

Feeding Strategies of Japanese Monkeys Against Deterioration of Habitat Quality

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ABSTRACT. Field observations of the feeding behaviour of Japanese monkeys were carried out from autumn to winter on Kinkazan Island which is covered with cool temperate forest. As a result, the following two points became clear: (1) the available food items were fixed for a long time; and (2) the habitat quality deteriorated monotonously because the monkeys themselves or their competitors, such as wild mice, utilized the food resources. Against the decrease in food intake caused by this deterioration of the habitat quality, the monkeys controlled the decrease in food intake by employing the following strategies: (1) they recovered their feeding speed by exploiting new food patches (patch-increase strategy); (2) they extended the time spent on feeding (time-extension strategy); and (3) they changed their food (food-change strategy). The former two strategies operated earlier than the third one.

Key Words: Feeding strategies; Habitat quality; Feeding speed; Cool temperate forest; Winter; *Macaca fuscata*.

INTRODUCTION

Among non-human primates, the Japanese monkey (*Macaca fuscata*) is the species whose distribution is the most northerly in the world. Many studies on the adaptation to cold districts have been carried out from various standpoints, such as the morphology, physiology, ecology, etc. of this species (e.g., SUZUKI, 1965; WADA, 1975; WATANABE, 1975; TOKURA et al., 1981; WADA & TOKIDA, 1981). However, studies on the feeding ecology of Japanese monkeys in snowy areas have concentrated on the food items and frequency of feeding on each item, habitat utilization, travel distance, home range size, etc. Research on adaptational strategy in the feeding behaviour of Japanese monkeys, based on estimations of the food intake or of the food environment in the home range, has never been carried out.

Deterioration of habitat quality generally occurs in cool temperate forest from autumn to winter. The present study was undertaken to clarify what kinds of feeding strategy the Japanese monkey employs against deterioration of its habitat quality. A field survey was conducted on Kinkazan Island, which is covered by cool temperate forest with a vegetation zone similar to that of snowy areas.

STUDY AREA AND MATERIALS

Kinkazan Island lies about 700 m offshore at its shortest distance from the Oshika Peninsula, Miyagi Prefecture (38°16'N, 141°35'E). The island is 5.1 km long and 3.7 km across. The total area is about 10 km². The highest peak is 444.9 m above sea level (Fig. 1).

The mean annual temperature is 11°C and the mean annual rainfall is about 1,500 mm. This island is seldom covered with snow, although it does sometimes snow in winter.

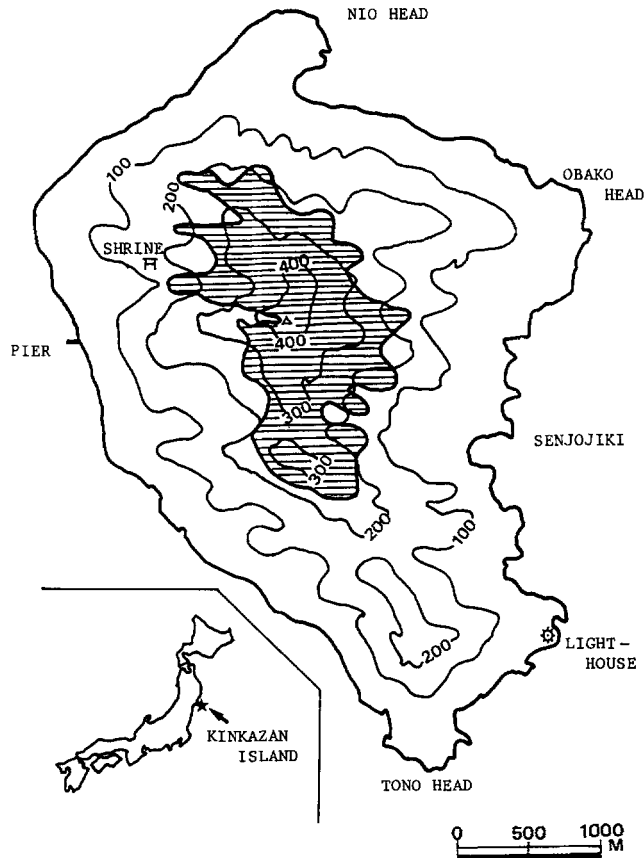


Fig. 1. Map of Kinkazan Island. The shaded portion shows the *Fagus crenata* zone.

The vertical distribution of vegetation on the island can be divided roughly into three: a *Fagus crenata* zone at more than 200 m above sea level; an *Abies firma* zone at less than 200 m above sea level; and a *Pinus thunbergii* zone around the coast. Besides this, several grasslands are patchily distributed on the island, and are dominated by *Zoysia japonica*, *Miscanthus sinensis*, and *Pteridium aquilinum* (YOSHII & YOSHIOKA, 1949; TAKATSUKI, 1980). The vegetation is strongly influenced by Sika deer which densely inhabit the island. Therefore, the sub-high tree stratum and low tree stratum are hardly developed (e.g., YOSHIOKA, 1960).

The Japanese monkeys on this island have been surveyed intermittently since 1959 and reports on the population size and food habits have been presented (YOSHIBA, 1959; IZAWA, 1963a, b; IZAWA & NISHIDA, 1963; AZUMA et al., 1967; YOSHIHIRO, 1980). Individual identification and long-term continuous observation by habituation have been carried out by IZAWA since 1982 (IZAWA, 1983, 1985a, b).

At present, more than 200 monkeys forming five troops inhabit the island. The A-troop of 20 animals which was habituated by SATO, IZAWA, and others was chosen as the subject of this study.

METHODS

A preliminary study was carried out from October 22, 1984 to November 12, 1984. The regular study was then carried out from November 13, 1984 to February 13, 1985 and from October 16, 1985 to December 1, 1985. The total focal animal sampling time was 736 hr 16 min.

The method of data collection was by focal animal sampling (ALTMANN, 1974). As a rule, one individual was followed all day long. Three adult females, one young female and two adult males were chosen as focal animals in 1984, while five adult females were chosen in 1985. The focal animal was changed day by day. However, the data for all individuals were analyzed together in this paper because the age-sex difference in the data was considered trivial.

Data were recorded as follows. The activities were divided into four categories, that is, feeding, moving, resting, and social activities, and were recorded in seconds. The food items were also recorded during feeding. When the duration of a feeding bout (as described later) on beech-seeds (*Fagus crenata*) and on torrey-seeds (*Torreya nucifera*) exceeded 5 min, the feeding speed (as described later) was calculated. Middle and high trees of food patches where the duration of a feeding bout exceeded 5 min were marked with vinyl number tape and their location was recorded exactly on a map.

The terms used in this paper may be defined as follows:

Feeding bout: Continuous feeding on the same food item for more than 1 min. However, when the interval between two continuous feedings on the same food item for more than 1 min was less than 2 min and, moreover, when the total moving time in this interval was less than 1 min, these two continuous feedings were regarded as one feeding bout (Ex. 1). Thus, when the total moving time in this interval was more than 1 min (Ex. 2) or when this interval was more than 2 min (Ex. 3), the activity was regarded as two different feeding bouts (Fig. 2).

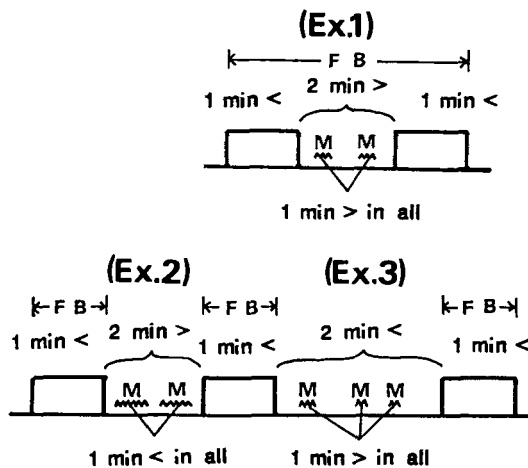


Fig. 2. Definition of a feeding bout. FB: Feeding bout; M: moving.

Food patch: One tree where feeding had been observed was usually regarded as one food patch. However, when beech-seeds and torrey-seeds were consumed on the ground, a food patch could not be specified because of their continuous distribution. In this case, the site within a radius of 15 m from the trunk of a beech and of 10 m from the trunk of a torrey tree was regarded as one food patch for the sake of convenience.

Feeding speed: The quotient of food intake divided by feeding time. The actual method for measuring the feeding speed was different between beech-seeds and torrey-seeds, as follows. **Beech-seeds**: When the monkeys came to the site where beech-seeds had fallen, they sat down, pushing fallen leaves aside and picked up seeds one by one with one or both hands. Picking up some seeds, they stood up and took a few steps. They then sat down and began to pick up some seeds again. The time duration from sitting down to standing up was measured with a stop-watch and the number of beech-seeds eaten during that time was counted. The feeding speed in a feeding bout was calculated by averaging the quotient of the number of seeds eaten divided by the time duration. The proportion of empty seeds and insect-damaged seeds was very high. Judging from the behaviour of the monkeys, however, they did not appear to eat only sound seeds (as described later). One seed was therefore counted as one seed even if it was an empty or insect-damaged one. **Torrey-seeds**: In some cases, the monkeys sat down and picked up seeds just as in the case of beech-seed feeding. In other cases, they pick them up during a walk. The feeding speed in a feeding bout was calculated by the following two methods. (1) A hand-held computer with a built-in clock (EPSON HC-20) was employed. By means of pushing the key board, the time when a monkey took a seed into its mouth was automatically recorded. In this case, the feeding speed was calculated from the total data input-time and total number of seeds eaten. (2) The alternative method was as follows. One-minute units were randomly set up in a feeding bout, and the feeding speed was calculated by averaging the number of seeds eaten per 1-min unit. The monkeys never ate all the albumen of a seed, even if they chewed and broke it. However, the seed was taken as eaten, since they usually left almost the same amount of albumen.

Number of seeds eaten in one day: This term was employed only in beech-seed feeding. For feeding bouts in which the feeding speed was measured, the number of seeds eaten was calculated by multiplying the average feeding speed in each bout by the duration of each feeding bout. For feeding bouts in which the feeding speed was not measured or for feeding lasting less than 1 min, the number was calculated by multiplying the daily average feeding speed by the total duration. The numbers of seeds eaten were then summed to give an estimated value for the number of seeds eaten in one day.

RESULTS

The main food of the monkeys was beech-seeds in 1984 because of the good beech crop. In contrast, the main food was torrey-seeds in 1985 due to a bad beech crop and a good torrey crop. The data for 1984 and the data for 1985 were therefore analyzed independently.

BEECH-SEEDS IN 1984

The beech crop was super-abundant in the autumn of 1984. The monkeys sometimes ate beech-seeds in the trees during the preliminary study. However, they ate them only on the

ground during the regular study period because almost all the fruits had fallen. The A-troop ranged mainly in the *Fagus crenata* zone throughout this study period. The home range size was 154 ha.

The study period was divided into six periods by half-months as follows: the latter half of November, the former half of December, the latter half of December, the former half of January, the latter half of January, and the former half of February. The food items were classified roughly into five categories as follows: (A) beech-seeds, which were always eaten from autumn to winter; (B) autumn food, comprising fruits which ripened and became available in autumn, but became non-available before long because of their disappearance due to consumption, rotting, outflow, etc.; (C, D) winter food, which was not eaten or eaten only a little in autumn despite its availability, but began to be eaten with lapse of time, and could be divided into the two categories of (D) barks and buds typical of winter and (C)

Table 1. Food-species list of the monkeys of the Kinkazan A-troop from November 1984 to February 1985.

Species name	Japanese name	Part eaten
A. <i>Fagus crenata</i>	Buna	Se
B. Autumn food		
<i>Rubus microphyllus</i>	Nigaichigo	Fr
<i>Carpinus tschonoskii</i>	Inushide	Se
<i>Quercus acuta</i>	Akagashi	Fr
<i>Perilla frutescens</i>	Remonegoma	Se
<i>Sorbus japonica</i>	Urajironoki	Fr
<i>Torreya nucifera</i>	Kaya	Se
<i>Zelkova serrata</i>	Keyaki	Se
<i>Clematis apiifolia</i>	Botanzuru	Se
<i>Quercus serrata</i>	Konara	Fr
<i>Cornus macrophylla</i>	Kumanomizuki	Fr
<i>Viburnum dilatatum</i>	Gamazumi	Fr
<i>Zanthoxylum piperitum</i>	Sansho	Fr, Se
<i>Rosa multiflora</i>	Noibara	Fr
<i>Callicarpa japonica</i>	Murasakishikibu	Fr
Fungi spp.		
C. Winter food except for barks and buds		
<i>Euonymus fortunei</i>	Tsurumasaki	Lf
<i>Pinus densiflora</i>	Akamatsu	Lf
<i>Trachelospermum asiaticum</i>	Teikakazura	Lf
<i>Viscum album</i>	Yadorigi	Fr
Herbs and grasses		
<i>Oplismenus undulatifolius</i>	Chijimizasa	
<i>Ixeris stolonifera</i>	Iwanigana	
<i>Ixeris japonica</i>	Ojishibari, etc.	
D. Barks and buds		
<i>Callicarpa japonica</i>	Murasakishikibu	Br
<i>Zanthoxylum piperitum</i>	Sansho	Br, Bu, Tw
<i>Fraxinus lanuginosa</i>	Aodamo	Br
<i>Ilex macropoda</i>	Aohada	Br
<i>Celastrus flagellaris</i>	Tsuruumemodoki	St
<i>Schizophragma hydrangeoides</i>	Iwagarami	Bu
<i>Cornus macrophylla</i>	Kumanomizuki	Bu
<i>Cornus kousa</i>	Yamaboushi	Bu
<i>Castanea crenata</i>	Kuri	Bu
<i>Symplocos chinensis</i>	Sawafutagi	Br
<i>Celtis sinensis</i>	Enoki	Bu
E. Soil and unidentified species		

Fr: Fruit; Se: seed; Lf: leaf; Br: bark; Bu: bud; Tw: twig; St: stem.

other winter food; and (E) other items including soils and unidentified species (Table 1). Fruits of *Viscum album* were the only food item which became newly available in winter because the fruits ripened in winter. The time spent feeding on insects was excluded from the time spent feeding because insect-feeding rarely occurred.

Figure 3 shows the proportion of time spent feeding on each food category with respect to the total feeding time in each period. Beech-seeds were one of the main food items throughout the study period and represented about 70% of the total. Food items other than beech-seeds changed gradually with lapse of time.

The change in feeding speed on beech-seeds is shown in Figure 4. Since each data point is based on the average feeding speed for each feeding bout, the standard deviation reflects the degree of unevenness in feeding speed among the feeding bouts in each period. Moreover, when the feeding bouts differed from each other, the food patch was usually also different. It was considered therefore that the standard deviation reflected the degree of unevenness in feeding speed among the food patches. The feeding speed was generally correlated to the food density. This was suggested by the following findings.

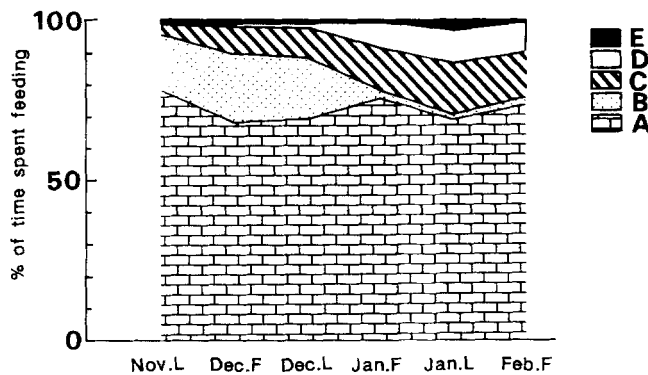


Fig. 3. Changes in percentage of time spent feeding on each food category from the latter half of November 1984 to the former half of February 1985. A: Beech-seeds; B: autumn food; C: winter food other than barks and buds; D: barks and buds; E: soils and unidentified species.

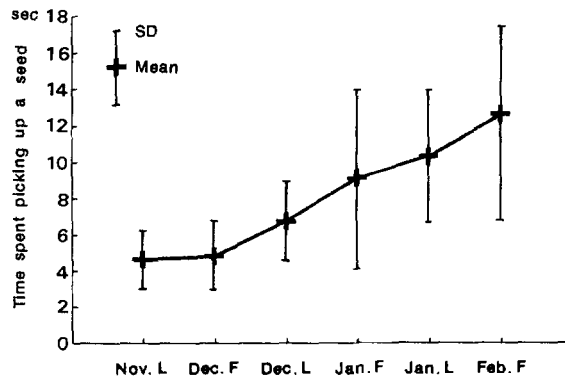


Fig. 4. Changes in feeding speed on beech-seeds from the latter half of November, 1984 to the former half of February, 1985. The ordinate shows the inverse of the feeding speed; that is, the time spent picking up a seed.

From the latter half of November to the former half of February, the feeding speed decreased monotonously with lapse of time. From the latter half of November to the former half of December, the feeding speed was very high and the values in both periods were almost equal (4.7 sec/seed). Also, the standard deviation was small; that is, the degree of unevenness was apparently small among the food patches. On the other hand, the feeding speed decreased with lapse of time (12.7 sec/seed) and the unevenness became increasingly larger among the food patches. The factors underlying these changes in feeding speed were considered to be as follows. From the latter half of November to the former half of December, the feeding speed converged at maximum because only a short time had passed since the beech fruits had fallen to the ground and the fallen seed density was very high. Subsequently, the feeding speed became dependent on the fallen seed density as the density dropped with lapse of time. Animals, including monkeys, non-uniformly utilize beech-seed patches and the fruit production differs among individual beech trees. This caused the unevenness in quality among the food patches to become larger. As a result, the variance in feeding speed became larger. Thus, the data in Figure 4 indicate a correlation between food density and feeding speed, and the feeding speed is therefore employed as an index of food density in this paper.

As the quality of the food patches deteriorated with lapse of time, the monkeys extended the proportion of their time spent feeding on beech-seeds with respect to the observation time from 27.0% to 48.7%. As a result, they extended the proportion of the total feeding time to the observation time from 34.4% to 66.3% (Fig. 5). The latter value was much higher than the 24% obtained at Yakushima (Maruhashi, 1981), 29% at Koshima (Kuroki, 1975), and 28% at Takagoyama (Yotsumoto, 1976).

The number of beech-seeds eaten per 1-hr observation time was estimated. The mean values for each period are shown in Figure 6. Since decreasing feeding speed influenced the number of seeds eaten more strongly than extension of the feeding time did, the number of seeds eaten decreased with lapse of time.

The present study period was divided into two periods: November and December, when

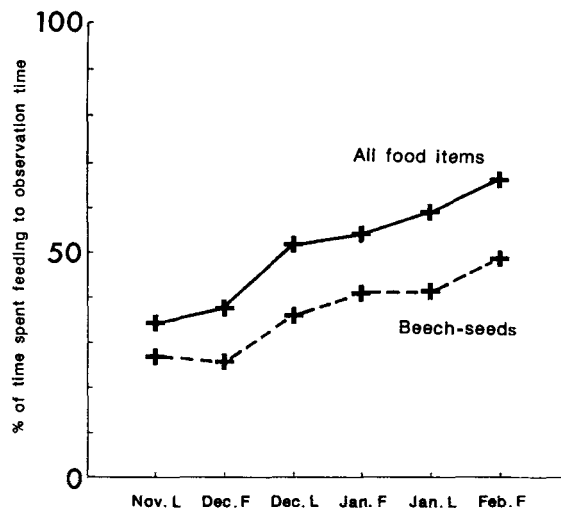


Fig. 5. Changes in percentage of time spent feeding on beech-seeds (broken line) and on all food items (solid line) to observation time from the latter half of November 1984 to the former half of February 1985.

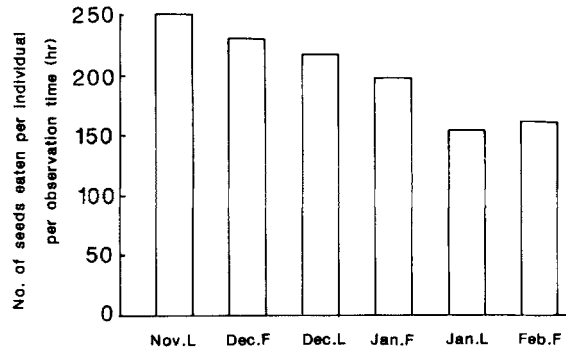


Fig. 6. Changes in number of beech-seeds eaten per individual per observation time (1 hr) from the latter half of November 1984 to the former half of February 1985.

Table 2. Percentage of time spent feeding on all food items except beech-seeds to total feeding time.

	<i>N</i>	After 3:00 p.m.	Before 3:00 p.m.
November–December	24	37%	24%
January–February	26	46*	23*

Comparison between after 3:00 p.m. and before 3:00 p.m. *t*-test: * $p < 0.05$.

the food other than beech-seeds was mainly autumn food; and January and February, when the food other than beech-seeds was mainly winter food (see Fig. 3). The proportion of time spent feeding on food other than beech-seeds with respect to the total feeding time was calculated, and the value before 3:00 p.m. was compared with that after 3:00 p.m. in each of the two periods (Table 2). The value after 3:00 p.m. was higher than that before 3:00 p.m. in both periods, but a significant difference was observed only in the January and February period (*t*-test, $p < 0.05$). Judging from this result and the data in Figure 6, the number of seeds eaten does not decrease significantly in the evening in autumn when large numbers of beech-seeds were eaten. In winter when only small numbers of seeds were eaten, the winter food was eaten in the evening as a means of supplementing the shortage of beech-seeds.

The beech-seed feeding by wild mice, and the fertility and insect-damage of beech-seeds, etc. were also examined.

First, the average feeding speed on beech-seeds shown in Figure 4 was separated into the feeding speed in each feeding bout (Fig. 7). As mentioned, the unevenness in quality among the food patches became greater with lapse of time. Moreover, the quality of the food patch itself gradually deteriorated in every patch regardless of whether the monkeys ate beech-seeds there or not. It is considered therefore that the deterioration of the beech-seed patches was more strongly influenced by other factors which acted uniformly on all food patches than by feeding by the monkeys. MIGUCHI and MARUYAMA (1984), who conducted an ecological study on Japanese beech forest, reported that 60–70% of the total fallen beech-seeds were eaten by wild mice in a mastyear. In view of the fact that at least *Apodemus argenteus* lives on Kinkazan Island (OHTA, 1967) and that a super-abundant crop of beech fruits slightly influenced the *Apodemus argenteus* population increase (MIGUCHI, 1983), it is quite possible that the uniform deterioration of the beech-seed patch is influenced by mouse-feeding.

Data concerning the fertility and insect-damage of the seeds are given in Table 3. With lapse of time, the proportion of empty seeds was constant (about 40%), but the proportion

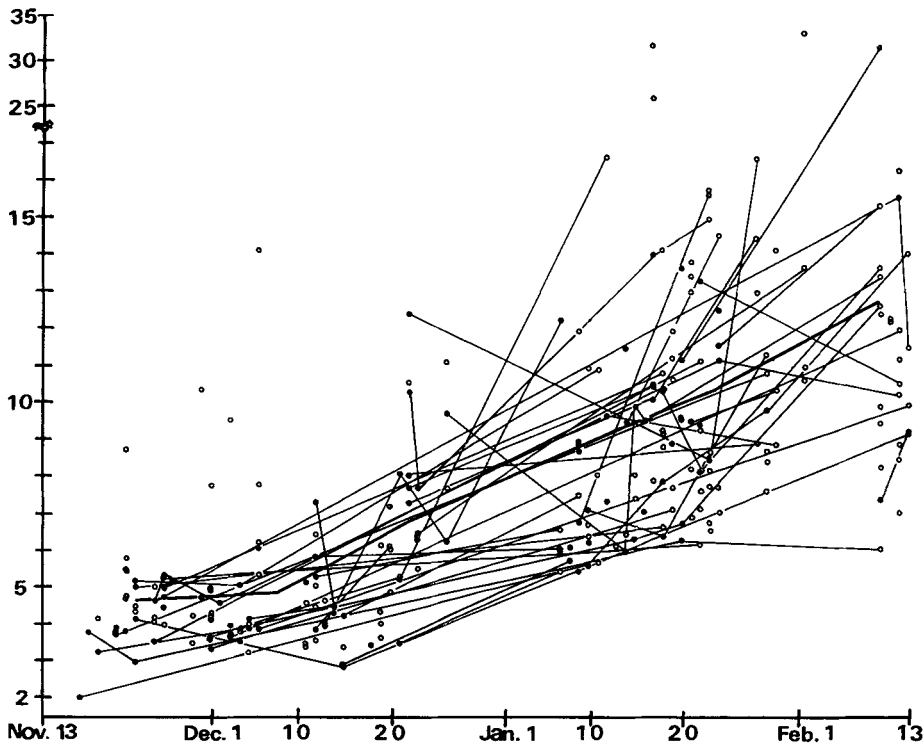


Fig. 7. Changes in feeding speed on beech-seeds at each food patch from November 13, 1984 to February 13, 1985. The ordinate shows the inverse of the feeding speed; that is, the time spent picking up a seed. Data points for the same food patch are connected with each other by thin line. The means for each half-month period are connected by the thick line.

Table 3. Percentages of sound, insect-damaged, and empty beech-seeds in each month.

	Sound seeds (%)	Insect-damaged seeds (%)	Empty seeds (%)
December	20.8	39.6	39.6
January	12.0	50.0	38.0
February	5.3	53.0	41.7

At the three periods, December 9 and 10, January 6, and February 14, respectively, 100, 150, and 150 beech-seeds were collected randomly in 3-5 food patches. Insect-damaged seeds had holes measuring 1 mm across which were made by insect larvae on their surface. In external appearance, an empty seed was difficult to distinguish from a sound one. However, when the shell was broken, the seed proved to be empty and an undeveloped ovule was found inside.

Table 4. Percentages of sound, insect-damaged, and empty beech-seeds at other localities.

Locality	Sound (%)	Insect-damaged (%)	Empty (%)	Animal-damaged (%)
Chugoku District ¹⁾	35	23	42	—
Chugoku District (stands of highest dominance) ²⁾	74.5	13.7	11.8	—
Wakayama Prefecture ³⁾	16.8	41.2	42.0	—
Yamagata Prefecture ⁴⁾	71.8	13.3	13.5	1.4

1), 2), 3) The seed fertility varied widely with the dominance of the beech trees. According to a study in the mastyear of 1973, it decreased with decrease of dominance (HASHIZUME & YAMAMOTO, 1974); 4) data for the mastyear of 1981 (MIGUCHI & MARUYAMA, 1984).

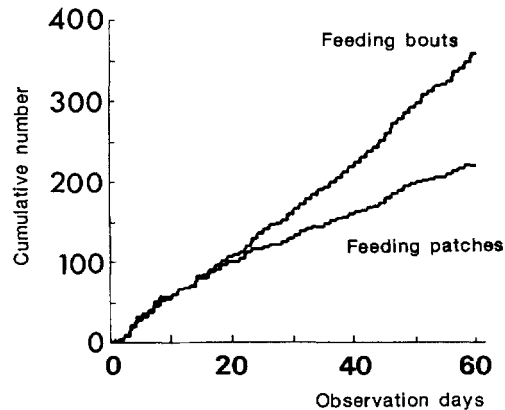


Fig. 8. Changes in cumulative numbers of feeding bouts and food patches in beech-seed feeding.

of sound seeds decreased and the proportion of insect-damaged seeds increased. Beech-seeds are not damaged by insects after falling (MIGUCHI & MARUYAMA, 1984). Judging from the monkeys' behaviour, they did not appear to eat only sound seeds. Considering all these observations, the decrease in proportion of sound seeds seemed to result from selective feeding on sound seeds by other animals, probably wild mice.

Comparing these results with those for other localities (Table 4), the proportion of sound seeds was comparatively low in the present study. This appeared to reflect the fact that the sample seeds of the present study were collected from December to February, at many days after the seeds had fallen, whereas the sample seeds in the other studies were collected soon after falling. This again suggested selective feeding on sound seeds by other animals. Judging from all these findings, the decrease in number of sound seeds eaten with lapse of time seemed to occur more rapidly than the data shown in Figure 6.

Finally, the feeding strategy through increasing food patches against deterioration of the food patch quality was examined (Fig. 8). Only feeding bouts lasting for more than 5 min were analyzed. The number of food patches always continued to increase throughout the study period as the number of feeding bouts increased. Although the monkeys appeared to employ the patch-increase strategy, recovery of feeding speed could not be confirmed as already shown (see Figs. 4 & 7), that is, this strategy seem to be ineffectual. It is possible that feeding on fallen beech-seeds by wild mice influenced the situation as demonstrated above.

TORREYA-SEEDS IN 1985

The torreyia crop was super-abundant in the autumn of 1985, although the beech fruits failed. The monkeys picked up and ate torreyia-seeds usually on the ground but sometimes in the trees. Seven items were compared between the beech-seed and torreyia-seed feeding (Table 5).

Figure 9 shows the changes in cumulative numbers of feeding bouts and food patches. Only feeding bouts lasting more than 5 min were analyzed in this study. From November 14 to 21, the number of food patches saturated for a time, although the number of feeding bouts was increasing. The number of food patches then began to increase again from November 22. The study period was divided into six periods of about a week. The changes in

Table 5. Comparison between the characteristics of beech-seed feeding and those of torreya-seed feeding.

	Beech-seeds	Torreya-seeds
1. % of time spent feeding to total feeding time	70%	30%
2. Distribution	Uniformly in the home range	Clumpily in a region of the home range
3. Competitors	Wild mice	Almost none (while seeds were covered with pulp)
4. % of non-sound seeds ¹⁾	79.2–94.7%	Almost 0%
5. Weight of edible part ²⁾	0.10 g	0.09 g
6. Caloric content/1 g edible part ²⁾	6.91 kcal	5.28 kcal
7. Density of fallen seeds	High	Low

1) The proportion of non-sound beech-seeds varied with the dominance of the beech trees: as shown in Table 3, it changed with lapse of time. For the torreya-seeds, 57 seeds on October 21 and 63 seeds on December 21 were collected as samples and examined: as a result, no non-sound seeds were observed; 2) NAKAGAWA, in prep.

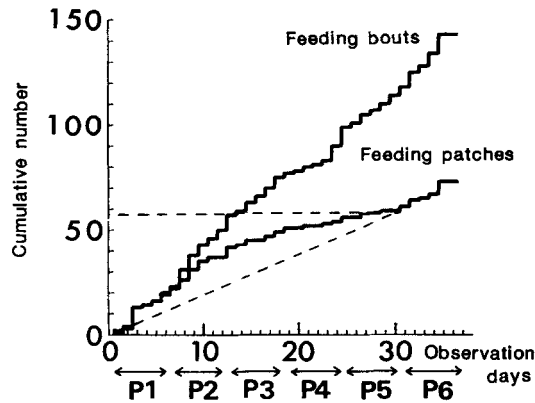


Fig. 9. Changes in cumulative numbers of feeding bouts and food patches in torreya-seed feeding. P1: Oct. 16–22; P2: Oct. 23–29; P3: Oct. 30–Nov. 5; P4: Nov. 8–13; P5: Nov. 14–21; P6: Nov. 22–Dec. 1.

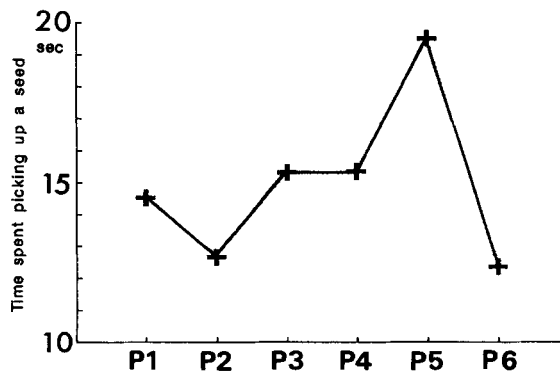


Fig. 10. Changes of average feeding speed on torreya-seeds from October 16 to December 1, 1985. The ordinate shows the inverse of the feeding speed; that is, the time spent picking up a seed. P1: Oct. 16–22; P2: Oct. 23–29; P3: Oct. 30–Nov. 5; P4: Nov. 8–13; P5: Nov. 14–21; P6: Nov. 22–Dec. 1.

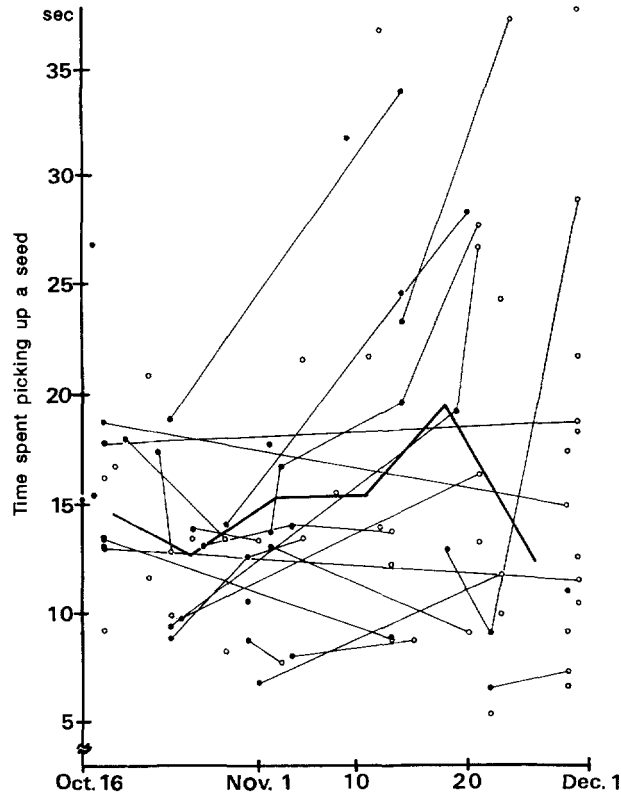


Fig. 11. Changes in feeding speed on torrey-seeds at each feeding bout from October 16 to December 1, 1985. The ordinate shows the inverse of the feeding speed, that is, the time spent picking up a seed. Data points for the same food patches are connected with each other by thin lines. The means for each period are connected by the thick line.

average feeding speed are shown in Figure 10. When the number of food patches saturated (from November 14 to 21), the feeding speed decreased to 19.5 sec/seed, but it recovered to 12.4 sec/seed when food patches were newly exploited.

Figure 11 shows the changes of feeding speed in each feeding bout. When the number of food patches saturated (from November 14 to 21), the feeding speed decreased markedly in repeatedly utilized food patches as expected. This finding suggested that deterioration of the food patch quality was caused by the feeding carried out by the monkeys. This could be ascribed to the much lower density of fallen torrey-seeds than of beech-seeds. On the other hand, when the monkeys exploited new food patches after November 22, the feeding speed was high in the newly exploited patches. This suggested that there was no competitor to the monkeys for the torrey-seeds when the seeds were covered with pulp. Thus, a food patch which the monkeys visited for the first time retained the same high quality as at the time of fruit-falling, and whether the quality of a torrey-seed patch was high or not was influenced by the visits and feeding by the troop.

The newly exploited food patches were plotted on a map (Fig. 12). The area enclosed by the solid line shows the home range during the study period. Since the monkeys ranged over almost the same area before November 21 as in the study period, the areas in which

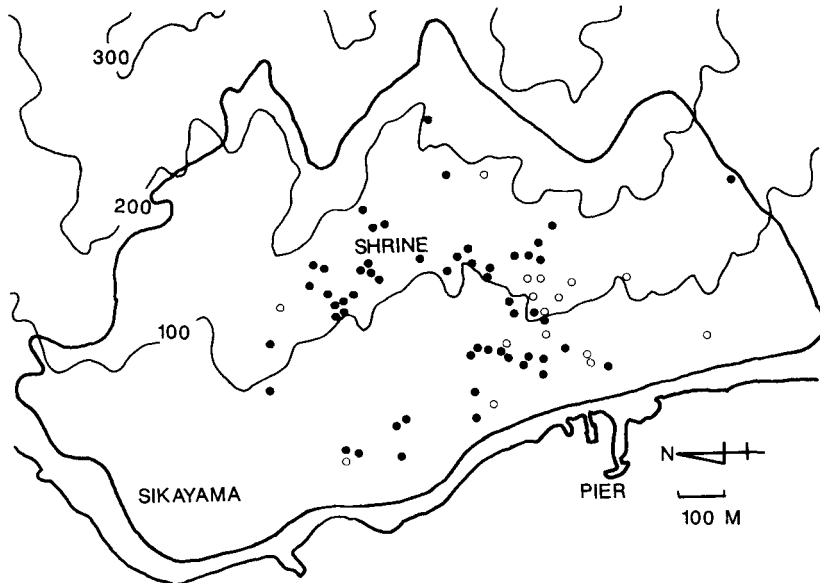


Fig. 12. Distribution of torreya-seed patches. The area enclosed by the solid line shows the home range of the A-troop from October 16 to December 1, 1985. Solid circles indicate food patches before November 21; open circles indicate food patches which the monkeys visited and fed at for the first time after November 22.

they newly exploited food patches of torreya-seeds had also been utilized for moving or for feeding on other food items. Thus, new patches were exploited only within the range which the troop had been utilizing before November 21. The distribution pattern of new food patches appeared to show that the monkeys newly exploited food patches in the peripheral area of the distribution of torreya trees which was located as a broad clump only around the shrine. The monkeys thus employed a strategy whereby they newly exploited food patches in the peripheral area of the torreya distribution and, in consequence, recovered their feeding speed against the deterioration of the quality of the torreya-seed patches caused by their feeding.

Just as in the case of beech-seeds, the monkeys extended the proportion of their time spent feeding on torreya-seeds with respect to the observation time from 10.3% in P1 to 20.2% in P6. As a result, they extended the proportion of the total feeding time to the observation time from 46.0% in P1 to 62.8% in P6. However, they did not eat the typical winter food (barks and buds) even in P6. In addition, the proportion of time spent feeding on other winter food (for example, *Oplismenus undulatifolius* and *Ixeris stolonifera*) to the total feeding time was only 10.4% even in P6.

DISCUSSION

The feeding strategies of the Japanese monkeys on Kinkazan Island from late autumn to late winter are shown schematically in Figure 13.

On Kinkazan Island, the autumn food including beech-seeds and torreya-seeds, decreased from autumn to winter. As a result, the quality of the habitat surrounding the monkeys

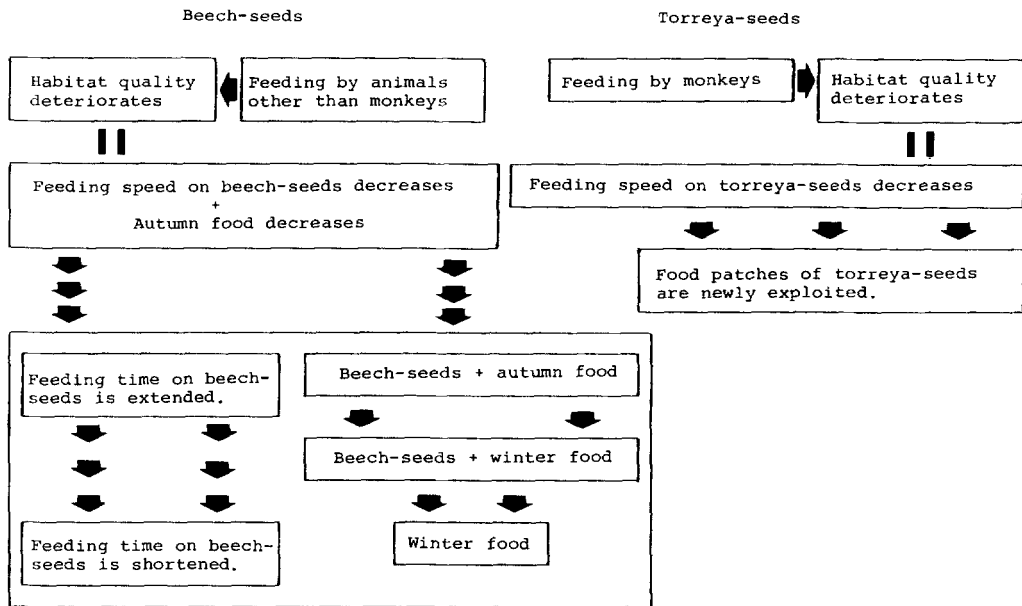


Fig. 13. Feeding strategies of Japanese monkeys against deterioration of the habitat quality.

deteriorated. This was reflected in the data for beech-seeds and torreya-seeds as main foods.

In the case of beech-seeds, the habitat quality deteriorated because fallen seeds were probably consumed by wild mice. Consequently, the monkeys controlled the decrease in their beech-seed intake by extending their feeding time on beech-seeds. They then changed their food other than beech-seeds from autumn food to winter food. This change advanced as follows. Since the beech-seed intake decreased in winter, the winter food was eaten in the evening as a means of supplementing the decreased beech intake. Even on the last observation day, February 13, 1985, the time spent feeding on beech-seeds still represented 70% of the total feeding time. The change to winter food was thus incomplete. However, IZAWA (pers. comm.) has observed that the monkeys did not eat beech-seeds but ate only winter food in early March 1985. This suggests that the monkeys do not extend their feeding time on beech-seeds forever, but that they eventually stop feeding on them and change their food entirely to winter food. In the case of torreya-seeds, of which the fallen number is much fewer than that of beech-seeds, when the habitat quality deteriorated because of feeding by the monkeys themselves, the monkeys recovered their feeding speed by exploiting new food patches.

The above analysis of feeding indicates that the feeding strategies used by the monkeys operate against a decrease of food intake to a certain level caused by deterioration of the habitat quality. The strategies can be separated into three, as follows: strategy-1: a patch-increase strategy; strategy-2: a time-extension strategy; and strategy-3: a food-change strategy. Moreover, the former two strategies are considered to operate earlier than the third one.

The Japanese monkeys live in cool temperate forest where the seasonal changes in environment are large but predictable. In such animals, the time-energy budgets need to fit the time of greatest stringency (principle of stringency; WILSON, 1975). If their time-energy budget

was fitted to the richest time for food resources, they would fall into crisis at the time of stringency. However, they are assumed to accumulate body fat in the autumn and to consume it during winter under poor food conditions (e.g., WADA, 1975, 1979; WADA et al., 1975; WADA & TOKIDA, 1981; NAKAGAWA, in prep.). Thus, the energy budget does not appear to be fixed so as to fit the time of greatest stringency exactly. The former two strategies operate to accumulate energy under conditions of surplus food, while the third one serves to restrict the consumption of accumulated energy under conditions of stringency.

Acknowledgements. I wish to express my deepest thanks to Dr. M. KAWAI, former Professor of the Primate Research Institute, Kyoto University, for his guidance at every stage of this study. I also wish to thank Dr. K. IZAWA of Miyagi University of Education and Ms. S. SATO of Yamagata University for offering information prior to my study and for their invaluable help. I am grateful to Drs. Y. SUGIYAMA, H. OHSAWA, A. MORI, U. MORI, members of the ecology seminar of the Primate Research Institute, Kyoto University, and Dr. T. MARUHASHI of Musashi University for their criticism of my preliminary draft. I am indebted to Ms. M. SETOYUCHI for her assistance with the computer programming.

In the field study, I was helped by members of the No. 29 joint-study room, Miyagi University of Education. I obtained excellent facilities for my field work from the staff of Kinkazan Koganeyama Shrine, especially the chief priest, M. OKUMI. I would like to thank all these persons.

This study was financed in part by the Cooperative Research Fund of the Primate Research Institute, Kyoto University, and also by a Grant-in-Aid for Special Project Research on Biological Aspects of Optimal Strategy and Social Structure from the Japanese Ministry of Education, Science, and Culture.

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—Received August 25, 1987; Accepted July 12, 1988

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