FORAGING ECOLOGY OF THE PHILIPPINE FLYING LEMUR (*CYNOCEPHALUS VOLANS*)

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Between August 1986 and September 1987, six Philippine flying lemurs (*Cynocephalus volans*) were observed foraging on 35 of 76 available species of trees, representing ≥12 families of ≥26 available families. Eight species were foraged on in amounts significantly greater than expected, given the tree's abundance on the study area, and four were foraged on significantly less than expected. The foraging strategy of *C. volans* involved foraging many times during the night, for short duration, in several different species of tree each night. This strategy differed from that of other arboreal folivores.

Key words: *Cynocephlaus volans*, Dermoptera, foraging ecology, behavior, arboreal folivore

Mammalian arboreal folivores that spend the majority of their time in trees and feed almost exclusively on leaves represent a unique assemblage of animals because of the many environmental constraints under which they function. They faced with feeding on a very low-quality food and secondary compounds that may limit palatability or quality of some plants (Freeland and Janzen, 1974; Milton, 1980). Spatial distribution of food and difficulty inherent in reaching this food make foraging complex (McNab, 1978; Parra, 1978). Members of this group that have been studied in the greatest detail—the three-toed sloth (*Bradypus variegatus*), the koala (*Phascolarctos cinereus*) and the greater glider (*Petauroides volans*)—use similar physiological and ecological strategies in dealing with these constraints (Cork and Foley, 1991; Cork et al., 1983; Foley and Hume, 1987; McNab, 1978). These strategies include low metabolic rate, variable body temperature, limited daily movement, long time for passage of digesta, and consumption of immature and mature foliage (Cork, 1996; Cork and Warner, 1983; Eberhard, 1978; Eisenberg, 1978; Foley and Hume, 1987; Montgomery

and Sunquist, 1978; Sunquist and Montgomery, 1973).

Recent work by Wischusen (1990) and Wischusen et al. (1994) suggests that the Philippine flying lemur (*Cynocephalus volans*) differs from the koala, greater glider, and sloth in having larger daily movements and shorter times for passage of digesta, suggesting that flying lemurs utilize a foraging strategy different from that of other arboreal folivores. Although there are some anecdotal reports on foods of flying lemurs, there are no quantitative studies of their foraging ecology (Beebe, 1913; Chapman, 1902; Chasen and Kloss, 1929; Liat, 1967; Wharton, 1950). In this paper, we describe the foraging ecology of the Philippine flying lemur and make comparisons with previously studied species.

METHODS AND MATERIALS

Research was conducted on private land in the town of Cabarisan, Davao City, Mindanao, Philippines, adjoining Mount Apo National Park (7°2′N, 125°20′E). The study area was ca. 5.3 ha of mixed primary and old second-growth forest that was classified as lower-montane rainforest and dominated by Dipterocarpaceae and Fagaceae (Whitmore, 1990). The topography was

gently rolling and generally sloped toward the east. Elevation ranged from 800 to 1,000 m.

Philippine flying lemurs were captured using nets placed near trees to which the animals had previously been observed gliding. After capture, animals were individually marked with reflective collars and radiotransmitters. Reflective collars allowed for individual identification of animals at distances ≤100 m (Wischusen and Richmond, 1989).

All trees ≥30 cm in diameter at breast height (dbh) within the study area were marked with a numbered tag, mapped, measured for height and diameter, and identified to species. Samples of leaves from species that could not be identified in the field were collected and identified at the herbarium of the University of the Philippines at Los Baños. Trees foraged on by flying lemurs, outside of the study area or having dbh <30 cm, were also tagged, measured, and identified.

Observations of marked animals were conducted nightly from 1730 to 0530 h using 7 by 50 binoculars and a flashlight. Individuals were rarely active outside that time (Rickart et al., 1993; Wischusen, 1990). The flashlight allowed us to confirm identity and behavior and was used as little as possible to minimize disturbance. All observations were conducted using the focal-animal sampling technique (Lehner, 1979). The behavior of the animal under observation was recorded at intervals of 1 min, along with its location (tree number) and, if it was feeding, the type of forage (leaf, fruit, or flower) and relative age (young or old) of forage. Complete foraging bouts were defined as continual foraging during which behavior was known for 1 min prior to and after the bout and in which ≤1 min passed during which the behavior of the animal could not be determined. We used the Kruskal-Wallis *H*-test (Freund and Wilson, 1997) to analyze data for differences in length of foraging bouts among individuals and hours of the night. We also used that test to analyze differences in number of species and families of forage consumed among individuals.

Preference indices were calculated for species, dbh, and height of the trees foraged on. Preference indices were calculated using the proportion of foraging bouts that took place in a tree with any particular character divided by the proportion of occurrence of trees with that character (Hobbs, 1982). To test for differences among preferred, neutral, and avoided species, a

95% *CI* was determined for each preference index using the *CI* for a binomial proportion (Snedecor and Cochran, 1980). If the confidence interval contained only numbers >1.0, the characteristic was preferred; if the confidence interval included 1.0, the characteristic was neutral; if the confidence interval contained only numbers <1.0, the characteristic was avoided.

Leafing phenology of marked trees was determined by surveying trees at ca. 2-week intervals. During each survey, presence or absence of young leaves was recorded for all marked trees on the study area. Percentage of preferred and avoided trees with young leaves was compared with the Wilcoxon signed-rank *t*-test (Freund and Wilson, 1997).

RESULTS

Foraging behavior of six flying lemurs was observed during 3,860 min of 22,690 min of total observations, accounting for 17% of all observations made from 1730 to 0530 h. Although foraging was observed throughout this period, activity was not evenly distributed. The overall pattern of foraging activity was bimodal with peaks just after sunset (ca. 1800 h) and a few hours prior to sunrise (ca. 0500 h; Fig. 1).

A total of 186 complete foraging bouts was observed, and the behavior of all individuals was generally the same during each bout. An animal would move to the end of a branch and feed on a few young leaves and then move to another branch and again feed on just a few young leaves. This would continue for the duration of the foraging bout. Small branches were often pulled to the mouth with a foreleg (Wharton, 1950), and then, leaves were grabbed by the mouth. After leaves were in the mouth, they were pulled off the branch; whatever came away in the mouth was chewed and consumed.

Mean duration of all complete foraging bouts was 9.4 min. Mean duration of foraging bouts for different individuals ranged from 3.0 to 13.8 min. There were no significant differences among individuals ($H = 3.69$, $d.f. = 4$, $n = 178$, $P > 0.25$). Mean duration of foraging bouts during different
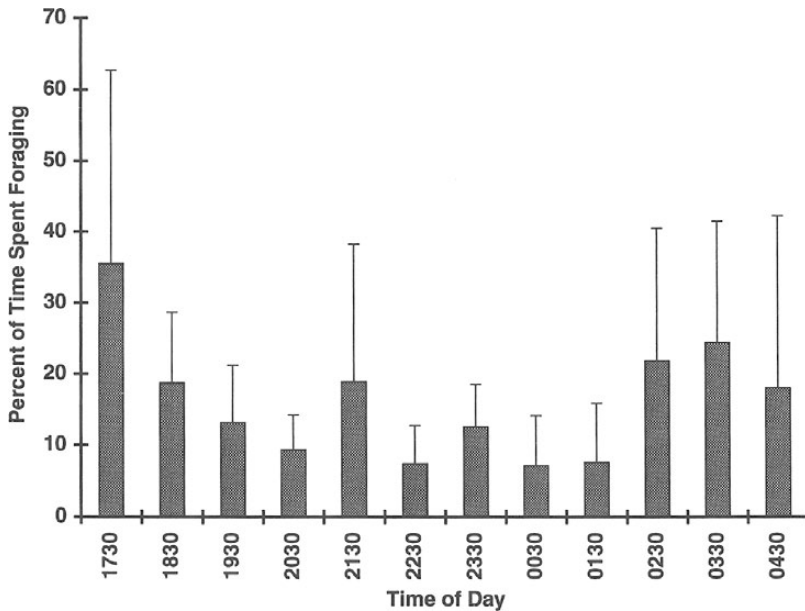
FIG. 1.—Percentage of time ($\bar{X} \pm SD$) flying lemurs (*Cynocephalus volans*) were engaged in foraging behavior during 1-h periods throughout the night.

hours of the night ranged from 4.2 min, between 0400 and 0459 h, to 13.2 min, between 2300 and 2359 h. Again there were no significant differences in length of foraging bouts during different times of the night ($H = 17.44$, $d.f. = 10$, $n = 185$, $P > 0.05$). Given the mean duration of a foraging bout (9.4 min) and the percentage of time animals spent foraging (17%), we calculated that the flying lemurs typically engaged in 12 foraging bouts/night, or 1 bout/h during their active period.

Philippine flying lemurs were observed foraging on 35 of 76 species of trees present in the study area (Table 1). These 35 species represented ≥12 of ≥26 available families. Individual flying lemurs foraged on 11–18 species representing 6–8 families, except for one individual (Table 1). This individual fed on only five species from three families, but it was observed for the shortest duration (3 months). Whenever the exact forage could be determined, the material was young leaves; however, there were many observations during which the type

and age of the forage could not be determined.

The number of different species of trees foraged on during a single night was calculated for each flying lemur for each night during which there was more than one complete observation of foraging activity. Mean number of trees foraged on per night for all individuals combined was two species in two families and ranged from one to four for both species and families. There were no significant differences among individuals for the number of species ($H = 0.72$, $d.f. = 4$, $P = 0.95$) or families ($H = 0.72$, $d.f. = 4$, $P = 0.95$) foraged on.

Eight of the 35 species consumed were foraged on in amounts significantly greater than expected given the tree's abundance on the study area (preferred); 21 were foraged on in amounts equal to that suggested by the tree's abundance (neutral), and four were foraged on in amounts significantly less than expected (avoided; Table 1). A preference index was not calculated for two species that were foraged on but not con-

Table 1.—*Preference indices and 95% CI for trees foraged in by Philippine flying lemurs (Cynocephalus volans).*

Species	Family	n^a	Preference Index	Preference 95% CI
Palaquium[b]	Sapotaceae	4	48.08*	30.74–65.41
Syzygium malaccense	Myrtaceae	2	12.46*	3.33–21.59
Palaquium luzoneinse	Sapotaceae	4	11.25*	7.62–14.88
Elaeocarpus[b]	Elaeocarpaceae	4	11.40*	7.66–15.14
Neolitsea[b]	Lauraceae	1	10.68*	2.22–19.15
Syzygium nitidum	Myrtaceae	2	9.50*	4.96–14.03
Mala mala[c]		2	5.34*	1.90–8.78
Syzygium[b]	Myrtaceae	2	5.34	0.67–11.36
Neolitsea vulcanica	Lauraceae	3	4.15*	2.03–6.28
Ficus[b]	Moraceae	2	2.85	0.90–4.80
Elaeocarpus ramiflorus	Elaeocarpaceae	1	2.54	0.99–4.09
Pos pos[c]		1	1.78	−0.68–4.24
Discocalyx cybianthoides	Myrsinaceae	1	1.78	−0.68–4.24
Canarium racemosum	Burseraceae	1	1.78	0.05–3.51
Palaquium philippense	Sapotaceae	2	1.72	−0.22–3.65
Ficus variegata	Moraceae	2	1.53	0.32–2.74
Astrocalyx calycina	Melastomataceae	2	1.07	−0.13–2.27
204[c]		1	0.89	−0.34–2.12
Cleistocalyx operculatus	Myrtaceae	3	0.89	0.12–1.66
Shorea squamata	Dipterocarpaceae	3	0.82	0.58–1.05
Shorea hopeifolia	Dipterocarpaceae	1	0.82	−0.55–1.69
Shorea almon	Dipterocarpaceae	4	0.78	0.53–1.04
Palaquium merrillii	Sapotaceae	4	0.73	0.26–1.21
Palaquium montanum	Sapotaceae	2	0.71	−0.27–1.70
Pygeum vulgare	Amygdalaceae	3	0.69	0.18–1.20
Shorea polysperma	Dipterocarpaceae	3	0.65	0.29–1.00
Breynia rhamnoides	Euphorbiaceae	1	0.59	−0.57–1.76
Narik[c]		1	0.59	−0.57–1.76
Castanopsis philippinensis	Fagaceae	2	0.55	0.07–1.04
Cinnamomum mindanensis	Lauraceae	1	0.30**	−0.28–0.88
Canarium multipinnatum	Burseraceae	1	0.22**	−0.21–0.66
Lithocarpus pruinosa	Fagaceae	2	0.11**	−0.04–0.26
Castanopsis javanica	Fagaceae	1	0.03**	−0.03–0.09
Litsea garciae	Lauraceae	1		
Unidentified[c,d]		2		

[a] Number of individual flying lemurs observed foraging in each species of tree.
[b] Unknown species within this genus.
[c] Species identified only by number or common name.
[d] Preference index could not be calculated because of the lack of similar species of trees in the marked sample.
* Preference index >1.0, $P \leq 0.05$.
** Preference >1.0, $P \leq 0.05$.

tained in the sample of marked trees. The families Elaeocarpaceae, Lauraceae, Myrtaceae, and Sapotaceae contained more than one species that were preferred (Table 1). The families Burseraceae, Fagaceae, and Lauraceae contained species that were avoided (Table 1).

Flying lemurs also exhibited preferences for large trees. Trees ≥60 cm dbh generally were preferred, and trees <60 cm dbh were avoided (Table 2). Trees of 30–39 m in height were preferred, and trees of 25–30 m in height were neutral; and trees <25 m and ≥45 m in height were avoided (Table 2).

Twenty surveys were conducted to deter-

TABLE 2.—*Preference indices and 95% CI for trees of different diameters at breast height and heights foraged in by Philippine flying lemurs (Cynocephalus volans).*

Class	n	Preference Index	95% CI
Diameter (cm)			
30–39.9	53	0.45**	0.34–0.56
40–49.9	51	0.77**	0.58–0.96
50–59.9	26	0.58**	0.37–0.80
60–69.9	41	2.51*	1.80–3.23
70–79.9	16	1.51	0.79–2.23
80–89.9	6	0.54**	0.11–0.96
90–99.9	41	3.86*	2.77–4.96
100–109.9	13	2.37*	1.11–3.63
110–119.9	24	10.50*	6.49–14.51
≥120	16	6.22*	3.27–9.18
Height (m)			
15–19	24	0.51**	0.32–0.71
20–24	54	0.63**	0.48–0.78
25–29	57	0.85	0.65–1.05
30–34	94	2.02*	1.68–2.36
35–39	48	2.29*	1.70–2.90
40–44	16	1.20	0.63–1.77
≥45	1	0.07**	−0.08–0.24

* Preference index >1.0, $P \le 0.05$.
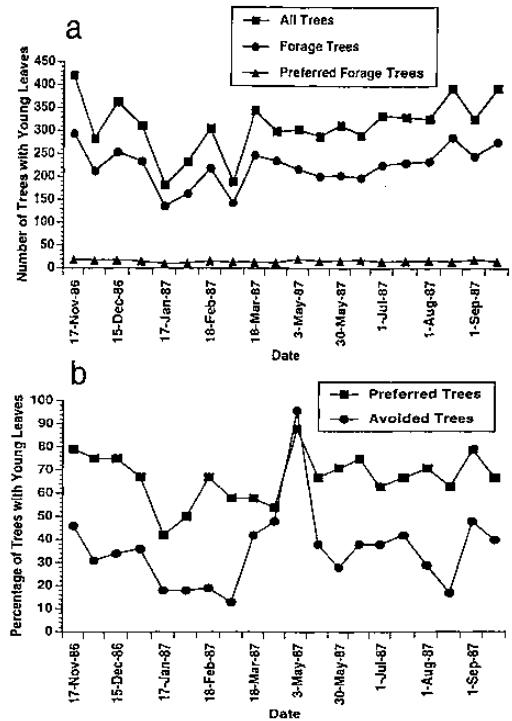** Preference index <1.0, $P \le 0.05$.

FIG. 2.—Number of trees with a) young leaves present and b) percentage of preferred and avoided species of trees containing young leaves on different dates in 1986–1987.

mine phenology of leaves. The number of trees on the study area that had young leaves present varied over time (Fig. 2a). The fewest trees with young leaves were recorded during January, February, and March. This was true for marked trees of all species combined and when only the species foraged on were considered. When only preferred species were considered, the overall pattern was somewhat similar, but seasonal variation appeared to be less. A comparison of the percentage of trees with young leaves present between preferred and avoided species that were foraged on revealed that a greater percentage of trees of preferred species had young leaves than trees of avoided species ($t = -3.85$, $P < 0.0001$; Fig. 2b).

DISCUSSION

Although foraging was observed during all active hours, there were differences in the amount of time that flying lemurs foraged during different hours of the night. Peaks in foraging were similar to peaks in the overall cycle of activity, which occurred just after sunset and a few hours prior to sunrise (Wischusen, 1990). Based on the amount of foraging activity observed during each hour of the night, it appears that flying lemurs initially fill their alimentary tracts and then maintain a high volume during the night by constantly ingesting more forage after brief periods of digestion.

Individual foraging bouts were short, often lasting only a few minutes, but there were many bouts during the course of the night. This lends support to the hypothesis that this species maintains a high volume in the alimentary tract—a pattern of foraging seen in many other herbivores (Batzli et al., 1981). The amount of foraging behavior varied with hour, but length of individual

foraging bouts did not. Thus, changes in the amount of foraging behavior observed during each hour were due to changes in length of time between foraging bouts (interbout length). As interbout length increased, the amount of foraging behavior decreased. As interbout length increased, presumably more digestion took place, and an individual was faced with consuming more to fill its alimentary tract. One would expect longer foraging bouts as the percent of time spent foraging decreased, but there was no increase in bout duration as the percentage of time spent foraging decreased.

The large number of species and families of trees foraged on by the Philippine flying lemur shows that it is a generalized forager. On an individual basis, the number of species and families foraged on were lower than for all individuals combined, but individuals still foraged on a large proportion of the species and families present. Individuals foraged on 31–51% of the total species foraged on by the group. With a longer study and more individuals under observation, the number of species and families foraged on would probably increase.

A comparison of the number of species and families of trees foraged on by other arboreal folivores suggests that the Philippine flying lemur, the three-toed sloth, and the proboscis monkey (*Nasalis larvatus*) are generalist foragers, feeding on 36, 31, and 90 species and 14, 31, and 39 families, respectively (Montgomery and Sunquist, 1978; Salter et al., 1985). Although there is little quantitative information on exact diet of the koala or the greater glider, they appear to have more specialized diets, feeding on ca. 10 species in one family each (Eberhard, 1978; Marples, 1973). However, these species inhabit forests dominated by only a few species of trees (Cork, 1996; Cork and Foley, 1991; Hindell et al., 1985), and composition of the forest may be more important in determining number of species consumed than preference for certain species or families of trees.

During a single night, flying lemurs for-

aged on several different species of trees. In one case, an animal foraged on four different species of trees during the course of 1 night. These results support the prediction of Freeland and Janzen (1974) that generalist herbivores should ingest several different species of forage over a short period of time. This results in individuals consuming smaller quantities of tree-specific secondary compound. An additional outcome of consuming leaves of several species during a single night would be to increase quantity of young leaves available on any given night, which would be beneficial if young leaves are in limited supply.

Avoidance of all species foraged on within one family (Fagaceae) was very interesting given the abundance of this family on the study area. This family represented >20% of all trees ≥30 cm in dbh and represented a significant part of the young leaves available in the study area and presumably throughout the region. Many members of the Fagaceae are known for their high content of tannins that inhibit digestion (Hagerman and Butler, 1991; Haslam, 1989; Van Soest, 1982).

In general, Philippine flying lemurs preferred larger trees for foraging in terms of diameter and height. Preference for larger trees could be the result of several characteristics of such trees. First, if large and small trees of the same species produce proportionally the same quantity of young leaves, larger trees represent larger or higher-quality food patches. According to departure rules for optimal patches, time allocated to better patches should be greater (Pyke, 1984), and our data appear to be consistent with this foraging model. Second, it may be easier for flying lemurs to climb or move in trees of larger diameters than trees of small diameters.

The consistency of production of young leaves may be an important criterion for determining forage preferences, if young leaves represent a limiting resource. Production of young leaves for all species appeared to decrease during December–Feb-

ruary, the drier months of the year, and to increase during March–November, the wetter parts of the year (Wischusen, 1990). These results were similar to the trends seen in Malaysian forests, where there was a distinct maximum in production of young leaves, just after the driest part of the year (Medway, 1972). When only preferred species of trees were analyzed, there was only a small change in number of trees with young leaves present. The preferred group also had a greater proportion of trees with young leaves during most times of the year.

Most, if not all, foraging occurred on young leaves. This is not surprising because young leaves have higher nutritional value tha old leaves (Hladik, 1978; Van Soest, 1982). Young leaves of preferred species were found in the study area during all months of the year and in stable numbers, suggesting that flying lemurs were not subjected to a time when there was a shortage of young leaves of preferred species.

Foraging ecology of the Philippine flying lemur appears different from that of other arboreal folivores in two ways. First, flying lemurs heavily used young leaves, whereas koalas, greater gliders, and three-toed sloths consume large quantities of mature foliage. Second, flying lemurs consume a varied diet, eating leaves of several tree species each night, whereas koalas and three-toed sloths generally consume only one species of leaf each night. These data suggest that there is a variety of strategies that can deal successfully with the environmental constraints associated with the lifestyle of an arboreal folivore.

ACKNOWLEDGMENTS

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