



Modeling Dietary Selectivity by Bornean Orangutans: Evidence for Integration of Multiple Criteria in Fruit Selection

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*Food patch visitation was compared to the availability of fruit patches of different species during 2 years in a Bornean lowland forest to examine orangutan (*Pongo pygmaeus*) diet selectivity. Feeding on both the pulp and the seeds of nonfig fruit varied directly with fruit patch availability, demonstrating preference for these foods over fig fruit or other plant parts (bark or leaves). Factors determining fruit selectivity rank were examined through multiple regression analysis. Modeling selectivity for 52 chemically unprotected "primate-fruit" pulp species revealed strong preferences for species of (i) large crop size (numbers of fruits ripening in an individual patch), (ii) high pulp weight/fruit, and (iii) high pulp mass per swallowed unit of pulp + seed, demonstrating orangutan sensitivity especially to patch size (g of pulp or total energy/patch) and perhaps to fruit handling time. Modeling selectivity for 18 fig species showed that 4 factors significantly influenced fig species rank: crop size, pulp weight/fruit, and 2 chemical variables, percentage digestible carbohydrate and percentage phenolic compounds in the fig fruit pulp. The selectivity rank based on the overall nutrient gain from feeding in the fruit patch (the product of the first 3 variables) is proportionally depressed by the percentage tannin content, demonstrating that orangutans integrate values for these variables in selecting fig patches. The conclusions from these results and from analysis of selectivity for seeds and for other fruit types are that orangutan foraging decisions are strongly influenced by the meal size expected from a feeding visit (i.e., by patch size), that tannins and other toxins deter feeding, and that the energy content, rather than the protein content, of foods is important in diet selection. The foraging strategy of orangutans is interpreted*

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relative to these results and to Bornean fruiting phenology. By integrating spatial, morphometric, and chemical variables in analysis, this study is the first to demonstrate the application of foraging theory to separate out the key variables that determine diet selection in a primate. Multivariate analysis should routinely be applied to such data to distinguish among the many covarying attributes of food items and patches; inferences drawn in previous studies of primate diet selection, which ignore key spatial and morphological variables and rely on univariate correlations, are therefore suspect.

KEY WORDS: diet selection; foraging theory; seed dispersal, seed predation; patch size; tannin; orangutan, *Pongo pygmaeus*.

INTRODUCTION

In this paper I explore the dynamics of dietary breadth of Bornean orangutans (*Pongo pygmaeus pygmaeus*) by comparing their diet with the relative availabilities of different fruits and by modeling fruit pulp selectivity as a function of distributional, chemical, and morphometric variables. One robust result from foraging theory (Krebs and Stephens, 1986) is that dietary breadth—the diversity and relative proportions of items in the diet—depends on the relative densities of the preferred items. An item that is important in the diet at one time can be completely neglected during another period, even if the item is at a higher absolute density, if more preferred items themselves are more common. Items eaten when rare—that are deliberately sought out and eaten—will typically be eaten in greater quantity as they become more common. Therefore, dietary breadth can dramatically fluctuate, even if the consumer consistently applies rules governing its decisions of selectivity rank among available items.

To build a predictive theory of diets, data should be collected and analyzed so they are “dynamically sufficient,” capable of generating predictions about dietary breadth under various conditions of the relative availabilities and spatial distributions of different potential food items (Leighton, 1992). This requires adequate sampling of the relative availabilities of items eaten and uneaten. The characteristics of uneaten, common items shed as much light on the factors underlying the decision rules of food choice as the rare, but vigorously consumed, highly preferred items do. A further step involves multivariate modeling of food item selectivity to determine which factors underlie decisions of food choice. Models will yield accurate results only if all relevant variables influencing selectivity are collected (Janson *et al.*, 1986). Selectivity indices compare the relative frequency of feeding on a food item with its relative availability (Cock, 1978; Chesson, 1978, 1983; Johnson, 1980). Items with high selectivity values are

deliberately searched for and/or disproportionately eaten once encountered. Items that are "neglected," that have low selectivity values, have been passed over relative to more highly preferred items.

Previous studies of orangutan feeding ecology and behavior (Rodman, 1988) established that orangutans are omnivorous, feeding on bark, the pith from palm and other monocot stems, leaves, flowers, fruit pulp, and seeds, and also on animal prey, often social termites or ants (MacKinnon, 1974; Rodman, 1977; Rijksen, 1978; Sugardjito *et al.*, 1987; Galdikas, 1988). It has been the impression of these field-workers that fruits are preferred items and that the incidence of bark-feeding, in particular, is high only during periods of low fruit availability. However, because phenological data have typically not been collected, dietary changes cannot be interpreted rigorously in relation to the fluctuating availabilities of preferred fruit patches. The study by Sugardjito *et al.* (1987) is an exception; they monitored the changing availabilities of fruiting figs versus nonfig fruiting plants but did not analyze dietary selectivity for food types or fruit species. Hypotheses about orangutan preferences among food and fruit types, and the variables responsible for these preferences, therefore remain unexamined.

Modeling Food Selecting

Which factors influence primate food selection? The pioneering studies of colobines by Waterman and colleagues (McKey *et al.*, 1981; Davies *et al.*, 1988) led them to conclude that protein (positively), fiber, and sometimes tannin content (negatively) influence leaf or seed selection. These inferences and those of others (Milton, 1979) were based on univariate analysis. The low correlation coefficients relating the presence or proportion of an item in the diet to single variables or indices of variables and the high covariance among chemical measures suggest caution in interpreting the results. Instead of implying that primates employ sloppy shopping rules of food choice or that the net rate of energy gain is unimportant, these inferences may be flawed for two reasons. First, biased field measures may lead to poor estimates of selectivity rank—the dependent variable. In all studies, a feeding visit to a patch was not scored as a single observation; instead, multiple samples for analysis were artificially created from some combination of the feeding group size and visit duration at one patch, violating parametric assumptions for the independence of samples. Thus, analysis of selectivity is confounded with a different question: What factors determine how much fruit is consumed once the animals decide to feed in the patch? In addition, the estimates of relative availability, if measured, were densities of sterile plants and not densities of food patches; these

may or may not be related, depending on the phenology of the plant species and the schedule with which feeding animals were observed.

Second, probably a more significant shortcoming of these studies is that selectivity was modeled using only chemical variables. These included both the macronutrients (fat, digestible carbohydrate, and protein) that might be generally limiting to consumers and the chemical or physical characteristics that could slow the rate of nutrient acquisition. Feeding deterrents may include fiber (Van Soest, 1981), tannins (Waterman and Choo, 1981; Wrangham and Waterman, 1983; Mole and Waterman, 1987), and toxic compounds such as alkaloids and terpenes (Freeland and Janzen, 1974; McKey *et al.*, 1981; Glander, 1982). All these chemical variables can be reasonably hypothesized to influence an item's selectivity rank and should be included in multivariate analyses.

However, if food choice is based on maximizing the long-term rate of energy intake, as proposed by foraging theory (Krebs and Stephens, 1986), chemical factors alone would predict an item's selectivity ranking only if items were searched for and ingested at equal rates. If we consider fruit pulp, for instance, we might expect that morphological features, such as husk toughness and thickness, and fruit and seed size, which vary widely among fruits, can dramatically alter rankings of fruit based on total nutrient content, because of gross differences in handling time (Leighton, unpublished).

In addition, Howe and Vande Kerckhove (1982) hypothesized that the ratio of fruit pulp to seed mass is important in determining fruit choice by birds because the seed is costly ballast that fills the gut, thereby preventing feeding on other items and increasing body mass and the costs of flying. Avian fruit selection is also influenced by how fruit is presented in the crown in relation to a bird's typical locomotor or perching methods of harvesting fruit (Moermond and Denslow, 1985). However, these variables of importance in avian fruit selection (Martin, 1985; Moermond and Denslow, 1985) may have little influence on primate fruit selection either because their use of teeth, hands, and positional behavior may render most fruits similar in their net rates of nutrient yield or because the fruits that primates eat do not vary sufficiently in handling difficulty to affect their selectivity rankings. Also, the decline in travel efficiency from carrying seed ballast (Martin, 1985) probably has limited consequences for primates; ratios of seed mass to body mass following a fruit meal influence the per distance costs of flight more than predicted for primate locomotion (see Calder, 1984, p. 190) and are likely to be much smaller for the most massive primates.

In addition to the morphological features of individual fruits, spatial distributional variables such as food patch size, patch density, and the density

of items within patches may influence selection because the rate of nutrient return is likely to be positively correlated with these variables (MacArthur and Pianka, 1966; Charnov, 1976; Leighton and Leighton, 1983; Schluter, 1982; Krebs and Stephens, 1986). An animal visiting large patches can maximize energy returns indirectly by reducing the number of patches required to obtain its daily ration, thereby minimizing the time and energy costs of travel.

The lack of predictive power of these prior attempts to explain primate dietary breadth from chemical factors alone is therefore not surprising, when reviewed from the perspective of optimal foraging theory. Rates of energy (or other nutrient) acquisition are expected to underlie dietary choice, and chemical variables may be overwhelmed in importance by morphological and spatial characteristics of fruit that more dramatically influence feeding efficiency.

To build predictive models, the selectivity ranking of a species must be modeled as a function of *all* the variables that might underlie dietary choice, so that multivariate analysis can determine which factors of food items or patches are used to make foraging decisions. If important variables are left out, factors which merely covary with causal factors or are relatively inconsequential can be mistakenly interpreted as determining selectivity and models may fail to explain or will explain less of the variance in selectivity among food items (Janson *et al.*, 1986), leading erroneously to the conclusion that the animal is not applying consistent criteria in ranking foods. By testing for the significance of the partial regression coefficients of each independent variable on selectivity, while statistically controlling for the effects of others, multiple regression analysis can expose the joint influence of several factors that are used by the animal to determine the relative selectivities of different items. The results would indicate if, in deciding which items to select or which patches of items to visit, the animal trades off various attractive and deleterious factors against one another, so that an integrated or weighted value is used for establishing selectivity rankings of items or patches (Schluter, 1982; Smallwood and Peters, 1986). Such an integration might be expected because few characteristics of fruit are likely to cause a straightforward change from acceptance to avoidance at some specific threshold value.

Specific Research Aims

The analyses presented here were designed to expose the factors underlying food, and particularly fruit, selectivity by Bornean orangutans. I posed the following questions:

- (1) Which types of foods (fruit pulp, seeds, bark, etc.) are preferred, and why?
- (2) Are there chemical or physical features of fruits that influence selectivity?
- (3) How does variability in fruit patch size and density influence fruit selection?
- (4) Are there interactional effects between factors, and if so, is there evidence of integration or weighing of measures for the different factors instead of threshold effects?
- (5) Are the significant factors that influence selectivity consistent with predictions from foraging economics?
- (6) Does the multivariate approach that I adopt in this study, with its underlying assumptions of complex orangutan decision making, based on foraging economics, compare favorably in its explanatory power vis-à-vis other approaches?
- (7) What do the results of dietary selectivity analyses imply about orangutan foraging strategies?

To address these questions, I sequentially examine selectivity for different subsets of food items, using each subset to control for some potentially confounding variables. Selection among food types is evaluated first. Next, selection among types of nonfig fruits exposes some chemical factors that influence fruit pulp selection. Selectivity rankings within a subset of these, the different "primate-fruit" species (Leighton and Leighton, 1983), which have similar chemistry and morphology, are then modeled. Finally, to control for fruit morphological differences, and to examine further multivariate interactions, factors influencing rankings among the set of fig fruits (*Ficus* spp.) are explored. Seed-eating is interpreted in light of the results of fruit pulp selectivity.

METHODS

Study Site

All field data were gathered during a 24-month interval (September 1977–August 1979) at the Mentoko Research Site, Kutai National Park, East Kalimantan, Indonesia (Leighton and Leighton, 1983). The site encompassed 35 km of mapped and marked trails, arranged roughly as a grid within 3 km² of rain forest on the south bank of the small Sengata River, 25 km from the east coast of central Borneo (0°24'N, 117°16'E). Most of the site is upland, well-drained, species-rich mixed dipterocarp

lowland rain forest (20–320 m in elevation), with a distinctive riparian sub-habitat of seasonally flooded alluvial bench forest in small pockets along the Sengata and the smaller Mentoko stream. The lowland forest of East Borneo [at least before the 1983 drought and forest fires (Leighton, 1986)] is among the most species-rich in the world; ≈ 780 species of woody plants reproduced within the small site during the 2 years of phenological monitoring. Wildlife had not been hunted. Other than some limited low-density hand-logging of some of the Bornean ironwood (*Eusideroxylon zwageri*) before the study, the full complement of plant and animal species, at relative population densities, presumably reflecting their recent evolutionary history, occupied the site during the study. Competitors of orangutans for pulp and seed resources at Mentoko are described by Leighton and Leighton (1983).

Aspects of social behavior and the general ecology of orangutans at Mentoko have been described by Rodman (1977, 1984) and Mitani (1985). The orangutan population included individuals that occupy stable, defined home ranges continuously for at least several years, and a much larger set of individuals that migrated in and out of the site (Leighton and Leighton, 1983). Migrations by subadults and adults of both sexes in January–April 1978 were responses to an unusually heavy fruiting season.

Methods of Measuring Food Selectivity

Sampling Diets

I measured the relative proportion of an item in the diet as the ratio of the number of independent observations of orangutans feeding in patches of the item to the total number of feeding observations. To conform to underlying biological and statistical assumptions, one observation is scored for each independent sighting of feeding orangutans, regardless of the number of individuals in the patch or how long they fed there. Fruits occurred in discrete patches in this species-rich forest, as individual fruiting trees, lianas, or hemiepiphytic figs, separated from conspecifics by the non-fruiting crowns of many other species. Therefore, orangutans “decided” to visit a *patch* of fruit, and not to eat an *item*, because once in the patch, only one fruit species is usually available. Consequently, the individual or group of individuals traveling together have made a single decision of what to eat from among the different food species available. In fact, orangutans typically travel and feed solitarily, except for a mother with a dependent juvenile and occasional pairs or trios of subadults (Rodman, 1988, personal observation; but see Sugardjito *et al.*, 1987).

My research assistants and I gathered feeding observations which I used for dietary selectivity analysis, during censuses for vertebrates along the set of trails within the study site, while following orangutans or, rarely, other animals. Feeding observations collected while watching fruit trees were excluded. Feeding orangutans were carefully observed to determine which maturational stage and part of each fruit was chewed up, which was discarded, and which was swallowed. I also compared discarded parts with entire fruits to help identify the ingested parts. In general, the orangutans ate either seeds or pulp, but not both, which enhanced how accurately I could classify observations. Further, these observations revealed that orangutans almost always select ripe fruits for pulp-eating and then almost invariably swallow the enclosed seed(s) within the pulp. By examining numerous fecal samples, I established that seeds within ripe pulp were passed undigested and viable through the digestive tract; consequently, orangutans are seed dispersers of these plants. In contrast, unripe fruits are typically selected for their seeds which are chewed up, and their fleshy parts are ignored, being either thrown away or incidentally swallowed. This distinction between ripe pulp eating and immature seed eating has also prevailed during studies at Gunung Palung, West Kalimantan, over the last 5 years (Leighton, 1992), though in a few cases orangutans fed on mature (=ripe) or immature pulp but discarded the seeds.

Sampling Fruit Patch Availability for Different Species

I calculated the relative availabilities of fruit patches of different species by monitoring the flowering and fruiting of all fruiting woody plants [>5 -cm diameter at breast height (dbh) in a set of phenological plots (30 0.5-ha plots in the first year, 41 0.25-ha plots in the second year] and along belt transects bisected by the midlines of the animal census trails. Flowering or fruiting plants were mapped by location and measured for dbh at 137 cm above the ground. Plots were initially selected from a stratified random design within the 3-km² study site. Belts were 20–50 m wide, depending on the size and taxa of tree or liana, and were used to monitor rare or large plants that were uncommon within the phenological plots. Densities of fruit patches of each species were calculated each month from tallies of the numbers of individuals with fruit at the appropriate stage of maturation, depending on whether the species' unripe seeds or ripe pulp was eaten by orangutans. Densities were adjusted to account for different areas that were monitored for different species; tallies for common and small plants that were sampled only within plots were multiplied accordingly by a factor to

extrapolate their density within the total 1.2 km² of forest monitored for the largest, rarest trees and lianas.

For each fruiting individual, the size of the crop of fruit was estimated, and the fruits were classified into one of three stages of fruit maturation: (1) an immature stage in which seed development had not proceeded to the stage at which vertebrates begin to prey on seeds (the few exceptions to this were noted); (2) a stage before fruit ripening at which the seed is relatively hard and typically is preyed upon by at least one species of the set of primate, squirrel, or psitticine arboreal predators; and (3) a ripe stage corresponding often to some dramatic change(s) in color, texture, fruit pulp softness, and/or husk dehiscence, that corresponds to seed dispersal by the appropriate vertebrate or inanimate agent. Because I followed crops of fruits of virtually all species throughout their developmental cycles, noting these changes, I learned the distinguishing features of ripe versus unripe fruit and could adjust phenological codes post hoc if initial interpretations proved incorrect. Botanical specimens were collected for 776 of the 781 species that fruited during the 2-year study and were identified, in most cases, by the expert for the taxon (Leighton and Leighton, 1983). Most genera could be correctly identified in the field, and an elaborate set of type individuals with their bark, leaf, fruit, and flower descriptions helped to classify species newly becoming reproductive.

Examining Selection of Food Types

The migrations of orangutans in and out of the study site, the proportion of time they spent active and feeding, and the relative census effort resulted in highly variable rates of accumulating feeding observations; therefore, observations were grouped into 11 successive intervals of 1 to 4 months, depending on sample size. To avoid bias, months were successively added until the total sample of independent feeding visits exceeded 25, except for the last interval (Table I). To describe seasonal changes in fruit availability, the "large" mid- and high-canopy trees (dbh \leq 25 cm, excluding figs) were singled out from other patches, because orangutans tend to select against (i.e., avoid) smaller trees, even if they contain palatable fruit pulp or seeds. Densities of these large fruit trees for each of the 11 sampling intervals (Table I) are calculated from phenological plots. An individual fruiting tree was usually tallied in two consecutive intervals: once when its fruit were "nearly ripe" (stage 2), when orangutan seed predation typically occurs, and again in the subsequent interval when the ripe pulp was eaten (and seed dispersal occurs). Periods of significant ripe fruit production were

Table 1. Densities of Fruiting Trees and Figs and Proportions of Food Types in Orangutan Diets During 11 Consecutive Periods of Study

Period ^a	Month midpoint ^b	Fruiting trees >K25 cm/ha	No. fruit tree spp.	Fruiting figs/ha	Dietary proportion ^d										N ^c (No. obs.)
					Flowers	Bark	Leaves	Imm. seeds	Imm. pulp	Ripe pulp	Imm. figs	Ripe figs			
son 77	2	1.9	13	0.93		0.06	0.12		0.09	0.68		0.03		34	
d 77	4	4.1	23	1.27			0.08		0.11	0.08	0.67	0.06		36	
i 78	5	11.8	40	1.33	0.09			0.29	0.03	0.57				35	
f 78	6	20.0	53	1.20				0.39	0.11	0.50				28	
m 78	7	19.7	61	0.87				0.08		0.92				25	
a 78	8	3.7	33	1.07				0.37	0.04	0.52	0.04			27	
mjj 78	10	2.1	7	0.87		0.17	0.30	0.13	0.07	0.27		0.07		30	
aso 78	13	1.9	7	0.78		0.27	0.12	0.30	0.09	0.03	0.12	0.06		33	
ndjf 78/79	16.5	1.7	7	0.87	0.05	0.16	0.03	0.08	0.14	0.16	0.08	0.30		37	
ma 79	19.5	4.3	23	1.03				0.15		0.73	0.09	0.09		33	
mija 79	22.5	1.3	4	0.93		0.04	0.04		0.04	0.35	0.13	0.39		23	

^a Months (abbreviated by single lowercase letter) included within period; e.g., "77" = 1977.

^b Refers to midpoint of period, with Sept. 1977 = 0 (see figures).

^c Total trees >25 cm in dbh maturing fruit within the phenology plots (see text).

^d Imm., immature or unripe; figs, *Ficus* spp.

^e Number of independent observations of orangutans feeding during period.

seldom longer than 4–6 weeks, so an individual was usually tallied only for the month when most of its fruit ripened.

Calculating Selectivity Ranks for Fruit Taxa

For each plant taxon i , during each 1- to 2-month interval, the ratio of independent observations of feeding on i to total observations was calculated (f_i). Relative availabilities of fruit patches (an individual fruiting plant) of a taxon (a_i) were calculated as the relative proportion of all patches of ripening fruit during the interval comprising patches of taxon i . The measure of selectivity used was the simple ratio, $S_i = f_i/a_i$. Most taxa were individual species, but if congeneric fruit species had very similar values of the variables examined for their correlation with selectivity rank, they were grouped together to help ensure that samples were independent (Clutton-Brock and Harvey, 1984). Without such grouping, for example, avoidance of *Litsea* fruits per se by orangutans could be misconstrued as avoidance of lipid-rich bird-fruits, because the 32 species of *Litsea* could dominate this class if each were assigned a separate selectivity measure.

Although continuous measures of selectivity have been designed and are preferable (Chesson, 1978, 1983; Cock, 1978), I assigned fruit pulp taxa into ordered selectivity ranks. All taxa of pulp eaten by orangutans were ranked. Taxa producing abundant patches of fruit (arbitrarily defined as >10) but not observed to be fed upon were also assigned ranks, in reverse order to their values of a_i (i.e., the more available, the lower the ranking), because more confidence can be placed in inferring a taxon's low preference the more common its patches were. Conversely, taxa of uneaten fruits that occurred in rare patches (<10) were excluded from analysis, because sampling error and factors affecting orangutan ranging behavior other than food patch choice more likely precluded estimating their true preference.

To examine selectivity of fruits of grossly distinctive types, the distributions of fruits of different seed dispersal syndromes into five rank classes were compared. Fruit taxa fitting the criteria for ranking were assigned to a class based on chi-square tests for significant differences between the classes and from neutrality, or no selection ($S_i = 1$). Note that the species for which $S_i = 1$ will be determined arbitrarily by the set of species included in the calculations because this will determine the total patches available (Johnson, 1980); however, definition of this set will not affect *relative* rankings. These five classes, from most preferred to most neglected or avoided, were numbered and defined as follows.

- (1) S_i significantly >1 .
- (2) $S_i >1$, but feeding on i and patches of i both rare (therefore, actual class may be 1 or 3).
- (3) S_i not significantly >1 ; patches of i common.
- (4) S_i significantly <1 (some $f_i = 0$), patches i common and S_i significantly $< S_i$ for class 3 fruits ($P < 0.05$).
- (5) $S_i = 0$ (all $f_i = 0$), patches of i very common, S_i more significantly $< S_i$ for class 3 fruits ($P < 0.01$) than were class 4 fruits.

To examine variables underlying fruit pulp selection, both primate-fruit and fig species were assigned selectivity ranks ranging from 1 (for the most preferred) to n , the sample size for the particular analysis, with the stipulations that (i) the highest ranks were allotted first to the species of class 1 and then to the successively numbered classes, as defined above and (ii) within each class, taxa were ranked by their relative S_i . In the case of ties among nonfig fruits, taxa fruiting during periods of higher fruit availability were given higher ranks because the much lower diversity of fruits available during fruit-poor periods likely resulted in higher numerical values for fruits that would have ranked lower if they had been available during a period of high competition among fruits for orangutan visits. Selectivity ranks for figs were computed for the period May 1978–August 1979, because fig-eating was virtually confined to this period (42 of 46 feeding observations), when more preferred fruits were scarce.

Methods of Measuring Patches and Fruits

Crop Size

Plants that contained fruit were scanned to estimate crop size (the number of fruit on an individual plant). Crop size was estimated on an exponential scale in which each order of magnitude was divided into three equal-sized classes; accordingly, classes were of 1–3, 4–7, 8–10, 11–39, 40–69, 70–99, 100–399, 400–699, 700–999, 1000–3999, . . . fruits, up to the largest crop of a few hundred thousand. The midpoint of the class was used as a point estimate in analysis. I estimated fruit number in sample units of canopy volume or surface, or of individual twigs or branches, dispersed around the crown. I then derived the total crop size by multiplying this mean number of fruits by the number of sample units. To ensure replicability, I estimated the great majority of the crop sizes analyzed here myself.

Chemical and Morphometric Measures of Fruits

Fresh fruits of most species, both eaten and uneaten by orangutans, were collected and scored or measured for seed number per fruit and the volumes, metric dimensions, and wet and dry weights of the dissected parts of fruits. Pulp and seed (the embryo and associated dicotyledons or endosperm) were preserved for later chemical analysis. For *Ficus* fruits ("figs"), the digestible, pulpy pericarp layer was weighed and analyzed separately from the indigestible inner layers of seeds and old floral parts. Chemical analysis of figs was restricted to the pulpy outer layer, because the inner layers are either discarded or are passed undigested by orangutans.

The data reported here were collected during a larger community study of vertebrate frugivory, from which it has been possible to classify fruits into syndromes of seed dispersal, marked by unique sets of covarying morphological and chemical traits (Leighton and Leighton, 1983; Leighton, 1992). Based on their primary agents of seed dispersal, the pulpy fruits were classified into the following types: primate-fruits, lipid-rich bird-fruits, sugary bird-fruits, and bat-fruits. Figs, which are generalized fruits eaten by a variety of vertebrates, were examined as a separate class. Primate-fruits, for which seed dispersal is predominantly by the three genera of seed-dispersing primates (*Pongo*, *Hylobates*, and *Macaca*) (Leighton and Leighton, 1983; Leighton, unpublished), are a special focus here. Their defining characteristics are an inedible, indehiscent yellow to red husk, which must be peeled before the pulp and its enclosed seeds can be swallowed, and a watery pulp that is rich in digestible carbohydrate (mostly sugars), but containing little protein and virtually no lipid, and almost invariably with low densities of chemical deterrents such as fiber, tannins, or toxic compounds.

Fruits selected for measurement and preservation were representative of a distinctive phase of maturity of the species. I preserved the separated pulp or seed parts by drying, or fixation in boiling ethanol, or both. After oven-drying at 45–55°C, samples were stored in plastic bags with desiccant until chemical analysis. Chemical analysis was performed mostly in the phytochemistry laboratory of Peter Waterman, University of Strathclyde, U.K., with some in the nutritional biochemistry laboratory of Biological Anthropology at Harvard University (Leighton, Waterman, and Marks, in preparation).

Multivariate Analyses of Selectivity

The independent variables that I used to model selectivity rank in multivariate analysis are defined below. All measures are median values for the sample of trees or fruits measured for a plant species or genus.

(i) *Fruit patch density*: the number of individuals of a taxon simultaneously fruiting within a 1.2-km² area (densities of common species were estimated from plots of smaller total area, then scaled proportionally upward).

(ii) *Crop size*: the number of fruit matured by an individual plant during a single fruiting episode. Crop size was estimated just before fruit maturation (to avoid counting immature fruits destroyed by insects or aborted before they became ripe and available). Crop sizes for any one species often showed a bimodal or skewed distribution due to sparse fruit production by some individuals (Leighton, unpublished). Because orangutans typically ignored these in favor of the denser patches, the crop size estimate used in analysis was the median among the largest 50% of measured crop sizes.

(iii) *Patch size*: the kilograms of dry edible pulp within a crop of fruit matured by the plant (the product of the median grams dry weight of pulp per fruit and the median crop size). Pulp dry weight was used as an estimator of the energy content of primate-fruit because most pulp of these species contains little indigestible fiber. Further, the assumption that orangutans ate fruit pulp to acquire energy is supported by the results. A more refined measure of patch size was used for the fig analyses. The percentage digestible carbohydrate (dc)—the energy-rich nutrient—of each fig was multiplied by the pulp dry weight/crop to yield to patch size estimator, grams dc per patch. The protein and fat fractions of both figs and primate-fruits are uniformly low, so carbohydrate is the only significant nutrient.

(iv) *dbh*: the diameter at breast height (137 cm above ground) of the bole of a tree; dbh has often been used as an estimator of patch size. For hemiepiphytic figs, dbh was the diameter of the main root above the point where it subdivides while descending to the ground.

(v) *Pulp weight/seed*: the dry weight of pulp surrounding an individual seed.

(vi) *Pulp weight/fruit*: the pulp weight/seed multiplied by the median seed number per fruit.

(vii) *Pulp + seed volume*: the volume of the unit of seed + pulp swallowed by an orangutan. This unit is the entire fruit in figs, but primate-fruits have inedible husks that are removed and that often contain several to many of these units.

(viii) $(Pulp\ weight/seed)/(pulp + seed\ Volume)$: the ratio expressing the benefit/cost ratio of ingesting nutrient-rich pulp vs consuming indigestible seed ballast (Howe and Vande Kerckhove, 1980).

(ix) *Length of feeding bout*: complete length of time feeding in a fruit tree during a feeding visit, calculated for 19 primate-fruit taxa, using the median value for multiple observations of a fruit taxon.

The chemical measures used in the fig analyses are each expressed as a relative percentage of fig pulp dry weight: (x) *digestible carbohydrate (dc)*; (xi) *protein*; (xii) *fat*; (xiii) *condensed tannin (ct)*; (xiv) *total phenolics (tp)*; and (xv) *fiber* (measured as acid detergent fiber). Digestible carbohydrate was calculated as the difference between 100% and the sum of the tannin, acid detergent fiber, fat, and protein extracts and is used here as the best estimator of the carbohydrate fraction utilizable for energy by the orangutan. In addition to soluble sugars, orangutans likely digest starch and some hemicelluloses in the foregut, and it is also probable, given their long retention times (Milton, 1984), that the structural carbohydrates, pectin and other hemicelluloses, are digested via hindgut fermentation (Milton, 1979; Van Soest, 1981; Robbins, 1983). Standard methods of chemical analyses were used to estimate the other components of figs (Davies *et al.*, 1988; Marks *et al.*, 1988).

Statistical Analysis

Before modeling selectivity rank by multiple regression, I first performed a factor analysis with varimax rotation [using Systat 5.1 for the MacIntosh (Wilkinson, 1989)] to eliminate independent variables that were too highly correlated with others (factor loadings of >0.80 or <-0.80). Variables i–ix were transformed by logs, and variables of percentage chemical content (ix–xiv) were transformed by arcsins before multivariate analyses. Residual plots from all regressions were examined to verify the fit of the data to model assumptions. Nonparametric tests followed Conover (1980).

RESULTS

Availability of and Preferences for Different Food Types

Temporal Changes in Fruit and Other Food Availability

During the 24 months of study, the densities of nonfig fruit patches varied over an order of magnitude, from 1 or 2 to 20 trees per ha (Fig. 1b, Table I); the species diversity of fruiting trees fluctuated in parallel with their density (Fig. 1a). A major fruiting peak occurred from January to March 1978 (months 5–7) and into early April, when the density of large fruiting trees was 5–10 \times higher than during baseline, nonfruiting seasons. Comparison with 5 recent years of phenological data, gathered in southwestern Bornean rainforest at Gunung Palung (Leighton, unpublished),

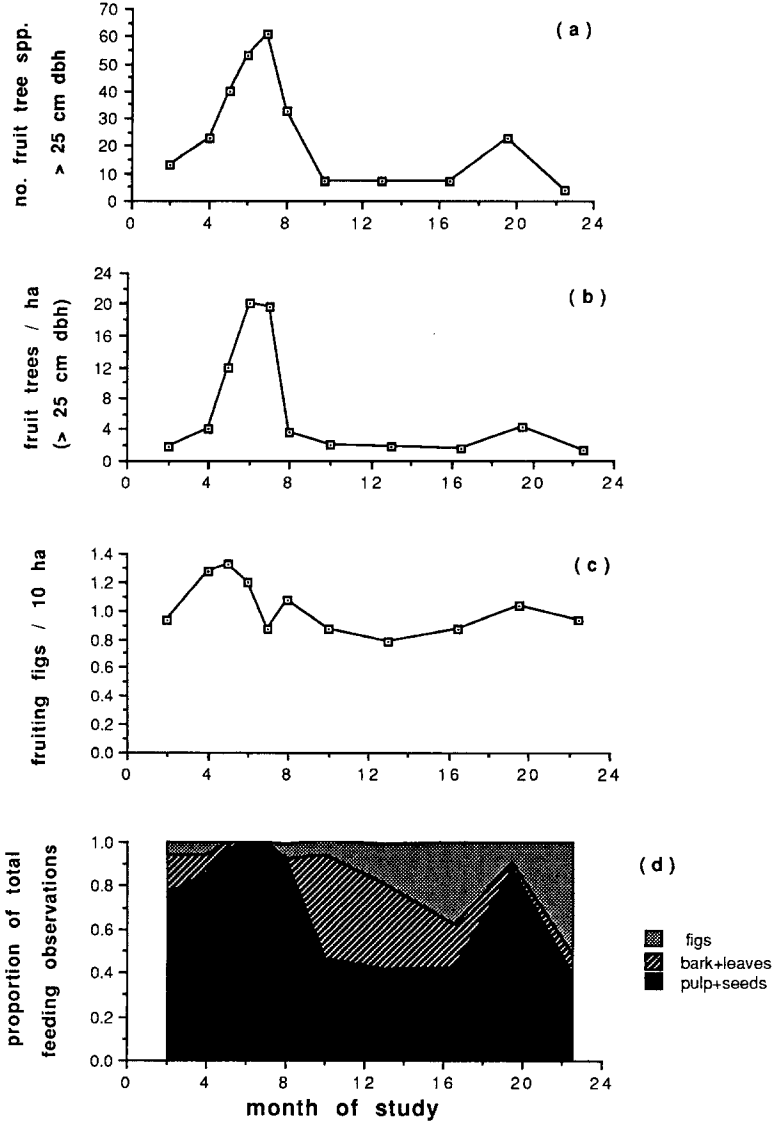


Fig. 1. Phenology of fruit production and of orangutan diet during 11 consecutive intervals (see Table I) of the 24-month study (month 1=September 1977). (a) Diversity (number of species) of large trees (>25-cm dbh) ripening fruit. (b) Density of large trees at peak ripe fruit production. (c) Density of ripe fig crops of large hemiepiphytic and climbing fig plants. (d) Seasonal changes in proportions of observations of orangutan feeding on three types of plant food.

suggests that this 1978 fruiting peak was a “minimasting” episode, in which 30–50% of the entire set of mast fruiting tree and liana populations (and individuals) synchronously fruited together. The relative intensity of the minimast varied with seed dispersal syndrome, plant size, and plant structural form (i.e., trees vs lianas), and with seed characteristics (Leighton and Leighton, 1983; Leighton, unpublished), but was evident in all classes of fruit defined by these criteria. Note that a much smaller fruiting peak occurred March–April 1979 (months 19–20; Figs. 1a and b).

Figs, in contrast, ripened crops seasonally, varying only from 0.9 to 1.3 fruiting individuals per ha during the 2 years (Fig. 1c, Table I). This set of figs included 32 species of mid- to high-canopy lianas and hemiepiphytic trees (Leighton, 1992). Nonfruit food types of orangutans were animal prey (especially social insects), “bark” [the phloem on the inner surface of bark from selected limbs and twigs (Rodman, personal communication)], young, growing leaves, and the leaf bases of a few palms and pandans. When orangutans switch to exclusive pulp- and seed-eating, these foods remained available, notwithstanding the facts that orangutans are selective feeders on certain species of leaves, bark, and insects and that these foods also may vary seasonally in their density. Orangutans therefore selected diets from a forest that fluctuated dramatically in the availability of nonfig fruit and seed resources but provided a relatively continuous supply of figs and nonfruit foods.

Preferences Among Food types

Orangutans strongly preferred pulp and seeds of nonfig fruit over other food types, as revealed by how the proportions of food types in the diet changed with the fluctuating availability of fruits and seeds (Figs. 1a and d; total $N = 341$ feeding observations; Table I). Pulp- and seed-eating both increased with overall fruit patch (i.e., fruit tree) density ($r_s = 0.54$, $P < 0.05$, and $r_s = 0.53$, $P = 0.05$, respectively). However, the combined proportion of feeding on both seeds and fruit pulp is what closely tracked nonfig fruit availability, measured by either the density of patches ($r^2 = 0.85$, $P < 0.001$; Fig. 2a; proportions transformed by arcsins, densities by logs) or the species diversity of patches ($r^2 = 0.94$, $P < 0.001$; Fig. 2b).

In contrast, fig-eating was unrelated to fig availability (Fig. 2c), demonstrating orangutans' relatively low preference for figs (see also Leighton and Leighton, 1983). Not surprisingly, pulp + seed-eating was inversely related to fig-eating ($r_s = -0.78$, $P < 0.005$; Fig. 3a) and to bark + leaf-feeding ($r_s = -0.86$, $P < 0.001$; Fig. 3b), establishing that these food types were eaten only when fruit pulp and seeds were rare. Bark and leaves

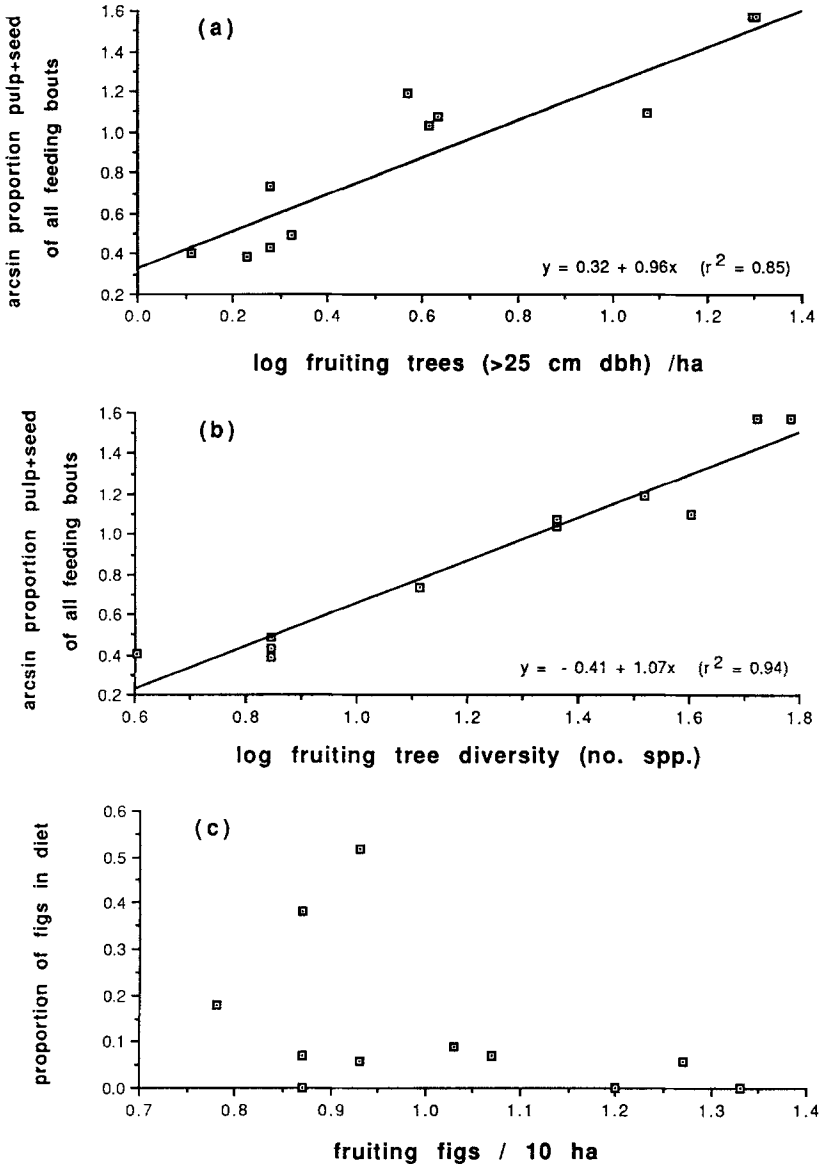


Fig. 2. Preference for plant food types as inferred from the correlation between the relative proportion of observations of orangutan feeding on each type and its availability during 11 sample periods (Table I). (a) Combined seed- and fruit pulp-feeding was directly related to the density of large fruit crops (of large trees). (b) The relative frequency of fig-eating was unrelated to the availability of ripe fig fruit patches, indicating that they were not preferred.

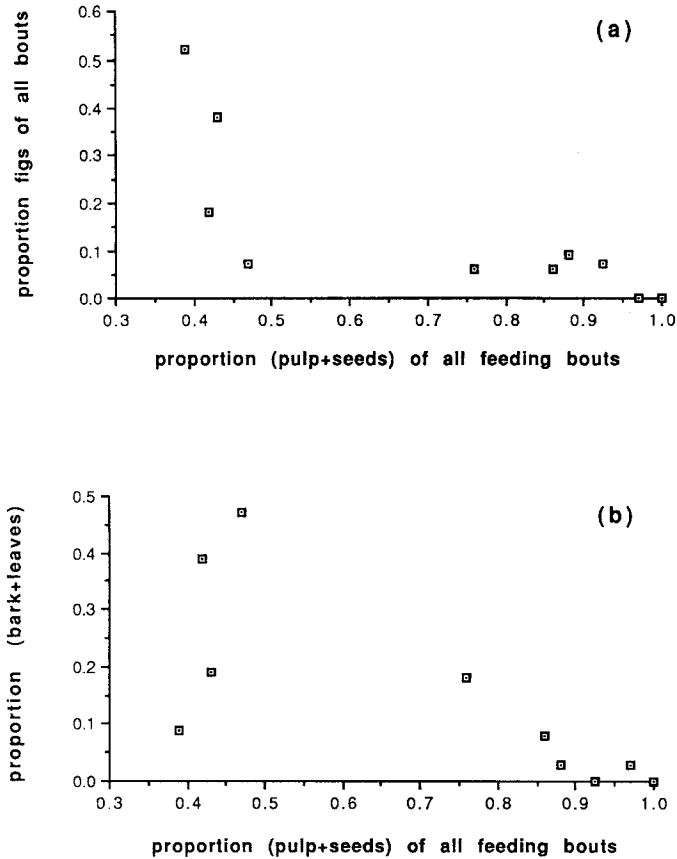


Fig. 3. The proportions of observations of (a) fig- and of (b) leaf+bark-feeding by orangutans were both inversely related to combined fruit pulp+seed-eating.

tended to be eaten during the same periods ($r_s = 0.68$, $P < 0.05$). Therefore, consumption of the preferred types, nonfig ripe pulp and unripe seeds, was limited by availability; these foods comprised >85-90% of all feeding observations when fruiting trees exceeded 4 trees/ha (Fig. 2a, Table I).

Preferences for Pulp Versus Seeds

Orangutans carefully selected immature seeds of some plant species (25 species from 15 genera of 10 families) and ripe fruit pulp of others

(47 species from 33 genera of 27 families) (Table II). With only one exception (*Willughbeia* sp.), they never ate unripe seeds from a species they subsequently harvested for its ripe pulp, nor did they eat seeds from ripe fruits at their stage of seed dispersal. Of the ripe pulp species eaten, 31, representing 26 genera and 20 families, were of the primate-fruit syndrome (Table II).

Analysis of preferences during the January–March 1978 fruiting minimast, when the greatest diversity and abundance of fruit and seed types were available, revealed that pulp and seeds were equally highly preferred as food types. Fortunately, the sample size of feeding observations was large during this minimast period (Table I), because high fruit availability attracted immigrant adults and subadults of both sexes into the study site (Leighton and Leighton, 1983) and because orangutans increased their rate of visiting fruit patches, thereby allowing a more accurate analysis of selectivity. Of the 10 highest-ranking items during this period, 5 were seed and 5 were pulp species (Table II). Orangutans thus showed strong species-specific preferences for either the immature seeds of some species or the ripe pulp of others, but treated these types as coequal.

Orangutans might be expected to eat more seeds during lean fruit periods because the combined pressure of seed predators would make ripe fruit less available [recall that predators ate immature stages, thereby limiting the quantities of ripening fruit (Leighton, unpublished)]. In fact, the converse of this hypothesis was supported; as noted above, seed-eating was positively correlated with fruit patch density.

Preferences for Fruit Pulp of Different Seed Dispersal Syndromes

Because the seed dispersal syndromes of fruit are associated with distinctive chemical and morphological features (Leighton and Leighton, 1983; Leighton, 1992), examining the distribution of fruit selectivity ranks across dispersal syndromes can expose factors influencing selection. This distribution was strongly biased ($\chi^2 = 64.8$, $P < 0.0001$; Fig. 4). Although the set of fruits preferred (ranks 1 and 2) or “neutral” (rank 3) included species from all syndromes, 59% of the 27 preferred species were primate-fruits, whose major or sole dispersal agents were primates. Only 36% of these species were avoided (classes 4 and 5, Fig. 4), whereas most species of the other dispersal syndromes were avoided (70% of bat-fruits, 93% of lipid-bird fruits, and 97% of sugar-bird fruits).

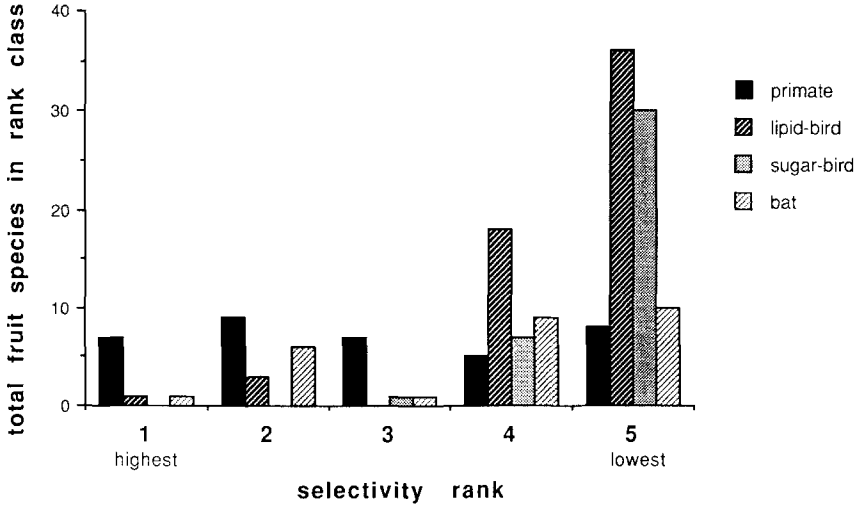


Fig. 4. The distribution of available fruit taxa of different seed dispersal type (see text) among classes of orangutan selectivity rank (rank 1 are taxa highly preferred and rank 5 are fruits never eaten, although common).

Factors Underlying Variation in Selectivity for Primate Fruits: Controlling for Chemical Differences

Rationale

Although they dominated the set of preferred fruits, primate-fruits were spread liberally among the other three selectivity classes (Fig. 4). This variation was exploited to investigate the effect on selectivity ranking of variables related to the rate of nutrient gain, while in essence holding chemical features constant, because the chemical compositions of different taxa of primate-fruits are virtually identical. This is supported by analysis of a set of primate-fruits from this site (Leighton and Waterman, unpublished) and from Gunung Palung in Southwest Borneo (Leighton and Zens, unpublished), for which chemical data are available ($N = 23\text{--}30$ species, each from a different genus of primate-fruit). In this set, the median values (by percentage of total pulp dry mass) and variation (10–90% quantiles of range) across species are total phenolics = 1.3% (0.2–3.1%), condensed tannins = 0.6% (0.1–1.3%), fiber = 21% (10–38%), protein = 6.4% (2.4–10.6%), fat = 1.5% (0.0–5.0%), water-soluble carbohydrates = 30% (6–63%), and digestible carbohydrates = 61.7% (32.8–86.4%) (Waterman *et al.*, 1981; Marks *et al.*, 1988). The protein and fat content of these fruits

Table II. Ecological Variables of Pulp and Seed Species Observed Eaten by Orangutans

Family	Species	Fruit type ^a	dbh (cm)	Density/ 1.2 km ²	Selectivity rank	
					Primate-fruits ^b	Fruiting peak ^c
Alangiaceae	<i>Alangium ridleyi</i>	Pulp: primate	30	11	1	
Alangiaceae	<i>Alangium</i> sp. 1	Pulp: primate	35	4	1	3
Anacardiaceae	<i>Dracontomelum costatum</i>	Pulp: primate	55	3	2	
Anacardiaceae	<i>Dracontomelum dao</i>	Pulp: primate	68	25	1	
Anacardiaceae	<i>Koordersiodendron pinnatum</i>	Pulp: primate	51	48	1	7
Anacardiaceae	<i>Mangifera quadrifida</i>	Pulp: bat	100	1		
Annonaceae	<i>Artabotrys</i> sp. 1	Pulp: primate	Liana	88	3	10
Annonaceae	<i>Goniothalamus</i> sp. 2	Pulp: primate	16	28	3	
Annonaceae	<i>Monocarpia marginalis</i>	Pulp: primate	12	92	3	
Annonaceae	<i>Uvaria cf. grandiflora</i>	Pulp: primate	Liana	132	3	
Annonaceae	<i>Xylopia malayana</i>	Seed	40	52		9
Annonaceae	<i>Xylopia</i> sp. 1	Seed	56	18		
Apocynaceae	<i>Willughbeia</i> sp. 1	Pulp: primate	Liana	16	1	2
Bombacaceae	<i>Durio acutifolius</i>	Seed	40	44		
Bombacaceae	<i>Durio griffithii</i>	Seed	37	21		
Bombacaceae	<i>Durio lanceolatus</i>	Seed	100	8		4
Bombacaceae	<i>Durio oxyleyanus</i>	Seed	70	3		
Burseraceae	<i>Dacryodes rostrata</i>	Pulp: lipid bird	31	12		13
Burseraceae	<i>Samiria oblongifolia</i>	Pulp: lipid bird	95	6		
Burseraceae	<i>Scutinanthe brunnea</i>	Pulp: primate	60	4	1	1
Celastraceae	<i>Terminalia foetidissima</i>	Pulp: bat	50	5		
Chrysobalanaceae	<i>Partinari canaroides</i>	Pulp: primate	80	1	2	
Convolvulaceae	<i>Erycibe</i> sp. 1	Pulp: primate	Liana	42	3	

Dilleniaceae	<i>Dillenia borneensis</i>	Pulp: bat	92	7	
Dilleniaceae	<i>Dillenia excelsa</i>	Pulp: bat	60	5	
Dilleniaceae	<i>Dillenia reticulata</i>	Pulp: bat	60	32	
Dipterocarpaceae	<i>Shorea polyandra</i>	Seed	112	28	8
Ebenaceae	<i>Diospyros</i> sp. 1	Pulp: primate	36	40	3
Ebenaceae	<i>Diospyros</i> sp. 2	Pulp: primate	19	48	3
Ebenaceae	<i>Diospyros</i> sp. 3	Pulp: bat	26	40	14
Euphorbiaceae	<i>Aporosa lucida</i>	Seed	25	140	19
Euphorbiaceae	<i>Aporosa subcaudata</i>	Seed	20	8	11
Euphorbiaceae	<i>Baccaurea ?edulis</i>	Pulp: primate	30	3	2
Euphorbiaceae	<i>Baccaurea costulata</i>	Seed	30	2	
Euphorbiaceae	<i>Baccaurea kunstleri</i>	Seed	28	10	16
Euphorbiaceae	<i>Baccaurea pyriformis</i>	Seed	37	19	
Euphorbiaceae	<i>Baccaurea trunciflora</i>	Seed	6	44	
Euphorbiaceae	<i>Chaetocarpus castanopsis</i>	Seed	26	96	15
Euphorbiaceae	<i>Omphalea bracteata</i>	Seed	Liana	324	20
Fagaceae	<i>Castanopsis</i> sp. 1	Seed	63	5	5
Fagaceae	<i>Castanopsis</i> sp. 2	Seed	48	1	
Fagaceae	<i>Lithocarpus</i> sp. 1	Seed	60	16	17
Fagaceae	<i>Lithocarpus</i> sp. 2	Seed	25	7	
Flacourtiaceae	<i>Ryparosa</i> sp. 1	Pulp: primate	74	2	1
Gnetaceae	<i>Gnetum cuspidatum</i>	Pulp: lipid bird	Liana	16	
Guttiferae	<i>Garcinia cf. bentharii</i>	Pulp: primate	40	5	2
Ilacinaeae	<i>Phytocrene racemosa</i>	Pulp: primate	Liana	200	1
Irvingiaceae	<i>Irvingia malayana</i>	Seed	90	11	

(Continued)

Table II. Continued

Family	Species	Fruit type ^a	dbh (cm)	Density/ 1.2 km ²	Selectivity rank	
					Primate-fruits ^b	Fruiting peak ^c
Lauraceae	<i>Eusideroxylon zwageri</i>	Seed	80	592		
Lecythidaceae	<i>Planchonia</i> sp. 1	Pulp: bat	90	1		
Leguminosae	<i>Adenanthera pavonina</i>	Seed	67	4		
Leguminosae	<i>Inisia palembanica</i>	Seed	122	5		6
Leguminosae	<i>Sindora coriacea</i>	Seed	75	5		
Loganiaceae	<i>Strychnos polytricantha</i>	Pulp: primate	Liana	84		
Meliaceae	<i>Aglaia odoratissima</i>	Pulp: sugar bird	59	28		
Meliaceae	<i>Aglaia</i> sp. G	Pulp: primate	17	40	2	
Meliaceae	<i>Aglaia tomentosa</i>	Pulp: primate	13	12	2	12
Meliaceae	<i>Reinwardtiodendron</i> sp. nov.	Pulp: primate	31	28	3	
Moraceae	<i>Artocarpus odoratissimus</i>	Pulp: primate	51	5	2	
Moraceae	<i>Ficus acamptophylla</i>	Fig: bird	13	8		
Moraceae	<i>Ficus bentjantina</i>	Fig: bird	28	4		
Moraceae	<i>Ficus binnendijkii</i>	Fig: bird	8	24		
Moraceae	<i>Ficus crassiramea</i>	Fig: bird	95	1		
Moraceae	<i>Ficus excavata</i>	Fig: bird	Liana	1		
Moraceae	<i>Ficus sagittata</i>	Fig: (galls)	Liana	12		
Moraceae	<i>Ficus</i> sp. 2	Fig: primate/bird?	20	1		
Moraceae	<i>Ficus stipenda</i>	Fig: bird	17	19		
Moraceae	<i>Ficus subiecta</i>	Fig: bird	9	25		

Moraceae	<i>Ficus subulata</i>	Fig: bird	Liana	2
Moraceae	<i>Ficus sumatrana</i>	Fig: bird	90	1
Moraceae	<i>Ficus surindata</i>	Fig: bird	6	39
Moraceae	<i>Ficus trichocarpa</i>	Fig: (galls)	Liana	12
Moraceae	<i>Ficus trichocarpa</i>	Fig: bird	Liana	12
Moraceae	<i>Ficus variegata</i>	Fig: primate?	23	2
Moraceae	<i>Ficus villosa</i>	Fig: bird	Liana	32
Moraceae	<i>Ficus xanthophylla</i>	Fig: bird	8	15
Myristicaceae	<i>Knema latericia</i>	Pulp: sugar bird	12	72
Myrtaceae	<i>Syzygium</i> sp.	Pulp: bat	39	6
Myrtaceae	<i>Syzygium tawhense</i>	Pulp: bat	45	15
Myrtaceae	<i>Syzygium</i> sp. 3	Pulp: bat	75	4
Sapindaceae	<i>Nephelium</i> sp. 5	Pulp: primate	45	2
Sapindaceae	<i>Paranephelium cf. nitidum</i>	Seed	40	32
Sapindaceae	<i>Pometia pinnata</i>	Pulp: primate	74	4
Sapotaceae	<i>Chrysophyllum roxburghii</i>	Pulp: primate	50	7
Tiliaceae	<i>Microcos ?crassifolia</i>	Pulp: primate	36	14
Tiliaceae	<i>Microcos ?stylocarpa</i>	Pulp: primate	38	8
Vitaceae	<i>Tetrastigma lanceolarium</i>	Pulp: primate	Liana	40
Vitaceae	<i>Tetrastigma pedunculare</i>	Pulp: sugar bird	Liana	164
Vitaceae	<i>Tetrastigma</i> sp. 3	Pulp: sugar bird	Liana	48
				21
				18
				2
				2
				2
				1
				2
				1

^a Syndrome of dispersal agent (see text).

^b Selectivity rank class of primate-fruits used in multivariate analyses (see text).

^c Selectivity rank of pulp and seed species eaten during major fruiting peak of Feb.-Apr. 1978.

is consistently low, so I have inferred that orangutans preferred primate-fruits because of their energy content, gained primarily from the high fraction of digestible carbohydrate. There is no evidence that primate-fruit pulp contains chemical feeding inhibitors; the pulp of these species is usually palatable to humans and is uniformly low in phenolic compounds and condensed tannin. If this wide variation in selectivity class was not due to chemistry, then what factors caused some primate-fruits to be highly preferred and others to be neglected by orangutans?

Results

Fifty-two tree and liana species of primate-fruits could be ranked for selectivity; estimates of crop size as well as the other variables were collected for 45 of these (29 tree and 16 liana species), whereas a second set of analyses using dbh, but not crop size, was based on a subset of 36 trees among the 52 species (Tables III and IV). In univariate analysis, selectivity rank was highly correlated with patch density, crop size, both predictors of patch size (dbh and pulp crop weight), pulp+seed volume, pulp weight/seed, and length of the orangutan feeding bout in the patch ($P < 0.01$ for all r_s ; Table III). However, these patch and fruit variables were also correlated with dbh ($P < 0.01$ for all r_s ; Table III), and many others covaried.

Multiple regression analysis unmasked those variables, which independently predicted selectivity rank (Table IV). Crop size ($P = 0.001$), pulp weight/fruit ($P = 0.04$), and pulp weight/seed ($P = 0.01$) were all significant predictors of selectivity rank among the 45 trees and lianas ($r^2 = 0.43$, $P < 0.0001$). The product of the first two variables (pulp weight/crop) is patch size, indicating that orangutans strongly preferred to feed in large patches. For the subset of 36 trees, dbh was the only significant predictor of rank ($P = 0.001$, $r^2 = 0.49$; Table IV). As expected, tree size, as estimated by dbh, better predicted overall reproductive output (total fruit biomass or the product of crop size and fruit size) than did crop size or one of the fruit size ratios alone. Consistent with this, the regression model predicting tree dbh demonstrated that crop size ($P < 0.001$), pulp weight/fruit ($P = 0.039$), and pulp+seed volume ($P = 0.011$) were all independently and positively correlated with dbh ($r^2 = 0.60$, $N = 29$) in the subset of these 36 trees for which crop size was measured. The preference of orangutans for large fruit patches, when estimated by pulp weight/crop or by dbh, is modeled in Figs. 5a and b, respectively. I interpret the correlation between selectivity and plant density ($r_s = 0.49$, $P < 0.01$; Table III) to be spurious. Orangutans did not

Table III. Matrix of Spearman Rank Correlation Coefficients (r_s) for Variables^a Influencing Orangutan Selectivity of Primate-Fruits

	Selectivity rank	dbh	Tree density	Crop size	Pulp crop wt.	Pulp + seed vol.	Pulp wt./seed	Pulp wt./fruit	(Pulp wt./seed)/p + s volume
Tree dbh	-0.68**								
Patch density ^b	0.49**	-0.63**							
Crop size	-0.44**	0.55**	-0.12						
Pulp crop weight ^c	-0.61**	0.69**	-0.15	0.73**					
Pulp + seed volume ^d	-0.60**	0.66**	-0.42**	0.16	0.25				
Pulp weight/seed	-0.49**	0.54**	-0.35*	0.17	0.45**	0.66**			
Pulp weight/fruit ^e	-0.15	0.25	-0.04	-0.21	0.39**	0.26	0.60**		
(Pulp weight/seed)/p + s volume	0.02	-0.05	0.03	-0.01	0.28	-0.27	0.46**	0.39*	
Length of feeding bout	-0.57**	0.49	-0.44	0.55*	0.68**	0.19	0.08	-0.33	-0.13

^aNote that variables positively associated with high preference have negative correlation coefficients. Sample sizes are the 45 tree and liana species for which median crop size estimates were obtained, except for two variables: for dbh, $n = 36$ tree species (overlapping the set of 45 species); and for length of feeding bout, $n = 19$, except crop and pulp weight crop ($n = 15$) and dbh ($n = 13$).

^bDensity of fruiting plants.
^c(Pulp weight/fruit) × median crop size.
^dVolume of the swallowed unit of one seed and its surrounding pulp.
^e(Pulp weight/seed) × (mean No. seeds)/fruit.
^{*} $p < 0.05$.
^{**} $p < 0.01$.

Table IV. Results of Multiple Regression on Selectivity Rank of Primate-Fruits for 45 Tree and Liana Species Measured for Crop Size ($r^2 = 0.43$, $P < 0.0001$) and for 36 Trees in Which dbh Substitutes for Patch Size ($r^2 = 0.49$, $P < 0.0001$)

Variable ^a	$n = 45$ trees & lianas		$n = 36$ trees	
	Slope ^b	P	Slope ^b	P
Crop size	-0.452	0.001		
dbh			-0.608	0.001
Pulp weight/seed	-0.405	0.010	-0.232	0.246
Pulp weight/fruit	-0.301	0.040	0.045	0.751
Pulp weight/(p + s) volume	0.225	0.101	0.066	0.678
Patch density	0.006	0.958		

^aEach variable log-transformed before factor analysis (see text) and multiple regression.

^bStandardized regression coefficients, giving the expected change, in standard deviations, in fruit selectivity rank for each standard deviation change in the variable.

avoid common trees with attractive fruit—these trees were merely of small dbh, and larger trees were less common than smaller trees ($r_s = -0.63$, $P < 0.01$; Table III).

Orangutans undoubtedly selected large trees in which to feed because they constituted large food patches. Patch size, as estimated by the mass of fruit pulp in a ripening crop of fruit, varied directly with dbh over four orders of magnitude among primate-fruit trees (Fig. 6). A large patch provides not only single large meals, but also a predictable resource patch that can be repeatedly visited, as orangutans do. Both attributes would result in greater feeding efficiency by lowering the time and energy costs of traveling, as contrasted with visiting more smaller patches. In conformance with this hypothesis, the median duration of a feeding bout in a patch of primate-fruits increased with the median pulp crop weight of patches ($r_s = 0.68$, $P < 0.01$, $N = 19$; Fig. 5c), and was highly correlated with selectivity rank ($r_s = -0.57$, $P < 0.01$, $N = 19$; Table III).

Orangutans also preferred primate-fruits with high ratios of pulp weight/seed, though it is noteworthy that because the factor analysis revealed that pulp weight/seed strongly covaries with pulp+seed volume, the latter was excluded from the regression analysis on biological, not statistical, grounds. The more reasonable biological interpretation is that nutrient ingestion rates (pulp weight/min) are higher when the individual units swallowed have higher amounts of pulp, instead of when these units are larger (of greater volume) *per se*. Note that because of the uniformly high percentage digestible carbohydrate content of primate-fruits, pulp mass predicts energy content very accurately. For 10 species (one per genus) for

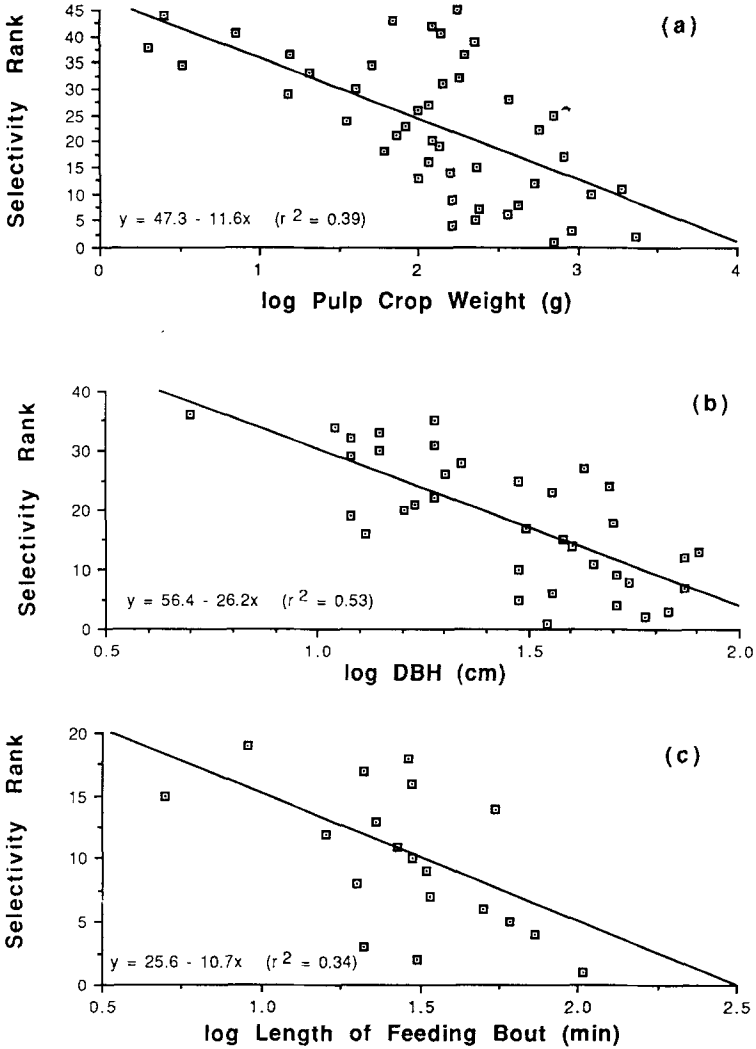


Fig. 5. The selectivity rank of a primate-fruit species was inversely related to (a) the weight of pulp in a crop ($N = 45$ tree and liana species), (b) the tree size (median dbh of fruiting individuals in each species population; $N = 36$ tree species), and (c) the media length of an orangutan feeding bout in a tree ($N = 19$ species), indicating that orangutans preferred primate-fruits occurring in large patches, where they fed for the longest period.

which protein, fat and carbohydrate were all determined, the correlation coefficient (after transforming by logs) between the total energy content

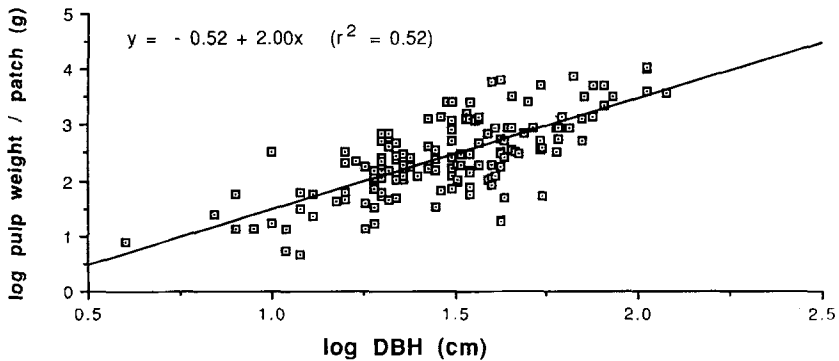


Fig. 6. The total mass of pulp available in a ripening crop of primate-fruits on a tree is directly related to the log dbh of the tree ($N = 151$ fruiting trees; species represented roughly according to the relative densities of fruiting individuals).

(kJ) in the pulp surrounding a seed and the pulp weight was 0.98. Consequently, the correlation of pulp + seed volume with selectivity is epiphenomenal; that is, fruits with larger seed+pulp units were disproportionately selected merely because they occurred in larger trees ($r_s = 0.66$, $P < 0.01$; Table III). Finally, the hypothesis that a cost is imposed by carrying indigestible seed ballast swallowed with the pulp (Howe and Vande Kerckhove, 1980) was not supported; the effect of the ratio pulp weight/seed volume was not significant (Table IV). Thus, in addition to choosing large patches where they obtained big meals, orangutans also were sensitive to the rate of energy gain while eating individual fruits, as this will be strongly influenced by the pulp weight/seed ratio.

Selecting Among Fig Species: Integrating Chemical, Morphological, and Distributional Variables

Rationale

Figs as a group ranked low in orangutan selectivity, as demonstrated by their ingestion only during the prolonged periods when the preferred large patches of primate-fruits and seeds were unavailable [Figs. 1 and 3, Table I (Leighton and Leighton, 1983)]. Nonetheless, figs provide an excellent opportunity to tease apart the relative importance of factors influencing fruit pulp selection. Figs of different species are virtually identical in morphological properties influencing handling times, because they are

berry-like fruits popped into the mouth singly, without processing. Handling time was thereby "controlled" because it was similar between fig species, unlike primate-fruits, which vary in their morphology and correspondingly, in the handling time required to extract and swallow the individual pulp+seed units.

In contrast, fig species are diverse in other fruit and patch measures which might influence selectivity based on net energy yield (Table V). These include five chemical components of pulp: the percentage dry weight of the potential attractive nutrients—%DC (digestible carbohydrate) and %PROTEIN—and of the feeding deterrents—%ADF (acid detergent fiber), %TP (total phenolics), and %CT (condensed tannins). Three alternative measures of fig fruit size were examined in models of selectivity: WT (g dry weight of pulp, excluding seeds and the largely indigestible old floral parts in the interior of the fig synconia), VOL (volume; cm^3), and DC·WT (the product of %DC and g dry weight of pulp per fig). Fruit size may influence the visibility of a patch, the visibility of figs within a patch and hence feeding rate, and/or the rate of nutrient ingestion. Nutrient ingestion rate increased directly with larger fig size because figs are eaten individually and rapidly; any slight decline in feeding rate (fruits/min) due to larger size was more than compensated by greater pulp content. Pulp weight/fig varied across two orders of magnitude (Table V), causing dramatic differences in rate of ingesting pulp. DC·WT was included to best express the nutrient payoff from ingesting a single fig. Variables associated with the meal size or the numbers of meals provided by a fruiting fig plant (i.e., patch size) were also included: DBH; CROP (crop size: the numbers of figs ripening each fruiting episode); and most accurately, DC·CROP·WT, or the grams digestible carbohydrate per crop (the product of median crop size and DC·WT). This last measure will closely reflect the available energy in the patch.

Thirty-one fig species could be analyzed for selectivity in relation to fig fruit and patch variables (Table V). Analysis of selectivity rankings for a subset of 18 of these fig species included chemical variables. Before multiple regression of rank for the set of 31 fig species, DBH was eliminated because of its high correlation with CROP, as revealed through the factor analysis. In the factor analysis for 18 fig species, four subsets of highly correlated variables were identified. The first variable listed in each of these subsets was used in the multiple regression analysis based on its direct biological relevance to orangutan feeding efficiency, and to avoid compound variables: (1) WT, VOL, and DC·WT; (2) CROP, DBH, and DC·CROP·WT; (3) DC and ADF; and (4) %TP and %CT.

Table V. Variables^a of 31 Fig Taxa Used in Multiple Regression Analysis of Orangutan Fig Selectivity

Rank ^c	18 spp.	31 spp.	Ficus species or variety	dbh ^b (cm)	Fig vol (cm ³) ^c	Pulp wt (g) ^d	CROP (Fruits) ^e	DC WT/CROP (g)	% DC ^f	% PROTEIN ^g	% ADF ^h	% TP ⁱ	% CT ^j
1		1	<i>Ficus crassiramea</i> Miq.	95	2.14	0.81	50000	1700	42.0	4.95	51.9	0.82	1.13
2		2	<i>Ficus</i> sp. 2	20	1.89	0.43	10000	1700					
3		3	<i>Ficus stipenda</i> Miq. var. <i>minor</i> Corner	17	10.8	3.0	2500	3800	50.7	3.85	44.6	0.45	0.83
4		4	<i>Ficus kerkhovenii</i> Val.	46	1.06	0.33	50000	6500					
3.5		6	<i>Ficus trichocarpa</i> Bl. var. <i>?obtusata</i>	7	4.82	2.4	2500	2875	48.1	7.67	43.8	0.83	0.00
6		6	<i>Ficus variegata</i> Bl.	23	8.85	0.96	5000	1850					
3.5		6	<i>Ficus sumatrana</i> Miq. var. <i>sumatrana</i>	90	0.47	0.135	85000	3825	33.0	5.50	56.1	3.07	5.43
5		8	<i>Ficus trichocarpa</i> Bl. var. <i>borneensis</i> (Miq.) Corner	9	0.52	0.20	10000	1050	52.9	4.84	40.8	1.46	0.70
9.5		9.5	<i>Ficus subgelidii</i> Corner var. <i>rigida</i> Corner	7	5.08	1.3	2500	1275					
6		9.5	<i>Ficus benjamina</i> L.	28	0.70	0.125	25000	575	18.5	6.55	75.0	0.36	0.00
11		11	<i>Ficus sagittata</i> Vahl (gall-figs)	8	0.64	0.11	5000	215					
7		12	<i>Ficus villosa</i> Bl. var. <i>appressa</i> Corner	6	0.64	0.17	8000	680	51.1	6.24	38.8	3.07	3.85
13		13	<i>Ficus trichocarpa</i> Bl. var. 2	7	1.65	0.60	5000	1150					
8		14	<i>Ficus binneidijkii</i> Miq. var. <i>latifolia</i> Corner	8	0.21	0.08	8500	382	56.4	4.64	49.2	1.10	0.70
9		15	<i>Ficus acamptopterylla</i> Miq.	13	1.30	0.53	5000	950	35.3	4.10	53.8	3.46	6.80

10	16	<i>Ficus xylrophylla</i> Wall.	8	6.37	2.38	2500	2525	42.3	4.94	48.2	3.81	4.61
11	17	<i>Ficus subsecta</i> Corner var. nov.	9	1.95	0.64	5000	1200	37.4	4.52	50.9	3.05	7.35
12	18	<i>Ficus deltoidea</i> Jack var. <i>lutescens</i> (Desf.) Corner	1	0.47	0.11	100	4.3					
13	19	<i>Ficus sundaica</i> Bl. var. <i>beccariana</i> (King) Corner	6	2.28	0.94	2500	800	34.5	4.09	50.1	3.13	11.3
14	20	<i>Ficus sumatrana</i> Miq. var. <i>microsyce</i> Corner	70	0.24	0.058	25000	400	28.2	5.07	56.1	3.12	10.0
15	21	<i>Ficus pisocarpa</i> Bl.	5	1.34	0.31	2500	300	39.1	5.25	48.2	2.33	7.46
16	22	<i>Ficus depressa</i> Bl.	8	6.10	1.6	500	270	33.8	5.60	58.8	1.35	1.75
17	23.5	<i>Ficus excavata</i> Wall.	6	0.0067	0.0086	8500	28					
18	24	<i>Ficus schwartzii</i> Koord.	5	20.6	1.4	500	240	34.5	8.72	54.7	2.08	1.75
19	25	<i>Ficus aff. ruginervia</i> Corner	5	21.2	4.7	8	14.7					
20	26	<i>Ficus delooyce</i> Corner var. <i>obtusata</i> Corner	11	0.13	0.037	8500	110	34.7	4.95	49.9	2.46	9.00
21	27	<i>Ficus pendens</i> Corner var. <i>appressa</i> Corner	3	0.067	0.017	2500	16					
22	28	<i>Ficus consociata</i> Bl.	6	1.24	0.37	2500	375	39.3	4.45	51.0	3.75	4.82
23	29	<i>Ficus pellucida-punctata</i> Griffith	5	2.20	0.61	2500	600					
24	30	<i>Ficus unglaukulosa</i> Wall. var. <i>parviflora</i> Miq.	2	0.13	0.031	2500	30					
25	31	<i>Ficus micloris</i> Corner	1	0.70	0.028	100	1.1					

^a Selectivity ranking (1 = highest) for the 18 figs measured for five chemical variables and for the larger set of 31 taxa (see text).

^b Adult population median for liana stem or main hemiepiphytic root(s).

^c Volume of fig fruit.

^d Weight of outer pulp layer without indigestible interior floral parts and seeds.

^e Median number of fruits/plant in each fruiting episode.

^f Total g digestible carbohydrate/crop (= product of DC, pulp wt., and crop).

^g Chemical variables are percentage of total dry weight.

Table VI. Matrix of Spearman Rank Correlation Coefficients (r_s) Between Orangutan Selectivity Rank, Fig dbh, Fig Fruit Weight, and *Ficus* Fruit and Patch Variables

	Rank		dbh	FRUIT WT
	$N = 31$ figs ^a	$N = 18$ figs ^b		
Fig fruit size				
FRUIT VOL (cm ³)	-0.23		0.06	0.96***
FRUIT WT (g)	-0.33	-0.16	-0.17	
% DC WT (g)		-0.18	-0.26	0.99***
Patch size				
DBH (cm)	-0.72***	-0.52*		0.15
CROP (No. fruits)	-0.53**	-0.45	0.75***	-0.67**
WT · CROP (g)	-0.79***	-0.76***	0.74***	
% DC · WT · CROP (g)		0.44	0.38	
Fig pulp chemistry				
%TP		0.49*	-0.23	-0.10
%CT		0.57**	-0.08	-0.24
%ADF		0.25	0.39	-0.18
%PROTEIN		0.01	-0.13	-0.10
%DC		-0.37	-0.25	0.21

^a Correlations with selectivity rank for 31 fig species with fig size and patch size data.

^b Eighteen species also analyzed for chemical features.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.005$.

Results

Univariate correlations between selectivity rank and the measured variables were numerous but consistently highest for the measures of patch size (Table VI). Rank was correlated most strongly with the most accurate estimator of food patch or meal size, the product of the three variables %DC·WT·CROP ($r_s = -0.82$, $P < 0.005$) (vs $r_s = -0.52$ for DBH in the same set of 18 species), even though neither WT nor %DC by itself was a significant predictor of rank (Table VI). Conforming to this result, rank was strongly correlated with DBH ($r_s = -0.72$, $P < 0.005$) and crop size ($r_s = -0.53$, $P < 0.01$) in the set of 31 species. Orangutan fig selection might be influenced by the avoidance of tannin, as high values of either %TP or %CT are associated with low-ranking species ($r_s = 0.49$, $P < 0.05$, and $r_s = 0.57$, $P < 0.01$, respectively). Rank bears no relation to protein content ($r_s = 0.01$). Although these univariate correlations hint that more

Table VII. Results of Multiple Regression on Fig Selectivity Rank for 18 Fig Taxa Measured for Patch, and Fruit Morphometric and Chemical Variables ($r^2 = 0.86$), and for 31 Fig Taxa Measured for Patch and Fruit Morphometric Variables ($r^2 = 0.52$)

Variable	<i>N</i> = 18 fig species		<i>N</i> = 31 fig species	
	Slope ^a	<i>P</i> level	Slope ^a	<i>P</i> level
CROP (No. fruits/plant)	-0.983	<0.0001	-0.670	<0.0001
WT (pulp wt/fruit)	-0.664	<0.0001	-0.532	<0.0001
%DC	-0.331	0.005		
%TP	0.292	0.013		
%PROTEIN	-0.073	0.482		

^a Standardized regression coefficients, giving the expected change, in standard deviations, in fig selectivity rank for each standard deviation change in the variable.

preferred figs may have a higher concentration of digestible carbohydrate ($r_s = -0.37$, $P < 0.10$) and may be larger ($r_s = 0.33$, $P < 0.05$), rank is seemingly unrelated to the nutrient quantity (%DC·WT) in a fig's pulp ($r_s = -0.18$, $P > 0.4$). Crop size and total pulp weight of a crop (WT·CROP) are correlated with dbh, but note that fig %TP, %CT, and %DC are unrelated to either patch (DBH) or fig fruit size. Like the analysis of primate-fruit selectivity, these univariate correlations suggest misleading inferences about which factors influence fig selectivity, as revealed by multivariate analysis.

The multiple regression of fig selectivity rank (Table VII) exposed four independent variables—patch size (CROP), fig fruit pulp weight (WT), and two chemical variables, sugar content (TDC) and total phenolics (%TP)—as highly significantly related to selectivity rank. Orangutans' relative preference for a fig species depended on how high values for each of the first three variables were, in combination with how low the concentration of phenolic compounds was in the fig's pulp. The greatest influence on fig species choice was exerted by fig patch size, as indicated by its large slope (Table VII), with pulp weight/fig of less importance, and sugar and phenolic content of even less effect. The high multiple regression coefficient ($r^2 = 0.86$) indicates that these four factors accounted for much of the variation in rank. The model for the larger sample of 31 figs substantiates the importance of crop size and pulp weight/fig in determining selectivity rank, but presumably because the chemical variables were left out, the regression coefficient was much lower ($r^2 = 0.52$). Scattergrams for the four variables that significantly predict rank are plotted in Fig. 7. A three dimensional graph (Fig. 8) displays the close dependence of fig selectivity rank on the percentage

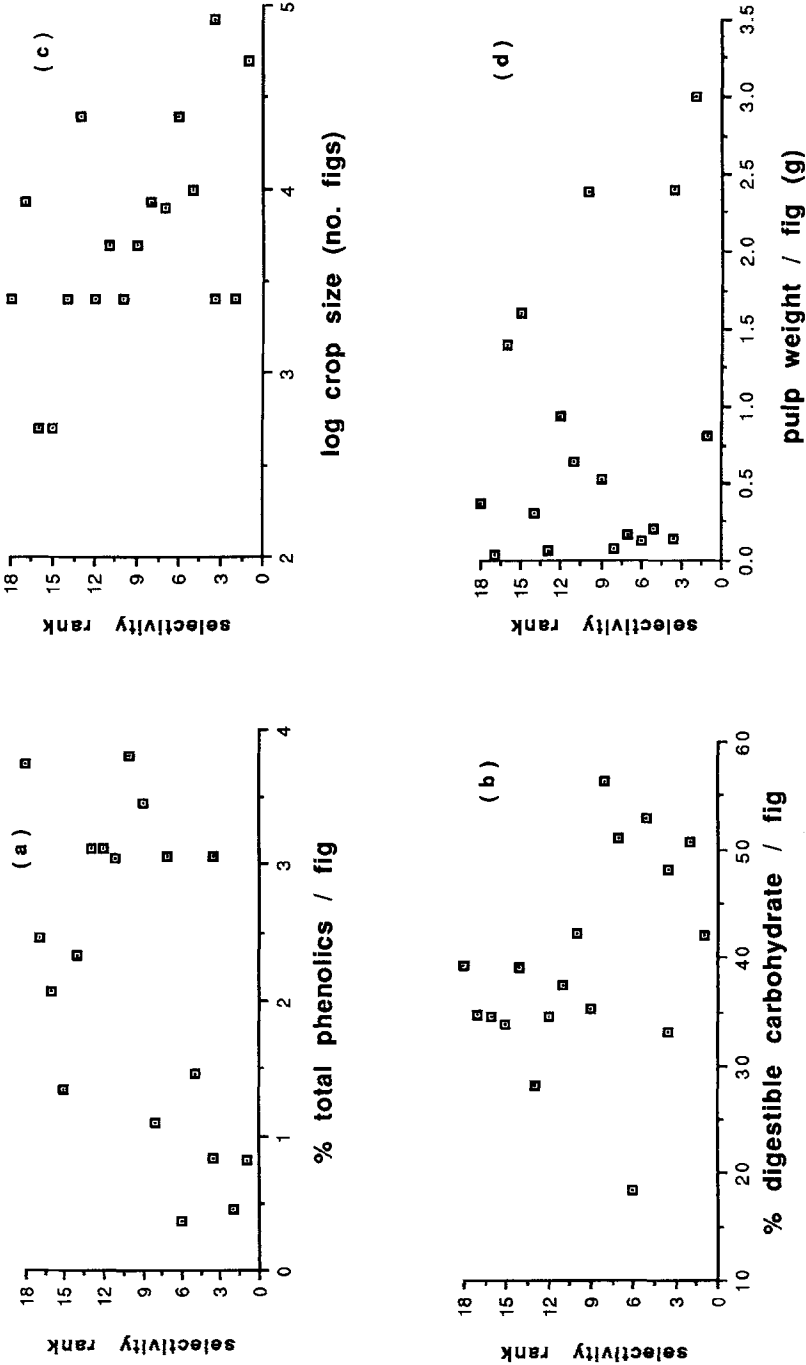


Fig. 7. Scattergrams of the selectivity rank of 18 fig species (1 = most preferred; 18 = least), and the four variables that influence fig selectivity by orangutans (Table VII): (a) percentage total phenolics in dry fig pulp ($r_s = 0.49, P < 0.05$); (b) percentage digestible carbohydrate in dry fig pulp ($r_s = -0.37, ns$), (c) median crop size (number of ripening figs per fruiting episode) ($r_s = -0.45, ns$), and (d) pulp weight/fig ($r_s = -0.16, ns$).

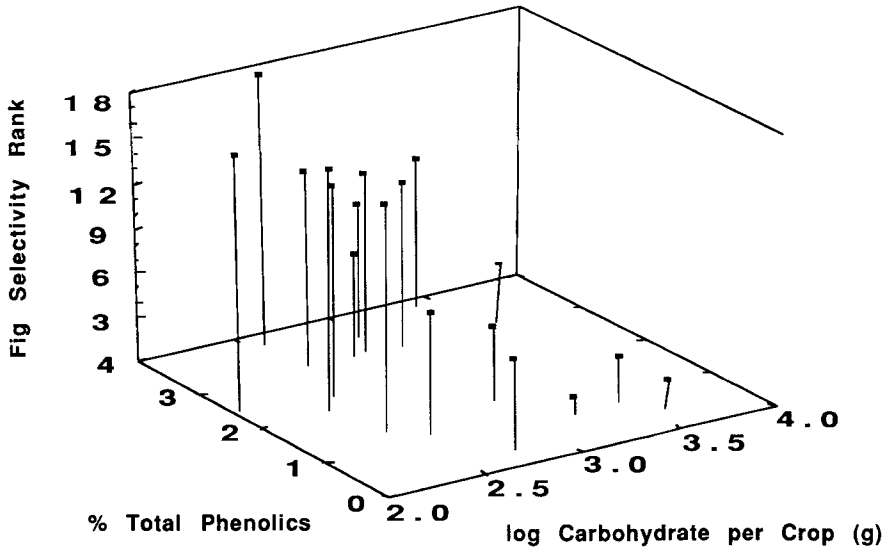


Fig. 8. Three-dimensional regression model for the dependence of orangutan fig selectivity ($N = 18$ species) on the percentage total phenolic compounds in fig pulp and on patch size, as estimated by the grams digestible carbohydrate in the median crop of ripening fig fruit ($r^2 = 0.81$, $P < 0.001$).

total phenolics and patch size ($r^2 = 0.81$), estimated here as the product of the other three significant variables (DC-CROP·WT), or the grams digestible carbohydrate per crop.

The phenolic concentration in fig pulp varied greatly, unrelated to fig plant and crop size (Table V), apparently causing a fig's selectivity rank to slide up or down accordingly. This is clearly revealed by examining the extreme outliers from the regression of rank on the total weight of pulp sugar/crop (the product of the other three significant variables) (Fig. 9). The three figs farthest above the regression line (*Ficus consociata*, *F. subsecta*, and *F. xylophylla*)—with a lower selectivity rank than predicted by patch size—have among the highest phenolic concentrations (including the two highest), while the three outliers farthest below the curve have among the lowest concentrations (Table V). If %CT is substituted for %TP in the multiple regression model, the coefficient is only slightly lower ($r^2 = 0.82$), and %CT content is only marginally significant ($P = 0.09$), suggesting that pulp components extracted in the assay for total phenolics other than condensed tannins (hydrolyzable tannins?) influence selection. However, this

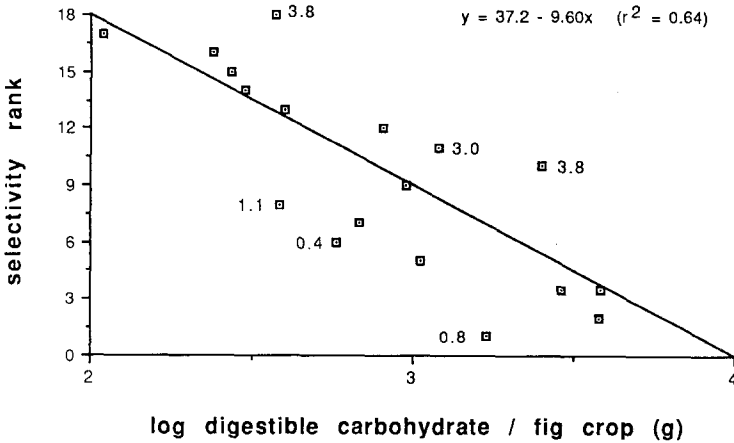


Fig. 9. The relationship of fig selectivity rank to patch size (=DC·WT·CROP) ($N = 18$), showing the percentage total phenolics/dry pulp in the six species farthest from the regression line.

conclusion seems unwarranted, given the uncertainty in comparative tannin assays (Mole and Waterman, 1987).

To illustrate how inferences of orangutan fig selectivity would have been affected if smaller, less complete, or different sets of variables had been measured, multiple regression models were fit to various subsets of the independent variables, excluding the others from analysis (Table VIII). First, models including only chemical variables (%DC and %TP or %CT model 1; Table VII), only fig fruit size (models 7 and 8), or combinations of them (model 2) explain none of the variation in fig selectivity. Second, if patch size is not the combination of crop size, pulp mass, and %DC, then models are much poorer (e.g., models 4–6 vs $r^2 = 0.86$ for the model presented in Table VII). For instance, if DBH is the surrogate for patch size, the model is a pathetic, albeit significant, predictor of selectivity ($r^2 = 0.46$, model 10; see also models 3 and 9), and the important effect of fig size is masked, appearing to be insignificant, as found for dbh models of primate-fruit selectivity.

In summary, analysis of fig selectivity confirms trends apparent in the analysis of primate-fruits. First, fig choice is strongly influenced by patch size. Second, chemical factors influence selection: Figs of high pulp phenolic content are devalued, while figs rich in digestible carbohydrate are evaluated more highly than the weight of the crop would predict by itself. By inference, it is the total amount of harvestable energy that so strongly

Table VIII. Results of Multiple Regression Models of Significant Factors Influencing Orangutan Fig Selectivity When Subsets of Variables^a are Excluded from Analysis

	r^2	Excluded variables
A. N = 18 fig taxa		
1. RANK = -18.92 DC - 203.46 TP + 13.82	0.16 (ns)	CROP, DBH, WT
2. RANK = -0.22 WT - 13.95 DC + 205.23 TP + 10.48	0.20 (ns)	CROP, DBH
3. RANK = -3.20 DBH* - 1.33 WT + 16.42	0.25*	CROP, DC, TP, CT
4. RANK = -5.42 CROP*** - 4.70 WT*** + 40.31	0.63***	DBH, DC, TP, CT
5. RANK = -2.13 CROP** - 18.40 DC* + 189.40 TP* + 31.18	0.56**	DBH, WT
6. RANK = -3.76 DBH** - 26.07 DC** - 0.94 WT + 123.64 TP + 26.13	0.61**	CROP
B. N = 31 fig taxa		
7. RANK = -0.85 WT + 16.67	0.09 (ns)	CROP, DBH
8. RANK = 0.06 VOL + 2.20	0.09 (ns)	CROP, DBH
9. RANK = -5.41 DBH*** + 27.93	0.43***	CROP, WT
10. RANK = -5.01 DBH*** - 1.43 WT + 25.26	0.46***	CROP

^a Weight (g), volume (cm³), DBH (cm), and number transformed by natural logs; read as ln(VARIABLE). All chemical variables (proportions of dry weight per fig) transformed by arcsins; read as arcsin(VARIABLE).

* P < 0.05.

** P < 0.01.

*** P < 0.001.

attracts feeding attention, not some facile single factor such as fruit size, sugar content, or plant dbh, each of which alone poorly predicts meal size and quantity. Most striking is that orangutans make choices among species by integrating information both on the qualities of separate items (tannin and digestible carbohydrate or energy content) and on the distribution of these into patches.

Seed Preferences

Although the seeds that orangutans eat rank as highly as fruit pulp, orangutans select seeds from an extraordinarily small range of plant taxa (Table II). The points presented below support the inference, based on results of pulp selection, that orangutans select chemically unprotected seeds that can be eaten as large meals.

Seed Chemistry

The chemical profile of eaten seeds indicates that orangutans select unprotected seeds, low in condensed tannin (CT) or phenolic concentration (TP) and inferred to be low in toxic compounds. Seed and pulp selectivity rank during the main fruiting period (Jan.–Apr. 1978), when most seeds were eaten, was uncorrelated with PROTEIN, TP, or CT (Spearman r_s , all $P > 0.10$; $N = 21$ genera). However, if eaten seeds ($N = 13$, 1 species/genus) are compared (all are means \pm SD) with a sample of presumably attractive, available uneaten seeds (those produced as large crops and without impenetrable seed coats; $N = 59$, 1 species/genus), then eaten seeds have less condensed tannin (0.8 ± 1.5 vs $4.6 \pm 7.0\%$; $z = -2.05$, $P = 0.02$, Mann–Whitney test) and less phenolics (1.7 ± 2.9 vs $4.7 \pm 7.2\%$; $z = -1.50$, $P = 0.07$) (Leighton and Waterman, unpublished). Exceptions to general taxonomic patterns are insightful. Within the Fagaceae, for instance, the spiny fruits of two *Castanopsis* species (chestnuts) were highly preferred (TP = 0.35–0.50%, CT = 0.0%; $N = 2$), but the large patches of acorns produced by a *Quercus* species (TP = 33%, CT = 4%) and by *Lithocarpus* species ranked low or were not eaten at all [TP = 2.7–27%, CT = 0.0–8.8%; $N = 3$ (Leighton and Waterman, unpublished)].

Selection for seeds that are high in protein might reasonably be hypothesized, especially during the peak fruiting season when orangutans restricted their diet to pulp and seeds (Jan.–Apr. 1978 and Apr.–May 1979; Table I). In support of this, the mean (\pm SD) protein content of seeds eaten ($7.9 \pm 2.7\%$; $N = 12$ species) was higher than pulps eaten

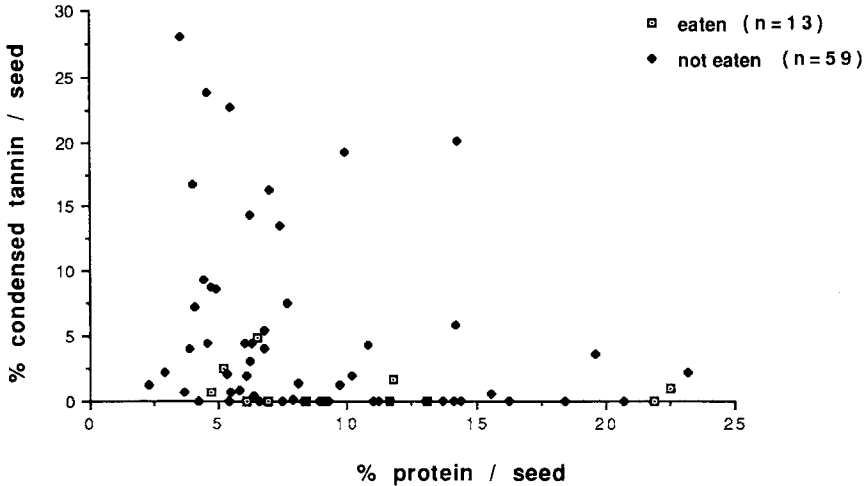


Fig. 10. Scattergram of condensed tannin vs protein content of seeds eaten by orangutans and seeds uneaten but available. One seed per genus was selected, based on completeness of chemical data; uneaten seeds were restricted to those occurring in large patches and of a morphology handled by orangutans (i.e., very small seeds or ones with hard seed coats were excluded).

($6.2 \pm 4.0\%$; $N = 16$ species) during these periods ($z = -2.07$, $P = 0.02$, Mann-Whitney test). The phenolic content of these seeds ($2.5 \pm 4.2\%$; $N = 12$) and pulps ($1.0 \pm 1.0\%$; $N = 17$) was low, but highly variable, and did not significantly differ ($z = 1.05$, $P = 0.15$). Nevertheless, there is no evidence that selection among seeds was based on protein content. Eaten seeds contained a similar percentage protein ($10.4 \pm 5.8\%$, $N = 13$, 1 species/genus) as uneaten seeds ($8.7 \pm 4.7\%$, $N = 59$, 1 species/genus) ($z = -1.07$, $P = 0.14$). Condensed tannins were lower in eaten seeds (0.8 ± 1.5 vs $4.6 \pm 7.0\%$; $z = -2.04$, $P = 0.02$), and the trend was for total phenolics to be lower in eaten seeds (1.7 ± 2.9 vs $4.7 \pm 7.2\%$ for uneaten seeds; $P < 0.10$). These 72 species (=72 genera) varied widely in their protein and condensed tannin content, but strikingly, in scattergrams showing the distribution of eaten vs uneaten seeds by condensed tannin and protein content (Fig. 10), the limited seed diet breadth of orangutans is unexplained by these two variables. Dozens of seeds had a favorable nutrient content and a low tannin and fiber content, and occurred as big, energy- and protein-rich patches, but were neglected. Because other explanations can be excluded, I hypothesize that many, if not the great majority, of these seeds were protected by toxins (alkaloids, terpenes, etc.) which deterred orangutan feeding.

Evidence for avoidance of seeds with toxic compounds is indirect, as chemical screening for these was not done. Nonetheless, it is suggestive. First, large seeds of some taxa (e.g., Myristicaceae, Apocynaceae, Loganiaceae, Meliaceae, and some genera of Rubiaceae and Euphorbiaceae), lacking morphological protection (e.g., hard seed coats), occurred as large crops that potentially are attractive to orangutans, and although they were consistently and commonly available, even during fruit-poor times, they were avoided. Many of these taxa were eaten by *Presbytis hosei* (Colobinae), which can presumably detoxify chemical poisons using its foregut flora (Waterman and Choo, 1981). Second, many seeds that were consumed by orangutans are harvested as food by humans, including *Parkia*, *Durio*, *Castanopsis*, and *Irvingia*. Third, seeds that are eaten by orangutans were biased toward the "masting" plant species and were consumed mostly during the January–March 1978 minimast. Preferred orangutan seed taxa of this type are *Castanopsis*, *Durio*, and selected genera of Euphorbiaceae, especially *Baccaurea*, *Chaetocarpus*, and *Aporusa*. The masting species rely primarily on a strategy of predator satiation for ripening seed past the bottleneck imposed by squirrels, primates, and psitticines (Leighton and Curran, unpublished). The relatively palatable seeds ripen synchronously in a huge flood of seed production every several years. This explains why orangutan seed-eating is prominent during infrequent periods of a few months every several years, despite the simultaneous abundance of ripe fruit pulp.

Selection for Large Seed Meals

The dbh size class distribution of seed-trees was biased toward large trees and did not differ significantly from that for pulp-trees ($z = -0.89$, $P = 0.19$, Mann–Whitney test; Fig. 7a), supporting the hypothesis that seed selection was influenced by the enhanced efficiency of feeding in large patches, as found for pulp-trees. Similarly, the durations of feeding bouts were similar at seed-trees and pulp-trees ($z = -0.24$, $P = 0.40$; Fig. 7b). This is not surprising, given that the harvestable patch size of a crop of seeds in a tree of a given dbh, compared with its pulp crop, is effectively greater because of the restrictive range of ripe fruit acceptable to orangutans. Only ripe or nearly ripe fruit, typically a low proportion of the entire crop, were consumed; return trips were made to harvest later-ripening fruits. In contrast, although seed predation was also restricted to a specific maturational stage, typically a month or so before a fruit ripened, I observed that a wider range of seed maturational stages was acceptable for consumption (presumably because they were more chemically similar than were ripe vs unripe pulp). Accordingly, orangutans typically stripped a tree of its seed crop during a single visit (e.g., the small *Aporusa*) or during

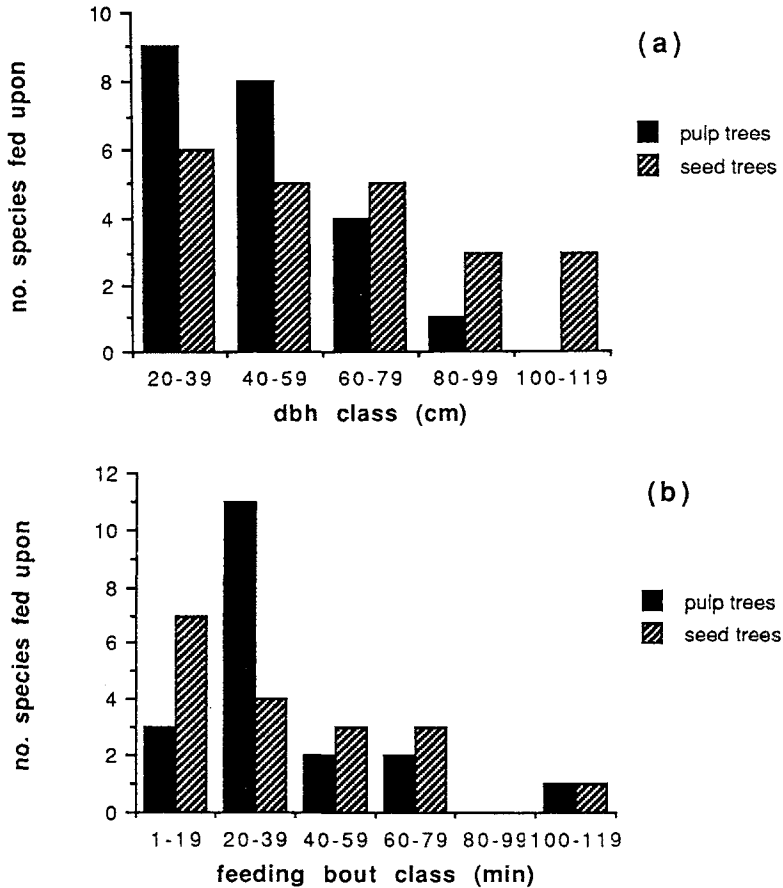


Fig. 11. Frequency distributions of the number of fruit pulp and seed species fed upon by orangutans among classes of (a) tree size (dbh) and (b) feeding bout lengths (min). Each tree species is represented by its median value in cases of multiple samples of dbh and feeding bout.

repeated visits over a few days or weeks (e.g., *Durio*, *Castanopsis*). Seed morphological defenses, even the sharp, tough spines of *Durio* and *Castanopsis*, were overwhelmed completely as orangutans bit and tore through husks and ate seeds rapidly, undeterred by substantial incidental ingestion of husk and seed coat parts.

Most taxa eaten, such as the Leguminosae, *Durio*, *Castanopsis*, *Irvingia*, and *Shorea*, had large seeds that matured in large crops on big trees. The small trees from which orangutans ate seeds (Fig. 11a), e.g.,

Euphorbiaceae, *Xylopia malayana*, and *Paranephelium*, have unusual features that resulted in large meals or high yields of energy per unit time. First, seed output during the minimast, when most of these were visited, was relatively massive compared to small trees fruiting at other times (Leighton, unpublished), presumably because of their storage of nutrient reserves and low investment in chemical or morphological defenses of seeds. Second, the seed-trees of small dbh, corresponding to the short feeding bouts depicted in Fig. 11b, were mostly small-seeded species of Euphorbiaceae. Their seemingly anomalous selection can be explained by how their seeds are packaged. When ingested 1–2 months before ripening, the entire fruits were simply crunched up, and the thin husks spit out, while the nearly undeveloped and small, soft seed coats were swallowed with the 3–6 seeds inside each fruit. Thus, individual fruits did not require processing. High yields of energy return were further augmented because 10–30 fruits are packed along clustered spikes issuing from the trunk or limbs, enabling orangutans to strip fruits from several spikes simultaneously through their mouth in one motion; these small seeds were processed at very high rates of >100 fruits (and 500 seeds!) per min. Similarly, *Xylopia* seeds are packaged 8–12 per fruit, and fruits are clustered at the tip of a short fruiting stem (the torus), so that a handful of fruits were bitten through in turn. Therefore, the short feeding bouts and small dbh's of seed-trees shown in Fig. 11a nonetheless represented large meals, rapidly ingested. Consequently, it is not surprising that these were intermingled in selectivity rank with large trees of some of the most palatable pulp species available during the same minimast period (Table II).

DISCUSSION

Selection for Food Types Based on a Foraging Strategy of Energy Maximization

The Seasonal Dichotomy in Diet

The strong correlation between nonfig pulp- and seed-eating and the availability of these items (Figs. 2a and b) establishes that orangutans preferred these items; in contrast, figs (Fig. 2b), leaves, and bark were constantly available yet were eaten only when preferred types were uncommon (Fig. 3). This low preference ranking for figs was shared by squirrels and hornbills (Leighton and Leighton, 1983) and is not surprising, given that almost all fig species produced nutritionally poor fruits (Table V).

In Table IX, I contrast the chemical properties of figs, which were completely ignored during the January–April 1978 fruit period, with the seed and pulp species for which I have chemical data eaten then. Fig pulp is nutritionally inferior to nonfig pulp and to seeds from every perspective, except in comparing the protein content of pulp. Digestible carbohydrate and protein are very low, and fat is absent (Table IX). Converting the contents of these macronutrients in each species by their standard physiological fuel values (Lloyd *et al.*, 1978) and summing, we find that the median metabolizable energy in fig pulp is 7.4 kJ/g, while nonfig pulp (12.4) and seeds (14.1) are nearly twice as energy-rich ($P < 0.01$, Mann–Whitney test; Table IX). Moreover, figs contain much higher tannin content and nearly twice the fiber. Recall, also, that the fig pulp surrounds indigestible, fibrous old floral parts and seeds, which makes up roughly half the total dry weight of a fig fruit. Therefore, ingested figs may be typically 75% indigestible fiber.

Although poor nutritional substitutes for nonfig pulp and seeds because of their low digestibility, figs presumably provide energy sources during fruit-poor times. Their low nutrient content (both of energy and protein) is compensated somewhat by their large patch sizes. The synchronized ripening of large crops of figs (Leighton, unpublished) enables orangutans to obtain large meals, a primary factor influencing their selection of fruit trees. Bark and leaves are similarly low-quality foods, containing little energy in relation to high fiber content, though orangutans are very selective feeders on new leaves, which have relatively low fiber content relative to mature stages (Milton, 1979; Davies *et al.*, 1988).

Like all generalized herbivores, orangutan dietary selection is constrained by the fluctuating availabilities of different potential food items, and although dietary shifts can appear capricious, the selectivity analysis presented in this paper provides insights into orangutan foraging and nutritional strategy. Faced by the extreme fluctuations of Bornean rainforest phenology, orangutans responded with a dichotomous dietary mixture of food types. During brief, 2- to 4-month periods of high fruit availability, orangutans achieved a nearly exclusive nonfig fruit pulp and seed diet. To illustrate the strong preference for these foods, during 100 consecutive days of the minimasting period of high fruit availability (January–early April 1978), 108 consecutive episodes of fruit pulp- and seed-eating were observed, to the complete exclusion of figs, bark, or leaves, which were apparently not required in the diet (data include all observation types except those from watching fruiting trees). But these fruit-rich times are separated by extended fruit-poor periods [comprising perhaps 80% of the time (Fig. 1) (Leighton, unpublished from West

Table IX. Contrasts in Median (25, 75% Quantiles) Chemical Content (% Dry Wt) Among Species of Nonfig Pulps and Seeds Eaten by Orangutans and of the Uneaten Figs Available During the Jan.-Apr. 1978 Fruiting Season

Variable	Pulps (eaten) (N = 14 species)	Seeds (eaten) (N = 8 species)	Figs (uneaten) (N = 18 species)
Digestible carbohydrate	56.5 (30.8, 73.2)	64.8*	38.2 (34.5, 48.1)
Protein	5.2 (3.1, 8.4)	7.5*	5.0 (4.5, 5.6)
Fat	1.7* (0.2, 10.7)	1.0*	0 (0-1 ?)
Acid detergent fiber	26.0 (11.3, 53.4)	24.0 (10.7, 28.0)	50.5* (48.2, 54.7)
Total phenolics	0.7 (0.3, 1.0)	0.4 (0.4, 1.2)	2.4* (1.1, 3.1)
Condensed tannin	0.0 (0.0, 0.2)	0.0 (0.0, 1.0)	4.2* (0.8, 7.4)
Energy density ^a (kJ/g)	12.4* (9.3, 14.4)	14.1* (12.1, 15.3)	7.4 (6.7, 9.3)
% kJ protein/total ^b	10.1 (5.4, 13.0)	10.2 (7.2, 12.7)	10.8 (10.4, 14.2)

^a From physiological fuel values (Lloyd *et al.*, 1978) of digestible carbohydrate, protein, and fat.

^b "Protein/energy" ratio, the percentage of all digestible kJ that could be derived from protein.

* $P < 0.01$, Mann-Whitney U test, for comparisons of seeds or pulps vs figs (all tests of seeds vs pulps were ns).

Borneo; Sugardjito *et al.*, 1987)], when orangutans must augment pulp and seed ingestion by scraping the phloem layer of bark, chewing up pith from the stems of palm leaves, pandans, and large herbs (e.g., gingers), and eating figs and the immature leaves of a few species, such as *Ficus*, *Dracontomelum*, and some Leguminosae.

Why this dichotomy of dietary mixtures? I hypothesize that the foraging strategy during fruit-rich periods is to achieve maximum fat reserves to sustain animals during recurrent periods with a high risk of sustained negative energy balance, which can result from a highly fibrous, low-energy diet. The fluctuating physical condition and weight of wild orangutans observed (though unmeasured) in field studies are consistent with this alteration (personal observation). A foraging strategy of energy maximization is consistent with strong selection for large patches of the most digestible food items (seeds and nonfig fruit pulp). Note that the costs of eating figs during fruit-rich times are incurred not only by their low energy density (only one-third that of seeds and pulp if the digestible inner parts are ingested with fig pulp), but also by the effect on passage rate of their high fiber content. Gut retention time is strongly related to fiber content (Demment and Van Soest, 1985), so that filling up on figs prevents ingestion of energy-rich items until the gut clears. The migratory pattern of orangutans, in which most individuals switch habitats according to relative fruit production (Leighton and Leighton, 1983; te Boekhorst *et al.*, 1990; Leighton, 1992), is driven by this foraging strategy of searching for energy-rich foods as a response to, and to take advantage of, phenological asynchrony between habitats or between different areas of the same rain-forest habitat.

The seasonal dichotomy in diet that I have outlined contrasts with the results of Sugardjito *et al.* (1987) from Ketambe in Sumatra, who found that orangutans continued to eat figs during their season of high availability of nonfig fruits. However, their data contrasting diet with phenology also show, similar to these, that figs are not preferred. Continued fig ingestion may be explained by at least two hypotheses: (i) the diversity or densities of large patches of preferred pulp and seeds were not nearly as high as those that I measured; and (ii) the major figs visited during the nonfig fruiting season contained pulp low in digestive inhibitors. The first hypothesis is supported by their description of forest structure. The fruit patches that are alternative to figs are on small trees (e.g., *Aglaia*), and the large trees producing preferred fruits in lowland Borneo are rare at this higher-elevation, relatively species-poor site. Instead, most Ketambe figs are large individuals that have strangled their hosts; in contrast, these comprise only 2% of adult fruiting figs at Mentoko (Leighton and

Leighton, 1983). Therefore, greater selectivity of figs at Ketambe may be driven by the relative paucity of large nonfig pulp and seed patches.

Balancing Protein and Energy in the Diet

It is striking that protein content seems to have little to do with fruit and seed choice. Protein ingestion during fruit-poor times would seem quite adequate because the immature leaves added to the diet are typically a good protein source (McKey *et al.*, 1981; Davies *et al.*, 1988). In addition, seeds rich in protein, such as the legumes *Parkia* (21.9%) and *Adenanthera* (22.5%), are eaten during fruit-poor periods (Leighton, unpublished). During these times, maximizing intake of the limiting nutrient, energy, could also drive patch and food item selection without compromising the acquisition of necessary protein. However, for >3 months (January–April) orangutan diets were composed solely of pulp (61% of 108 observations), with a median protein content of 5.2% among species, and seeds (29% of observations), with median = 7.5% (Table IX). The actual time spent feeding and the relative quantities of pulp vs seed ingested are probably roughly proportional to the percentage of feeding observations. This protein density is low for herbivore diets, given that the apparent digestibility of crude protein in pulp and seeds is probably about 60–80% (Lloyd *et al.*, 1978; Milton, 1979; Robbins, 1983). If this imposes a constraint, then a reasonable hypothesis for the avoidance of figs at this time is that their high condensed tannin content (Tables V and IX) might precipitate the available protein (Freeland and Janzen, 1974). Arguing against this is the lack of seed or pulp selectivity based on protein content ($P > 0.10$, r_s on seed and pulp selectivity rank vs protein content during fruiting peak; $N = 17$ species), and the higher energy returns from eating nonfig pulp and seeds.

How do orangutans specialize on pulp and seeds if their protein content is so low? First, they do not seem to ingest food for maintenance during these all pulp+seed periods, so acquiring sufficient protein is not a problem; it can be met merely from consuming large amounts of these plentiful foods. But this diet would seem to impose problems from the perspective of its ratio of protein/energy. For maintenance, and to prevent loss of appetite, protein intake for humans should provide at least 17% of total energy (Lloyd *et al.*, 1978). The median ratios among seed species (10.0%; $N = 6$) and pulp species (10.1%; $N = 10$; Table IX) appear too energy-rich or protein-poor. This obliges the orangutan to shunt the excess energy into fat deposition in order to achieve protein balance.

Second, the daily crude protein requirement for maintenance scales as energy does, to the 3/4 power of body mass; e.g., for humans, the requirement is estimated as $2.45W^{0.75}/d$, where W is body weight (kg), and d is the digestibility coefficient of the protein (Lloyd *et al.*, 1978; Robbins, 1983). Therefore larger mammals require proportionally lower percentages protein in their diets than smaller ones do. In sum, scaling protein requirements and shunting excess energy to fat may allow orangutans to pursue an energy maximization strategy on a diet of all pulp and seed without special attention to protein intake. A second scaling rule, the enhanced ability of larger-bodied species to survive starvation periods (Calder, 1984), goes hand in hand with this extreme seasonal dichotomy in the dietary mixture and is an additional element in their foraging strategy. Paradoxically, from the perspective of the Jarman-Bell principle (Richard, 1985), because of the scaling of protein requirements and the low protein content of these fruits, larger frugivores may be more able to subsist on an all-pulp and/or all-seed diet than smaller frugivores (e.g., gibbons), which might be forced to ingest proteinaceous immature leaves during the season of pulp plenty. As a further prod to this niche difference, the locomotor mode of most smaller arboreal mammals may preclude them from employing the fat-binging strategy of orangutans. For instance, gibbons presumably would incur much greater risks and time/energy costs during travel if they were obliged to fatten up by selecting this diet. In contrast, the slow, cautious scrambling mode of arboreal travel (Wheatley, 1982; Sugardjito, 1982), and ground travel, by orangutans, would seem not to impose equivalent costs and risks.

Preferences for Different Types of Fruit: Avoiding Small Patches and Toxic Pulp

Preference for primate-fruits does not result from circularity in the definition of these fruits. This seed-dispersal syndrome has been established from observations that seed dispersal is performed by gibbons and/or macaques in addition to orangutans, and typically not by other taxa, and the tight association of characters that define the syndrome (Leighton and Leighton, 1983; Leighton, unpublished). In fact, there is no a priori reason to expect that animals which are the significant seed dispersal agents for a species would actually prefer to eat that species. It is entirely possible that the frugivore may consistently eat a pulp species and dominate seed dispersal quantitatively but not prefer it to other types of fruits.

What distinguishes the preferred primate-fruits from the fruits of other dispersal syndromes, which comprise the majority of available fruits, and are mostly avoided (Fig. 4)? The distinction cannot be due to morphological defenses because the pulp of the other fruit dispersal types can be easily ingested or scraped off by orangutans. The evidence indicates instead that selection of primate-fruits was due to their chemistry, specifically their high sugar and low tannin and toxin content, and to the large meals that some of them provided. The importance of these factors was established through the fig selectivity analysis, supported by the results of primate-fruit selectivity. Patterns of selection of species of other seed dispersal fruit types can be interpreted with regard to these same factors.

I hypothesize that most sugar-rich bird fruits and primate-fruit lianas were avoided because they occur as small patches, thereby would yield a small proportion of a meal and would cause orangutans to incur the time and energy costs of visiting more patches. Sugar-rich bird fruits dominate the flora [$>40\%$ of species (Leighton, unpublished)] and also have high median values of digestible carbohydrate (58 vs 62% for primate-fruits; ns, Mann—Whitney test) and low tannin contents in their pulp (Leighton and Waterman, unpublished). But sugar-rich bird-fruits overwhelmingly occurred as small patches, mostly as understory trees, lianas, and epiphytes, and were neglected. In contrast, a few that were large trees (e.g., some *Eugenia*; Table II) ranked highly in selectivity (Fig. 4). In addition, these fruits yield low kilojoules per minute compared to primate-fruits (Leighton, unpublished) because their grams of pulp per fruit values are relatively very low. Many also may be defended against unwanted exploiters by toxins in their pulp (Herrera, 1982).

Similarly supporting the small patch size explanation, only 3 of 16 (19%) liana species producing primate-fruits were of high preference (classes 1 and 2), compared with 50% of 36 trees producing primate-fruits ($X^2 = 4.5$, $P = 0.03$; Fig. 4). I compared the median patch sizes (g dry weight pulp/crop) of liana vs tree primate-fruits for those species for which crop size and pulp weight/fruit had been measured. Liana species produced patches less than half the mean (\pm SD) size (146 ± 167 g pulp/crop; $N = 16$; mean among species medians) of the average tree species (412 ± 559 g pulp/crop; $N = 29$). Solving the regression model of patch size on tree dbh (Fig. 6) indicates that the average liana species produced patches equivalent to 22-cm-dbh, small understory trees. Moreover, the variance of these mean values (and Fig. 6) illustrates that orangutans can enjoy far larger meals by selecting large trees (see Figs. 5a and b).

However, instead of patch size, avoidance of bat-fruits and lipid-rich bird fruits (Fig. 4) must be based on deterrent chemicals in the pulp, as

these fruits commonly occurred as large patches produced on large trees. Bat-fruit pulp was as low in energy and protein content as figs (Table IX), and most were high in tannins (median = 4.6%) (Leighton and Waterman, unpublished). As the analysis of fig selectivity demonstrated, these levels are in the range that presumably would deter feeding by orangutans (Wrangham and Waterman, 1983). The *Syzygium* bat-fruits in selectivity class 2 (Fig. 4) had an anomalously low tannin content (Leighton and Waterman, in preparation); conspecifics that were similar in other features, but high in tannin, were avoided.

Although many lipid-rich bird fruits were high in tannin, many other neglected species were low in tannin and fiber but high in fat and protein (Leighton and Waterman, unpublished), and occurred as common, large patches while orangutans were feeding on low-quality foods. These should have been the most attractive patches available, potentially yielding extraordinary rates of energy return to orangutan feeding effort, outstripping even good primate-fruit patches. Many of these pulps were bitter or spicy-tasting and are of taxa known to be high in alkaloids, terpenes, and other toxic secondary compounds. A recently completed comparison of primate feeding in West Borneo strongly supports the hypothesis that the high terpene content of these pulps most significantly deters orangutan feeding (Zens and Leighton, in preparation). The occasional high-ranking lipid-rich fruits (e.g., *Gnetum cuspidatum* and *Dacryodes rostrata*; Table II, Fig. 4) were low in tannin and, presumably, do not contain toxins.

The hypothesis that orangutans avoid fats in their diet per se was not supported by the fact that a few very high-ranking items were lipid-rich (e.g., *Dacryodes* pulp, 24%; *Iringia* seeds, 68%). Although the ratios of protein/energy for many of the lipid-rich bird pulps were unfavorable, many were not, and could have been mixed into the diet during fruit-poor times. Instead, I interpret the apparent avoidance of lipid-rich pulp by orangutans as an epiphenomenal correlate of selection to restrict ingestion of seeds to high-quality dispersal agents, such as hornbills and some other birds (Herrera, 1982; Leighton, 1992).

The sensitivity of orangutans to toxic compounds is shared with many monogastric vertebrates that lack foregut microorganisms to detoxify these compounds before absorption in the small intestine. The avoidance of the highly nutritious, lipid-rich bird-fruits, if it is due to toxic compounds in the pulp, then leaves unanswered the question of why the hornbills, pigeons, and other large birds that prefer these are insensitive to the compounds. Similarly, the avoidance of tannins by orangutans is clear from these results. Other monogastric mammals (e.g., the sympatric seed-eating tree squirrels) tolerate much higher tannin concentrations in their food. These different abilities for detoxification and tolerance of chemical feeding

inhibitors are as yet unexplained at the physiological level, for any monogastric vertebrate.

Support for the Foraging Economics Perspective

The analyses presented here indicate that the robust results from foraging and dietary breadth models (Krebs and Stephens, 1986) provide guidelines for examining the problem of dietary choice in a generalized primate omnivore like the orangutan. In order to integrate variables, I avoided formulating this as a complex nutrient- and toxin-mixing optimization problem, which seems incapable of incorporating spatial variables like patch size (Freeland and Janzen, 1974; Westoby, 1974). In fact, I have not considered the optimal mix of fruit species in the diet at any given time. The success of this modeling further depended upon separating fruit selectivity from selection of other food types like bark and leaves, because quantifying the critical spatial, chemical, and morphometric variables of food items was possible for fruit. Strong correlations were found between selectivity and features of fruit that can be readily interpreted in terms of foraging economics and basic considerations of physiology and morphology. Orangutans clearly avoided tannins, although, because measures of total phenolics and condensed tannins strongly covaried, and because there is still confusion over the biological implications of the compounds measured by each analysis (Mole and Waterman, 1987), it is unclear to what degree avoidance was due to palatability, and/or the binding of condensed tannins with protein, and/or the toxic effects of absorbed hydrolyzable tannins. Tradeoffs between nutrients and tannins or other toxic compounds would be best demonstrated through experimental food preference trials.

The overwhelming influence of patch size on fruit (and seed) selection can be interpreted in terms of the high costs of travel for orangutans and their high energy demands (Calder, 1984). The 90-kg males and 50-kg females travel slowly and inefficiently (in terms of direct-line travel) when arboreal, in comparison with gibbons and macaques (Wheatley, 1982; Rodman, 1984). Terrestrial travel, especially employed by males, involves costs of vertical climbing to reach food patches and, perhaps, a decline in the efficiency of discovering arboreal food patches (Rodman, 1984). Orangutans seem inordinately concerned with acquiring both large individual meals and successive large meals from the same fruit patch visited over several consecutive days, while apparently foregoing feeding on small patches of even more nutritious items in order to minimize daily travel. The costs in time and energy of the alternative strategy, visiting more small

patches of higher mean quality of food items, cannot be calculated from available data, but can only be surmised in comparison with other frugivorous primates. For instance, gibbons, which travel perhaps an order of magnitude more rapidly (Cannon and Leighton, in preparation), do not show such a strong proclivity to limit feeding to large patches (Robbins and Leighton in preparation). Although both the implied high costs for orangutans in traveling to many small patches and the scaling of their energy requirements may be important elements influencing their selection of large patches, sensitivity to patch size is not predicted to be limited to large individuals or groups of individuals (Charnov, 1976; Schluter, 1982).

The most striking result concerns the apparent ability of orangutans to integrate measures of different food-related variables and to shift selectivity rankings according to an *integrated* measure of net benefit. The fact that several variables contributed independently (and significantly) to predicting selectivity rank in the multivariate regressions forces us to conclude that orangutans make complex decisions about fruit choice. That is, figs of a high tannin content are not neglected per se; if they occur in large patches, they "move up" the rank order of selectivity to a position commensurate with their combined negative and positive features. Similarly, orangutans do not simply go to the patch with the largest crop; choice is weighted proportionally not only by the chemistry of the pulp but also by the pulp weight per swallowed unit, for both figs and primate-fruits, indicating that orangutans are sensitive to handling time while in the patch. I suspect that a broader set of chemical data on seed species would show that a similarly complex integration of deterrent chemical content, net yield per item (including handling time), and patch size underlies seed selection. Of course, from the perspective that feeding efficiently is of great selective importance to free-ranging orangutans and most other animals, this is not surprising. It would be surprising if properly designed studies of other omnivorous primates did not reveal similar abilities to select foods based upon complex, integrated multiple criteria.

These results suggest reassessment of inferences drawn from previous studies of primate dietary selection. Although these papers mention foraging theory in passing, the critical spatial variables (patch size, relative availability) and morphometric variables (those associated with handling time) identified by foraging theory as influencing net rate of energy (or protein) gain were not measured. Chemical measures of foods (e.g., fiber, tannin, energy, carbohydrate or sugar content) typically covary strongly, but multivariate analyses have not been used to demonstrate which of them are independent variables that influence dietary choice. To give but one example that could be selected from any study, Davies *et al.* (1988)

concluded that “N, ADF and CDIG all influence foliage selection,” an assertion not supported by the subsequent clause of the sentence: “however, they are not independent of each other.” The need for multivariate analysis is compounded by the fact that food item energy content can covary with patch size (Table III) or crown volume (Janson, 1986; Leighton, unpublished). Future studies should incorporate these methodological aspects and better estimates for some variables. For instance, I failed to measure both handling time and total meal size per patch visit for different fruit species in this study, and their estimation would have allowed more careful exploration of foraging models and diet selectivity.

Analyzing Selectivity as a Window into Other Problems

Identifying the factors underlying food selectivity is important for evaluating hypotheses about orangutans other than the basis of the dynamics of their diet breadth (Leighton, 1992).

Socioecological hypotheses for orangutan solitariness (Galdikas, 1988; MacKinnon, 1974; Rodman and Mitani, 1987; Rijksen, 1978; Rodman, 1977, 1984; Schurmann and van Hooff, 1986; Sugardjito *et al.*, 1987) depend fundamentally on untested assumptions about orangutan selectivity for fruits and patches of particular types, and on their sizes. The results of this study support the hypothesis that orangutans prefer big patches. Previously, this had been inferred from the fact that they feed there longer (Rodman, 1984). Recall that in my study, even though orangutan selectivity rank was positively correlated with patch size, multivariate analysis was required to disentangle this variable from other features of fruits that also strongly covaried with tree size and selectivity rank.

The coevolutionary role of orangutans in rainforest communities as either seed predators or mutualistic agents of seed dispersal for plants can be inferred from careful observation of feeding behavior and by modeling their selectivity for different fruits and seeds (Leighton, 1992). Selective pressure is exerted by the frugivore on those fruit and fruiting traits underlying fruit pulp or seed choice (Janson *et al.*, 1986). Although most prior studies of orangutans do not separate out seed-eating from fruit pulp-eating, classifying both under the rubric of “fruit-eating,” these are taxonomically, physically, chemically, and even phenologically very different food types.

The predictive power from these models could be applied to conservation biology: A dangerously low orangutan population density in a forest reserve, for instance, could be augmented by enrichment planting of the

food species that are most uniquely preferred and that fruit during periods of limited fruit availability (Leighton, 1992). This requires simultaneous modeling of selectivity for the competing species of the same frugivorous guild, especially other primates and squirrels.

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