fl	EH
12	Castanopsis cuspidata	Fagaceae	Sudajii	Fr*	EH
13	Pasania edulis	Fagaceae	Matebashii	Fr**	EH
14	Morus dustralis	Moraceae	Shimaguwa	L**	DH
15	Ficus pumila	Moraceae	Oitabi	Fr*	ĔV
16	Ficus stipulata	Moraceae	Himeitabi	Fr	ĒV
17	Ficus stipulata Ficus erecta			L, Fr**	DH
		Moraceae	Inubiwa	Fr**	EH
18	Ficus microcarpa	Moraceae	Gajyumaru		EH
19	Ficus wightiana	Moraceae	Ako	L*, Fr**	EB
20	Villebrunea frutescens	Ulticaceae	Iwagane	L*, Fr	EB
21	Debregeasia edulis	Ulticaceae	Yanagiichigo	L	
22	Taxillus yadoriki	Loranthaceae	Obayadorigi	Fr	E
23	Polygonum chinense	Polygonaceae	Tsurusoba	<u>L</u>	H
24	Cinnamomum camphora	Lauraceae	Kusunoki	Fr	EH
25	Machilus thunbergii	Lauraceae	Tabunoki	Sh, Br	EH
26	Lindera citriodora	Lauraceae	Aomoji	L**, Fr**, St*	DH
27	Actinodaphne longifolia	Lauraceae	Baribarinoki	Fr**, L	EH
28	Hydrangea angustipetala	Saxifragaceae	Yakushimaajisai	L, Fl	DB
29	Rubus sieboldii	Rosaceae	Horokuichigo	Fr*, St	EB
30	Rubus grayanus	Rosaceae	Ryukyuichigo	Fr, St	DB
31	Rubus rosaefolius	Rosaceae	Ryukyubaraichigo	Fr**	DB
32	Rubus crataegifolius	Rosaceae	Kumaichigo	Fr	DB
33	Zanthoxylum ailanthoides	Rutaceae	Karasuzansho	Pt, Fr, Br	DH
34	Daphniphyllum teijsmannii	Euphorbiaceae	Himeyuzuriha	L*	EH
35	Glochidion obovatum	Euphorbiaceae	Kankonoki	L, Br	EL
36	Mallotus japonica	Euphorbiaceae	Akamegashiwa	Se**, Br	DH
37	Rhus succedanea	Anacardiaceae	Haze	Fr**, L	DH
38	Ilex integra	Aquifoliaceae	Mochi	Fr*	EH
39	Ilex goshiensis	Aquifoliaceae	Tsugemochi	L	EL
40	Euscaphis japonica	Staphyleaceae	Gonzui	Se*	DH
41	Ampelopsis brevipedunculata		Nobudo	Fr*	DV
42	Ampelopsis leeoides	Vitaceae	Udokazura	Fr*	DV
43	Parthenocissus tricuspidata	Vitaceae	Tsuta	Fr	DV
44	Elaeocarpus japonicus	Elaeocarpaceae	Kobanmochi	Fr*	EH
45	Actinidia rufa	Actinidiaceae	Shimasarunashi	L*, Fr**	DV
46	Camellia japonica	Theaceae	Yabutsubaki	L, Fl	EL
47	Ternstroemia gymnanthera	Theaceae	Mokkoku	Fr	EH
48	Cleyera japonica	Theaceae	Hisakaki	Fr	EL
49	Eurya japonica	Theaceae	Sakaki	Fr*	EL
49 50	Eurya japonica Eurya emarginata	Theaceae	Hamahisakaki	Fr	EL
51	Aralia elata	Araliaceae	Taranoki	Fr*	DH
-1	mana ciana	manactat	i al allUNI	* *	~~··

Appendix 1. Food species list of the Yakuzaru (Macaca fuscata yakui), identified by direct observation, in 1975 and in 1976, in Yakushima Island, Japan.

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52	Shefflera octophylla	Araliaceae	Fukanoki	Fr, L	EH
53	Vaccinium bracteatum	Ericaceae	Shashanpo	Fr	EH
54	Cornus brachypoda	Cornaceae	Kumanomizuki	Se**	DH
55	Maesa tenera	Myrsinaceae	Shimaizusenryo	L, Fr, St	EB
56	Ardisia sieboldíi	Myrsinaceae	Mokutachibana	Fr**	EH
57	Myrsine seguinii	Myrsinaceae	Taimintachibana	Fr*	EH
58	Lysimachia sikokiana	Primulaceae	Morokoshiso	L	н
59	Diospyros japonica	Ebenaceae	Shinanogaki	Fr**	DH
60	Buddleja venenifera	Loganiaceae	Urajirofujiutsugi	L	EB
61	Anodendron affine	Apocynaceae	Sakakikazura	Se	EV
62	Hoya carnosa	Asclepidiaceae	Sakuraran	L	EV
63	Callicarpa japonica	Verbenaceae	Omurasakishikibu	L**, Fr	DB
64	Clerodendrum trichotomum	Verbenaceae	Kusagi	Fr**, L	DB
65	Aeginetia indica	Orobanchaceae	Nanbangiseru	Fl	н
66	Morinda umbellata	Rubiaceae	<b>Hanagasa</b> noki	Fr*, L	EV
67	Psychotria rubra	Rubiaceae	Bochoji	Fr	EB
68	Damnacanthus indicus	Rubiaceae	Aridoshi	Fr, L	EB
69	Paederia scandens	Rubiaceae	Hekusokazura	L**, Fr, Fl	DV
70	Farfugium japonicum	Compositae	Tsuwabuki	St, L	H
71	Bidens biternata	Compositae	Sendangusa	Se, L	н
72	Lapsana humilis	Compositae	Yabutabirako	L, Fl	н
73	Crepidiastrum lanceolatum	Compositae	Hosobawadan	L	н
74	Ixeris japonica	Compositae	Jishibari	Fl	н
75	Youngia denticulata	Compositae	Yakushiso	Fl, L, St	н
76	Psychotria serpens	Rubiaceae	Shiratamakazura	Fr	EV

#### Appendix 1. (continued)

L: Leaf; Fr: fruit; St: stem; Se: seed; R: root; Bb: broad bud; Fl: flower; Sh: shoot; Pt: petiole; Br: bark. EH: Evergreen high tree; EL: evergreen low tree; EB: evergreen bush tree; EV: evergreen vine; DH: deciduous high tree; DL: deciduous low tree; DB: deciduous bush tree; DV: deciduous vine; F: fern; G: grass; H: herb; E: epiphytes. \*\*: Major food; \*: common food.

#### REFERENCES

- ALDRICH-BLAKE, F. P. G., 1970. Problems of social structure in forest monkeys. In: Social Behaviour in Birds and Mammals, J. H. CROOK (ed.), Academic Press, London & New York, pp. 79-101.
- ------, T. BUNN, R. DUNBAR, & P. HEADLEY, 1971. Observations on baboons, *Papio anubis*, in an arid region in Ethiopia. *Folia Primat.*, 15: 1-35.
- ALTMANN, J., 1974. Observational study of behavior: sampling method. Behaviour, 49: 227-265.
- CASIMIR, M. J., 1975. Feeding ecology and nutrition of an eastern gorilla group in the Mt. Kahuji region (Republique of Zaïre). Folia Primat., 24: 81-136.
- CLUTTON-BROCK, T. H., 1975. Feeding behaviour of red colobus and black and white colobus in East Africa. Folia Primat., 23: 165-207.
- ———, 1977. Methodology and measurement. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, London & New York, pp. 585–590.
- DUNBAR, R. I. M., 1977. Feeding ecology of gelada baboons: a preliminary report. In: Primate Ecology, T. H. CLUTTON-BROCK (ed.), Academic Press, London & New York, pp. 251–273.
- FREELAND, W. J. & D. H. JANZEN, 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Amer. Natur., 108: 269-289.
- GROVES, C. P., P. ANDREWS, & J. HORNE, 1974. Tana river colobus and mangabey. Oryx, 12: 565-575.
- HADDOW, A. J., 1963. Field study of African redtail monkey: the composition and behavior of bands. In: *Primate Social Behavior*, C. H. SOUTHWICK (ed.), D. van Nostrand, New York, pp. 52–67.
- HATSUSHIMA, S., 1972. Plants of Yaku Island. In: The Wildlife of Yaku Island, Y. MATSUDA (ed.), Yaedake-shobo, Tokyo, pp. 168–180. (in Japanese)
- HLADIK, C. M., 1977. A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, London & New York, pp. 323-353.

- IKEDA, J. & T. WATANABE, 1966. Morphological studies of Macaca fuscata. III. Craniometry. Primates, 7: 271-288.
- ITANI, J., 1963. Vocal communication of the wild Japanese monkey, Macaca fuscata fuscata. Primates, 4(2): 11–66.

— & K. TOKUDA, 1954. The nomadism of the wild Japanese monkey, Macaca fuscata fuscata, in Takasaki-Yama. Jap. J. Ecol., 4: 1–7.

- IWAMOTO, M., 1964. Morphological studies of *Macaca fuscata*. I. Dermatoglyphics of hand. *Primates*, 5(1-2): 53–73.
- IWAMOTO, T., 1974. A bioenergetic study on a provisioned troop of Japanese monkeys (Macaca fuscata fuscata) at Koshima Islet, Miyazaki. Primates, 15: 241-262.

—, 1979. Feeding ecology. In: *Ecological and Sociological Studies of Gelada Baboons*, M. KAWAI (ed.), S. Karger, Basel, pp. 279–310.

- KAWAI, M., 1965. Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Island. *Primates*, 6: 1–30.
- KAWAMURA, S. & J. ITANI, 1952. Monkey and deer of the Yakushima Island. (in mimeo.) (in Japanese)
- KING, G. E., 1976. Society and territory in human evolution. J. Human Evol., 5: 323–332.
- KLEIN, L., 1974. Agonistic behavior in neotropical primates. In: Primate Aggression, Territoriality, and Xenophobia: A Comparative Perspective, R. HALLOWAY (ed.), Academic Press, New York & London, pp. 77–122.
- KOGANEZAWA, M., 1975. Food habits of Japanese monkey (*Macaca fuscata*) in the Boso Mountains. In: Contemporary Primatology, S. KONDO, M. KAWAI, & A. EHARA (eds.), S. Karger, Basel, pp. 380–383.
- MARUHASHI, T., 1977. A study of group movement of a wild troop of Yakuzaru (Macaca fuscata yakui) in Yakushima. M. Sc. dissertation, Kyoto Univ.
  - -----, 1978. The Japanese monkeys in Yakushima---short report. Nihonzaru, 4: 74-77.
  - ——, in prep. Activity patterns of a troop of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan.
- SHOTAKE, T., Y. OHKURA, & K. NOZAWA, 1975. A fixed state of the PGM<sup>2</sup><sub>2mac</sub> allele in the population of the Yaku macaque (*Macaca fuscata yakui*). In: Contemporary Primatology, S. KONDO, M. KAWAI, & A. EHARA (eds.), Karger, Basel, pp. 67–74.
- STRUHSAKER, T. T., 1975. The Red Colobus Monkey. Univ. of Chicago Press, Chicago.
- SUSSMAN, R. W., 1977. Feeding behavior of *Lemur catta* and *Lemur fulvus*. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, London, New York, & San Francisco, pp. 1–36.
- SUZUKI, A., 1965. An ecological study of wild Japanese monkeys in snowy areas, focused on their food habits. *Primates*, 6: 31–72.
  - —, 1969. An ecological study of chimpanzees in a savanna woodland. Primates, 10: 103–148.
- ——, K. WADA, S. YOSHIHIRO, E. TOKITA, S. HARA, & Y. ABURADA, 1975. Population dynamics and group movement of Japanese monkeys in Yokoyugawa Valley, Shiga Heights. *Physiol. Ecol.*, 16: 15-23.
- TAGAWA, H., 1979a. Shoyojurin no Syushi kara Seiju e (From seeds to the adults in laurel-leaved forest; natural regeneration of forest). Shizen, 396: 38-44. (in Japanese)
- \_\_\_\_\_, 1979b. Yakushima Kuniwaridake Nishi-shamen no Shokusei (Vegetation on the western slope of Mt. Kuniwari, Yakushima Island). unpublished. (in Japanese)
- UEHARA, S., 1975. The importance of the temperate forest elements among woody food plants eaten by Japanese monkeys (*Macaca fuscata*) and its possible historical meaning for the establishment of the monkey's range. A preliminary report. In: *Contemporary Primatology*, S. KONDO, M. KAWAI, & A. EHARA (eds.), S. Karger, Basel, pp. 392–400.

—, 1977. A biogeographic study of adaptation of Japanese monkeys (*Macaca fuscata*), from view point of food habits—an essay on reconstruction of the history of Japanese monkeys' distribution. In: *Morphology, Evolution and Primates*, Y. KATO, S. NAKAO, & T. UMESAO (eds.), Chuokoron-sha, Tokyo, pp. 189–232. (in Japanese)

-Received June 26, 1979; Accepted August 13, 1979

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