FOOD PREFERENCES OF KINKAJOUS (*POTOS FLAVUS*): A FRUGIVOROUS CARNIVORE

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The diet of the kinkajou (*Potos flavus*) is described from analyses of feces and observations of habituated individuals. Ripe fruit was the primary food comprising 90.6% of feeding bouts and present in 99% of feces. Leaves and flowers made up <10% of the diet. No animal prey was eaten. Seventy-eight species of fruit from 29 families were detected. Moraceae was the main plant family in the diet and *Ficus* was the most important plant genus. Kinkajous preferentially fed in large fruit patches. Selection indices were calculated for 37 fruit species. Compared with other large mammalian frugivores in central Panama the diet of kinkajous is most similar to the spider monkey (*Ateles geoffroyi*).

Key words: *Potos flavus,* kinkajou, frugivore, fruit, arboreal, canopy, diet, *Ficus,* Panama

The kinkajou (*Potos flavus*) is a medium-sized procyonid common throughout most neotropical forests (Ford and Hoffmann, 1988). Despite their nocturnal and arboreal habits, numerous authors have commented on the diet of kinkajous, mainly from studies of stomach contents or chance observations (e.g., Bisbal, 1986; Charles-Dominique et al., 1981; Goldman, 1920). From those observations, kinkajous appear to eat primarily fruit, and supplement their diet with insects, flowers, and leaves. Some have suggested that kinkajous eat small vertebrates or bird eggs (Alvarez del Toro, 1952; Husson, 1978), although there is no direct evidence for this. Insects, especially ants, may be an important seasonal resource in some localities (Redford et al., 1989). No long-term study has examined quantitatively the diet of kinkajous.

Detailed description and analysis of diet are critical for understanding behavioral ecology (Chapman et al., 1995; Wrangham, 1980; Zhang, 1995) and conservation biology (Dietz, 1997; Mittermeier and Cheney, 1987). This may be especially true for a species with an unusual diet (e.g., *Ailuropoda melanoleuca*—Schaller et al., 1985). Likewise, many aspects of the biology of kinkajous have converged with primates including their diet, morphology, and social structure (Hershkovitz, 1972; Kays and Gittleman, 1995; Kortlucke, 1973). However, because details of the natural history of kinkajous remain unknown, precise comparisons to reveal evolutionary forces behind convergence with primates are not possible.

I studied the diet of kinkajous for 1 year to determine their dietary preferences by comparing relative use of individual fruit species with their relative availability. I showed how kinkajous fit into the large frugivore guild of central Panama by highlighting dietary similarities with other carnivore and primate taxa.

MATERIALS AND METHODS

Study site.—Field research was conducted in lowland forest of Parque National Soberanía in the Republic of Panama (22,100 ha; 9°9′N, 79°44′W). Work was centered around the trail network of the 104-ha Limbo research plot (Robinson, 1998). Elevation within the plot varied from 35 to 80 m above mean sea level, and surrounding areas reached an elevation of 225

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m. Vegetation was classified as tropical moist forest. Annual rainfall was ca. 2,600 mm with 90% falling during the wet season in late April to mid-December (Dietrich et al., 1982).

The Limbo plot was a heterogeneous mix of forests of various ages, ranging from a few years old in recent blowdowns to ca. 400 years in remnant patches of tall forest (Karr, 1971). The forest within 10–30 m of the single-lane gravel Pipeline Road was ca. 30 years old and had grown tall enough to have closed the canopy above the road through most of the study area. South of the road, the forest was 60–120 years old, having been disturbed by farmers and the United States military earlier this century (Foster and Brokaw, 1982).

Despite regular hunting pressure, the animal community of the Limbo plot was largely intact, including top predators such as jaguar (*Panthera onca*) and puma (*Felis concolor*) (O. Moore and T. Robinson; pers. comm.). The spider monkey (*Ateles geoffroyi*) was the only frugivorous mammal extirpated from the area. Other arboreal frugivores seen frequently on the Limbo plot included olingos (*Bassaricyon gabbii*), howler monkeys (*Alouatta palliata*), capuchins (*Cebus capucinus*), night monkeys (*Aotus trivirgatus*), and several species of opossums. Density of kinkajous around the Limbo plot was ca. 12 individuals/km^2 (R. Kays, in litt.).

Trapping and observation.—Twenty-five kinkajous were captured 192 times with 50 Tomahawk live traps (32 by 32 by 102 cm). Traps were baited for 1,292 trap nights with banana and hung in trees 4–25 m above the ground using a hoistable trap design. Newly-captured animals were immobilized with 0.3 cc of a solution of 80% Ketamine hydrochloride and 20% Zylazine hydrochloride, and standard physical measurements were made. Ten kinkajous were fitted with radio collars that were marked with a unique pattern of colored reflective tape. Fifteen kinkajous were fitted with a similar reflective identification collar without a radio transmitter.

Marked kinkajous habituated quickly and could be followed and observed without obvious disturbance. Radio-collared animals were followed on 74 half-nights for 380 h, either from when they left their sleeping den at dusk until midnight or from midnight until they entered their sleeping den at dawn. Focal animals were observed from the ground with binoculars and were illuminated with a 6-V head lamp. A red filter was used when an animal was in the understory and a 12-V spotlight was used when an animal was in the upper canopy. Care was taken to not shine lights continuously on the focal animal. Animals could not always be seen clearly because of understory vegetation and darkness. Therefore, sporadic visual observation, falling fruit, and sounds were used in combination to determine a focal animal's behavior. Generally, kinkajous could be seen directly while they were feeding or resting in a tree. As they moved through the trees, however, they could be seen only intermittently, and I had to rely on telemetry to follow traveling animals.

Each time a kinkajou fed on fruit, flowers, or leaves the following were recorded: plant species, location, diameter at breast height (DBH) of the plant, and a categorical estimation of the number of fruits or flowers on the ground under the plant (<10, <50, <100, <500, <1,000, >1,000). For unknown species, samples of fruit and leaves were collected and identified.

Dietary measures.—Diet was measured by behavioral observation and analysis of feces. Behavioral feeding data were collected while following focal animals. A feeding bout began when a focal animal entered a fruiting patch to feed and ended when the animal left. A fruiting patch usually consisted of a single fruiting tree or vine but occasionally included two fruiting plants if their canopies were adjacent. Kinkajous did not feed continuously in bouts longer than ca. 30 min. Therefore, measures of bout length and total feeding time were not actually measures of time ingesting food but time spent in feeding patches. Behavioral data were analyzed in terms of percentage of total feeding bouts (n = 202) and percentage of total feeding time (out of 138 h).

A total of 194 fecal samples was analyzed; two-thirds were collected from free-ranging animals and one-third came from animals in traps. Kinkajous do not use latrines but defecate while feeding and traveling in trees; their feces fall to the ground and are scattered by understory vegetation. I collected as much of each defecation as possible, but that was usually some fraction of the total actually eliminated. Defecations collected from the bottom of traps were complete feces. Banana bait in feces was excluded from analysis.

Feces were refrigerated until analyzed, usually overnight. Feces were weighed, dissected,

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and divided into component parts. Relative volume of each component was visually estimated. Fruit pulp, seeds, and flower parts were identified and a reference collection was made. Eaten fruits were analyzed in terms of percentage of total number of feces in which they occurred and percentage of total feces volume. Percentage of total feces did not sum to 100 across food species because many individual feces contained more than one species.

Monitoring of fruit.—Production of fruit on the Limbo plot was monitored at the beginning and middle of each month from February 1996 to December 1996 using transect counts of fallen fruit. The transect covered most of the Limbo plot and was 0.5 m wide and 11.4 km long. To minimize censusing dispersed fruits, only patches with more than 2 fruits were included in the census. Wind dispersed species and fruits >2 weeks old were not counted. When more than two, new, non-wind dispersed fruits were encountered, they were identified by species, location along the transect, number of fruits on the 0.5 m wide transect, and, estimated total number of fruits laying on the ground by category (<10, <50, <100, <500, <1,000, >1,000). When the fruiting tree was easily located, its DBH also was measured. A fruit species was classified as edible if it was detected in the diet of kinkajous at least once.

Data analysis.—Selectivity indices were calculated for all fruit species that were eaten by kinkajous and detected in the census of fruits. The index was a simple ratio, $S_i = f_i/a_i$ where f_i was the relative amount of the diet occupied by a fruit species and a_i was the relative abundance of that species in the census of fruits compared with other edible fruit species (Leighton, 1993). Selection indices >1.0 indicated that a species was eaten more than expected given its availability; values <1.0 indicated that the species was eaten less than expected.

Results

Fecal and behavioral data showed that kinkajous were almost exclusively frugivorous; 90.6% of feeding bouts and 90.7% of total feeding time was on fruit and 99.0% of feces examined contained fruit. Flowers made up 1.6%, 6.9%, and 8.6% of the feces, feeding bouts, and feeding time, respectively. Leaves comprised only 2.6%, 2.0%, and 0.7% of feces, feeding bouts, and feeding time, respectively. Kinkajous were not recorded to feed on animal matter. Small insect fragments were found in feces twice, but the amount and type were expected from accidental ingestion with fruits or flowers.

Nearly all fruit eaten was ripe. Unripe fruit of only one species, *Astrocaryum standleyanum,* was eaten twice when fruit was not abundant in November. Kinkajous ingested seeds while feeding on many fruit species, which did not appear to harm seeds. Physically damaged seeds were rare in the feces. All observed feeding was on arboreal food.

Kinkajous were observed eating 51 species of fruit, and 58 species were found in the fecal analyses; a total of 78 fruits from 30 plant families were eaten. Thirteen of those species remain unidentified. Of the 29 families, 14 were represented by only 1 species, 9 by 2 species, 5 by 3 species, and 1 by 15 species. The Moraceae, including genera *Brosimum, Cecropia, Ficus, Poulsenia,* and *Pourouma,* was the most represented family in diets of kinkajous.

Seven species of flowers from four families were eaten; none were eaten frequently. Kinkajous destroyed some flowers as they ingested floral components (e.g., *Philodendron*). Female palm flowers were ingested, but the cluster of flowers was never destroyed completely (e.g., *Astrocaryum standleyanum, Oenocarpus panamanus,* and *Scheelea zonensis*). Flower species from which only nectar was ingested were handled more carefully by kinkajous; the same individual flower was often visited more than once per night, and white pollen could be seen on the kinkajou's facial fur (e.g., *Ochroma pyramidale, Pseudobombax septenatum,* and *Tetrathylacium johansenii*). Leaves were found in seven fecal samples in six months, always in small amounts. Leaves in four samples were *Ficus.*

Fig fruits were the most important food of kinkajous (Table 1). *Ficus insipida* was

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TABLE 1.—*The most important fruits in the diet of kinkajous on the Limbo plot selected by choosing the five most important fruit species from each feeding measure.*

Family	Species	Vegetation type	Feeding bouts	Feeding time	Feces	Fecal volume
Boraginaceae	*Cordia panamensis*	Shrub	3.5	4.1	9.8	7.6
Mimosoideae	*Inga*	Tree	6.0	5.3	13.4	9.2
Moraceae	*Ficus insipida*	Tree	10.9	24.3	18.0	16.3
Moraceae	*Ficus* sp.?		1.0	0.8	15.5	8.1
Moraceae	*Ficus paraensis*	Hemiepiphyte	4.5	1.00	7.2	4.3
Palmae	*Astrocaryum standleyanum*	Understory	7.4	6.7	10.8	5.1
Palmae	*Scheelea zonensis*	Tree	6.9	9.1	0	0
Polygonaceae	*Coccoloba parimensis*	Liana	2.5	4.6	4.1	3.5
Sapindaceae	*Chrysophyllum cainito*	Tree	5.9	7.5	6.2	4.6
Total			48.6	63.4	N/A	58.7
All figs			21.8	29.6	44.9	32.06
All Moraceae			28.7	35.4	56.7	39.16

the most important species in all four dietary measures. Furthermore, most *Ficus* sp.? in feces were probably *F. insipida* which could not be identified to species at the beginning of the study. The nine most important fruits comprised 48.5–63.4 % of the total kinkajou diet, depending on the method used to assess diet.

The majority (55.5%) of fruits eaten by kinkajous were from trees, 36.5% were from climbers, and 8.0% were from shrubs. Compared with available patches of edible fruit, kinkajous fed in larger fruit patches, as measured by DBH ($\chi^2 = 136$, $d.f. = 6$, $P < 0.001$) and number of fruits on the ground ($\chi^2 = 172$, $d.f. = 5$, $P < 0.001$).

Bi-monthly census of fruit revealed strong seasonal changes in availability of fruit (Fig. 1). The subset of species eaten by kinkajous followed the trend shown by all fruiting species on the Limbo plot—a sharp increase in abundance from February to a peak in May followed by a slow decrease until the low point in December. Greater density of edible fruits was correlated negatively with distance between patches of edible fruit ($r^2 = 0.566$, $P = 0.0076$).

Four types of fruits were selected to illustrate three patterns of fruit availability and consumption by kinkajous. *Chrysophyllum cainito* (Fig. 2a) was a rare fruit but was frequently eaten by kinkajous in February and therefore strongly preferred. *Astrocaryum standleyanum* (Fig. 2b) was one of the most common fruiting species on the plot but was eaten rarely relative to its abundance. Fruits of *Chrysophyllum* and *Astrocaryum* occurred seasonally, as is typical of most species eaten by kinkajous, and were only available for a few months a year. Peak abundance of fruit in patches occurred 1 month after the peak of those species in the diet of kinkajous. That suggested that fruits were available to kinkajous in the trees ca. 1 month before they were detected with the census of fruits on the ground. Unlike most fruit species, no seasonality was evident in the fruiting pattern of fruits of *Ficus* (Figs. 2c and 2d).

Selection indices (S_i) were calculated for 37 fruits eaten by kinkajous and detected in the census of fruits. S_i for percent feces and percent volume were strongly correlated ($r^2 = 0.917$, $P < 0.0001$) and the data for percent feces is presented with the S_i for percent feeding bouts and hours (Fig. 3). The three indices gave similar values for most fruits but were contradictory for some species that were marginally selected for or against.

Comparison with other frugivores.—Kinkajous ate a higher percentage of fruit than any large frugivore that has been stud-

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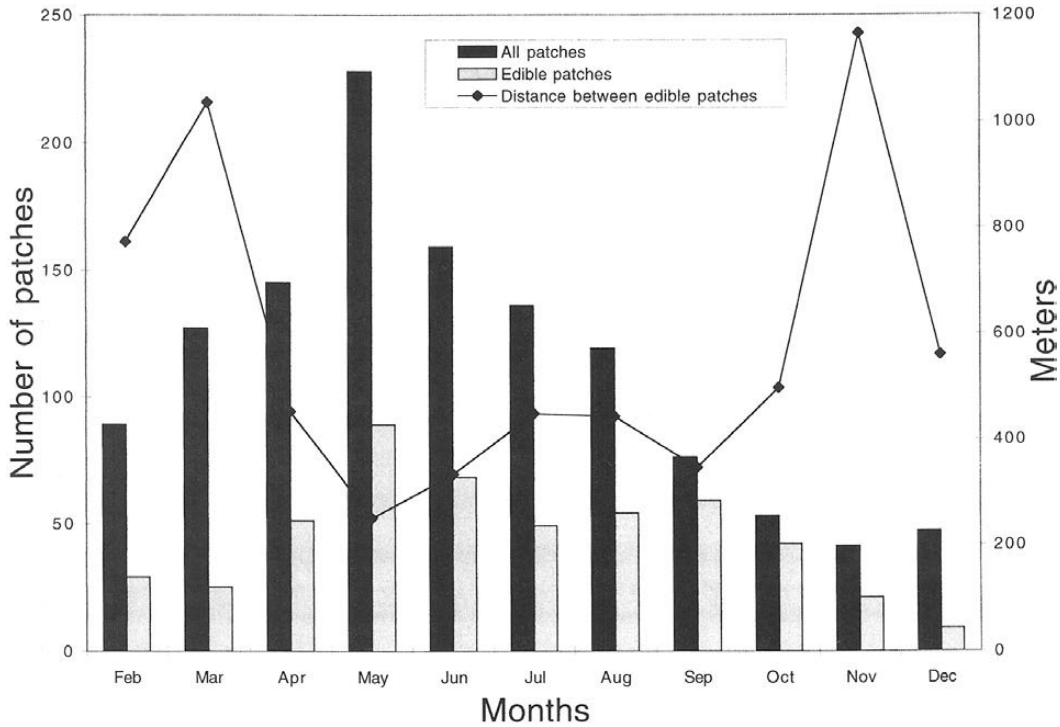

FIG. 1.—Availability of fruits and average distance between feeding patches on the Limbo plot in 1996 revealed by the number of non-wind dispersed fruit patches encountered on bi-monthly counts of fallen fruit on 11.4-km transects. Edible species are those that kinkajous ate during the study. Fruits actually were available to arboreal kinkajous ca. 1 month before they were detected in the census.

ied in central Panama and were closest to *Ateles* in overall dietary patterns (Table 2). I calculated the overlap of the specific fruits eaten by kinkajous and four other large frugivores studied on the nearby Barro Colorado Island, Panama. To compensate for fruit species eaten by frugivores on Barro Colorado Island that were not available on the Limbo plot, I calculated the total number of fruit species shared and the number shared from the subset of fruits detected on the Limbo plot by my census of fruits. Again, diets of kinkajous and *Ateles* were most similar. *Alouatta* also shared a high percentage of fruits eaten with kinkajous, but *Cebus* and *Nasua* shared <50% of the total fruit species and <60% of the species detected in the Limbo census of fruits. Like kinkajous, both *Ateles* and *Alouatta* also fed on a large number of figs and other Moraceae.

DISCUSSION

Kinkajou ecology.—Kinkajous on the Limbo plot were almost exclusively frugivorous. The proportion of their diet made up by fruit was higher than other carnivores (Charles-Dominique, 1978; Joshi et al., 1995; Lovari et al., 1994) and primates (Defler and Defler, 1996; Hladik & Hladik 1969; Leighton, 1993; Peres, 1994), and may be the highest of any non-volant mammal. However, not all populations of kinkajous are as frugivorous as the one in the present study (Estrada and Coates-Estrada, 1985; Redford et al., 1989).

Because kinkajous ingest, but seemingly do not damage seeds from most fruits, they

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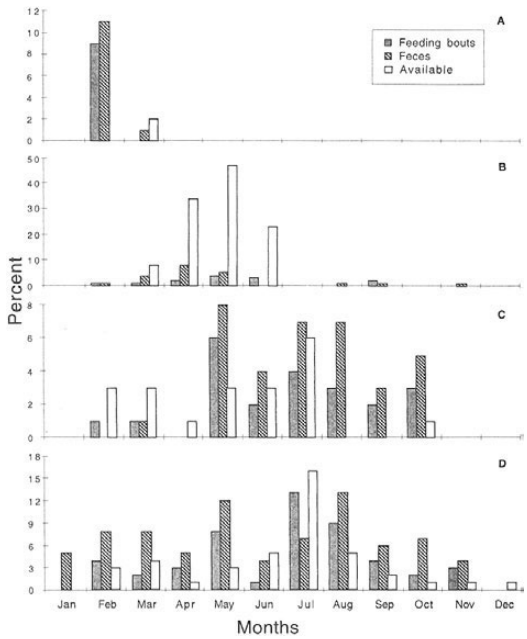

FIG. 2.—Availability and use of four fruit types for kinkajous. A) *Chrysophyllum cainito,* B) *Astrocaryum standleyanum,* C) *Ficus insipida,* and D) all *Ficus.* Intensity of use by kinkajous is shown by the number of feeding bouts and feces involving each fruit; availability is shown by the number of fruit patches encountered in the census of fruits.

apparently disperse seeds for many plant species. Kinkajous also may be acting as pollinators for those flower species from which they drink the nectar but do not damage flowers. The palm *Scheelea zonensis* was used often based on behavioral observations but was not detected in fecal analysis (Table 1). This may be related to the unusual way kinkajous fed on their large, hard fruits; they chewed on single fruits for ≤30 min before dropping the large seed under the tree. Such extended mastication may allow kinkajous to ingest juice and oils from the fruit that would not be detected in feces.

Kinkajous preferentially fed in large fruiting patches. This has been observed in other large-bodied primate frugivores (Leighton, 1993; Strier, 1989) and permits individuals to feed longer in one patch, visit fewer feeding patches, and travel less (Zhang, 1995). Of the fruits that were eaten, the majority were from trees, but 36.5% were from climbing vegetation. Climbing plants are difficult to census using a tree-based census of fruits (e.g., tree transects or fruit trails—Chapman and Wrangham, 1994); thus, if a tree-based census of fruits had been the only census method used, more than one-third of the species eaten by kinkajous would have been missed. This illustrates the importance of a ground-based census of fruits to study potentially available fruit when the diet of a frugivore is unknown.

All fleshy fruits, and the subset of species eaten by kinkajous on the Limbo plot in 1996, showed seasonal changes in abundance similar to that reported for Barro Colorado Island (Croat, 1978; Milton, 1980). The 1-month time lag between when fruits were available to arboreal kinkajous and when they were observed with the ground-based census also was reported by Zhang and Wang (1995) in their comparison of census methods for fruit.

Fruit preferences of kinkajous.—The selection indices (S_i) illustrate the relative amount a fruit was eaten compared with its relative availability. A high S_i for feeding bouts indicated that kinkajous visited a fruiting species more often than expected, a high S_i for feeding time indicates that kinkajous spent more time in a species than expected, and a high S_i for feces indicated that kinkajous ingested a fruit species more frequently than expected. These values may conflict with each other if, for example, kinkajous visited many trees of a certain species but did not spend much time in any one tree because it was small and had little fruit per tree.

Of the most important fruits in the kinkajou's diet (Table 1), only *Astrocaryum* was eaten substantially less than expected (Fig. 3). *Coccoloba paramensis* was eaten slightly less and *Scheelea* slightly more than expected. The other five species were selected for by kinkajous. Kinkajous selected all but

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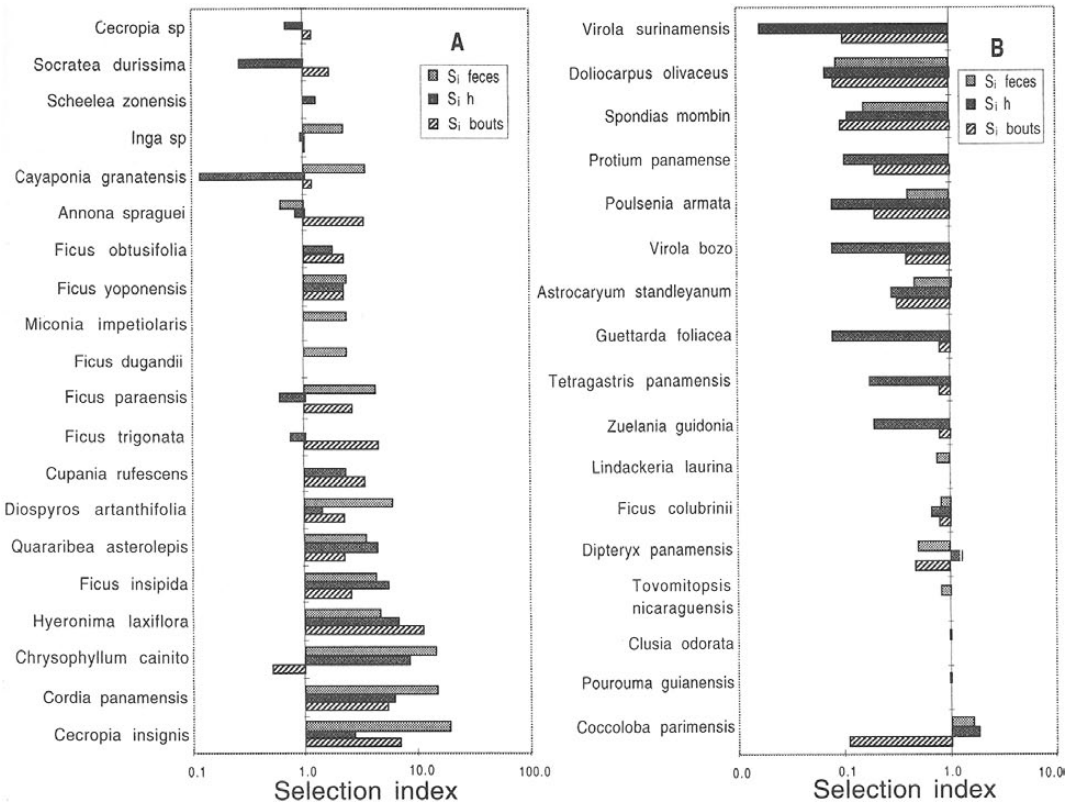

FIG. 3.—A) High and B) low selection indices (S_i) for fruits eaten by kinkajous. (>1 = selected for, <1 = selected against). High S_i-values for feeding bouts indicated that kinkajous visited a fruiting species more often than expected; high S_i-values for hours feeding (h) indicated that they spent more time in a fruit species than expected; high S_i-values for feces indicated that they ingested a fruit species more frequently than expected.

one fig species. *Ficus columbrinii* was not selected; this species differs from the other figs eaten in that it is small, red, and considered to be a bird-dispersed fruit (Kalko et al., 1996). The other eight species of figs selected by kinkajous are large, green, and dispersed by large mammals or bats.

In addition to 13 unidentified fruits, 27 species were eaten by kinkajous but were so rare they were not detected in the census of fruits. Clearly, these species also are selected but can not be directly compared with selection indices. These fruits were rarely eaten; the three most frequently eaten species not detected in the census of fruits were *Abuta racemosa* (4.6 % of feces), *Passiflora nitida* (2.6 % of feces), and *Brosimum alicastrum* (2.1 % of feces).

Importance of figs.—The only plant family that had more than three fruit species eaten by kinkajous was the Moraceae, which was represented by 15 species, including nine *Ficus*. Figs were the most important fruits for kinkajous, and most were selected over other fruits. *Ficus insipida,* a large free standing fig, was the single most important species of fruit eaten. The nine species of figs formed 21.8%—44.9% of the kinkajou's diet, depending on the dietary measure.

Because of their abundance and year-round availability, figs are important for

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TABLE 2.—*Dietary importance and overlap of figs, moraceous fruits, and all fruit species eaten by kinkajous and large frugivorous mammals from central Panama. Censused fruits are those detected at least once with the fruit census on the Limbo plot.*

Species	Method	Fruit	Flowers and leaves	Prey	Figs only % (*n*)	All Moraceae % (*n*)	Total fruit species eaten (*n*)	Total species shared with *Potos* (*n*)	Total species shared with *Potos* %	Censused fruit species eaten (*n*)	Censused species shared with *Potos* (*n*)	Censused species shared with *Potos* %	Reference
Potos	Percent time	90.7	9.3	0	14.1 (9)	23.4 (15)	64			40			This study
	Percent occurrence in feces	99	5.2	0									
Nasua	Percent time	26.8	0	73.2	6.5 (3)	15.2 (7)	46	20	43.5	26	15	57.7	Russell, 1982; Gompper, 1994
	Percent time	55.4	0	44.6									
	Percent occurrence in feces	72.1	0	41.9									
Alouatta	Percent time	42.1	57.8	<1	20.0 (9)	35.5 (16)	45	20	44.4	22	18	81.8	Milton, 1980; Hladik and Hladik, 1969
	Observations and stomach contents	60	40	<1									
Ateles	Observations and stomach contents	80	20	<1	8.3 (2)	29.2 (7)	24	15	62.5	13	13	100	Hladik and Hladik, 1969; Milton, 1993
Cebus	Observations and stomach contents	65	15	20	3.8 (3)	9.1 (7)	77	22	28.6	33	18	54.5	Hladik and Hladik, 1969
Aotus	Observations and stomach contents	65	30	5									Hladik and Hladik, 1969
Saguinus	Observations and stomach contents	60	10	30									Hladik and Hladik, 1969

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frugivores throughout the tropics (Janzen, 1979). However, there is controversy over their nutritional importance. Some authors have asserted that figs have low or baseline nutrient levels, are eaten because they are abundant, and therefore are not selected for, especially in the Old World (Conklin and Wrangham, 1994; Leighton, 1993; Milton, 1980). However, recent comparisons of the nutrient content of figs and non-fig fruits showed that figs are an excellent source of calcium and other minerals for frugivores, especially in the New World (O'Brien et. al., 1998). Furthermore, Panamanian figs have higher levels of lipids, protein, and carbohydrates, and lower tannin levels than Ugandan figs (M. Wendeln, in litt.). These high nutrient levels help explain why kinkajous on the Limbo plot preferred figs over most other fruits.

The frugivorous guild.—Although no large mammalian frugivores have been studied on the Limbo plot, diets of coatis (*Nasua narica*) and five primates (*Alouatta palliata, Aotus trivirgatus, Ateles geoffroyi, Cebus capucinus* and *Saguinus geoffroyi*) have been reported for Barro Colorado Island, <10 km E of the Limbo Plot.

A comparison of diets of this guild shows that kinkajous are the most frugivorous, and most similar to *Ateles* in broad dietary description (Table 2). Furthermore, kinkajous and *Ateles* also are the most similar in overlap of specific fruits eaten, sharing 100% of fruits known to occur on the Limbo plot and eaten by *Ateles* on Barro Colorado Island. Although *Alouatta* eat many more leaves and flowers than kinkajous, most of the fruits consumed overlap between species. Number of fruit species eaten is highest in *Cebus* and lowest in *Ateles*. However, each species has been studied with different intensity, and this number may not reflect actual dietary diversity.

The diet of kinkajous is most similar to *Ateles*—a large, diurnal, arboreal primate. Preliminary results from studies of kinkajous suggest that these two species also have similar social organizations, with individuals from a group or community usually foraging alone or in small groups and stronger social bonds between adult males than females (Kays and Gittleman 1995; Robinson and Janson, 1987). Future work with kinkajous should test hypotheses concerning similarity in diet between *Ateles* and *Potos* and convergence in their social organizations.

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