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Field Observations of the Feeding Behavior in the Japanese Giant Flying Squirrel, *Petaurista leucogenys*

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Field observations were carried out on *Petaurista leucogenys*, a tree dwelling glider, together with an analysis of stomach contents. The animal seldom perched on low branches to feed, and hardly sat on twigs of lcm and less in diameter or on branches with steep inclinations. In addition, the animal always fed at a sitting posture and put the hindpaws at a right angle to the branch. In spite of restrictions on feeding positions and feeding postures, the animal was able to get food at a distance by applying feeding techniques such as gnawing off or bending of branches. Feeding habits of the animal are characterized by the follwing facts: i. e. lack of storing habit, repeated visits to the same feeding site, infrequent shifts during a feeding bout, and long feeding bout on a tree together with the fact that ingested food remained in the stomach for a long time. The facts mentioned above indicated that the feeding habits of this animal are adapted for feeding on abundant items on a tree, particularly on fibrous ones such as leaves.

INTRODUCTION

An arboreal life is always associated with many difficulties. Branches, the only support for an animal on a tree, distribute only linearly in the three-dimensional space, and effort for keeping bodily balance is always necessary. This problem is important when the animal tries to harvest from terminal branches. Ecological and functional-morphological studies on mammalian adaptations to arboreal life has been carried out mainly on primates, and attentions have been extended that the feeding techinques on a tree is related with the morphology and the mode of locomotion of the species (Clutton-Brock, 1977). Although inter-specific difference in the feeding strategy has been studied in rodents as well (Reichman, 1981), studies on arboreal species from this point of view are still few. Particularly, the feeding behavior of gliders is hardly known yet. Therefore, we conducted field observations of the Japanese giant flying squirrel, *Petaurista leucogenys*, which occurs commonly in the forests throughout Japan, except Hokkaidō, to clarify the characteristics of foraging, picking, chewing and digesting.

STUDY AREA

Field observations on the animal were carried out at following eight areas; (1) Yakuoin in Hachidji, Tokyo Met., (2) Suiyō Shrine and Kamiakizuki-hachiman Shine in Amagi, Fukuoka Pref., (3) Ōnamuchi Shrine in Amagi, Fukuoka Pref., (4) Kumo-hachiman Shrine in Yabakei, Ōita Pref., (5) Takachiho Shrine in Takachiho, Miyazaki Pref., (6) Ōkawachi-hachiman Shrine in Shiiba, Miyazaki Prcf., (7) Kirishima Shrine in Kirishima, Kagoshima Pref. and (8) Kamiyokoyama in Jyoyō, Fukuoka Pref. Study areas (1) (7) were precincts of shrines with areas of one to a few hectare, locating at the foot or the side of mountains. Except the grove at Ōnamuchi which was isolated by the surrouding rice field, most groves of shrines had canopies which were contiguous to the coniferous plantations in the hillside. Those groves were represented by evergreen broad-leaved forest or mixed forest with evergreen and deciduous trees, including many big trees of *Cryptomeria japonica*, *Zelkova serrata*, *Cinnamomum camphora*, *Castanopsis cuspidata* and some *Quercus* species which were hundreds years old and 20-30 m high. Those trees provided the animal with suitable tree hollows for nests, and the animal was found easily at those areas at night. Area (8) was a plantation of Japanese cedar, where trees suffered severe damage from debarking by the animal.

METHOD

Feeding behavior of the flying squirrel was observed for 440 hours from 1975 to 1981. We used a flashlight with red filter for locating the animal and a starlight-scope (manufacture of NAC Inc.) for continuous observation of its behavior. On moonlight nights, we were able to watch the animal with binoculars (Nikon, 7x50) as a silhouette without any lightings. This method was rather effective for observing the detailed movements of the animal. Once the feeding animal was located, the height of the animal's position from the ground and species of tree were recorded. The diameter and the angles to the ground of the branch on which the animal perched were also recorded whenever the animal moved to new branch during feeding activities. Behavior of the animal was also analyzed by using 8 mm and 16mm movies (18 frames per sec.) and still photography.

In the preliminary investigation, it was known that the animal did not sit on a branch which bent 30 degrees and more by its weight. We measured, thus, the distance from the tip of a branch to a point at which it began to bend 30 degrees and more by hanging a weight of 1,200 g (equal to an average weight of an adult) on a horizontal branch of various kinds of trees. Moreover, stomach contents of fifteen inividuals caught in the nests during the day for pest control at Ōkawachi-hachiman Shrine and Kamiyokoyama were investigated.

RESULTS

1. Feeding sites

The flying squirrel did not explore its home range frequently. The animal, which emerged from its nest after dusk, often glided directly to a feeding tree. After arriving at a branch, the animal immediately started feeding. Some individual often visited some particular trees to feed repeatedly. For example, at Kamiakizuki-hachiman Shrine a particular individual was always found in a tree of *Diospyros* ***kaki*** from September to the following February, until all the fruits were eaten. A tree of *Robinia* ***pseudo-acacia*** *(9* m high) at Yakuōin lost all the leaves as the result of consecutive feeding by the animal for three months. The animal tended to damage intensively some particular trees even when it fed on common tree species such as *Cryptomeria japonica* or ***Cinnamomum*** *camphora* in the habitat. Moreover, in case of a big tree, the animal even showed a tendency to visit some particular boughs repeatedly.

In most case, the animal fed on at branches of 5 m or more at their heights. On the above-mentioned tree of *Diospyros* ***kaki,*** the animal did not come down to branches below 5 m to feed until it consumed the fruits at high branches. Feedings at the height of less than 5m were only seen when the animal fed on favorite food items such as fruits of *Diospyros kaki* or flower buds of *Camellia japonica.* Further, feeding at the height of below 3 m was seen only on trees growing at the middle of cliffs or steep slopes. At Yakuōin, seasonal change in the heights of feeding place was noticed. This was due to the fact that the animal fed on relatively low trees such as *Prunus* ***jamasakura*** and *Acer palmatum* from April to June, while big trees such as some *Quercus* species from September to November (Fig. 1).

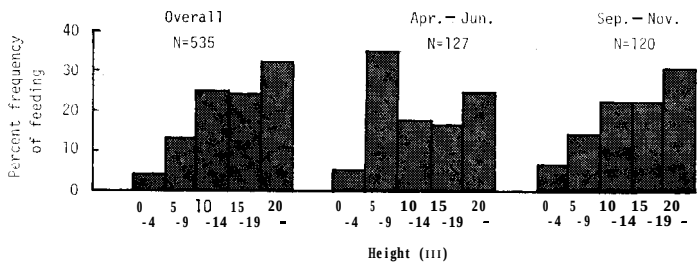

Fig. 1. Percent frequency of feeding by height class at Yakuōin during *197551977.*

The animal did not frequently sit on branches with diameter of less than 10 mm to feed; those of less than 8 mm in diameter were not utilized at all (Table 1). Branches of deciduous trees were slender and flexible in general. Accordingly, the length of terminal branches on which the animal was not able to perch was long, e. g. 109 cm in *Robinia* ***pseudo-acacia*** (n=50), 103cm in

Table 1. Distribution of diameters and angles to the ground of branches used by the flying squirrel while feeding.

Diameter (Dmm)	Angle (θ°)				Total
	$\theta \leqq 30$		$30 < \theta \leqq 60$	$60 < \theta$	
$D \leqq 10$	22	(5.7)	11 (2.8)	0 (0.0)	33 (8.5)
$10 < D \leqq 20$	115.5	(30.0)	54 (14.0)	7.5 (1.9)	177 (45.9)
$20 < D \leqq 40$	69.5	(18.0)	46.5 (12.0)	7 (1.8)	133 (31.9)
$40 < D \leqq 80$	20	(5.2)	11.5 (3.0)	1.5 (0.4)	33 (8.5)
$80 < D$	12	(3.1)	6 (1.6)	2 (0.5)	20 (5.2)
Total	239	(61.9)	129 (33.4)	18 (4.7)	386 (100.0)

Figures in parentheses mean percent.

Prunus jamasakura (n=30) and 85cm in *Acer palmatum* (n=100). On the other hand, the length was 38cm at most in *Camellia japonica* (n=40), an evergreen tree, and branches of *Quercus* often did not bend at all even when the weight was hung at the tip of a branch. The mean diameter of branches at the point where bending of 30 degrees was recorded by hanging the weight was between 8.4 mm and 12. Omm for every tree species tested.

The animal preferred branches with an angle of 30 degrees and less for supporting its body. When the animal fed at a branch with an acute angle, it selectively sat at a stable place such as a stump of broken branches. The animal was not able to feed in the posture of clinging to a vertical trunk. For this restriction, the animal was only able to eat the stem bark within the reach of its mouth while sitting on a branch with hindpaws (Fig. 2).

2. Feeding postures and techniques

The basic feeding posture of the animal was a sitting posture on a branch with hindpaws (Fig. 3a). The animal often twisted or extended the body to find or get food (Figs. 3b–f) and always turned back to the sitting posture to eat the detached food. Varied extended postures were shown when the animal fed on food such as bark or winter-sprout without detaching it from a branch. The animal had easy access to the food in the front and in the upper front of the branch on which it sat, while it found difficulty in obtaining food beneath it. Regardless of the diameter of the branch, the animal always put its hindpaws at a right angle to the axis of the branch (Fig. 4). Hindpaws were kept in touch with the branch only by the pads, and claws made no contact with the branch during feeding activities. The tail also did not touch with any branches, nor was it wagged positively to be well balanced.

The animal got food by drawing a whole branch to the mouth with forearms (Fig. 5) or by gnawing off a piece of branch together with the food attached to it (Fig. 4). Bending or hauling of branches was seen frequently in case of trees with long and flexible branches, while gnawing off was observed in case of evergreen trees with thick branches. The maximum length bent by the animal reached a length of 110 cm in ***Robinia pseudo-acacia***

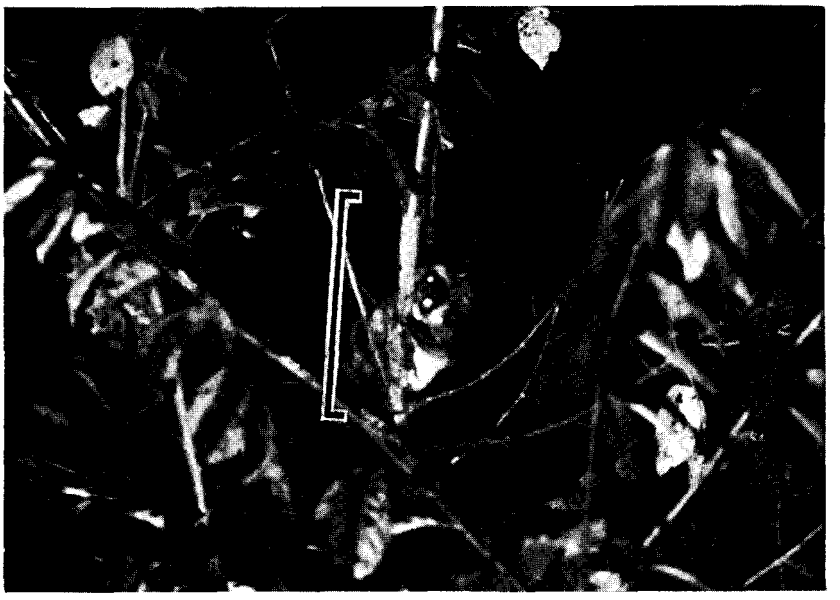

Fig. 2. Photo showing feeding on bark of *Prunus jamasakura*. The brace represents the range of feeding on the bark of stem.

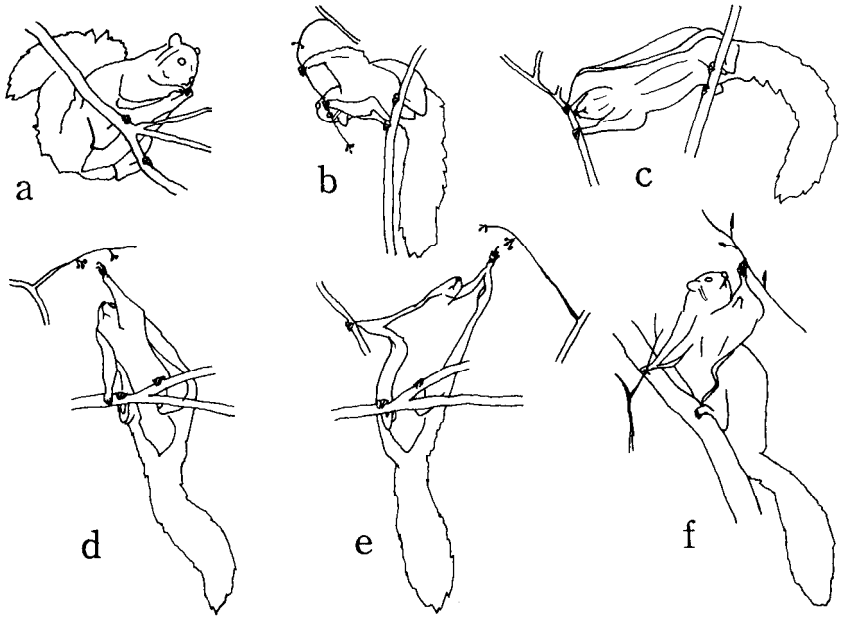

Fig. *3.* Feeding postures. a, normal sitting posture; b-f, twisted or extended posture when procuring food.

Fig. 4. The flying squirrel feeding on winter-sprouts of *Acer palmatum* after gnawing off a twig.

and *Acer palmatum*. The animal often tried to draw near the tip of the branch on which it was sitting. In such a case, the animal occasionally almost fall from the branch as it was forced to strike a shaky posture by turning sideways.

The Frequency of gnawing off branches generally depended on the flexibility of branches, the attaching state of food parts to branches, the size of

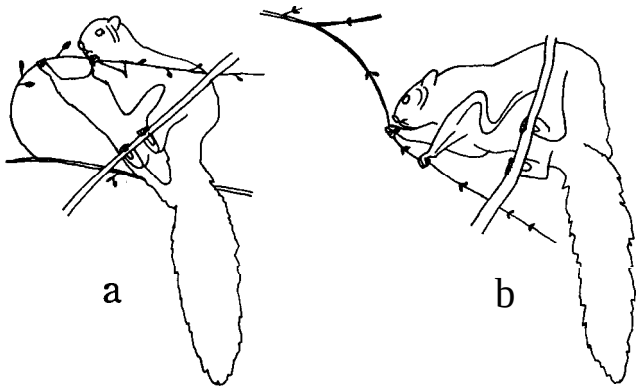

Fig. 5. The flying squirrel trying to get food by bending (a) and hauling (b) a twig.

Table 2. Frequency of gnawing off behavior according to food items

Food part	Plant species	Frequency	Food part	Plant species	Frequency
Young leaves	***Prunus jamasakura***	++	Fruits, seeds and nuts	*Zelkova* ***serrata***	++
	Zelkova serrata	+		***Eurya japonica***	+
	Aesculus ***turbinata***	+		***Cryptomeria japonica***	
	Fagus ***japonica***	–		***Torreya*** *nucifera*	
	Fagus crenata	–		***Quercus gilva***	+
	Acer ***palmatum***	–		***Quercus glauca***	+
				Quercus acuta	
Mature leaves	***Cryptomeria japonica***	+		Cinnamomum *camphora*	
	Quercus gilva	+		*Fagus* ***crenata***	
	Quercus glauca	+		*Pinus densiflora*	
	Quercus acuta	+		***Camellia japonica***	
	Cinnamomum *camphora*	+		***Prunus jamasakura***	
	Robinia pseudo-acacia	–		*Prunus* ***persica***	
	Zelkova serrata	–		*Acer* ***palmatum***	
	Prunus persica	–		***Tilia miqueliana***	–
Flowers and buds	***Chamaecyparis*** *obtusa*	+	Winter sprout	***Larix*** *leptolepis*	++
	Camellia japonica	++		***Zelkova serrata***	++
	Pruns jamasakura	++		***Prunus jamasakura***	++
	Quercus glauca	+		*Acer* ***palmatum***	++
				Quercus glauca	
Bark	***Prunus jamasakura***	++		***Quercus acuta***	+
				Cinnamomum *camphora*	+
Gall	***Cryptomeria japonica***	++		***Magnolia obovata***	

The symbols of –, + and ++ show no, a few and many occurrences of gnawing off during a bout of feeding, respectively.

food, and feeding position of the animal on a branch (Table 2). The animal took the food such as winter-sprouts which attached directly to a branch by gnawing off the whole branch. On the other hand, it took leaves or fruits which had flexible petioles or carpophores by slightly bending the stem toward its mouth with forepaws. Small food items which were hard to handle, however, were gnawed off with branches even when they possessed petioles or carpophores. This difference was seen when the animal fed on flowers and fruits of ***Prunus jamasakura.*** Although both of them attached to branches with flexible peduncles or carpophores, the former which were difficult to hold between incisors were always taken together with twigs, and the latter which were easy to snap were pulled apart one by one from the carpophore with incisors. In case of feeding on bark, the animal peeled it directly from the branch when it was sitting on a thick branch, while the animal ate it after gnawing off the branches when it was on a slender branch.

The length of branches gnawed off varied with both tree species and parts eaten (Fig. 6). Namely the animal occasionally gnawed off branches up to 1 m in length and 8 mm in diameter when it fed on bark or winter-sprout, although the length of branches cut off was usually short when it fed on leaves, flowers or nuts. Occasionally, the animal cut off a branch into a few

short sections. In case of feeding on leaves or large fruits, it frequently threw away a cut twig held in the forepaws before eating up all edible part attached to the piece, and gnawed off a new twig. In case of feeding on winter-sprouts, however, the animal usually consumed entire buds on the cut twig.

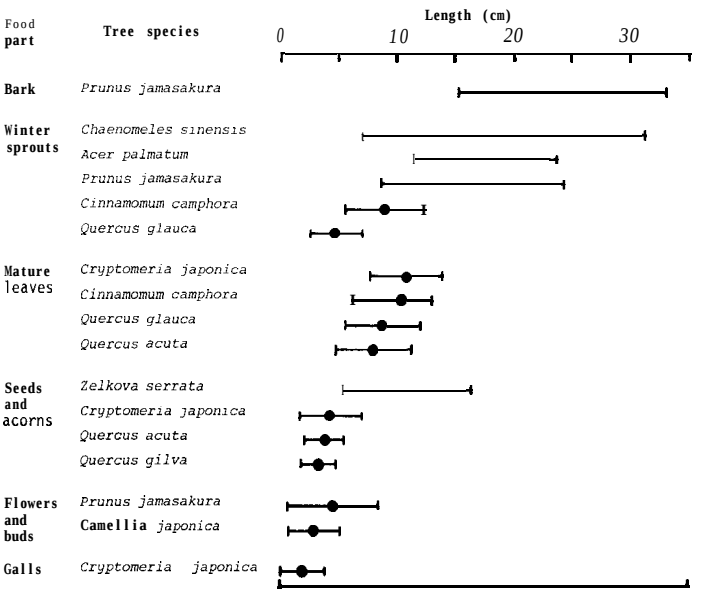

Fig. 6. Differences in length of twigs gnawed off according to food items. Solid circle, mean ; horizontal line, standard deviation.

There was observed an individual difference in the way of feeding, e.g. between two individuals eating on the same branch, one frequently gnawed off the branch, while another seldom used this technique to take food. In case of feeding on cherries, most animals ate only the pulp of fruit and dropped the seed to the ground. On the other hand, some animals fed on the albumen, too, after cracking the shell of seed, and a few exceptional animals even swallowed the seed at one gulp without cracking.

3. Duration of a bout of feeding and frequency of shift while feeding

The flying squirrel very seldom carried food, except in case of feeding on persimmons. The animal sometimes dropped the fruit to the ground by accident because most of the fruits were born near the tip of the thin branches. When the animal detached the fruit successfully, it often ate the fruit after carrying it up to a high and horizontal branch. Persimmons carried into the nest by the animal were discovered in three of nest boxes set for the animal at Ōkawachi-hachiman Shrine (Andō et al., 1983). As the nearest persimmon trees from those nest boxes stood at the distance of 10–40 m, those fruits seemed to have been carried by way of gliding.

Once the animal started feeding, it usually kept feeding without break. The time of a bout was sometimes extended over two hours. Obvious differences were not found in the time of a feeding bout according to food items (Fig. 7). Now and then the animal shifted the position at which hind-paws were put during a bout, but did not move a long distance by gliding. Frequency and distance of shifts during a feeding bout differed according to food items (Fig. 8). In case of feeding on acorns of *Quercus glauca*, the ani-

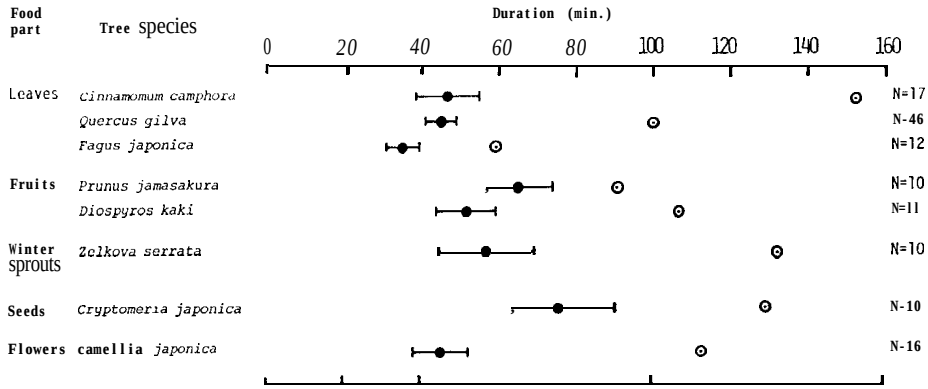

Fig. 7. Time required for a bout of feeding. Solid circle, mean; double circle, maximum ; horizontal line, standard error.

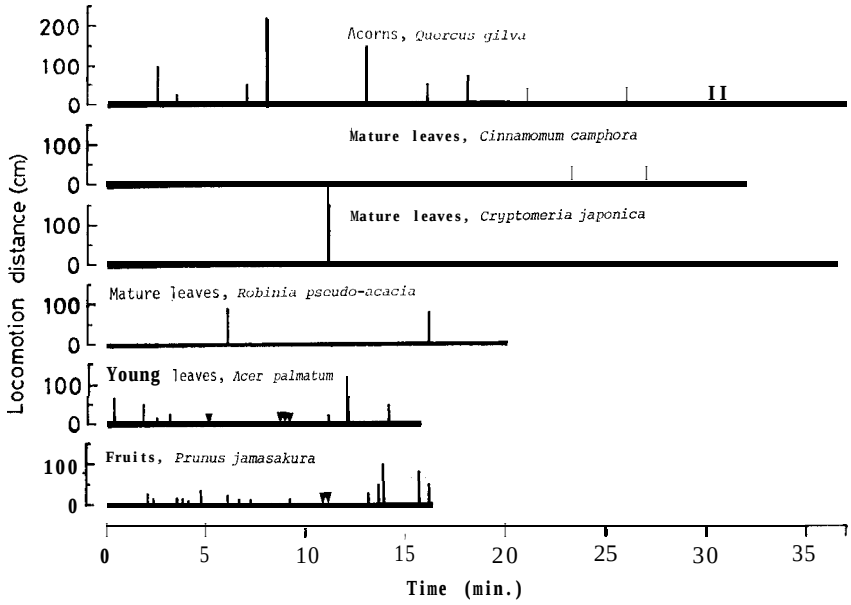

Fig. 8. Frequency of shift during a bout of feeding. Horizontal line, duration of a bout; solid triangle, occurrence of turning round without shift of feet; vertical line, occurrence and distance of locomotion on a tree.

mal moved a long distance from one branch to the other, because acorns were mainly born near the tip of each branch. The animal often did not move at all for more than 30 miuntes when it fed on mature leaves of *Cryptomeria japonica*, *Cinnamomum camphora*, ***Robinia pseudo-acacia*** and some ***Quercus*** species. On the other hand, it repeated short shifts frequently while eating young and small leaves of *Zelkova* ***sewata***, *Acer palmatum* and *Prunus jamasakura*, and also fruits of *Prunus jamasakura*. The bark of *Zelkova serrata* and *Prunus jamasakura* were eaten as the animal slided its feeding position inch by inch.

Further detailed analysis of the feeding behavior in a bout indicated that one bout consisted of repetition of three behavioral units, i. e. 1) extending the body to find and draw the food toward the mouth by gnawing off or bending and returning to the sitting posture, 2) gnawing and chopping the food with incisors, and 3) grinding the food with molars. The time spent in each unit varied according to the food items (Fig. 9). In most food, the animal spent little time for foraging. Exceptionally, it spared a considerable time for eating cherries, as it always sniffed them one by one to select ripe one. In case of eating winter-sprouts attached to a cut piece of twig, the animal sometimes sniffed the twig from end to end, while holding it in the forepaws and moving it sideways before it began to eat. The time needed for cutting or bending a twig was short. For example, a flowered twig of *Prunus jamasakura* with the diameter of 4 mm was gnawed off in only 6 seconds by the animal, and the time spent gnawing itself was no more than 0.6 seconds. Generally, bending and gnawing off of branches was not so frequent because the animal could get more than several food pieces from one twig gnawed off. In case of almost all food items, the greater part of the feed-

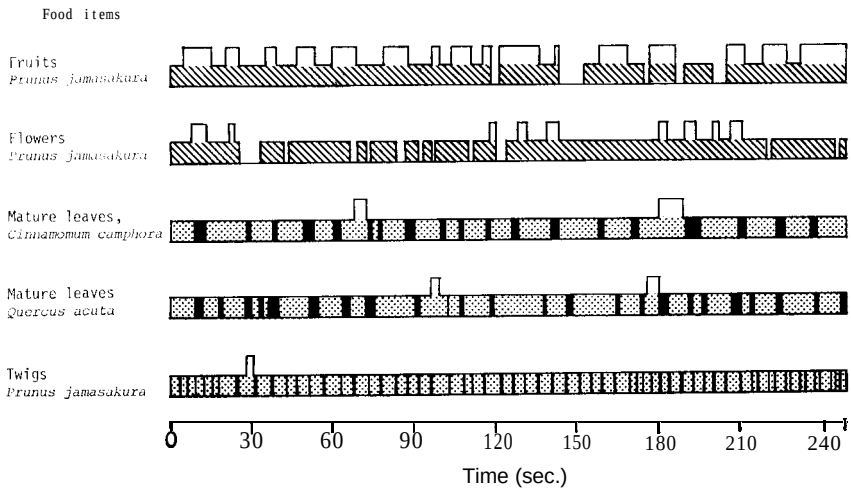

Fig. 9. Scheme of the feeding procedure of the animal at some point of time within a bout of feeding. Open column, forage ; solid column, gnawing and chop with incisors ; dotted column, grind with molars ; hatched column, mastication including gnawing, chop and grind.

ing time was spent on chopping and grinding. The animal kept masticating even while it was foraging. This phenomenon was most obvious when the animal fed on cherries. Chopping and grinding were distinguished clearly and were repeated alternatively, when the animal fed on fibrous food such as mature leaves of evergreen tree. On the other hand, they were not distinguished obviously in case of eating soft materials such as fruits.

4. **Feeding rate and analysis of stomach contents**

In the field, an adult consumed 81 mature leaves of *Cinnamomum camphora* in 60 min., 10 mature leaves of *Quercus acuta* in 21 min., 28 acorns of *Castanopsis cuspidata* in 21 min., 4 unripe cones of *Pinus densiflora* in 22 min., bark (660 cm^2) of *Zelkova serrata* in 60 min., 18 cherries of *Prunus jamasakura* in 4 min. and 20 sec., and 6 fruits of *Diospyros kuki* in 107 min. (79 min. except the time of break), respectively. Feeding rate of the juvenile was slower than that of the adult, i. e. a mother ate up 7 unripe nuts of *Camellia japonica* in 28 min. while her accompanied juvenile spent 80 min. to eat 9 nuts. The feeding rates (in wet weight) calculated by applying mean wet weight of each food item to above-mentioned results were as follows: 0.5 g/min. for leaves of *Cinnamomum camphora*, 3.5 g/min. for cherries of *Prunus jamasakura* and 2.8 g/min. for nuts of *Camellia japonica*.

A feeding bout of the animal was observed between just after sunset and just before sunrise. The relationship between the weight of stomach contents and the captured time in 15 animals was shown in Fig. 10. The weight of stomach contents occupied 5.7-7.0 % of the body weight in animals

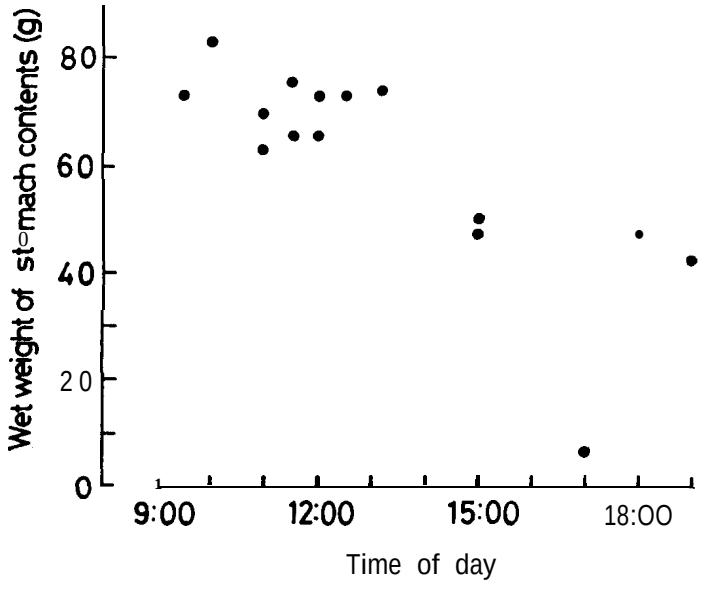

Fig. 10. Relationship between the wet weight of stomach contents and the captured time in adults.

Table 3. Analysis of stomach contents in the flying squirrels captured at Kamiyokoyama and Ōkawachi.

Place of capture	Individual number	Date of capture	Food item				
			Leaf	Bark	Acorn	Flower	Unidentified
Kamiyokoyama	1	Jan. 10 1982	14	86	0	0	0
	2	Jan. 10 1982	0	100	0	0	0
	3	Jan. 10 1982	+	100	0	0	0
	4	Jan. 10 1982	1	96	0	0	0
	5	Jan. 10 1982	92	5	0	3	
	6	Jan. 10 1982	90	10	0	0	0
	7	Jan. 10 1982	48	52	0	0	0
Ōkawachi	8	Feb. 5 1981	83	0	0	+	17
	9	Apr. 30 1981	90	0	0	0	10
	10	Apr. 30 1981	100	0	0	0	0
	11	Jul. 28 1979		0	0	0	0
	12	Jul. 28 1979	100	0	0	0	0
	13	Oct. 10 1979	0	0	100	0	0
	14	Oct. 10 1979		0	100	0	0

Figures mean percent. +, trace.

captured in the morning. Although the weight of stomach contents decreased as time went by, a fair amount of contents still remained in the stomach even in the evening. Except an animal which had almost empty stomach, it was characteristic in most animals that stomach contents were composed of only one or two kinds of food items (Table 3). In Kamiyokoyama, the animal fed mainly on leaves and bark in January, while in Ōkawachi-hachiman Shrine, it fed on leaves during winter to summer and on acorns in autumn. The animal matter was not eaten at all.

DISCUSSION

1. Feeding sites and feeding techniques

The animal seldom fed on at low branches. This may be to avoid predators. In general, carrying food is a procedure to feed at safer place (Bindra, 1948). The fact that the animal scarcely displayed carrying habits means that the arboreal space is free from dangers. *Sciurus vulgaris* and *Tamias sibiricus* often carry food from the ground to branches to feed, but they hardly do so when the arboreal visibility becomes good after defoliation (unpublished). It is worth while noticing that the animal carried only heavy items such as a persimmon (110 g) which was equal to about 10 % of the body weight. Accordingly it may be said that carrying habit has a meaning to seek after a stable place for feeding. *Sciurus aberti* (Hall, 1981), *Sciurus lis*, *Sciurus vulgaris*, *Tamias sibiricus* and *Pteromys volans* (unpublished) also carry food frequently from the tip of branches to thick and horizontal branches.

The animal was not able to sit on narrow twigs nor on branches with steep inclination. In addition, the hindpaws were always put on the branch at a right angle to it, and the feeding posture was always limited to the sitting

one. In the habitat of the animal, however, restrictions caused by the angle of branches did not seem serious, for few trees extend their branches vertically. The animal was also able to get food at a distance by gnawing off or bending branches. Although these feeding techniques are used by other squirrels as well (Reynolds, 1966), the application of these techniques to large branches as in the case of this animal has not been reported yet. Consequently, the animal was able to obtain almost all resources in trees, in spite of restrictions arising from the body weight and the feeding posture. In addition, these techniques were beneficial for the animal, 1) to take food which was hard to hold directly by the mouth despite of its propinquity, e. g. acorns or winter-sprouts which attached to the wrong side of the branch, 2) to save time for obtaining many pieces of food from a twig and 3) to eat food which was too small to handle with forepaws.

By the removal of terminal branches during the animal's feeding, the damaged tree shoots out many small lateral twigs from the remained part of the branch, and it grows thicker in the following years. As new lateral branches generate at more suitable position for the animal to gnaw off, cuttings by the animal may become more intensive in the following year (Imaizumi, 1983). Thus, a tree may be changed into a more suitable form for the animal to feed on by the pruning effect.

2. Feeding habit

Food storage is a habit seen widely among Sciuridae including gliders (Muul, 1968; MacClingtock, 1970; Thompson and Thompson, 1980; Hall, 1981; Wrazen and Wrazen, 1982). Except this species, the lack of food storage habit among this family is only known in some ***Ratufa*** species which live in tropical rain forest (Payne, 1980). This uniqueness in the Japanese giant flying squirrel seems to have derived from the dietary pattern that it depends on the food such as leaves available throughout the year (Andō and Imaizumi, 1982 ; Baba ***et*** al., 1982). Moreover, the following feeding habits may also be related with folivorous habit, i. e. repeated visits to the same feeding tree, and infrequent shifts and long feeding on a tree during a feeding bout. On the other hand, squirrels which feed mainly on seeds and insects search for their food eagerly (Emmons, 1980; Thompson and Thompson, 1980).

The animal spent almost all time of feeding bout for mastication of food, and did not spare much time for locomotion, searching and obtaining food. Accordingly, amount of food intake per unit time is chiefly decided by the feeding rate of each food item. Although feeding rate varied considerably according to food items, duration of each feeding bout did not differ so much. This means that the amount of food intake in a feeding bout is variable. Further, the fact that a considerable amount of food is still remained in the stomach even in the evening suggests that it takes long time for the animal to digest leaves or bark. On the other hand, the stomach of *Schoinobates volans*, a marsupial glider which resembles the animal in the diet and the body size, becomes nearly empty before sunset (Marples, 1973). This difference may be explained by the fact that the former continues feeding up to just

before sunrise, while the latter ceases its activity after midnight. Thus the time needed for digestion may give influences onthe pattern of feeding activity (Wrangham, 1977 ;Andō and Imaizumi, 1982).

From the facts mentioned above, it can be concluded that the animal overcomes restrictions concerning feeding sites and feeding postures by using feeding techniques such as bending and gnawing off branches, and that the feeding habit of the animal is adapted for feeding on abundant fibrous food items such as leaves.

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