International Journal of Primatology, Vol. 16, No. 4, 1995

Dietary Selection by Yakushima Macaques (*Macaca fuscata yakui*): The Influence of Food Availability and Temperature

Naoki Agetsuma[1]

Received January 13, 1995; accepted March 9, 1995

I examined dietary selection by Yakushima macaques (Macaca fuscata yakui) *in relation to food availability and air temperature. Multiple regression analysis indicates that both food availability and temperature influenced the selection of foods. Feeding on young leaves, seeds, and flowers was affected more by availability, while feeding on fruits, mature leaves, and fallen seeds was affected more by temperature. Feeding on insects is strongly correlated with temperature, perhaps because availability of insects increased with temperature. These results suggest that temperature influences dietary selection of Yakushima macaques by changing the energy expenditure required for thermoregulation and through its influence on the accessibility to insects, which are an important protein source for the monkeys.*

KEY WORDS: dietary selection; food availability; air temperature; *Macaca fuscata yakui*; thermoregulation.

INTRODUCTION

For the efficient intake of nutrients, animals should vary their selection of foods in relation to several factors including food quality and availability in the habitat, and the animals' metabolic rate (Schoener, 1971). Estrada (1984), Harrison (1984), Yeager (1989), Davies (1991), Lucas and Corlett (1991), Stanford (1991), Strier (1991), and Newton (1992) have studied the relationship between selection and the availability of plant foods, such as fruits, flowers, and leaves, in several primate species. They imply that for

[1]Primate Research Institute, Kyoto University, Inuyama Kanrin, Aichi 484, Japan.

0164-0291/95/0800-0611$07.50/0

some foods feeding is related to availability, while for others it is not. In general, foods of a relatively high quality, and which vary greatly in availability, such as fruits, flowers, and young leaves, tend to be fed on according to their availability (Estrada, 1984; Harrison, 1984; Yeager, 1989; Lucas and Corlett, 1991; Newton, 1992).

Selection of foods by primates is also related to body weight (Clutton-Brock and Harvey 1977; Sailer *et al.,* 1985), age, and sex (Gautier-Hion, 1980; Harrison, 1983, Watanuki and Nakayama, 1993). These factors influence the nutritional requirements of the individual animals. Larger species tend to feed more on leaves because they need more energy, but they have a lower metabolic rate per body weight than smaller species (Sailer *et al.,* 1985). It has also been suggested that female monkeys of some species tend to feed more on foliage than males do, because of a greater protein requirement (Gautier-Hion, 1980; Harrison, 1983), and that pregnancy and lactation may lead to an increase in female metabolic rate (Portman, 1970). Further, the type of digestive system a species has, i.e., monogastric or sacculated stomach, will be related to the selection of fibrous foods, reflecting the animals ability to break down plant fibers (Davies, 1991).

Air temperature influences the metabolic rate of monkeys by causing changes in the energy required for thermoregulation. Accordingly, it might affect their dietary selection. Primate species increase their metabolism below around 20–35°C (Nakayama *et al.,* 1971; Mahoney, 1980; Le Maho *et al.,* 1981; Muller *et al.,* 1985). Heat production by a female Japanese monkey of 8 kg is 515 W/day at 30°C and 1262 W/day at 5°C (Nakayama *et al.,* 1971). The former figure approximates the basal metabolic rate. Therefore, as temperature decreases, energy requirements increase (Iwamoto and Dunbar, 1983), and it is predicted that monkeys will adjust their selection of foods to increase the efficiency of nutritional intake. However, the influence of temperature on the selection of foods by primates has received little attention (Watanuki and Nakayama, 1993).

In this paper, I examine the influence of air temperature on dietary selection in Yakushima macaques (*Macaca fuscata yakui*), which are one of two subspecies of Japanese macaques. They live only on Yakushima island. They inhabit forest dominated by evergreen broad-leaved trees, where temperature varies between 3 and 29°C annually. The monkeys feed mainly on fruits, seeds, leaves, and insects (Maruhashi, 1980). Seasonal variation of diet is great, though details of their diet have been reported only for limited months [August to December (Maruhashi, 1980), May and August (Maruhashi, 1986)]. Thus, the Yakushima macaque is a good subject to the influence of food availability and temperature on dietary selection. I describe characteristics of the food availability at different times of year and patterns of consumption from 10 months of data and examine the influence of food availability and temperature on dietary selection.

STUDY AREA

The study site is on the northwest coast of Yakushima island (30°N, 131°E), Japan, where the annual rainfall is about 2600 mm and the mean temperature is 21°C (Tagawa, 1980). The area is covered by primary and secondary warm temperate broad-leaved forest (0–350 m above sea level), which consists mainly of evergreen species of the Fagaceae, Myrsinaceae, and Lauraceae. Deciduous species, including several of *Ficus*, also occur in the forest. The study area includes various types of vegetation: primary forest, mixed primary and secondary forest, patches of early successional deciduous trees along the road, and coastal vegetation.

METHODS

Feeding Behaviors

I observed feeding behaviors of Yakushima macaques in a well-habituated group [P Group (Hill, 1991a)] intermittently from January 1990 to April 1992. Group size varied between 5 and 19 members (2–6 adult males, 2–5 adult females) as a result of births, deaths, emigration, and immigration by males.

Every 10 min I conducted a 5-min scan (Altmann, 1974) and recorded the behavior of all visible members of the group, except suckling infants. I also noted the foods—parts and species of woody plants, herbs, ferns, fungi, insects, and other items—upon which the monkeys fed.

I classified the food items of the monkeys eight categories according to their spatial distribution and nutritional characteristics, as follows: *fruits*—whole fruits including seeds; *seeds*—seeds and nuts without pulp which were fed on in the trees; *fallen seeds*—nuts, seeds, and dried fruits in the leaf litter, *flowers*—nectar and petals; *mature leaves*—blades completely open; *young leaves*—immature blades, buds, and new shoots; *insects*—true insects and other animal matter; and *other*—bark and branches of woody plants, herbs, ferns, fungi, and unidentified foods. I determined the time spent feeding on each item by calculating the number of records of feeding on a food item as a proportion of the total number of feeding records in each calendar month, regardless of sampling year. I calculated the annual time spent feeding on each item by averaging the time spent feeding on the item in each of 10 calendar months, to compensate for differences in data for each month. I regard food items that account for ≥1% of the annual time spent feeding as main food items and those that account for ≥0.1% as common food items.

Measuring Temperature

I attached a maximum and minimum thermometer to a tree in the forest 1.3 m above ground and 7 m from an ephemeral stream. On every field day I recorded the maximum and minimum temperatures. I recorded daily maximum temperatures 30 times on average (range, 14–65 times) for each calendar month. I combined the data and averaged each month regardless of sampling year.

Survey of Food Availability

I surveyed vegetation of the study area from September 1990 to May 1992. I established 98 5 × 50-m belt transects uniformly over 25 ha within the range of the study group (about 32 ha). I estimated the crown area of all trees of ≥5-cm DBH which lay on the transect belt as follows. First, I measured a line that corresponded to the crown width at its greatest point (*A*). Next, I measured a second dline (*B*) that was perpendicular to the first. Then I expressed the crown area as the area of an ellipse with long axis (*A*) and short axis (*B*). This method produces an estimate of actual crown area that can be compared between species at one location and between locations (Agetsuma and Noma, 1995). I summed estimated crown areas for each species.

In the study area, most plant species (excluding *Ficus* species) show clear seasonality in flowering and fruiting (Noma, 1989; Agetsuma, 1995). I censured the period in which each plant food item was available during the observation of monkeys and the vegetation survey. I recorded calendar months when at least one individual of a species of food plant had fruits, seeds, flowers, mature leaves, or young leaves available (Agetsuma, 1995).

I calculated the availability of each category of plant food, except fallen seeds, in each calendar month as follows. For each calendar month, I summed the total crown area of common food species of that category, which were available in that month, regardless of sampling year. The month with the maximum total crown area has a value of 1, and the total crown areas in the other months are proportions of 1: the index of availability.

Hill (1991b) observed Yakushima macaques foraging on the ground for fallen seeds frequently from winter to spring. To estimate the availability of fallen seeds, I sampled five sites where the monkeys foraged terrestrially over 8 months: 17 and 22 September, 9 November, and 8 and 9 December 1991 and 3 and 4 February and 24 April 1992. I bounded 25-m^2 quadrat at each site and sampled fallen seeds within the quadrat. I identified and counted the seeds in the laboratory.

I express availability as the density of fallen seeds of common foods and the availability index of each item as the relative density in each sampling month.

RESULTS

I obtained a total of 10,733 feeding records during the study period. Feeding records in July and October are too few to be analyzed. The data for August are from 1 year, those for February from 3 years, and those for other calendar months from 2 years. Yakushima macaques fed on at least 84 species (151 items) of plants. They ate fruits, seeds, and nuts of 58 species, flowers of 14 species, and leaves, shoots, and buds of 45 species of woody plants, in addition to herbs and grasses of 3 species, ferns of 4 species, and several unidentified species of fungi. There are 21 main plant-food items (17 species), which account for ≥1% of annual feeding time and 71 common food items (52 species), which account for ≥0.1% of annual feeding time. Main plant-food items account for 62.5%, and main and common items account for 81.4%, of annual feeding time. The monkeys also fed on several species of insects and vertebrates, which account for 8.9% of annual feeding time. Less common food items and unidentified items account for the remaining 9.7% of annual feeding time.

The lowest minimum temperature recorded is 3°C and the highest maximum temperature is 29°C in the study area during the study period. Mean monthly maximum temperature varied from 13 (January) to 28°C (August).

Periods of Availability and Consumption Patterns for Each Food Item

Monkeys fed arboreally on the seeds of *Lithocarpus edulis* (Fagaceae) in August and September. Thereafter, they foraged intensively on fallen seeds. The density of seeds on the ground (seeds/m^2) is 3.26 in September, 8.04 in November, 5.18 in December, and 2.05 in February. By the last sampling in April, the density of seeds was only 0.50/m^2, and 6.5% of them had already germinated. Accordingly, the estimated period of availability for fallen seeds of *L. edulis* is between August and March.

Mature fruit of *Neolitsea aciculata* was available from September to November. Although there is one feeding record for immature fruit of this species in February, I regard the period of availability to be from September to November.

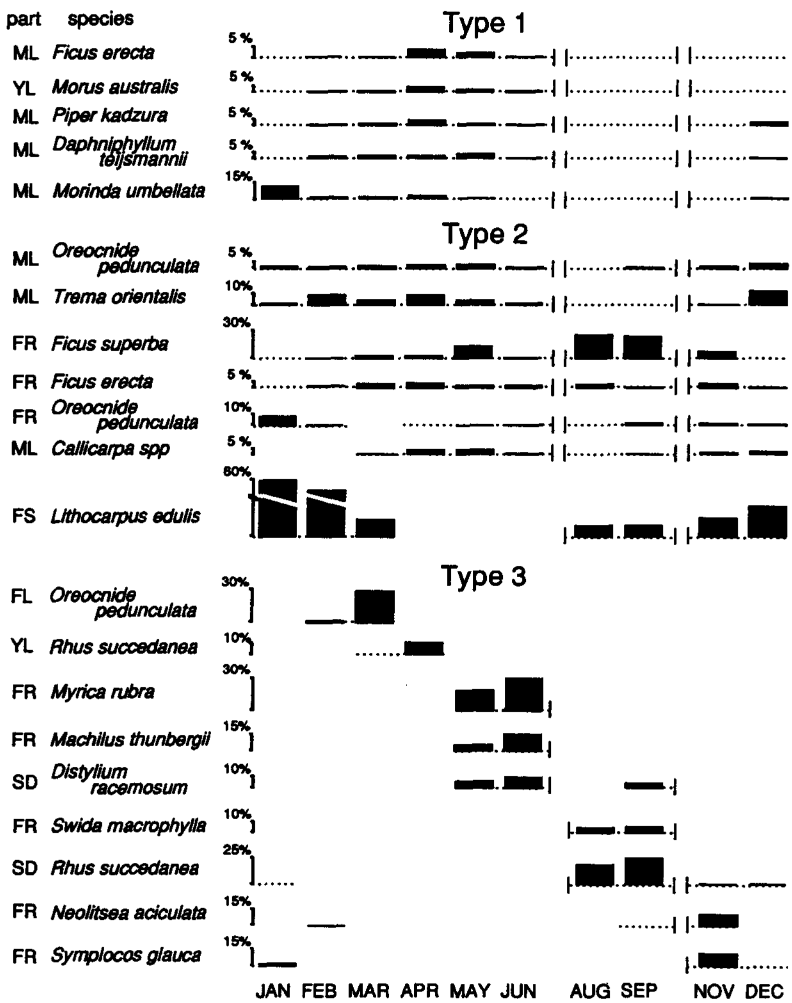

Fig. 1. Period of availability and time spent feeding on main plant food items. Dotted line shows available periods of the items. Solid bars show time feeding on the items. ML, mature leaves; YL, young leaves; FS, fallen seeds; FL, flowers; FR, fruits; SD, seeds.

Periods of availability and consumption patterns of 21 main plant-food items are in Fig. 1. Leaf-food items tended to be available for long periods, but were consumed in only small amounts each month. Contrarily, fruit-food items were available for shorter periods and were consumed in much greater amounts during that time.

Characteristic plant-food items of Yakushima macaques could be classified into three types, in terms of periods of availability and consumption patterns (Table I). Type 1 foods are available in ≥6 of the 10 calendar months, though they were fed on in less than two-thirds of the available period. Most of the common mature leaf-food items are Type 1.

Type 2 foods were available for ≥6 months and were fed on in more than two-thirds of the available period. Three main mature leaf-food items, including *Oreocnide pedunculata* and *Trema orientalis*, which are pioneer species along streams and roadsides, and five common fruit-food items, including two species of *Ficus*, *O. pedunculata*, and the fallen seed of *L. edulis*, are of this type.

Type 3 foods were available <6 months. Most common fruit-food items, seed-food items and young leaf-food items, and all common flower-food items are Type 3.

Annual time feeding on Type 1 common foods is 15.9%, that on Type 2 common foods is 35.0%, and that on Type 3 common foods is 30.5% (Fig. 2). Type 2 common foods include only seven items (Table I), however, they constituted a considerable proportion of the diet of the monkeys.

Table I. Types of Common Plant-Food Items

	No. common items (main items)			
Food category	Type 1	Type 2	Type 3	Total
Young leaves	1 (1)	—	5 (1)	6 (2)
Flowers	—	—	6 (1)	6 (1)
Seeds	1 (0)	—	9 (2)	10 (2)
Fruits	10 (0)	3 (3)	14 (5)	27 (8)
Mature leaves	16 (4)	3 (3)	—	19 (7)
Fallen seeds	—	1 (1)	—	1 (1)
Others	2 (0)	—	—	2 (0)
Total	30 (5)	7 (7)	34 (9)	71 (21)

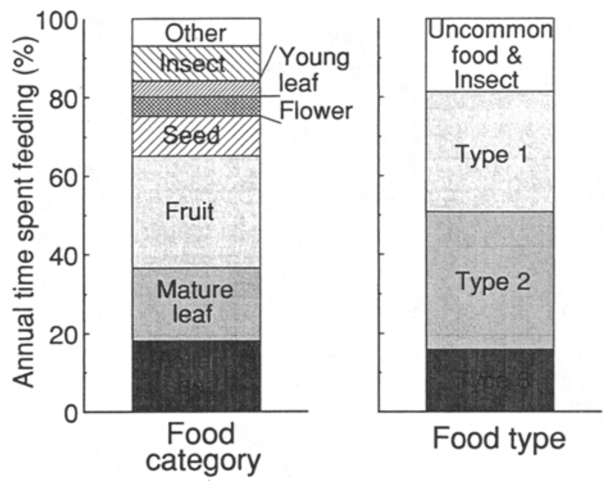

Fig. 2. Time feeding on each food category (left) and each food type (right) on average over 10 calendar months of data.

Seasonal Variation of Diet

Annual time spent feeding on each food category is in Fig. 2. The monkeys spent 28.6% of annual feeding time on fruits, 18.5% on mature leaves, 18.1% on fallen seeds, 10.1% on seeds, 8.9% on insects, 4.9% on flowers, 3.9% on young leaves, and 7.0% on others.

Times feeding on each food category in each month are in Fig. 3. There were great monthly differences in the proportion of each food category in the diet. Variation in the diet was greatest from December to May. During this period, the top category of food changed in turn from fruits (December), fallen seeds (January and February), flowers (March), and mature leaves (April) to fruits (May). In contrast, from May to December, fruit feeding was dominant. The monkeys ate various species of insects throughout the year, but insect-eating was most common in the summer.

Influence of Food Availability and Temperature on Dietary Selection

Availability of each plant food category and mean maximum temperature for each month are in Fig. 3. Monkeys fed on fallen seeds intensively from September to March. Only the seed of *L. edulis* reached the main and common food criterion within the food category of fallen seeds. Moreover, 88.5% of all sampled fallen seeds from five quadrats (N = 2625) are

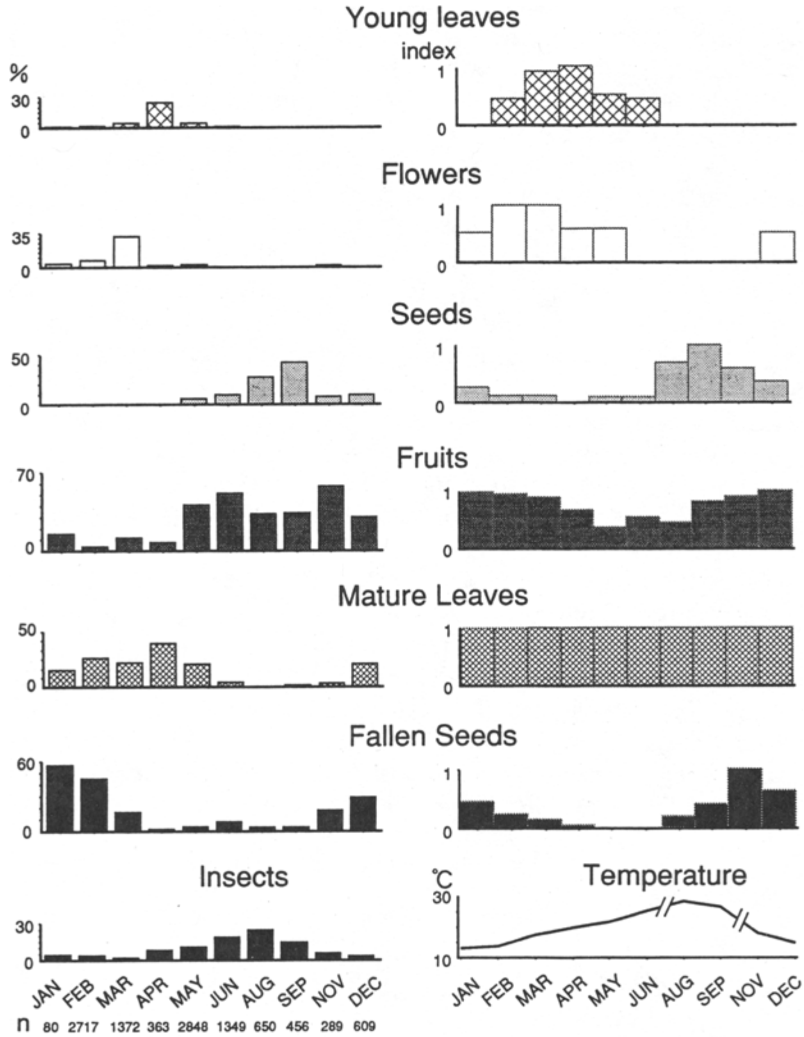

Fig. 3. Time feeding on each food category (left) availabilities of each plant food category (top right) in each month, and monthly temperatures (bottom right). The availability index of each month of each food category shows the relative availability of the food category given that the month with maximum availability has the value 1.

of this species. Because monthly density of the seed varied greatly on the forest floor, I report the availability index for this item as the relative density in each month: August, 0.21 (value for Sept. divided by 2); September, 0.41; November, 1.00; December, 0.64; January, 0.45 (mean values for Dec. and Feb.); February, 0.25; March, 0.16 (mean values for Feb. and Apr.); and April, 0.06. The availability in other months is 0.

Correlations between availability of each food category and temperature (Fig. 3) are in Table II. The availability of both fruits ($r = -0.76$, $P < 0.05$; $n = 10$) and flowers ($r = -0.78$, $P < 0.01$) is negatively correlated with temperature. The availability of other food categories had no significant correlation with temperature.

There are significant positive correlations between feeding on seeds and feeding on insects ($r = 0.67$, $P < 0.05$), and between mature leaves and young leaves ($r = 0.76$, $P < 0.01$), but negative correlations between feeding on mature leaves and feeding on fruits ($r = -0.72$, $P < 0.05$), seeds ($r = -0.66$, $P < 0.05$), and insects ($r = -0.59$, $P < 0.1$), and between fallen seeds and insects ($r = -0.59$, $P < 0.1$) (Table III).

Coefficients of simple regressions between feeding on each food and its availability and temperature are in Table IV. Feeding on young leaves ($r = 0.75$, $P < 0.05$), flowers ($r = 0.62$, $P < 0.1$), and seeds ($r = 0.86$, $P < 0.01$) positively correlated with their availability. Feeding on seeds ($r = 0.76$, $P < 0.05$) and insects ($r = 0.92$, $P < 0.001$) are positively correlated with temperature. Contrarily, mature leaves ($r = -0.56$, $P < 0.1$) and fallen seeds ($r = -0.82$, $P < 0.01$) are negatively correlated with temperature.

I analyzed the degree to which food availability and temperature influence feeding on each plant food category via multiple regression analysis. Multiple and partial regression coefficients for each food category are in Fig. 4. Feeding on seeds (multiple correlation coefficient: $R = 0.95$, $P < 0.001$) and fallen seeds ($R = 0.82$, $P < 0.05$) yields significant multiple

Table II. Correlation Between Availability of Each Food Category and Temperature

Food category	r	P
Young leaves	−0.09	ns
Flowers	−0.78	<0.01
Seeds	0.48	ns
Fruits	−0.76	<0.02
Mature leaves	0.63	ns
Fallen seeds	−0.35	ns

Table III. Correlation Between Food Categories

	Flowers	Seeds	Fruits	Mature leaves	Fallen seeds	Insects
Young leaves	0.06	−0.36	−0.45	0.76**	−0.31	−0.15
Flowers	—	−0.37	−0.44	0.30	0.12	−0.48
Seeds	—	—	0.32	−0.66**	−0.47	0.67**
Fruits	—	—	—	−0.72**	−0.41	0.42
Mature leaves	—	—	—	—	0.16	−0.59*
Fallen seeds	—	—	—	—	—	−0.59*

*$P < 0.1$.
**$P < 0.05$.

Table IV. Regression Coefficients Between Food Categories and Availability and Temperature

Food category	Availability	Temperature
Young leaves	0.75**	−0.06
Flowers	0.62*	−0.31
Seeds	0.86***	0.76**
Fruits	−0.35	0.47
Mature leaves	−0.20	−0.56*
Fallen seeds	0.35	−0.82***
Insects	—	0.92****

*$P < 0.1$.
**$P < 0.05$.
***$P < 0.01$.
****$P < 0.001$.

regression coefficients. Partial regression coefficients indicate that temperature is more clearly related to feeding on fruits, mature leaves, and fallen seeds than food availability is. Higher temperature is associated with an increase in feeding on fruits and a decrease in feeding on mature leaves and fallen seeds. This means that, even if availability of these food categories remained unchanged, time spent feeding on these foods would

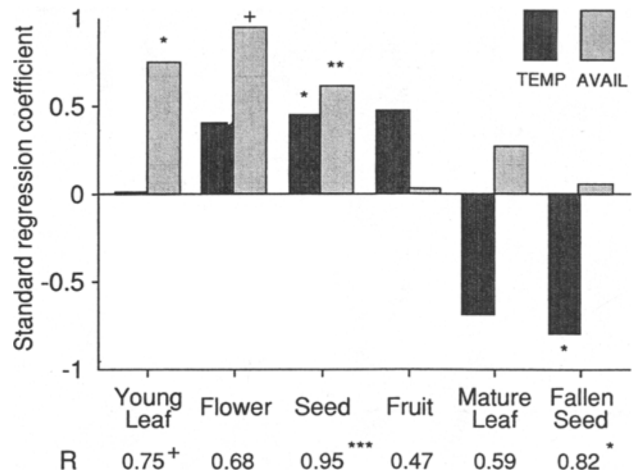

Fig. 4. Standard regression coefficients of temperature and availability from multiple regression analysis. Figures at the bottom show coefficients of multiple regression (R). $^{+}P < 0.1$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

change with temperature. Availability is more strongly associated with feeding on young leaves and flowers.

DISCUSSION

Characteristics of Food Items

Plant-food items (species and part) of Yakushima macaques may be classified into three types in terms of periods of availability and patterns of consumption (Table I). Type 1 foods are available for a long period but are consumed for a limited period. Most mature leaf-food species are Type 1. Type 2 foods are available and consumed over a long period. They are mainly fruits and some mature leaves. Type 3 foods are available and are consumed for short periods. Most young leaf foods, seed foods, and fruit foods and all flower foods are Type 3.

Fruits, seeds, and flowers are high-quality foods, implying more readily available energy and fewer secondary compounds than leaves contain (Harrison, 1985; Milton, 1993). Accordingly, Type 1 foods are lower-quality items and Type 3 are higher-quality items, in terms of energy. Type 2 foods are a mixture of higher- and lower-quality items. Yakushima macaques fed basically on stable Type 2 foods and opportunistically on variable Type 3 foods. They fed on Type 1 foods mainly when Type 2 and Type 3 foods were difficult to obtain, from March to May (Fig. 1).

The quality per unit weight of fallen seeds will be approximately equal to seeds on trees in terms of readily available energy. Searching for dispersed fallen seeds in the leaf litter may take more time, but it will require less energy than searching for them in trees, because the monkeys do not have to move on and climb up and down trees. Therefore, overall feeding on fallen seeds yield relatively low nutritional intake with low cost in a unit time.

Mature leaves are low-quality food in terms of readily available energy (Harrison, 1985; Chapman and Chapman, 1990; Milton, 1993). However, mature leaves were very important foods for the monkeys as "backstop" foods (Harrison, 1984). Mature leaves ensure against the failure of opportunistic foraging for higher-quality, but more variable, Type 3 foods by assuring reliable food intake. Green monkeys (Harrison, 1984) and capped langurs (Stanford, 1991) may also have similar backstop foods. But to avoid the accumulation of secondary compounds, monkeys may have to feed on various species of mature leaves rather evenly (Coelho *et al.,* 1976; Marsh, 1981; Agetsuma and Noma, 1995) in each month (Fig. 1).

Seasonal Variation of Diet

Annual variation in the diet of Japanese macaques has been reported only in cool temperate deciduous forests (Suzuki, 1965; Koganezawa, 1975). My results imply nearly annual variation of Japanese macaques in warm temperate evergreen forest. Yakushima macaques showed large seasonal variation of diet (Fig. 3). Their monthly diet varied from nearly folivorous to fruigivorous, to a mixture of fruigivorous and insectivorous (Hill, 1991b, 1995). Great seasonal variation in diet has also been reported for other populations of Japanese macaques, both in cool temperate (Suzuki, 1965; Koganezawa, 1975; Wada, 1980) and in warm temperate regions (Iwamoto, 1982). Thus, great variability of diet may be common in any habitat of Japanese macaques.

Japanese macaques in cool temperate forest frequently feed on bark and branches of trees from January to March when most leaves are not available (Suzuki, 1965; Koganezawa, 1975; Wada, 1980; Nakagawa, 1989a). Therefore, bark and branches, which are available in any seasons, are probably backstop foods for Japanese macaques in cooler habitats. However, the nutritional value of mature leaves is higher than that of bark or branches (Nakagawa, 1989b, 1994). Population densities of Yakushima macaques are higher than those found in other habitats in Japan (Takasaki, 1981), and this may be a result of the higher quality of their backstop foods.

Influence of Temperature on Dietary Selection

My results imply that dietary selection by Yakushima macaques is influenced not only by the existence of alternative foods and food availability, but also by air temperature. Temperature had a negative influence on feeding on mature leaves and fallen seeds, and a positive one on feeding on seeds and fruits (Fig. 4). Apparently in winter, while availability of fruits was highest, time feeding on fruits was lower (Fig. 3 and Table II). At lower air temperatures, monkeys need to use more energy to maintain their body temperatures (e.g., Nakayama *et al.*, 1971). When Yakushima macaques feed on fruits, they have to move for a long time, because fruits have a more dispersed distribution than those of other foods. However, Yakushima macaques can move and feed for only about 7 hr per day (Agetsuma, 1995), so it would be difficult to compensate for the greater energy requirement at lower temperatures simply by feeding on fruits. Therefore, in winter they shift to foods such as mature leaves, which require less energy expenditure.

The highly significant positive correlation between feeding on insects and temperature (Table IV) may reflect both increased activity of insects and larger populations at higher temperature. The numbers of most insects at the field site increase from May to September. This is particularly clear for *Geisha distinctissima* (Hemiptera), which the monkeys frequency ate and which is found from June to September (Kagoshima Prefectural Museum, 1991) when the temperature is higher (Fig. 3).

Thus, temperature may influence dietary selection both directly and indirectly. There are two mechanisms by which temperature may influence dietary selection. One is through its influence on the energy required for thermoregulation. Generally, within the variation of temperature in the study area (3–29°C), the lower the temperature becomes, the more energy the monkeys need for thermoregulation (e.g., Nakayama *et al.*, 1971). Heat production of Japanese monkeys at 5°C is about 2.5 times greater than at 30°C (Nakayama *et al.*, 1971). Accordingly, at low temperatures they feed on foods that require less energy to find, such as fallen seeds and mature leaves. In contrast, at higher temperatures, the monkeys need relatively less energy for thermoregulation, and also they can pursue higher-quality, but more widely dispersed food items, such as seeds and fruits, by expending more energy while foraging.

Another mechanism is via the influence of temperature on the chance of capturing insects as a source of protein. Insects and mature leaves are probably the main protein sources for Yakushima macaques. In general, mature leaves contain higher protein and lower energy than fruits do (Milton, 1993). When the temperature is high, and many insects are available, monkeys can depend on insects as a protein source and on fruits and seeds as an energy source. But at lower temperatures, when insects are less available, monkeys must feed on leaves for long periods to obtain their protein requirement. In fact, time feeding on insects is positively correlated with feeding on fruits ($r = 0.42$, NS) and seeds ($r = 0.67$, $P < 0.05$) but negatively correlated with feeding on mature leaves ($r = -0.59$, $P < 0.1$; Table III). These two mechanisms are not exclusive, and it is possible that both influence dietary selection by Yakushima macaques.

In general, monkeys that need more energy or protein or both such as species with heavier body weights (Cultton-Brock and Harvey, 1977; Sailer *et al.,* 1985), pregnant or lactating females (Portman, 1970; Gautier-Hion, 1980; Harrison, 1983), and groups in cooler habitats (Iwamoto and Dunbar, 1983) or in cooler seasons, like the Yakushima macaques, tend to have more folivorous diets.

ACKNOWLEDGMENTS

I thank Dr. D. A. Hill of the University of Hong Kong, Prof. T. Iwamoto of Miyazaki University, Dr. Y. Muroyama, Profs. T. Kano, H. Ohsawa, Y. Sugiyama, and N. Masataka of Kyoto University, and Prof. N. Nakagawa of Shion Junior College for helpful suggestions and comments on the manuscript and Dr. N. Noma for identification of plant species. I also thank Shimo-Yaku Forestry Office for permission to undertake the survey and many friends on Yakushima island for their support and hospitality during the fieldwork.

The study was supported by funds from the Nihon Life Insurance Foundation and the Cooperative Research Fund of the Primate Research Institute, Kyoto University, and a Grant-in-Aid for Encouragement of Junior Scientists from the Japanese Ministry of Education, Science and Culture.

REFERENCES

Agetsuma, N. (1995). Foraging strategies of Yakushima macaques (*Macaca fuscata yakui*). *Int. J. Primatol.* 16: 595-609.

Agetsuma, N., and Noma, N. (1995). Rapid shifting of foraging pattern by Yakushima macaques (*Macaca fuscata yakui*) as a reaction to heavy fruiting of *Myrica rubra. Int. J. Primtaol.* 16: 247-260.

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour* 49: 227-265.

Chapman, C. A., and Chapman, L. J. (1990). Dietary variability in primate populations. *Primates* 31: 121-128.

Clutton-Brock, T. H., and Harvey, P. H. (1977). Species differences in feeding and ranging behavior in primates. In Clutton-Brock, T. H. (ed.), *Primate Ecology,* Academic Press, pp. 557-594.

Coelho, A. M., Bramblett, C. A., Quick, L. B., and Bramblett, S. S. (1976). Resource availability and population density in primates: A socio-bioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. *Primates* 17: 63-80.

Davies, G. (1991). Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of Northern Borneo. *Int. J. Primatol.* 12: 119-144.

Estrada, A. (1984). Resource use by howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Veracruz, Mexico. *Int. J. Primatol.* 5: 105-131.

Gautier-Hion, A. (1980). Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *J. Anim. Ecol.* 49: 237-269.

Harrison, M. J. S. (1983). Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus. Anim. Behav.* 31: 969-977.

Harrison, M. J. S. (1984). Optimal foraging strategies in the diet of the green monkey, *Cercopithecus sabaeus,* at Mt. Assirik, Senegal. *Int. J. Primatol.* 5: 435-471.

Harrison, M. J. S. (1985). Time budget of the green monkey, *Cercopithecus sabaeus:* Some optimal strategies. *Int. J. Primatol.* 6: 351-376.

Hill, D. A. (1991a). The influence of a heavy fruiting of *Myrica rubra* (Myricaceae) on ranging and other behaviors observed in a troop of wild Japanese macaques in Yakushima. In Ehara, A., Takenaka, O., and Iwamoto, M. (eds.), *Primatology Today,* Elsevier Science, Amsterdam, pp. 105-106.

Hill, D. A. (1991b). Seasonal and annual variation in the feeding behavior of wild Japanese macaques (*Macaca fuscata yakui*) in Yakushima. *Am. J. Primatol.* 24: 108.

Hill, D. A. (1995). Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in Yakushima (in preparation).

Iwamoto, T. (1982). Food and nutritional condition of free ranging Japanese monkeys on Koshima Islet during winter. *Primates* 23: 153-170.

Iwamoto, T., and Dunbar, R. I. M. (1983). Thermoregulation, habitat quality and the behavioral ecology of gelada baboons. *J. Anim. Ecol.* 52: 357-366.

Kagoshima Prefectural Museum (1991). *Three Hundred Species Found on the Roadside in Kagoshima,* Nisshin Insatsu, Kagoshima (in Japanese).

Koganezawa, M. (1975). Food habits of Japanese monkeys (*Macaca fuscata*) in the Boso Mountains. In Kondo, S., Kawai, M., and Ehara, A. (eds.), *Contemporary Primatology,* Basel, Karger, pp. 380-383.

Le Maho, Y., Goffart, M., Rochas, A., Felbabel, H., and Chatonnet, J. (1981). Thermoregulation in the only nocturnal simian: The night monkey *Aotus trivirgatus. Am. J. Physiol.* 240: R156-R165.

Lucas, P. W., and Corlett, R. T. (1991). Relationship between the diet of *Macaca fascicularis* and forest phenology. *Folia Primatol.* 57: 201-215.

Mahoney, S. A. (1980). Cost of locomotion and heat balance during rest and running from 0 to 55°C in a patas monkey. *J. Appl. Physiol.* 49: 789-800.

Maruhashi, T. (1980). Feeding behavior and diet of the Japanese monkey (*Macaca fuscata yakui*) on Yakushima island, Japan. *Primates* 21: 141-160.

Maruhashi, T. (1986). Feeding ecology of Japanese monkeys in Yakushima Island. In Maruhashi, T., Yamagiwa, J., and Furuichi, T. (eds.), *The Wild Japanese Monkeys on Yakushima Island,* Tokai Daigaku Shuppankai, Tokyo, pp. 13-59 (in Japanese).

Marsh, C. W. (1981). Time budget of Tana River red colobus. *Folia Primatol.* 35: 30-50.

Milton, K. (1993). Diet and primate evolution. Many characteristics of modern primates, including our own species, derive from an early ancestor's practice of taking most of its food from the tropical canopy. *Sci. Am.* Aug: 70-77.

Muller, E. F., Nieschalk, U., and Meier, B. (1985). Thermoregulation in the slender loris (*Loris tardigradus*). *Folia Prmatol.* 44: 216-226.

Nakagawa, N. (1989a). Feeding strategies of Japanese monkeys against deterioration of habitat quality. *Primates* 30: 1-16.

Nakagawa, N. (1989b). Bioenergetics of Japanese monkeys (*Macaca fuscata*) on Kinkazan Island during winter. *Primates* 30: 441-460.

Nakagawa, N. (1994). *Various View-points of Feeding Ecology on Japanese Monkeys.* Heibonsha, Tokyo (in Japanese).

Nakayama, T., Hori, T., Nagasaka, T., Tokura, H., and Tadaki, E. (1971). Thermal and metabolic responses in the Japanese monkey at temperatures of 5–38°C. *J. Appl. Physiol.* 31: 332-337.

Newton, P. (1992). Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). *Int. J. Primatol.* 13: 245-285.

Noma, N. (1989). Flowering, fruiting and seed dispersal of woody plants in a warm temperate broad-leaved evergreen forest on Yaku-Shima Island: From the viewpoint of the relationship between sapfruits and animals. Master's thesis, Kyoto University, Kyoto (in Japanese).

Portman, O. (1970). Nutritional requirements of non-human primates. In Harris, R. (ed.), *Feeding and Nutrition of Non-human Primates,* Academic Press, London, pp. 276-319.

Sailer, L. D., Gaulin, S. J. C., Boster, J. S., and Kurland, J. A. (1985). Measuring the relationship between dietary quality and body size in primates. *Primates* 26: 14-27.

Schoener, T. W. (1971). Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2: 369-404.

Stanford, C. B. (1991). The diet of the capped langur (*Presbytis pileata*) in a moist deciduous forest in Bangladesh. *Int. J. Primatol.* 12: 199-216.

Strier, K. B. (1991). Diet in one group of wooly spider monkeys, or muriquis (*Brachyteles arachnoides*). *Am. J. Primatol.* 23: 113-126.

Suzuki, A. (1965). An ecological study of wild Japanese monkeys in snowy areas. Focused on their food habits. *Primates* 6: 31-72.

Tagawa, H. (1980). Vegetation on the western slope of Mt. Kunwaridake, Yakushima island. *Sci. Rep. Kagoshima Univ.* 29: 121-137 (reprint; in Japanese).

Takasaki, H. (1981). Troop size, habitat quality, and home range area in Japanese macaques. *Behav. Ecol. Sociobiol.* 9: 277-281.

Wada, K. (1980). Seasonal home range use by Japanese monkeys in the snowy Shiga heights. *Primates* 21: 468-483.

Watanuki, Y., and Nakayama, Y. (1993). Age difference in activity pattern of Japanese monkeys: Effects of temperature, snow, and diet. *Primates* 34: 419-430.

Yeager, C. P. (1989). Feeding ecology of the proboscis monkey (*Nasalis larvatus*). *Int. J. Primatol.* 10: 497-530.