

American Society of Mammalogists

Food Availability and Food Habits of Indian Giant Flying Squirrels (*Petaurista philippensis*) in Taiwan

Author(s): Chi-Chien Kuo and Ling-Ling Lee

Source: *Journal of Mammalogy*, Vol. 84, No. 4 (Nov., 2003), pp. 1330-1340

Published by: American Society of Mammalogists

Stable URL: <http://www.jstor.org/stable/1384019>

Accessed: 14/05/2009 04:09

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=asm>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



American Society of Mammalogists is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Mammalogy*.

<http://www.jstor.org>

FOOD AVAILABILITY AND FOOD HABITS OF INDIAN GIANT FLYING SQUIRRELS (*PETAURISTA PHILIPPENSIS*) IN TAIWAN

CHI-CHIEN KUO AND LING-LING LEE*

Department of Zoology, National Taiwan University, Taipei, Taiwan, Republic of China

We assessed seasonal variation in food habits of Indian giant flying squirrels (*Petaurista philippensis*) and food availability at Fushan Experimental Forest in Taiwan. Between July 1997 and December 1998, giant flying squirrels consumed at least 79 species-specific parts belonging to 30 plant species from 19 families. *Castanopsis cuspidata* was eaten most often (24.95% of annual diet), followed by *Ficus superba* (14.67%) and *Glochidion acuminatum* (12.18%). *P. philippensis* fed mainly on young leaves (27.7% of annual diet) and mature leaves (24.0%). Leaf parts (including buds, petioles, young leaves, and mature leaves) constituted 74.0% of the annual diet. Monthly and annual diet variation was obvious, and this was related to availability of species-specific plant parts. *P. philippensis* fed on mature leaves and petioles in winter; buds, young leaves, and fruit in spring; and young leaves and fruit in summer and autumn. They preferred buds, young leaves, flowers, and fruit to mature leaves and petioles. However, mature leaves and petioles seemed to be relied on when more favorable food items were scarce.

Key words: folivore, *Petaurista philippensis*, phenology, Taiwan

Impact of plant phenology on primary consumers has gained much attention in recent years (Curran and Leighton 2000; Terborgh 1986; van Schaik et al. 1993; White 1998). Spatial and temporal fluctuation in the production of plant parts contributes to changes in the diets of animals (Agetsuma 1995; Chapman 1987; Dasilva 1994; Kawamichi 1997), their ranging behavior (Doran 1997), activity patterns (Dasilva 1992; Stoner 1996), and reproduction (van Schaik and van Noordwijk 1985). Seasonal or multi-annual variation in availability of resources suggests the presence of behavioral, physiological, and morphological adaptations in consumers (van Schaik et al. 1993) and may influence the composition of vertebrate faunal communities (Fleming et al. 1987). Furthermore, certain species of plants provide alternative food sources during seasons of food scarcity and may be

vital for population persistence (Terborgh 1983).

Dietary variation in response to plant phenology and changes in availability of resources has been reported in frugivores, particularly primates and birds (Agetsuma 1995; Guillotin et al. 1994; Leighton and Leighton 1983; Poulsen et al. 2001), but little information exists for folivores (Dasilva 1992; Kool 1993; Peres 1994), perhaps because leaves are considered a stable and ample food source. However, leaves are often a low-quality food because they possess chemical or mechanical deterrents to consumption. Folivores may use behavioral adaptations to counteract plant defenses, i.e., by selecting food of higher quality or parts of plants low in cellulose, such as buds, young leaves, flowers, or fruit, instead of mature leaves (Cork and Foley 1991). However, preferred food may be seasonal (Rathcke and Lacey 1985), and folivores may shift to different species and parts of plants when availability of food changes.

* Correspondent: leell@ccms.ntu.edu.tw

Giant flying squirrels of the genus *Petaurista* inhabit areas of India, southeastern Asia, and northern Asia, including Korea and Japan (Corbet and Hill 1992). They are larger in size (body mass 1.0 to 2.5 kg—Nowak 1999) than flying squirrels of most other genera. Studies of their diet indicate that they are mainly folivorous (Ando et al. 1985; Kawamichi 1997; Lee et al. 1986; Muul and Liat 1978). Muul and Liat (1978) compared 11 species of flying squirrels from 7 genera on the Malaysian peninsula and reported that those in the genus *Petaurista* have the longest cecum, which correlates with the finding that they have the highest degree of folivory. However, Ando et al. (1985) and Kawamichi (1997) reported the diet of *Petaurista leucogenys* (0.7 to 1.5 kg) to be seeds or foliage, depending on the season.

Petaurista philippensis (1.3 kg—Lee 1998) was classified previously as *P. petaurista* (Corbet and Hill 1992). It is 1 of 3 flying squirrel species native to Taiwan, where they occur in low- to medium-elevation forests. Lee et al. (1986) described its diet in central Taiwan to be mainly leaves, occasionally including buds, flowers, or fruit. However, little quantified information on seasonal and annual variation in the diet of this species has been reported. In this study, we report seasonal variation in the diet of *P. philippensis* and describe its relationship to local plant phenology.

MATERIALS AND METHODS

Study site.—The study was conducted in the Botanical Garden of Fushan Experimental Forest Station (24°46'N, 121°34'E) at the border of Taipei and Ilan counties in northeastern Taiwan. The Botanical Garden is situated 600–800 m in elevation. Average monthly temperatures from July 1997 to December 1998 ranged from 12.1 to 24.4°C. Monthly rainfall varied from 66.5 to 1,082.5 mm (Y. J. Hsia, pers. comm.).

The study site is a subtropical moist hardwood forest, with 515 plant species belonging to 329 genera and 124 families recorded (Taiwan Forestry Research Institute 1989). The dominant species of trees are in the families Lauraceae and

Fagaceae. The site contained 4 general habitats: *Ficus erecta* type, secondary forest beside creeks; *Phoebe formosana* type, primary forest beside creeks dominated by *P. formosana* and *Persea japonica*; *Engelhardia roxburghiana* type, primary woodland in slope area dominated by *E. roxburghiana*, *Castanopsis cuspidata*, *Limlia uraiana*, and *Machilus thunbergii*; and *C. cuspidata* type, primary forest along mountain ridges (Chang et al. 1986). *Aeschynanthus acuminatus*, *Pothos chinensis*, and *Pileostegia viburnoides* are the most common epiphytes (C. Y. Lee, pers. comm.).

Feeding observation and diet analysis.—Between July 1997 and December 1998, we spent at least 5 nights per month observing flying squirrels. Each night around dusk, we walked along a transect (7.1 km) and observed flying squirrels with a spotlight and binoculars. We recorded behavior of individual flying squirrels continuously using instantaneous sampling (Altmann 1974) at 1-min intervals until the flying squirrel disappeared from view. If the flying squirrel was found eating at the beginning of each sampling minute, it was counted as 1 feeding record. The species and parts of plants eaten were also recorded. Parts of plants eaten were divided into 8 categories: buds, young leaves, mature leaves, fruits, seeds, flowers, petioles, and bark.

When estimating monthly diets, the proportion of time spent feeding on a particular species or part of plants was calculated by dividing the number of feeding records on that species or part by the total number of feeding records for that month. Because the number of feeding records each month differed, monthly proportions of feeding time for every species or part were averaged to give the annual ratio. Data from July to December were collected in both 1997 and 1998 and were averaged across years in our analysis.

We used the index of species-specific plant part overlap (shared percentages of feeding time on each species-specific plant part—Chapman 1987; Harrison 1984) to evaluate diet similarities between 2 months. For example, if Y part of X plant species constituted 25% and 40% of feeding time in 2 different months, the shared percentage of feeding time on that species-specific plant part is 25%.

Vegetation survey, diet selection, and plant phenology.—To assess whether flying squirrels

selected food in proportion to availability, we surveyed vegetation of 8 randomly selected 0.05-ha sampling plots where flying squirrels have access. Trees with diameter at breast height ≥ 5 cm were identified to species and measured in each plot. We calculated the modified importance value (Curtis and McIntosh 1951), which is the mean rather than the sum of relative density, frequency, and dominance of a plant species, to represent the relative importance of each tree species. Thus, the value of a modified importance value can vary between 0% and 100%. We never found flying squirrels feeding on shrubs or small trees, so trees with diameter at breast height < 5 cm were excluded from calculations.

We then calculated the selection ratio (Clutton-Brock 1975), which is an estimate of the extent to which animals consumed a plant species in proportion to its availability, to evaluate whether flying squirrels had preference for certain food plants. The selection ratio equals the percentage of feeding time on a species divided by the modified importance value of that species.

Phenology data for 20 dominant species (80 trees) was collected monthly by K. Y. Wang (pers. comm.) between October 1997 and December 1998. Because 5 species were not used by *P. philippensis* during the observation period, data for 15 species (62 trees, Appendix I) were analyzed to evaluate the relationship between abundance of various plant parts and composition of the diet of flying squirrels. The phenology of a species of plants was categorized into 9 phases: leaf budding, unfolding leaf buds, unfolding young leaves, unfolded young leaves, foliage shed, flower budding, flower blooming, immature fruit, and ripe fruit. To quantify changes in abundance of each phase, we used a piece of clear plastic (Plexiglas, 30 by 25 cm) marked with a grid of 100 squares (each measuring 2 by 2 cm). By superposing the image of the tree crown on the Plexiglas, we counted the number of squares each phase occupied and scored it from 1 to 5 (Kuo 1997). Phases that appeared over 0–20 squares were scored as 1, 21–40 squares scored 2, and so on to a maximum score of 5.

Mean scores of the first 2 phases represented abundance of available buds, whereas mean scores of the 3rd and 4th phases represented abundance of young leaves. Mean scores of the

6th and 7th phases represented flowers, and scores of phases 8 and 9 represented abundance of fruits or seeds. Most species of plants at the site shed some leaves during the year, but only 2 species, *Lagerstroemia subcostata* and *Rhus succedanea*, are deciduous. Thus, the availability of mature leaves or petioles of other species was always indicated by the score 5.

Abundance of each plant part of a particular species was counted by averaging scores of all trees of that species. The sum of scores for all species gave an abundance index for the parts of plants available to flying squirrels.

RESULTS

Annual diet.—We collected 7,376 feeding records during 827 h of field observation. *P. philippensis* consumed at least 79 species-specific parts of plants belonging to 30 species from 19 families (Table 1). Woody plants dominated the diet, with 26 species contributing to $>99\%$ of annual feeding time. Vines and epiphytes were exploited rarely. We never observed *P. philippensis* eating insects or animal parts. Among 30 species of plants eaten, 18 species contributed to $>1\%$ of the annual diet of *P. philippensis*. *C. cuspidata* was the most commonly consumed species (25.0% of annual diet), followed by *Ficus superba* (14.7%) and *Glochidion acuminatum* (12.2%). These 3 species constituted nearly half of the annual diet of *P. philippensis*.

Young leaves, mature leaves, and fruits comprised 27.7%, 24.0%, and 16.8% of the annual diet of *P. philippensis*, respectively. *P. philippensis* consumed other parts as follows: petiole, 15.9%; bud, 6.4%; flower, 5.4%; seed, 1.9%; bark, 1.0%; unknown, 0.9%. Withered leaves were consumed once (0.02%) but were not included in diet analysis. Leaf parts (including mature leaves, young leaves, petioles, and buds) comprised 74.0% of the annual diet. Therefore, *P. philippensis* can be categorized as a folivore.

Plants in the family Fagaceae were exploited most commonly (32.5% of annual diet), followed by plants in the families Moraceae (15.1%), Lauraceae (12.6%), and Euphorbiaceae (12.2%). *P. philippensis* ex-

TABLE 1.—Plant species and parts consumed by *Petaurista philippensis* at Fushan Experimental Forest, Taiwan between July 1997 and December 1998. (Part: ML = mature leaves; YL = young leaves; Bu = buds; Fr = fruits; S = seeds; Fl = flowers; LP = petioles of leaves; Ba = barks; W = withered leaves; ? = nonidentified plant parts. IV: Importance value, see text for definition.)

| Family | Species | Part | % feeding time | Rank | IV ^a (%) | Selection ratio ^b |
|----------------|---------------------------------|------------------------|----------------|------|---------------------|------------------------------|
| Myricaceae | <i>Myrica rubra</i> | YL | 0.16 | 25 | <0.4 | >0.4 |
| Juglandaceae | <i>Engelhardia roxburghiana</i> | ML, Bu, Fr | 3.56 | 9 | 11.05 | 0.32 |
| Fagaceae | <i>Castanopsis cuspidata</i> | ML, YL, Bu, Fr, LP, Ba | 24.95 | 1 | 9.7 | 2.57 |
| | <i>Limnites uraiata</i> | Bu | 0.22 | 24 | 2.23 | 0.1 |
| | <i>Cyclobalanopsis gilva</i> | ML, YL | 0.56 | 21 | <0.4 | >1.4 |
| | <i>C. longinux</i> | ? | 0.01 | 30 | 0.59 | 0.02 |
| | <i>Pasania hartlandii</i> | YL, Bu, Fr, Fl, LP | 6.24 | 4 | 4.23 | 1.48 |
| | <i>P. hancei</i> | Fr, ? | 0.54 | 22 | 2.83 | 0.19 |
| Moraceae | <i>Ficus superba</i> | ML, YL, Bu, Fr | 14.67 | 2 | <0.4 | >36.68 |
| | <i>F. sarmentosa</i> | ML, YL | 0.38 | 23 | | |
| Polygonaceae | <i>Polygonum chinense</i> | ML | 0.04 | 26 | | |
| Lauraceae | <i>Cryptocarya chinensis</i> | W | 0.02 | 29 | 2.54 | 0.01 |
| | <i>Lindera communis</i> | ML, YL, S | 1.74 | 15 | 0.63 | 2.76 |
| | <i>Litsea acuminata</i> | ML, YL, Bu, Fr, Fl, Ba | 4.51 | 5 | 15.32 | 0.29 |
| | <i>Machilus japonica</i> | Fr | 2.59 | 11 | <0.4 | >6.48 |
| | <i>M. thunbergii</i> | ML, YL, Bu, Fr | 1.36 | 18 | 12.49 | 0.49 |
| | <i>M. zuihoensis</i> | ML, YL, Bu, Fr | 2.41 | 12 | | |
| Theaceae | <i>Pyrenaria shinkoensis</i> | ML, S, Fl | 4.21 | 6 | 3.95 | 1.07 |
| Euphorbiaceae | <i>Glochidion acuminatum</i> | ML, YL | 12.18 | 3 | 1.72 | 7.08 |
| Anacardiaceae | <i>Rhus succedanea</i> | ML, YL, Bu, Ba | 1.89 | 14 | <0.4 | >4.73 |
| Sabiaceae | <i>Meliosma squamulata</i> | Bu | 0.86 | 19 | 2.41 | 0.36 |
| Aquifoliaceae | <i>Ilex ficoidea</i> | ML, YL | 1.54 | 16 | <0.4 | >3.85 |
| Elaeocarpaceae | <i>Elaeocarpus sylvestris</i> | ML, YL | 1.46 | 17 | <0.4 | >3.65 |
| Lythraceae | <i>Lagerstroemia subcostata</i> | YL, Bu, Fr, Fl, Ba | 0.76 | 20 | 0.72 | 1.06 |
| Araliaceae | <i>Schefflera octophylla</i> | YL, Fr, Fl, LP | 3.18 | 10 | 9.28 | 0.34 |
| Myrsinaceae | <i>Ardisia sieboldii</i> | ML, LP | 4.01 | 7 | 7.62 | 0.53 |
| Ebenaceae | <i>Diospyros morristana</i> | ML, YL, Fr, Ba | 3.76 | 8 | 3.43 | 1.1 |
| Styracaceae | <i>Alniphyllum pterospermum</i> | ML, YL | 2.25 | 13 | <0.4 | >5.63 |
| Fabaceae | <i>Pueraria montana</i> | YL | 0.03 | 27 | | |
| Araceae | <i>Pothos chinensis</i> | ML | 0.03 | 27 | | |

^a Vines or shrubs, not surveyed; *M. thunbergii* and *M. zuihoensis* were pooled together.

^b Selection ratio: % of feeding time on specific species/importance value of that species; vines or shrubs, not calculated.

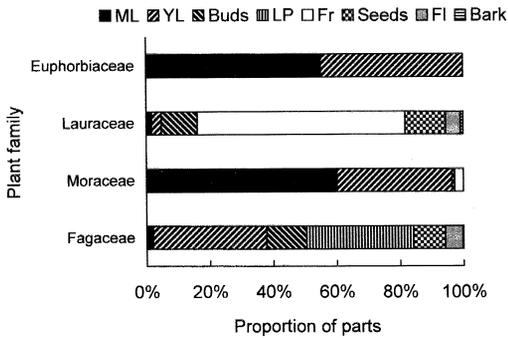


FIG. 1.—Percentage of plant parts of the 4 most exploited plant families consumed by *Petaurista philippensis* at Fushan Experimental Forest, Taiwan, from July 1997 to December 1998. ML, mature leaves; YL, young leaves; LP, petioles of leaves; Fr, fruit; Fl, flowers.

exploited different parts of plants in different families (Fig. 1). For example, they ate primarily young leaves (35.7%) and petioles (33.7%) of Fagaceae, whereas fruits (65.6%) and mature leaves (60.1%) were the most commonly eaten parts of Lauraceae and Moraceae, respectively.

Diet selection.—Twenty-eight plant species with a diameter at breast height ≥ 5 cm were recorded in the 0.4-ha survey plot. Data from *M. thunbergii* and *M. zuihoensis* were pooled together to calculate the importance value of *M. thunbergii*, since we could not reliably distinguish the 2 species in the field.

Litsea acuminata had the highest importance value (15.3%, Table 1), followed by *M. thunbergii* (12.4%), *E. roxburghiana* (11.1%), *C. cuspidata* (9.6%), and *Schefflera octophylla* (9.2%). Correlation between proportions of feeding time on the top 10 most commonly consumed species and their importance value (excluding *F. superba* because no tree was surveyed due to its scarcity) showed that *P. philippensis* did not feed on species of plants in proportion to abundance (Spearman rank correlation, $r_s = -0.18$, $P > 0.05$).

The selection ratio indicated that *F. superba* (selection ratio > 36.68 , calculated on the basis of the smallest importance value

surveyed [0.4%]) was the most preferred food plant of *P. philippensis* (Table 1). *G. acuminatum* (selection ratio = 7.08), *Machilus japonica* (> 6.48), and *Alniphyllum pterospermum* (> 5.63) were also favored highly. By contrast, *L. acuminata*, *E. roxburghiana*, and *M. thunbergii* were avoided (selection ratio = 0.29, 0.32, 0.49, respectively) despite their abundance on the study site.

Monthly and annual diet change.—Although *P. philippensis* fed mainly on leaves throughout the year, there was monthly variation (Fig. 2). For instance, monthly proportion of fruit consumed ranged from 0% to 83.2%, indicating that *P. philippensis* could be categorized as frugivorous rather than folivorous in some months. Mature leaves were also consumed variably. *P. philippensis* fed more often on mature leaves and petioles in winter, but rarely exploited them in other months. Buds, young leaves, and fruit were eaten in spring, and young leaves and fruits were consumed in summer and autumn.

On average, *P. philippensis* consumed 10.4 species of plants (5–15) each month. However, the 3 most consumed species accounted for more than half the monthly diet (53.8% to 97.2%), indicating that flying squirrels fed mainly on a few species each month. For instance, they ate 16 species in March 1998, but the 3 most eaten species accounted for 80.3% of their diet in that month. Three of 14 species consumed in July 1998 also accounted for 72.8% of their diet in that month. *C. cuspidata* was consumed every month, but flying squirrels fed on different parts of *C. cuspidata* in different months (Fig. 3). For example, young leaves were dominant in October 1997, but between November 1997 and February 1998, *P. philippensis* fed mainly on petioles of this plant.

The low index of species-specific plant part overlap (15.5%) supports the idea that monthly diet of *P. philippensis* was highly variable. In general, composition of diet was most similar between consecutive

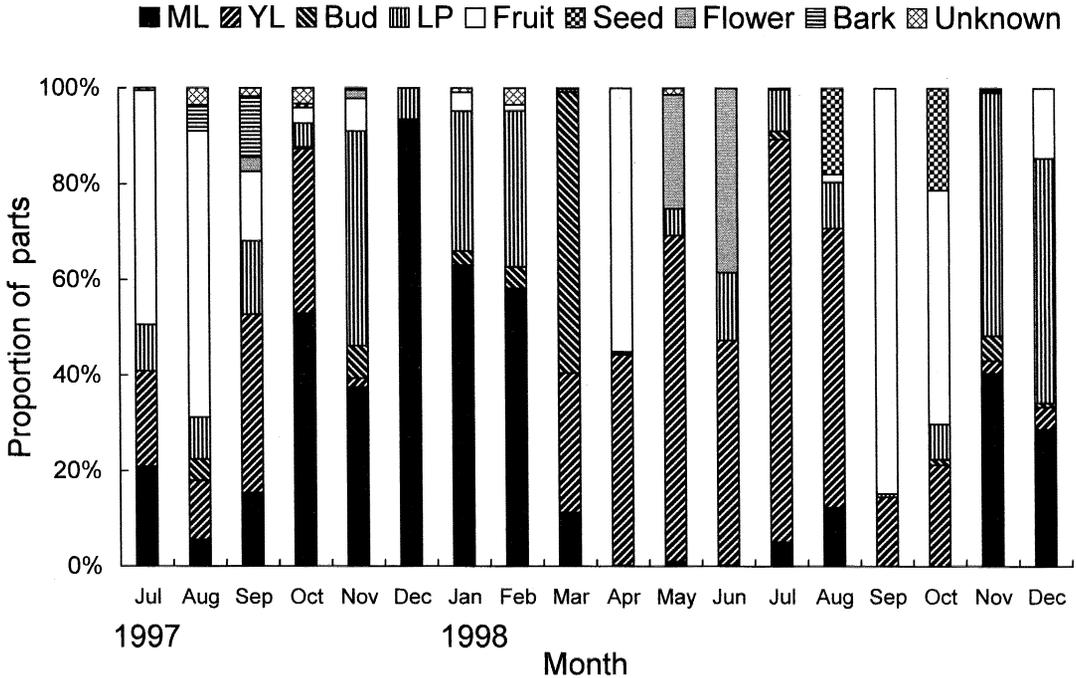


FIG. 2.—Monthly diet composition of *Petaurista philippensis* at Fushan Experimental Forest, Taiwan, from July 1997 to December 1998. ML, mature leaves; YL, young leaves; LP, petioles of leaves.

months. However, the index of species-specific plant part overlap was higher between winter months (>45%, except in December 1997), indicating that the food habits of *P. philippensis* changed less during this period. In winter their main food was the mature leaves of *F. superba* and *G. acuminatum*, along with petioles and mature leaves of *C. cuspidata*.

Annual variation in diet was observed (Fig. 2). Fruit was the main food in July and August 1997, whereas leaves were most important in these 2 months in 1998. In September and October 1997, leaf predominated in the diet of *P. philippensis*, whereas fruits and seeds were the most consumed food items in September and October 1998. The low index of species-specific plant part overlap (20.3%) between these months in different years implies that food habits of *P. philippensis* varied annually.

Diet change and food availability.—Phenology data exhibited intraspecific and inter-specific temporal variation. Generally,

buds peaked in March, young leaves were most abundant in April, flowers peaked from April to June, and fruit peaked from July to September. Except for deciduous species, mature leaves were abundant all year round (Fig. 4).

Spearman rank correlations showed that *P. philippensis* did not exploit plant parts according to their availability ($r_s = -0.11$ to 0.51 , $P > 0.05$). However, because not every part of all surveyed species was exploited by *P. philippensis*, we checked whether certain parts of a specific plant were favored. Feeding of *P. philippensis* was correlated with appearance and abundance of certain parts of specific species. For example, consumption of *C. cuspidata* buds was related to their availability ($r_s = 0.73$, $P < 0.01$) in March 1998. The young leaves of *G. acuminatum* were eaten more often when they were more abundant ($r_s = 0.59$, $P < 0.05$). The flowers of *Pasania harlandii*, *L. acuminata*, and *Pyrenaria shinkoensis* were exploited in relation to

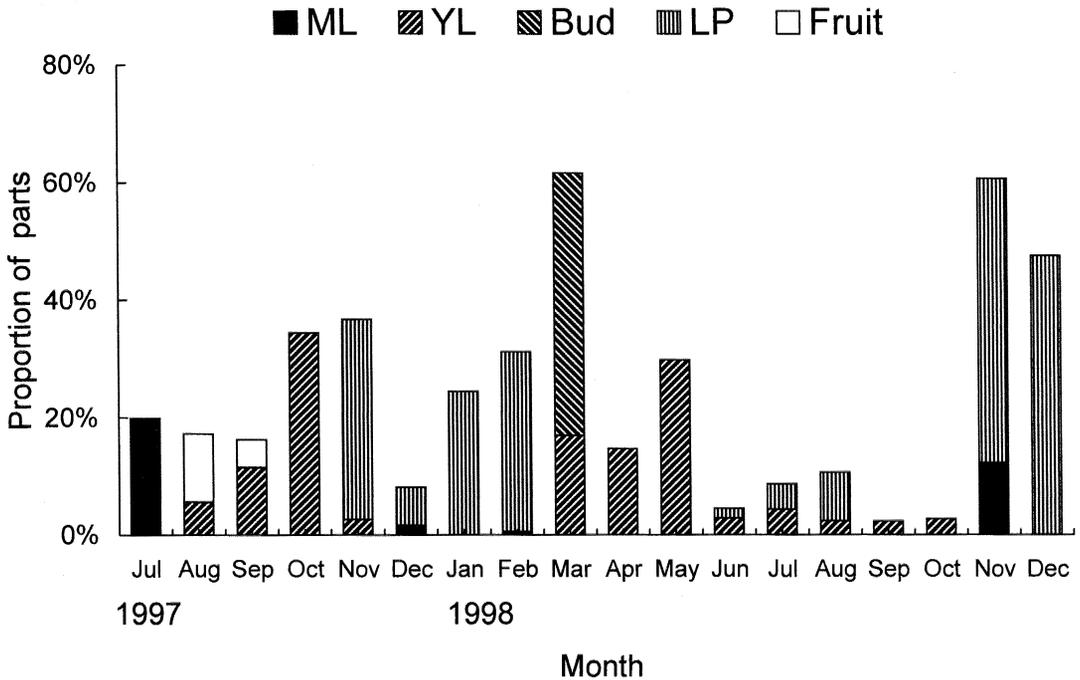


FIG. 3.—Monthly variation in the composition of parts of the tree *Castanopsis cuspidata* exploited by *Petaurista philippensis* at Fushan Experimental Forest, Taiwan, from July 1997 to December 1998. ML, mature leaves; YL, young leaves; LP, petioles of leaves.

their availability ($r_s = 0.56, 0.62, 0.99$, respectively; and $P < 0.05, 0.05, 0.01$, respectively). Consumption of fruit did not correlate with abundance of immature fruit

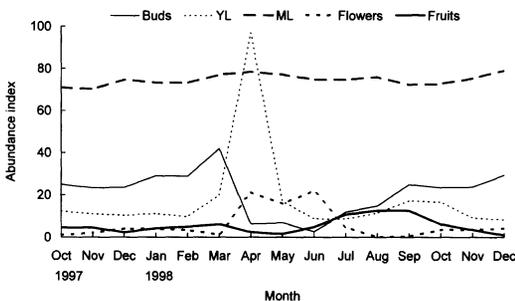


FIG. 4.—Monthly variation in abundance of phenological phases of 15 plant species consumed by *Petaurista philippensis* at Fushan Experimental Forest, Taiwan, from October 1997 to December 1998 (calculated from data collected by Wang, pers. comm.). ML, mature leaves; YL, young leaves. Abundance of seeds and petioles are the same as those of fruits and mature leaves, respectively.

($r_s = -0.16$ to 0.22 , $P > 0.05$). However, feeding frequency on the fruit of at least 5 species (*Diospyros morrisiana*, *E. roxburghiana*, *L. acuminata*, *P. harlandii*, *S. octophylla*) was correlated with the abundance of ripe fruit ($r_s = 0.63, 1.00, 0.68, 0.63, 0.73$; $P < 0.05, 0.001, 0.01, 0.05, 0.005$). Certain species-specific plant parts were exploited moderately, irrespective of their abundance. Abundance of the mature leaves of *G. acuminatum* and petioles of *C. cuspidata* was constant all year, but they were eaten mostly in winter when other plant parts were less available.

DISCUSSION

Characteristics of diet.—In our study, *P. philippensis* fed primarily on leaves (74.0% of annual diet, including buds, petioles, young and mature leaves). Other studies of diet on species in this genus also show that they are extensively folivorous (Ando et al. 1985; Kawamichi 1997; Lee et al. 1986;

Muul and Liat 1978). However, studies on northern (*Glaucomys sabrinus*) and southern flying squirrels (*G. volans*) (Dolan and Carter 1977; Wells-Gosling and Heaney 1984) reveal that they feed mainly on seeds, nuts, or fungi. These differences may be related to body size. Muul and Liat (1978) compared 11 species of flying squirrels in Malaysia and found that the larger the species, the higher the proportion of foliage in its diet. Because large mammals have lower mass-specific metabolic rates than small ones (Parra 1978), giant flying squirrels are better able to exploit low-energy foliage than are smaller northern and southern flying squirrels (body mass 50 to 185 g, Nowak 1999).

Petaurista philippensis is a highly selective forager. Only 18 plant species contribute to >1% of its annual diet. Furthermore, they consumed only a few species of plants each month. The 3 most commonly exploited species comprised >50% of the monthly diet. A study in central Taiwan showed that *P. philippensis* fed on no more than 16 species (Lee et al. 1986). Japanese giant flying squirrels (*P. leucogenys*) are also reported to be highly selective (Ando et al. 1985; Kawamichi 1997). Janzen (1978) stated that, relative to terrestrial animals, arboreal species are unable to store large amounts of fat, which would restrict their movements and increase the risk of falling. Furthermore, because arboreal folivores rely on relatively poor quality food, they may be constrained by their ability to convert energy (Eisenberg 1978). Freeland and Janzen (1974) noted that food selection by mammals is a trade off between ingestion of nutrients and intake of digestive inhibitors and toxins. Toxic compounds in some plants may reduce ingestion efficiency. These limitations may favor selectivity for increased nutritional uptake and lower their intake of toxic substances. Moreover, because smaller animals need more energy per unit body mass, most arboreal folivores are large (1 to 5 kg) as an adaptation to the low energy content of foliage (McNab 1978). *P. philip-*

ensis, with its small size compared to other arboreal folivores, should be a more selective forager.

Although not reported in other studies on *Petaurista* (Ando et al. 1985; Kawamichi 1997; Lee et al. 1986), petioles were consumed by *P. philippensis* in our study (15.9% of annual diet). Garber (1987) noted that there are smaller amounts of cellulose and secondary compounds in petioles than in mature leaves. This may explain why they were eaten by *P. philippensis*, especially in winter. However, in other studies, petioles have often not been treated separately from leaves or stems, which may explain why they have not been recorded as food items.

Petaurista philippensis preferred *F. superba*, *G. acuminatum*, *M. japonica*, and *A. pterospermum*. Except for *M. japonica*, *P. philippensis* fed mainly on young and mature leaves of the 3 other species. *F. superba*, *G. acuminatum*, and *A. pterospermum* are pioneer species. Preference for pioneer species has been observed in other herbivores (Cates and Orians 1975). Coley (1983) showed that young and mature leaves of pioneer species contain fewer digestion reducers such as cellulose, tannins, and lignin and are relatively palatable to herbivores. Furthermore, pioneer species often have higher leaf turnover rates (Coley 1983) and should, therefore, contain more nitrogen for rapid growth and fewer secondary compounds to reduce the risk of autotoxicity (Coley and Barone 1996).

Food availability and diet change.—The diet of *P. philippensis* changed in relation to plant phenology. No significant correlation was found between availability of parts of plants and feeding frequency, implying that Indian giant flying squirrels did not select food on the basis of total availability. Rather, availability of parts of some species was important. A striking example is consumption of ripe fruit of *E. roxburghiana* (76.3% of monthly diet) in September 1998. Increased intake of fruit in July and August 1997 relative to 1998 correlated

with the availability of fruit of genus *Machilus* only in 1997. The fact that leaves were used throughout the year suggests that foliage is a complementary food when fruits and flowers of some species are not available. Hence, *P. philippensis* foraged on favorable but ephemeral food sources but relies on stable low-quality food when necessary.

Primary consumers have morphological, behavioral, and physiological adaptations to periodic resource scarcity (see review by van Schaik et al. 1993). For example, primates switch their diets to mitigate the impact of food shortage (Terborgh 1983). In our study, *P. philippensis* alleviated the effect of food scarcity in winter by consuming low-quality but abundant leaves and petioles. They consumed mature leaves of *F. superba* and *G. acuminatum*, along with the petioles of *Castanopsis cuspidate*. Mature leaves of most other species were not used despite their availability, indicating that *P. philippensis* remained selective even when food resources were relatively scarce.

Some presumably favorable parts were avoided by *P. philippensis* even when food was scarce. For example, buds of *M. thunbergii* and *M. zuihoensis*, flowers of *S. octophylla*, and figs of *F. superba* were abundant in winter, but were not consumed. It is unknown why *P. philippensis* avoided these food items. Formosan macaques (*Macaca cyclopis*) at Fushan fed on these parts extensively in the same winter (Chang 1999; Chen 1999).

It may be that *P. philippensis* avoids nutritious foods that have secondary compounds that they are unable to process. Bryant and Kuropat (1980) reviewed feeding by several subarctic browsers in winter and concluded that secondary compounds were more important in selection of food than nutritional content. Some secondary compounds (resins) extracted from plants are detrimental to cecal microbes and reduce production of microbial proteins, vitamins, and volatile fatty acids in the cecum. A study of gray squirrels (*Sciurus carolinensis*—Chung-MacCoubrey et al. 1997)

shows that tannins and phenols may inhibit consumption of red oak acorns relative to those of white oaks, even though the former contain more fat and energy. Although some animals avoid the effects of toxic secondary compounds by feeding on a variety of foods (Freeland and Janzen 1974), this may not be possible for *P. philippensis* because it would require larger home ranges to increase the chance of encountering more potential food items. With a small home range in winter (Kuo 1999), *P. philippensis* may consume low-quality but abundant foods that contain easily processed secondary compounds and minimize energy consumption by moving less. Nutritional analysis of these foods will enable us to test this hypothesis.

ACKNOWLEDGMENTS

We are grateful to Fushan Experimental Research Station of the Taiwan Forestry Research Institute for providing facilities, lodging, and assistance during the study. We also thank J. T. Lin and C. B. Huang-Wu of Fushan Research Station for their assistance in identifying plants. Special thanks are given to P. F. Lee, C. M. Kuo of National Taiwan University, L. K. Lin of Tunghai University, J. T. Chao of Taiwan Forestry Research Institute, J. S. Scheibe, and 2 anonymous reviewers for their valuable comments on the manuscript. We thank R. W. Thorington for confirming the taxonomic status of *Petaurista philippensis* for us. We are indebted to K. Y. Wang for providing phenology data and for her assistance in vegetation survey. We are very grateful to K. Y. Chang, C. E. Chen, D. L. Chen, Y. T. Chen, C. Chiu, B. J. Hsieh, T. M. Horng, C. H. Kao, J. King, W. W. Kuo, C. Y. Lee, Y. Y. Lee, P. J. Lin, and I. B. Tzeng for their help with laboratory and field work. Acknowledgment is also given to many assistants and students of the Wildlife Research Lab of the Department of Zoology, National Taiwan University. This study is supported partially by a grant of the National Science Council, the Republic of China, NSC-86-2621-B-002-013-A07.

LITERATURE CITED

- AGETSUMA, N. 1995. Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): the influence of

- food availability and temperature. *International Journal of Primatology* 16:611–627.
- ALTMANN, J. 1974. Observational study of behavior: sampling method. *Behaviour* 49:227–265.
- ANDO, M., S. SHIRAIISHI, AND T. A. UCHIDA. 1985. Food habits of the Japanese giant flying squirrel, *Petaurista leucogenys*. *Journal of the Faculty of Agriculture, Kyushu University (Japan)* 29:189–202.
- BRYANT, J. P., AND P. J. KUROPAT. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics* 11:261–285.
- CATES, R. G., AND G. H. ORIANS. 1975. Successional status and the palatability of plants to generalized herbivores. *Ecology* 56:410–418.
- CHANG, F. S., Y. S. LIN, S. WANG, Y. WANG, K. Y. LUE, K. S. HSU, AND L. L. SEVERINGHAUS. 1986. The survey on the natural resources of Ha-pen area. Council of Agriculture, Taipei, Taiwan, Ecological Research Report No. 13 (in Chinese).
- CHANG, K. Y. 1999. Foraging strategies of Formosan macaques (*Macaca cyclopis*) in Fushan experimental forest, I-Lan. M.S. thesis, National Taiwan University, Taipei, Taiwan (in Chinese).
- CHAPMAN, C. A. 1987. Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica* 49:90–105.
- CHEN, C. E. 1999. The influence of Formosan macaques (*Macaca cyclopis*) on seed dispersal in Fushan experimental forest. M.S. thesis, National Taiwan University, Taipei, Taiwan (in Chinese).
- CHUNG-MACCOUBREY, A. L., A. E. HAGERMAN, AND R. L. KIRKPATRICK. 1997. Effects of tannins on digestion and detoxification activity in gray squirrels (*Sciurus carolinensis*). *Physiological Zoology* 70:270–277.
- CLUTTON-BROCK, T. H. 1975. Feeding behavior of red colobus and black and white colobus in East Africa. *Folia Primatologica* 23:165–207.
- COLEY, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53:209–233.
- COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305–335.
- CORBET, G. B., AND J. E. HILL. 1992. The mammals of the Indomalayan region: a systematic review. Oxford University Press, Oxford, United Kingdom.
- CORK, S. J., AND W. J. FOLEY. 1991. Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. Pp. 134–166 in *Plant defenses against mammalian herbivory* (R. T. Palo and C. T. Robbins, eds.). CRC Press, Boca Raton, Florida.
- CURRAN, L. M., AND M. LEIGHTON. 2000. Vertebrate responses to spatiotemporal variation in seed reproduction of mast-fruiting Dipterocarpaceae. *Ecological Monographs* 70:101–128.
- CURTIS, J. J., AND R. P. MCINTOSH. 1951. An upland forest continuum in the prairie forest border region of Wisconsin. *Ecology* 32:476–496.
- DASILVA, G. L. 1992. The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *Journal of Animal Ecology* 61:79–91.
- DASILVA, G. L. 1994. Diet of *Colobus polykomos* on Tiwai island: selection of food in relation to its seasonal abundance and nutritional quality. *International Journal of Primatology* 15:655–680.
- DOLAN, P. G., AND D. C. CARTER. 1977. *Glaucomyss volans*. *Mammalian Species* 78:1–6.
- DORAN, D. 1997. Influence of seasonality on activity pattern, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology* 18:183–206.
- EISENBERG, J. F. 1978. The evolution of arboreal herbivores in the class Mammalia. Pp. 135–152 in *The ecology of arboreal folivores* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- FLEMING, T. H., R. BREITWISCH, AND G. H. WHITESIDES. 1987. Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics* 18:91–109.
- FREELAND, W. J., AND D. H. JANZEN. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist* 108:269–289.
- GARBER, P. A. 1987. Foraging strategies among living primates. *Annual Review of Anthropology* 16:339–364.
- GUILLOTIN, M., G. DUBOST, AND D. SABATIER. 1994. Food choice and food competition among the three major primate species of French Guiana. *Journal of Zoology (London)* 233:551–579.
- HARRISON, M. J. S. 1984. Optimal foraging strategies in the diet of the green monkey, *Cercopithecus sabaues*, at Mt. Assirik, Senegal. *International Journal of Primatology* 5:435–471.
- JANZEN, D. H. 1978. Complications in interpreting the chemical defenses of trees against tropical arboreal plant-eating vertebrates. Pp. 73–84 in *The ecology of arboreal folivores* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- KAWAMICHI, T. 1997. Seasonal changes in the diet of Japanese giant flying squirrels in relation to reproduction. *Journal of Mammalogy* 78:204–212.
- KOOL, K. M. 1993. The diet and feeding behavior of the silver leaf monkey (*Trachypithecus auratus sondaicus*) in Indonesia. *International Journal of Primatology* 14:667–700.
- KUO, C. C. 1999. Diet, home range and activity pattern of red-giant flying squirrels (*Petaurista petaurista*) in Fushan experimental forest. M.S. thesis, National Taiwan University, Taipei, Taiwan (in Chinese).
- KUO, C. M. 1997. Research on forest plant community and phenology in Fushan area. Global climate change: long-term ecological research in Fushan. National Science Council, Taipei, Taiwan (in Chinese).
- LEE, P. F. 1998. Body size comparison of two giant flying squirrel species in Taiwan. *Acta Zoologica Taiwanica* 9:51–57.
- LEE, P. F., D. R. PROGULSKE, AND Y. S. LIN. 1986. Ecological studies on two sympatric *Petaurista* species in Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica* 25:113–124.
- LEIGHTON, M., AND D. R. LEIGHTON. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pp. 181–196 in *Tropical rain forest: ecology and management* (S. L. Sutton, T. C. Whitmore,

- and A. C. Chadwick, eds.). Blackwell Science Publications, London, United Kingdom.
- MCNAB, B. K. 1978. Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. Pp. 153–162 in *The ecology of arboreal folivores* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- MUUL, I., AND L. B. LIAT. 1978. Comparative morphology, food habits, and ecology of some Malaysian arboreal rodents. Pp. 361–368 in *The ecology of arboreal folivores* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- NOWAK, R. M. 1999. *Walker's mammals of the world*. 6th ed. Johns Hopkins University Press, Baltimore, Maryland 2:837–1936.
- PARRA, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pp. 205–230 in *The ecology of arboreal folivores* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- PERES, C. A. 1994. Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagotricha cana*) in central Amazonia: comparisons with other Atelines. *International Journal of Primatology* 15:333–372.
- POULSEN, J. R., C. J. CLARK, AND T. B. SMITH. 2001. Seasonal variation in the feeding ecology of the gray-cheeked mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology* 54:91–105.
- RATHCKE, B., AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16:179–214.
- STONER, K. E. 1996. Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica. *International Journal of Primatology* 17:1–30.
- TAIWAN FORESTRY RESEARCH INSTITUTE. 1989. A list of native plants of Fu-shan experimental forest. Taiwan Forestry Research Institute Press, Taipei, Taiwan (in Chinese).
- TERBORGH, J. 1983. *Five new world primates: a study in comparative ecology*. Princeton University Press, Princeton, New Jersey.
- TERBORGH, J. 1986. Community aspects of frugivory in tropical forests. Pp. 371–384 in *Frugivores and seed dispersal* (A. Estrada and T. H. Fleming, eds.). Dr. W. Junk Publishers, Dordrecht, the Netherlands.
- VAN SCHAİK, C. P., J. W. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.
- VAN SCHAİK, C. P., AND M. A. VAN NOORDWIJK. 1985. Interannual variability in fruit abundance and reproductive seasonality in Sumatran long-tailed macaques (*Macaca fascicularis*). *Journal of Zoology* (London) 206:533–549.
- WELLS-GOSLING, N., AND L. R. HEANEY. 1984. *Glaucomys sabrinus*. *Mammalian Species* 229:1–8.
- WHITE, F. J. 1998. The importance of seasonality in primatology. *International Journal of Primatology* 19:925–927.

Submitted 7 June 2002. Accepted 11 December 2002.

Associate Editor was Thomas J. O'Shea.

APPENDIX I

Plant species (by family) and number of stands (in parentheses) surveyed for phenology from October 1997 to December 1998 at Fushan Experimental Forest, northeastern Taiwan.

Juglandaceae, *Engelhardia roxburghiana* (5); Fagaceae, *Castanopsis cuspidata* (4), *Pasania harlandii* (5), *Pasania hancei* (4); Lauraceae, *Litsea acuminata* (5), *Machilus thunbergii* (3), *Machilus zuihoensis* (4), *Machilus japonica* (5); Theaceae, *Pyrenaria shinkoensis* (5); Euphorbiaceae, *Glochidion acuminatum* (6); Anacardiaceae, *Rhus succedanea* (2); Sabiaceae, *Meliosma squamulata* (5); Lythraceae, *Lagerstroemia subcostata* (2); Araliaceae, *Schefflera octophylla* (5); Ebenaceae, *Diospyros morrisiana* (2).