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Food Habits of Formosan Rock Macaques (*Macaca cyclopis*) in Jentse, Northeastern Taiwan, Assessed by Fecal Analysis and Behavioral Observation

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*We studied the food habits of the Formosan rock macaques (*Macaca cyclopis*) in Jentse via fecal analysis and direct field observation from October 1991 to September 1992, and recorded macaques eating 51 plant species and insects of ≥5 orders. Macaques in Jentse spent more time feeding on fruits than on other plant parts or insects. However, there was seasonal variation in their food habits, i.e., they spent a higher proportion of time feeding on fruits and insects in summer, and on leaves and stems in winter. The major plant species consumed and the patterns of seasonal variation in the macaque diets identified by fecal analysis and field observation are similar. However, there are discrepancies between results from the two methods in some of the finer details of estimated dietary composition.*

KEY WORDS: *Macaca cyclopis*; food habit; fecal analysis; field observation.

INTRODUCTION

Fruits are a major food source for many Asian species of *Macaca* (Wheatley, 1980). The diet of rhesus macaques (*Macaca mulatta*) in a Siwalik forest, north India, was 65–70% frugivorous (Lindburg, 1977). Caldecott's

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(1986) study of pig-tail macaques (*Macaca nemestrina*) in the Malaysian Peninsular showed that they spent 74.2% of their feeding time on fruits. A study of long-tailed macaques (*Macaca fascicularis*) in Kalimantan Tengah, Indonesia, showed that fruits comprised 66.7% of their feeding records (Yeager, 1996). O'Brien and Kinnaird (1997) reported that crested black macaques (*Macaca nigra*) spent 66% of feeding time on fruits from 145 plant species. However, many studies also indicated intraspecific variation in the proportions of different plant parts in the diet due to factors such as food availability in different vegetation types and seasonal influences (Agetsuma, 1995; Yeager, 1996; Hill, 1997).

Formosan rock macaques (*Macaca cyclopis*) are the only nonhuman primate native to Taiwan. They are distributed extensively throughout Taiwan from an elevation of 100 m to >3,000 m and live in many different habitats, including natural broadleaf and coniferous forest, artificial forest plantation, bamboo forest, grassland, and orchard (Lee and Lin, 1987; 1990). They eat ≥78 plant species representing 34 families, as well as insects, crustaceans and mollusks (Lee, 1991). However, macaques that inhabit different elevations and habitats eat different plant species and consume different proportions of various plant parts. The dietary composition also changes from season to season. In the Kenting area of southern Taiwan, which has low altitude and is covered with subtropical monsoon forest, macaques ate 27 species of plants. They ate the leaves of *Pueraria montana* and *Ficus irisana* throughout most of the year; however, the fruits of *Palaquium formosanum*, *Diospyros discolor*, and some *Ficus* species made up a major part of their diet during the fruit season (Wu and Lin, 1987). Along the Nanshi logging road in central Taiwan (1,730–2,670 m asl), where vegetation is a mixture of primary broadleaf and coniferous forest, macaques ate 12 species of plants, the main food items being leaves (46.7%) and young stems (33.3%). Fruits accounted for only 20% of the diet (Lin *et al.*, 1988). Two studies along the Central Cross-island Highway (30–580 m and 580–2,550 m asl) showed macaques eating ≥26 species of plants. Macaques primarily fed on fruit and leaves, and there was seasonal variation in the number of feeding records on different plant parts (Lin and Lu, 1989; 1990). One of the two studies (at 30–580 m asl) indicated that the macaques ate leaves more often than fruit, while the opposite occurred during the other study. However, the total number of feeding bouts recorded in these two studies is only 88 in two years.

Due to the rugged topography of most of the study sites in Taiwan and the occasional disturbance of macaques by local people, the Formosan rock macaques are often not completely habituated to researchers and cannot be observed continuously for a long period of time. In addition, the food habits of Formosan rock macaques reported from previous studies were often based

on a limited amount of observation because feeding behavior was only a small part of a broader research agenda. The aim of our research was to study the food habits of the Formosan rock macaques in Ilan, northeastern Taiwan. By using both fecal analysis and direct field observation, we hoped to obtain a more complete picture of their food habits in the area and to compare the results of the two different methods of study.

STUDY SITE AND METHODS

Study Site

Jentse (24°33′N, 21°30′E) is in a mountainous area of Ilan County in northeastern Taiwan. The elevation ranges between 500 and 900 m. Jentse is a recreation area famous for its hotsprings. It is situated in a valley, surrounded by rugged mountain slopes. One paved road and two dirt trails are the main access routes to the area (Fig. 1).

The climate is generally humid and warm. Mean annual temperature falls between 16.1°C and 28.3°C, and mean monthly precipitation ranges between 237 and 583 mm. The rainy season lasts from October to February. The dominant vegetation is secondary broadleaf evergreen forest forming a mosaic with patches of grass and artificial plantations of conifers. The major broadleaf tree species at the study site include *Trema orientalis, Machilus japonica, Mallotus japonicus, Broussanetia papyrifera, Schefflera octophylla, Liquidambar formosana* and *Ficus microcarpa*.

Methods

There were ≥6 troops of macaques in Jentse, the largest of which contained 31 individuals (Su, 1993). From October 1991 through June 1992 (excluding January), we visited the study site twice per month and stayed 3–4 days each time to conduct fieldwork on the macaques. In January 1992, we visited the site only once, but stayed for 6 days. To assess whether more intensive observation would affect the results in terms of macaque dietary composition, we also stayed at the study site for longer spans and conducted fieldwork intensively between July and September 1992. The total number of working days during these months is 44. The total time spent in the field during the course of the study is 1,286 hours. Each month we routinely surveyed the same sections of paved road and trails (survey routes) to look for macaques and to collect their feces (Fig. 1). Once the macaques were spotted, we followed them to record their behavior until they were out of view.

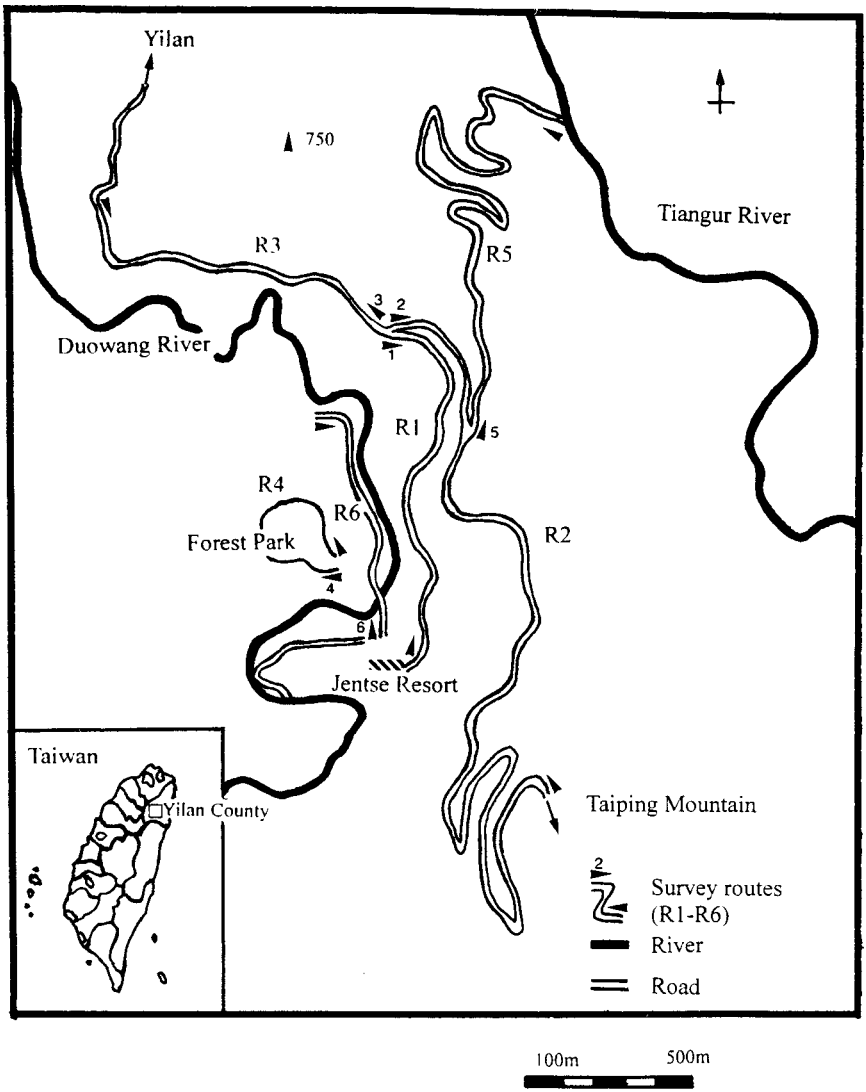

Fig. 1. Map of the Jentse area, showing the survey routes.

Fecal Analysis

We tried to collect 10 fecal samples each month from different parts of the survey routes to increase the possibility that they were from different troops of macaques. We brought the samples back to the laboratory

and dried them in an oven at 80–90°C for 2–3 days and stored them in airtight containers. Before analysis, we dried the fecal samples again until their weights changed little upon further drying, then we recorded their weights. We soaked each sample separately in hot water, stirred it evenly, and took one quarter of each sample randomly for identification and to record its contents (Korschgen, 1980). We first divided the contents of each subsample into four types of food item: fruits, plant body, flower, and animal matter. We pooled the remains of seed, peel and pulp in the feces as fruit, and the fiber of stems and leaves as plant body. We could identify flowers by their calyxes. We then tried to identify the food items to species, as far as possible.

In the analysis, we recorded the presence or absence of each food item and plant species in each sample and calculated their frequency of occurrence in samples analyzed each month (Leopold and Krausman, 1986). In order to compare the relative importance of each food item in the feces, we first estimated the proportion by volume of each food item in the fecal sample and gave it a score on a scale of 1–10. Since only the calyxes were left in the feces, the relative importance of flowers in the feces is negligible. The total score of the three food items that make up the bulk of the macaque diet, i.e., fruits, plant body and animal matter, would be 10 for each fecal sample. Thus, the relative importance (RI) of each food item would be:

$$\mathrm{RI} = \left[\sum_{i=1}^{n} (\mathrm{Wi} \times \mathrm{Si}) \Big/ \sum_{i=1}^{n} (\mathrm{Wi} \times 10) \right] \%$$

in which, Wi is the dry weight of each fecal sample, Si is the score of each food item, and n is the sample size (Wise *et al.*, 1981).

Field Observation

On sighting macaques, we followed and observed them via binoculars (8×30) and a telescope (20 or 40×60), and recorded their activity and feeding behavior using the scan-sampling method (Altmann, 1974) at 10-min intervals. We defined feeding behavior as when macaques collect food orally or manually, ingest food, or handle food. During scan sampling, we collected data on sex, age and activity of each visible troop member in turn, which usually took about 5 min. For each individual that was feeding, we counted the scan sample as one feeding record. Between scan sampling, we observed the macaques *ad libitum* and recorded the plant species consumed by them.

We calculated the monthly percentage of time spent consuming each food item or plant species based on the scan samples from the number of

feeding records for each food item or plant species divided by the total number of feeding records each month (Maruhashi, 1980; Lawes, 1991). We calculated the annual dietary composition of the macaques by dividing the number of feeding records for each food item by the total number of feeding records obtained by scan sampling during the course of the study. To reduce potential bias due to the fact that more observation time was spent during the intensive observation period from July through September 1992, we used only feeding records collected during two sets of 3–4 working days in each of these months to calculate the annual diet.

RESULTS

Food Habits Constructed from Fecal Analysis

The number of fecal samples collected each month between October 1991 and September 1992 varied. Although we attempted to collect and to analyze 10 fecal samples each month, fewer were collected in December and between January and March (Table I). The total number of fecal samples analyzed is 101. As only one sample was collected in February, we excluded it from the data analysis.

The frequencies of occurrence of fruits, plant bodies, flowers, and animal matter in macaque feces are 96%, 98%, 3%, and 83.2%, respectively. The frequencies of occurrence of fruits and plant body are >80% every month and show no seasonal variation, whereas the frequencies of occurrence of flowers and animal matter evidence seasonal variation. Flowers were present only in the feces from March and April. Insect remains were in most feces during the summer and early fall, but their frequencies dropped to <60% in winter.

The relative importance of fruits, plant bodies, and animal matter in feces is 46.2%, 47.6%, and 6.2%, respectively. Flowers occurred only in trace amounts. The relative importance of each food item in the feces varied seasonally (Fig. 2). The importance of both fruits and animal matter increased in summer (except in June) and early fall, whereas the importance of plant body increased in winter. According to the relative importance of individual plant parts, leaves and stems constitute >60% of the macaque diet from November to April.

We discovered the remains of ≥46 species of fruits in the feces, and could distinguish 44 of them by their seeds, which changed little in appearance, size, shape, and color during digestion. Twenty-two of them could be identified to species, including 5 species that were not observed to be eaten by the macaques during field observation (Table I). We could not identify the other

Table I. Fruit species in the feces of the Formosan rock macaques in Jentse, and their frequencies of occurrence

Plant type	Species\month	1991 10	11	12	1992 1	3	4	5	6	7	8	9
Large	*Broussanetia papyrifera*									0.3	0.11	
Evergreen tree	*Adinandra formosana**			*0.63*								
	Ficus erecta	0.3								0.1	*0.67*	*0.8*
	Ficus superba	0.1	0.1		0.14			*0.5*	*0.5*	*0.5*		
	Ficus variegata	*0.6*	0.3	0.13			0.1				0.11	0.3
	Machilus japonica									0.3	0.11	0.3
	Saurauia tristyla		0.2					0.2	0.3	0.3		
	Trema orientalis			0.13							0.11	0.4
	Turpinia formosana	*0.6*							0.1		*0.78*	*0.8*
Small	*Callicarpa dichotoma*	0.1	*0.5*	0.38						0.1	0.22	0.2
Evergreen tree	*Debregeasia orientalis*						*0.7*	1				
	Oreocnide pedunculata		0.1	*0.88*	*0.57*							
Shrub	*Rubus swinhoei**							*0.5*	0.3			
Herbaceous tree	*Musa formosana*	0.3	0.2					0.1		0.2	0.22	0.3
Herb	*Alocasia macrorrhiza*									*0.8*	0.22	0.4
	*Codonacanthus pauciflorus**	0.2	0.4	*0.75*								
	*Duchesnea chrysantha**								0.2	0.4		
Woody vine	*Ficus pumila*	*0.7*				0.33	0.2			0.2	0.22	0.4
	*Passiflora edulis**								0.2			
	Schefflera odorata			0.38								
	Vitis kelungensis										0.11	
Herbaceous vine	*Thladiantha nudiflora*	0.1										
	# of feces analyzed	10	10	8	7	6	10	10	10	10	9	10
	# of plant species identified	19	14	13	3	6	9	11	14	17	18	11

*Species that were not observed to be ingested by macaques.
Italic: frequency of occurrence >50%.

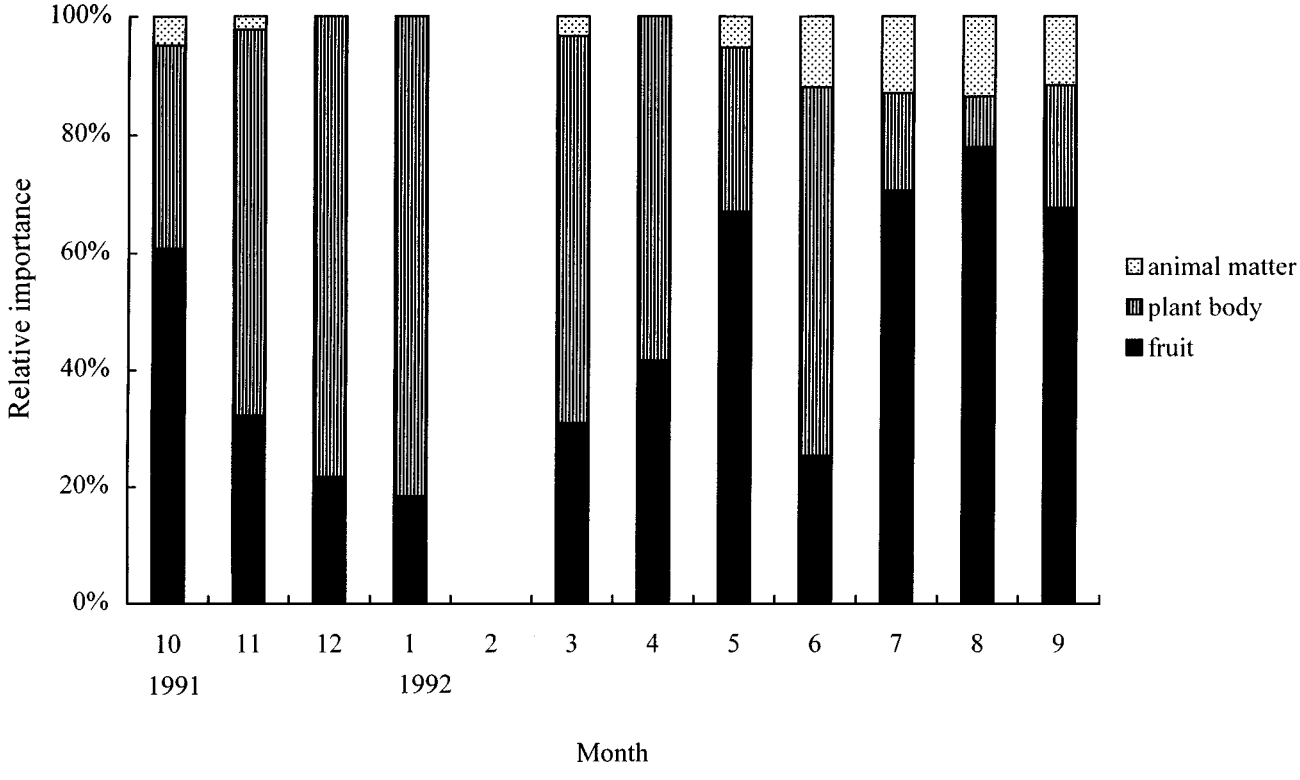

Fig. 2. Seasonal variation in relative importance of various food types in the feces of the macaques collected monthly from October of 1991 to September of 1992 (except February) (n = 101).

24 fruits to species, but they include two species each of *Ficus* and *Rubus*, and one species of each of the Cucurbitaceae and Araceae. Most of them had low frequencies of occurrence. The seeds came from plants which we did not see being eaten by the macaques and which occurred mostly in the understory. The major fruit species in the macaque diet, ones with higher frequencies of occurrence (Table I), are *Alocassia macrorrhiza, Turpinia formosana, Ficus erecta, F. variegata* and *F. pumila* in summer and *Oreocnide pedunculata, Adinandra formosana* and *Codonacanthus pauciflorus* in winter.

Among the partially digested remains of leaves and stems, only those of one species could be reliably identified: *Pueraria montana*, whose cilia resist digestion and are identifiable in the feces. The frequency of occurrence of *Pueraria montana* is >50% from October 1991 to May 1992, but no cilia of *P. montana* appeared in the feces from July and August 1992.

Animal matter in the feces included beetles (Coleoptera), grasshoppers (Orthoptera), cicadas (Homoptera), caterpillars and cocoons (Lepidoptera), and the stem section of hives of Hymenoptera. The remains of beetles had the highest frequency of occurrence (86.2%) among all insect remains. Remains of caterpillars and cocoons occurred at higher frequency in summer (25.4%) than in winter (4.9%).

Food Habits Constructed from Field Observation

There was considerable variation in the amount of data available for each month, due to changes in visibility of the macaques and differences in field time (Table II). In particular, the intensive data collection from July to

Table II. The observation times, number of scan samples, and number of feeding records during behavioral observations on the monkey troops in Jentse each month between October 1991 and November 1992

Month	Observation time (min.)	Number of scan samples	No. of feeding records
Oct., 1991	268	20	12
Nov.	180	22	14
Dec.	205	49	13
Jan., 1992	557	153	61
Feb.	323	38	8
Mar.	653	71	15
Apr.	526	124	63
May.	430	59	30
Jun.	159	42	9
Jul.	1247	159	121
Aug.	1966	694	258
Sep.	518	179	91

September produced more feeding data than are available for other months. To reduce potential biases, when examining the annual diet we used records collected during two sets of 3–4 field days in each month. However, when comparing the percentage of time macaques spent on different plant species or parts in each month, we used all the data to increase sample sizes.

We observed the macaques eating 46 identifiable plant species and 10 unidentified plant species in Jentse. The former included 29 species that had not previously been recorded as foods of Formosan rock macaques. Besides fruits, flowers, leaves, stems, and shoots of plants, the macaques occasionally ate the bark of *Trema orientalis* and *Lagerstroemia subcostata* (Table III). When eating fruit, macaques generally ate whole fruits, including the pulp and core. We did not observe the macaques eating only the seeds. However, most seeds of the fruit species were also ingested, and could be found in the feces.

By categorizing the food eaten by the macaques into various food types, including fruits, flowers, leaves, stems and shoots, we found that fruit comprised the highest proportion of the annual diet of the Formosan rock macaques (53.8%). Flowers comprised 7.32% of the diet, while leaves made up 14.92%, stem occupied 11.76%, shoots 2.44%, and insects constituted 9.76% of the annual diet.

There was seasonal variation in the proportion of each food type in the diet of the macaques (Fig. 3). The proportion of fruit in their diet increased in summer. The macaques spent most time eating the fruit of *Trema orientalis* during July, August, and September (27.5%, 25%, and 27.5%, respectively). They also spent a high proportion of time eating fruit of *Ficus irisana* in November. They consumed leaves and stems every month, but the peak time spent (>50%) on leaves and stems was in winter months (excluding November). In October, they spent most feeding time consuming the immature leaves and stems of *Broussanetia papyrifera*. Between December and February, they ate the leaves and stems of vines, especially *Pueraria montana, Clematis gouriana* and *Polygonum multiflorum*. From March to May, they spent more time on shoots and immature leaves of *Broussanetia papyrifera*. In April, they spent more time on flowers, particularly *Broussanetia papyrifera*. Insects, including cocoons and occasionally flying insects, constituted around 20% of seeding effort in July and August. Feeding on insects dropped sharply in September.

Comparison of Results from Fecal Analysis and from Field Observation

A total of 51 plant species were in the Jentse macaque diet based on fecal analysis and field observation; 33 of them are new records for the diet

Table III. Plant species and plant parts consumed by the Formosan rock macaques in Jentse between October 1991 and September 1992

Plant type	Family name	Species\Plant part	Fruit	Flower	Leaf	Stem	Bud	Bark
Conifer	Taxodiaceae	#*Cryptomeria japonica* (L. f.) D. Don		*		*	*	
		#*Cunninghamia konishii* Hayata					*	
Large broadleaf tree	Ulmaceae	*Trema orientalis* (L.) Bl.	*			*	*	*
	Moraceae	*Broussanetia papyrifera* (L.) L'Herit. ex Vent	*	*	*	*	*	
		Ficus erecta Thunb. var. *beecheyana* (Hook. & Arn.)	*		*	*	*	
		F. irisana Elm	*					
		F. nervosa Heyne ex Roth	*					
		F. superba (Miq.) Miq. var. *japonica* Miq.	*					
		F. variegata Bl. var. *garciae* (Elm) Corner	*			*		
	Lauraceae	*Machilus japonica* Sieb. & Zucc. var. kusanoi (Hayata) Liao	*		*	*		
		#*Phoebe formosana* (Hayata) Hayata	*					
	Actinidiaceae	#*Saurauia tristyla* DC. var. *oldhamii* (Hemsl.) Finet & Gagncp.	*		*	*		
	Theaceae	@#*Adinandra formosana Hayata var. formosana.*	*					
		#*Eurya gnaphalocarpa* Hayata	*					
	Rosaceae	*Eriobotrya deflexa* (Hemsl.) Nakai	*					
		#*Prunus campanulata*	*					
		#*P. phaeosticta* (Hance) Maxim.	*					
	Erythroxylaceae	*Bischofia javanica* Blume	*		*			
	Euphorbiaceae	*Mallotus japonicus* (Thunb.) Muell. -Arg.		*	*			
		M. paniculatus (Lam.) Muell.-Arg.					*	
	Staphyleaceae	#*Turpinia formosana* Nakai	*					
	Lythraceae	*Lagerstroemia subcostata* Koehne		*				*
	Ebenaceae	#*Diospyros morrisiana* Hance	*					
Small broadleaf tree	Moraceae	*Morus australis* Poir.	*		*	*	*	
	Urticaceae	*Debregeasia orientalis* C. J. Chen	*	*				
		#*Oreocnide pedunculata* (Shirai) Msamune	*			*		
	Stachyuraceae	#*Stachyurms himalaicus* Hook. f. & Thomson ex Benth.				*		
	Araliaceae	#*Tetrapanax papyriferus* (Hook.) K. Koch			*			

(*Continued*)

Table III. (*Continued*)

Plant type	Family name	Species\Plant part	Fruit	Flower	Leaf	Stem	Bud	Bark
	Verbenaceae	#*Callicarpa dichotoma* (Lour.) K. Koch	*					
	Arecaceae	#*Arenga engleri* Beccari	*					
Shrub	Rosaceae	#*Rubus fraxinifoliolus* Hayata	*					
		@#*R. swinhoei* Hance	*					
	Araceae	#*Alocasia macrorrhiza* (L) Schott & Endl.	*					
Herbaceous tree	Musaceae	#*Musa formosana* (Warb.) Hayata	*					
Herb	Rosaceae	@#*Duchesnea chrysantha* (Zoll. & Mor.) Miq.	*					
	Acanthaceae	@#*Codonacanthus pauciflorus* Nees	*					
	Asteraceae	#*Crassocephalum rabens* (Juss. ex Jacq.) S. Moore			*			
	Cyperaceae	#*Scirpus ternatanus* Reinw. ex Miq.	*					
	Poaceae	#*Miscanthus floridulus* (Labill.) Warb. ex Schum & Laut.			*	*		
		#*Setaria pallide-fusca* (Schumach.) Stapf & G. E.			*			
Woody vine	Moraceae	*Ficus pumila* L. var. *awkeotsang* (Makino) Corner	*					
	Vitaceae	#*Vitis kelungensis* Moriyama	*					
	Araliaceae	#*Schefflera odorata* (Blanco) Merr. & Rolfe	*					
Herbaceous vine	Polygonaceae	#*Polygonum multiflorum* Thunb. ex Murray var. *hypoleucum* (Ohwi) Liu, Ying & Lai	*		*	*		
	Ranunculaceae	#*Clematis gouriana* Roxb. ex DC. Subsp. *Lishanensis*		*	*	*		
	Convolvulaceae	*Pueraria montana* (Lour.) Merr.		*	*	*	*	
	Cucurbitaceae	#*Thladiantha nudiflora* Hemsl. ex Forbes & Hemsl.	*		*	*		
	Passifloraceae	@ *Passiflora edulis* Sims.	*					
	Asclepiadaceae	#*Hoya carnosa* (L. f.) R. Br.		*	*			
	Asteraceae	#*Senecio scandens* Ham. ex D. Don			*			
	Araceae	#*Pothos chinensis* (Raf.) Merr.	*		*			

#: Newly recorded plant species in the Formosan rock macaque's diet.
@: Found only in fecal samples.

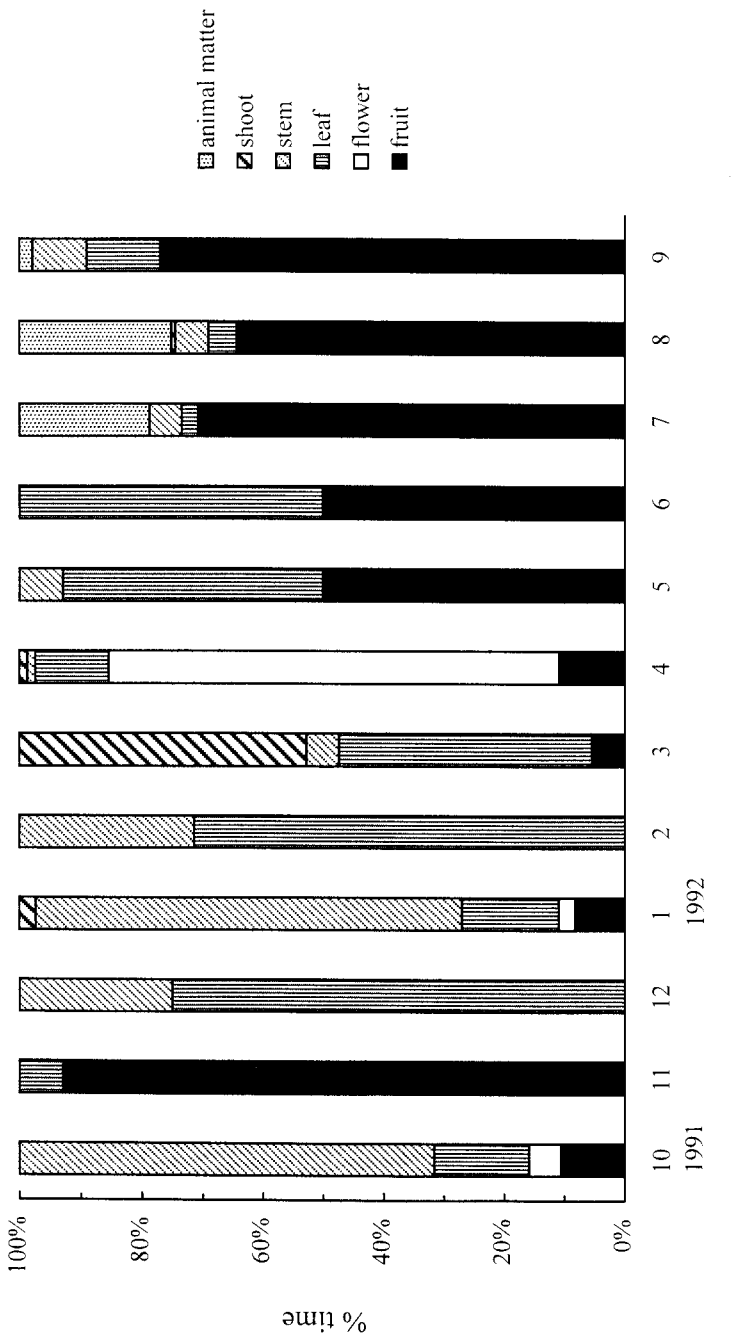

Fig. 3. Percentage of time spent feeding on various food types by the macaques as estimated via scan sampling from October of 1991 to September of 1992.

of Formosan rock macaques (Table III). There are some discrepancies in results obtained from the two methods. Some plant species, such as *Adinandra formosana, Codonacanthus pauciflorus, Passiflora edulis, Rubus swinhoei, Duchesnea chrysantha* and other unidentifiable seeds of vine and understory plants, were in macaque feces, but we never saw macaques eating them. Conversely, we saw macaques eating, *Ficus irisana, Prunus phaeosticta, Pothos chinensis* and *Diospyros morrisiana*, but they were not in the fecal samples.

We recorded fruit of 17 species as macaque foods by both methods, but the proportions of these fruit in the macaque diet differed between methods. The seeds of *Ficus variegata, F. superba, F. pumila, Musa formosana, Saurauia tristyla, Oreocnide pedunculata, Debregeasia orientalis* and *Alocasia macrorrhiza* were in macaque feces from more months than those we recorded via observation. For example, the macaques ate *Musa formosana* only in September, but the seeds of *M. formosana* were in feces from May and between July and November.

The monthly variation in the importance of different food types in the macaque diet show similar patterns by both methods (Figs. 2 and 3). However, the importance of insects in their diet was better represented by fecal analysis. We observed them eating insects only from July to September, and only pupae were identified on such occasions. However, the remains of insects were in feces from each month throughout the study period, and we identified 5 orders of arthropods by fecal analysis.

DISCUSSION

Comparison of Different Study Methods

Various methods have been used to assess the dietary compositions of animals, including direct observation in the field (Clutton-Brock, 1977; Oates, 1988; Nakagawa, 1989; Grether *et al.*, 1992), fecal analysis (Moreno-Black, 1978; Putman, 1984), feeding experiments (Baker, 1987), and analysis of gut contents (Gautier-Hion, 1978). However, an animal's complete diet often cannot be fully revealed by one of these methods alone. The use of multiple methods is preferable in order to obtain more complete information about the animal's diet. Accordingly, we conducted both fecal analysis and field observation in order to have a better understanding of the dietary composition of Formosan rock macaques.

We did not distinguish between feeding on fruits and feeding on seeds because the macaques generally ate whole fruits rather than only pulp or seeds. This is probably due to the fact that the seeds of the majority of the

fruit species consumed by Jentse macaques are very small. According to a study on the fate of seeds consumed by the Formosan rock macaques at Fushan, northeastern Taiwan, where trees of Lauraceae predominate, seeds $<3.5 \times 5$ mm were swallowed with the pulp by the macaques, and seeds larger than this size were either spat out or chewed up (Chen, 1999). As the seeds of many species occurred in the Formosan rock macaque feces, and as seeds are quite different from pulp in terms of nutritional content and chemical deterrents (Waterman and Kool, 1994; Corlett, 1996), it is important to find out whether it was seeds or pulp that attract the Formosan rock macaques.

Vine and shrub plant species like *Rubus swinhoei, Debregeasia orientalis, Codonacanthus pauciflorus, Alocasia macrorrhiza* and *Passiflora edulis* were in Jentse macaque feces, but feeding on these species is difficult to observe. Therefore, their importance could not be fully represented in the macaque diet without conducting fecal analysis. Feeding on insects posed another challenge to field observation. We saw the macaques eating insects only from July to September, and the prey were mostly non-flying insects and pupae. However, insects occurred in feces throughout the year, and more orders of insects were in feces than were observed being eaten. This shows that field observation alone is inadequate to estimate the presence and variety of insects in the diet. This may also be the reason why insects have so seldom been reported as being eaten during other observational studies of Formosan rock macaques (Wu and Lin, 1987; Lin *et al.*, 1988; Lin and Lu, 1989; 1990).

Since the contents of feces represent the undigested remains of foods, it was difficult to identify them to specific level, especially the leaves and stems. The different digestibility of food items would also affect the proportion of their remains in feces (Putman, 1984). Due to these problems, the remains of each food item in feces could not be used to estimate its importance in the diet. Therefore, conducting both field observation and fecal analysis concurrently enabled us to obtain more complete information on the dietary composition of the Jentse macaques.

The Diet of Formosan Rock Macaques

Many Asian macaques have been defined as frugivores, since fruits comprises >50% of their diet (Lindburg, 1977; Caldecott, 1986; Yeager, 1996; O'Brien and Kinnaird, 1997). Caldecott (1986) suggested that the food habits of macaque species consists of 50–90% fruits and seeds, while other plant parts account for 10–30%, and animal matter for 1–10% of the diet. The dietary composition of Formosan rock macaques, based on data from scan sampling in Jentse, shows that they spent the highest proportion of their feeding time (53.8%) on fruit, whereas plant parts and insects constituted only

36.4% and 9.8% of their feeding time, respectively. This result is qualitatively similar to that in the Kenting area, where the Formosan rock macaques also spent more annual feeding on the fruit of various plant species (Wu and Lin, 1987). These results indicate that Formosan rock macaques are frugivores. However, in the studies conducted in central Taiwan at mid-elevation (1,730–2,670 m) and along the Central Cross-island Highway at low elevation (30–580 m), leaves comprised the highest proportion of the macaque annual feeding records (58.3% and 50.94% respectively) (Lin *et al.*, 1988; Lin and Lu, 1989).

Many factors may contribute to differences in the proportion of fruit in the diet as reported in various studies. Different methodology and sampling periods may lead to different results. In the Kenting and Jentse studies, macaque troops were followed and observed as long as they were visible, whereas in the studies in central Taiwan and along the Central Cross-island Highway, the macaques were observed during a transect walk. The feeding behavior of each macaque troop spotted in the latter studies was observed for $\leq$20 min before the researcher moved on to find other macaque troops. Although some troops were occasionally followed for longer spans, such observation was infrequent and few feeding records were accumulated annually ($n = 53$) (Lin *et al.*, 1988; Lin and Lu, 1989).

Leaves and stems are predominant food types in the Formosan rock macaque diet during the winter season when the availability of fruit is low (Wu and Lin, 1987; Lin and Lu, 1989; Su, 1993). In at least one study, poor weather and road conditions prevented data collection throughout a significant portion of the summer (July to August) (Lin *et. al.*, 1988), which might have caused a bias towards leaves and stems in calculating the annual diet.

Variation in food availability due to differences in vegetation and plant phenology at different study sites or in different years may also affect macaque diets. Two recent studies on the dietary composition of Formosan rock macaques at Fushan Experimental Forest (600–800 m asl), in northeastern Taiwan, revealed that the proportion of fruit in their diet varied from 38% to 52% in different years (Chang, 1999; Chen, 1999). Such results also make it difficult to assign the Formosan rock macaque as a frugivore.

Furthermore, although fruit accounted for 53.8% of Formosan rock macaque annual diet, this proportion is low in comparison with the proportions of fruit in the diets of other macaque species reported by Caldecott (1986). Japanese macaques (*Macaca fuscata yakui*) in the lowland forest of Yakushima are dietary generalists, and their diet is not readily assigned to a simple dietary category (Hill, 1997). For Formosan rock macaques, further studies in different habitats and more long-term studies are required to determine whether they actually have a lower tendency toward frugivory than those of other *Macaca* species.

Of the 33 newly recorded plant species eaten by Jentse macaques, half are vines and herbaceous plants, which are widely distributed. Furthermore, of the 8 identified vine species, which were eaten by macaques, the leaves and stems of *Pueraria montana, Clematis gouriana* and *Polygonum multiflorum* were their main food resource in winter. Dasilva (1994) pointed out that *Colobus polykomos* at Tiwai, Sierra Leone, prefer liana to tree leaves and suggested that this is a result of the lower amount of secondary compounds in vine plants than in evergreen plants. Richard (1985) suggested that tannin and alkaloids, which are abundant in the leaves of evergreen plants, retard macaque digestion. The Formosan rock macaques ate various kinds of vines simultaneously, which may be a strategy to avoid accumulating too much of a single toxic or digestion retardant secondary compound (Milton, 1979; Agetsuma, 1995; Hill, 1997). Phytochemical analysis and comparison of leaves eaten and those not selected by the macaques may help to reveal how the Formosan rock macaques select their food in the wild.

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