Gibbon Foraging Decisions and the Marginal Value Model

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We use data from an observational field study of frugivory in two sympatric gibbons, lar (Hylobates lar) *and siamang* (H. syndactylus), *to test assumptions and predictions of the marginal value model (MVM). A key prediction of the MVM is that marginal gain rates at the time of leaving the patch are equal across patch types. We found that this is not the case for gibbons: rates of energy intake at the end of feeding sessions were significantly different for different types of fruit, and we could not attribute this to temporal variation in fruit availability. Initial and final caloric intake rates were highly correlated. This suggests that gibbons do not adjust the time spent in patches in order to maximize the average rate of energy intake. Similar results were obtained for all other currencies considered. Gibbon foraging appears to satisfy several, but not all, assumptions of the MVM. As required by the model, fruit patches occur as discrete units, patches are encountered sequentially, travel time between patches exceeds search time between items within a patch, search for and search within patches are incompatible activities, and intake rates decline over time spent in a patch. However, the declining rates we detected may be an effect of satiation instead of patch depletion, patches probably are not encountered at random, and group members may not forage independently. Thus, our results suggest that the MVM is not an adequate model of gibbon foraging behavior, but they do not invalidate the MVM per se.*

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INTRODUCTION

In this paper we apply a model from optimal foraging theory, the marginal value model (Charnov, 1976; Parker and Stuart, 1976), to examine the foraging behavior of two sympatric gibbons: lar (*Hylobates lar*) and siamang (*H. syndactylus*). Primates and other mammalian herbivores are poorly represented in the optimal foraging literature (Stephens and Krebs, 1986). In part this may be a consequence of the widespread opinion that the diets of herbivores, and the constraints under which they forage, are too complex to expect simple rate-maximizing models to apply (Milton, 1979; Freeland and Janzen, 1974; Schoener, 1987). Herbivores may need to select a diverse array of food types in order to meet dietary requirements (Crawley, 1983) or to minimize the deleterious consequences of particular plant toxins and digestibility reducers (Rosenthal and Janzen, 1979). Some herbivores may be able to synthesize what they do not eat, however, or to maximize the rate of energy intake subject to other dietary constraints (Belovsky, 1978; 1984; Schoener, 1987). Alternatively, herbivores may maximize some other currency, such as the ratio of protein to fiber gain (Milton, 1979), in a manner analogous to the marginal value model (Krebs and McCleery, 1984). Stephens and Krebs (1986) suggest that the emphasis on food quality for herbivores has prevented us from finding out how complex their foraging decisions actually are.

The marginal value model (MVM) (Charnov, 1976; Parker and Stuart, 1976) generates predictions regarding the behavior of animals utilizing a heterogeneous array of depletable food patches. In the model, foragers equipped only with knowledge of average path conditions travel from patch to patch and leave each patch when their rate of energy intake in that patch drops to the net rate of gain over all other patch types. Despite its restrictive assumptions and theoretical limitations (Mangel and Clark, 1988), the basic model has held up well to considerable testing (Krebs and McCleery, 1984; Stephens and Krebs, 1986; Schoener, 1987; but see Gray, 1986). Some studies have yielded results at odds with the model, but these are often flawed by a failure to test its assumptions (Stephens and Krebs, 1986).

Frugivorous primates have several attributes that may make them more suitable than other mammalian herbivores for studies of foraging behavior under natural conditions: (1) individuals can often be consistently monitored from patch to patch, (2) patches usually occur as readily distinguishable, nonarbitrary units (i.e., trees), (3) food items usually occur in discrete units that can be unambiguously counted during feeding, and (4) frugivores, in general, may be virtually free from the constraints imposed

on other herbivores by plant defenses. A discontinuous distribution of food is especially important for the MVM, and for sequential patch models in general, since these require that searching for and foraging within patches are mutually exclusive activities (Stephens and Krebs, 1986). On the other hand, primate sociality introduces complexities that are not easily incorporated into optimality models.

Our data on the foraging behavior of gibbons enable us to test a qualitative prediction of the MVM: that foragers will leave patches of all types at the same marginal (energy) gain rate (Charnov, 1976; Parker and Stuart, 1976). Gibbons do not meet rigidly all the assumptions of the MVM, however, so our data do not allow a rigorous test of the MVM itself. Instead, we aim to determine whether the MVM suffices as a model of gibbon patch-leaving decisions. Unless gibbon foraging deviates substantially from what the MVM predicts, there is little basis for considering more complex models.

METHODS

Study Area, Species, and Groups

This study was conducted at the Ketambe Research Station, Gunung Leuser National Park, northern Sumatra, Indonesia (3°40'N, 97°40'E), located in fairly undisturbed lowland tropical rain forest (Rijksen, 1978; van Schaik and Mirmanto, 1985). The two groups of each gibbon species (*Hylobates lar* and *H. syndactylus*) included in this study were the exceptionally well-habituated subjects of a long-term study conducted by RAP. Both species are highly territorial, live in socially monogamous family units (Chivers, 1972, 1978), and feed extensively on fig (*Ficus* spp.) fruit, though they differ in the proportion of leaves, nonfig fruit, and animal matter (primarily invertebrates) in their diets (Gittins and Raemaekers, 1980). For the most part, these dietary differences are quantitative. Siamang include more leaves in their diet; lar include more nonfig fruit, although this appears to vary from site to site (Chivers, 1978; Gittins and Raemaekers, 1980). Groups were composed of one adult male–female pair and one to three juveniles. Siamang group sizes were two and three; lar group sizes were three and two to five [the size of the latter group varied both within and between days (Palombit, 1992). Two adult females, one siamang and one lar, were pregnant or lactating during this study. Siamang territories overlapped extensively with lar territories.

Sampling Protocol

Observations were made by GFG between August and December 1987. Full dawn-to-dusk focal samples were distributed as evenly as possible across the eight adults (four male and four female) included in the study (72 focal samples; ca. 648 observation hr; mean of 9 follows per individual; range, 2–14). The individual for which only two full follows were obtained was a partially habituated adult male, which was only occasionally present in one *H. lar* group. Only *Ficus* feeding data on this individual were included in the analysis. Whenever possible, individuals were followed from the time they exited a sleep-tree at daybreak until they entered (and remained within) a sleep-tree in the late afternoon.

During focal samples, continuous activity records were compiled by calling off transition times into a cassette recorder. Recorded activities included resting, traveling, feeding, foraging on invertebrates, and drinking water trapped in tree cavities. Patch entry and exit times defined a feeding session. Behavioral transitions were recorded within and between sessions. The onset of resting during a feeding session was identified by a characteristic pause in food processing. Typically, delays of greater than 1 min between hand-to-mouth movements were counted operationally as resting, except when food processing took more than 1 min (e.g., *Myristica* spp. and large *Ficus* fruit). During feeding sessions, each hand-to-mouth movement made by the focal animal was announced into a continuously running tape recorder, along with an estimate of the number of items per handful, whenever such movements were clearly visible. Preliminary data collected in August were not included in the analyses. For most of the analyses, only data from the most complete sessions are utilized, as described below.

The data were transcribed from cassette tape onto a microcomputer equipped with a millisecond timer by means of a custom program in BASIC.

Patch Definition and Fruit Type Classification

In this study a patch was defined as the crown of a fruit tree or liana. Only data on the consumption of fruit (by far the largest dietary component of both species) are presented in this report. Nonfig fruit were classified by species. Since few of the large number of *Ficus* species at Ketambe were fed in by more than two individuals, analysis by fig species was not possible. Instead, *Ficus* fruit were classified as "small figs" or "large figs" according to the way in which gibbons processed the fruit. Gibbons placed small figs

directly into their mouths one or more at a time, but they bit large figs repeatedly while grasping them manually, before proceeding to the next item.

Analyses to Detect Patch Depression

The MVM assumes that intake rates decline with time spent feeding within patches. Two approaches were taken to test this assumption. First, the Spearman rank correlation between instantaneous intake rate and time spent feeding was calculated for each feeding session. Instantaneous intake rates were obtained by dividing the number of items in a handful by the corresponding interval between hand-to-mouth movements. When the number of items in a particular handful could not be counted, the average for that feeding session was substituted in its place. Session correlations were averaged by fruit type to obtain a mean value for each individual on each fruit type.

Our second approach was to compare intake rates near the beginning and end of feeding sessions. In order to improve the accuracy of our rate estimates, particularly the rate of feeding at the end of feeding sessions (our estimate of the marginal rate), we analyzed a subset of the data in which less than 40 sec was missing from the end of the feeding session and more than 50% of the time spent feeding in the session was included in the sample. "Missing" time occurred when the observer was unable to see the focal animal clearly enough to count hand-to-mouth movements accurately. Each of the selected sessions was divided into quarters (i.e., the first 25% of hand-to-mouth movements counted in a session were allocated to the first quarter, and so on; remainders were allocated by a rounding rule), and mean intake rates were calculated separately for each quarter based on the number of items eaten and the time spent actually feeding (i.e., excluding "rests" and other activities). The mean rate for the first quarter served as a measure of the "entry" intake rate, i.e., the rate of feeding near the beginning of the feeding session. The mean rate of intake over the last three intervals (between hand-to-mouth movements) of each session provided an estimate of the marginal (or "exit") intake rate. Entry and exit rates were analyzed in a split-plot design repeated-measures ANOVA using Statistical Analysis System's GLM procedure with the RANDOM and TEST statements for Satterthwaite approximate F tests (SAS version 6). The split-plot design was necessary to accommodate missing cells (not all individuals were observed on all fruit types.)

Table I. Mean Spearman Rank Correlations Between Instantaneous Intake Rate (the Reciprocal of Intervals Between Food Items) and Time Spent Feeding (Time Spent in the Patch Minus Time Spent There in Nonfeeding Activities)

Pair	Sex	*Ficus* fruit			Non-*Ficus* fruit		
		Mean	SE	N^a	Mean	SE	N^a
Lar							
A	m	−0.061	0.051	19	−0.043	0.055	23
A	f	−0.041	0.051	24	−0.232	0.079	18
M	m	−0.107	0.084	4	—	—	—
M	f	−0.035	0.067	23	−0.142	0.067	36
Siamang							
C	m	−0.154	0.065	12	−0.051	0.063	19
C	f	−0.118	0.077	9	−0.150	0.074	16
P	m	−0.078	0.041	10	−0.141	0.051	19
P	f	−0.038	0.068	8	−0.255	0.068	9

[a] The number of feeding sessions included per individual.

Marginal Gain Rate Analyses

In order to test the MVM prediction of equal marginal gain rates across patch types, the product of exit rate, grams dry weight per item, and kilocalories per gram was used as an estimate of the marginal caloric gain rate (mean fruit weights and nutritional information courtesy of C. van Schaik and S. Djojosudharmo, respectively). Marginal protein and protein/fiber gain rates were estimated similarly. Both dry weights and nutritional data were available for six fruit types. Fruit types and patch types were assumed to be one and the same. These data were analyzed as repeated-measure ANOVAs. Intake rates were square root-transformed.

RESULTS

Change in Intake Rates over Time Spent Feeding

The MVM assumes a negative relationship between intake rate and time spent feeding within a patch. In our sample of 249 fruit-feeding sessions, 69% of the Spearman rank correlations between instantaneous intake rate and time spent feeding were negative. The *mean* correlation for each animal was negative, on both figs and combined nonfig fruit (Table I). The likelihood of this occurring by chance is small (one-tailed Sign test:

Table II. Results of the Split-Plot ANOVA of Entry and Exit Rates

	Lar			Siamang		
Source	df	F	P	df	F	P
Period	1,7.47	1.119^a	0.3231	1,3.29	51.129^a	0.0041
Individual	3,8.99	7.725^a	0.0074	2,5.34	5.845^a	0.0391
Fruit type	7,23	5.698	0.0007	7,35	7.869	0.0001
Period × individual	3,23	0.292	0.8306	3,35	0.283	0.8372

^{a} Quasi F statistic (Satterthwaite approximation).

$P < 0.004$, $n = 8$, for figs; $P < 0.008$, $n = 7$, for nonfig fruit; n includes both gibbon species). No significant difference was found between the mean values for lar and siamang on figs (Mann–Whitney, $P > 0.10$, $n_1 = n_2 = 4$) or nonfig fruit ($P > 0.10$, $n_1 = 3$, $n_2 = 4$). Thus, these data indicate a deceleration of intake rate over the course of the most feeding sessions for both lar and siamang.

The results of the ANOVA of entry and exit intake rates can be summarized as follows. The difference between entry and exit rates was significant for siamang but not lar (Table II, Fig. 1). For both species, there were significant individual and fruit type effects but no significant individual × period interaction (where "period" refers to entry or exit). These results are consistent with the results of the rank correlation analysis (using the full data set) for siamang but not for lar. Individual differences, combined with the small sample size, may account for the lack of a significant period effect in lar: four of the data points above zero in Fig. 1 correspond to one lar female.

Gain Curve Shapes

The shape of the gain curves (fruit consumed versus time) can be inferred from the plots of intake rate versus session period. Plots for different fruit types fell roughly into two categories, corresponding to simple exponential (Fig. 2a) and sigmoid (Fig. 2b) gain functions. Fruit types in Fig. 2b appear to require some "startup" time before gibbons reach maximum intake rate. Nine of the ten fruit types exhibit a deceleration between the second and the third quarters. This rules out the possibility that intake rates decline only when gut capacity is closely approached but does not rule out other satiation effects.
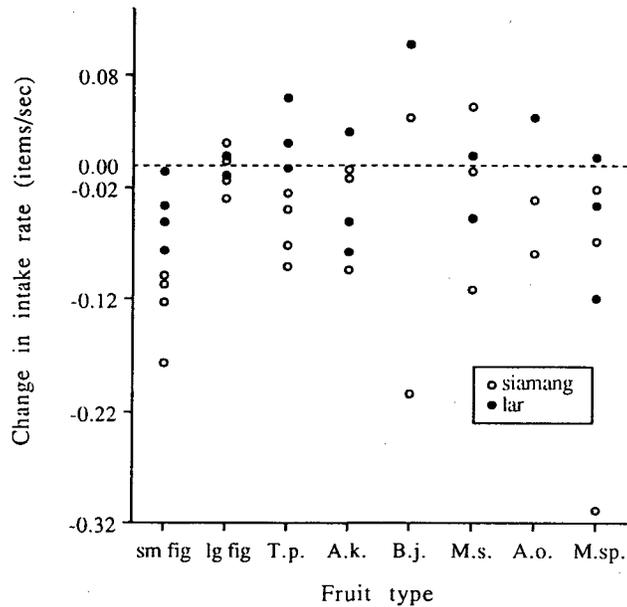
Fig. 1. The change in intake rate (items/sec) between the first
quarter and the last three intervals of feeding sessions for both
gibbon species on eight fruit types. Each point represents the
mean change for a particular individual feeding on a particular
fruit type, averaged over several sessions. Abbreviations for fruit
types translate as follows: sm fig, small *Ficus* fruit; lg fig, large
Ficus fruit; T.p., *Tinomiscium phytocrenoides*; A.k., *Aglaia
korthalsii*; B.j., *Biscoffia javanica*; M.s., *Mallotus sphaerocarpus*;
A.o., *Aglaia odoratissima*; and M.sp., *Myristica sp.* Overlapping
points were separated slightly for graphical presentation but so as
to preserve the original order with respect to the vertical axis.

Marginal Gain Rates

The effect of fruit type on caloric gain rate was significant (Table III,
Fig. 3). No difference was detected between the exit gain rates of lar and
siamang, and no fruit type × species interaction was detected. Thus, con-
trary to the prediction of the MVM, patch types differ with respect to the
average rate at which gibbons take in calories just before exiting the patch.
The effects of fruit type on protein, on protein/fiber, and on dry and wet
weight exit gain rates were also significant (Table III); neither gibbon spe-
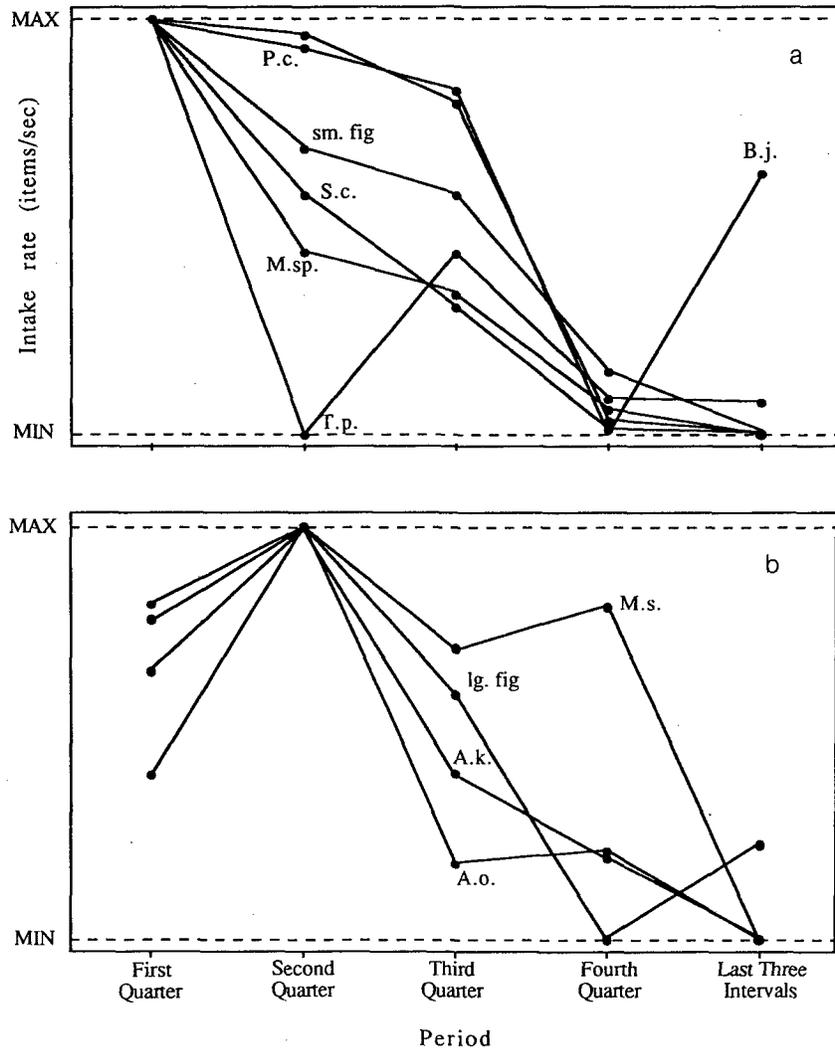cies nor the interaction term had a significant effect.

Fig. 2. Caloric gain rate plotted against session period to indicate the shape of the gain curves. Inferred gain curves fall roughly into two categories: (a) simple exponential and (b) sigmoid. Each point represents the mean of individual mean caloric intake rates for a particular fruit type during a particular period. Lines connect the data points corresponding to the same fruit type. The vertical axis has been standardized from the minimum value to the maximum value in order to make data for different fruit types comparable. Abbreviations for fruit types are as in the legend to Fig. 1, with the following additions: S.c., *Siphonodon celastrineus*; P.c., *Pyonarrhena cauliflora*.

Table III. Split-Plot ANOVA Results for Exit Gain Rates Using Five Different Currencies

Source	Caloric			Protein			Protein/fiber		
	df	F	P	df	F	P	df	F	P
Species	1,10.9	0.077[a]	0.7861	1,13.6	0.183[a]	0.6759	1,10.8	0.042[a]	0.8421
Indiv. (sp.)	6,17	0.438	0.8434	6,17	0.282	0.9378	6,17	0.453	0.8331
Fruit type	5,17	22.525	0.0001	5,17	34.800	0.0001	5,17	18.235	0.0001
Fruit × sp.	5,17	0.223	0.9477	5,17	0.216	0.9507	5,17	0.286	0.9141

[a] Quasi F statistic (Satterthwaite approximation).

Table III. Continued

Source	Dry weight			Wet weight		
	df	F	P	df	F	P
Species	1,10.3	0.158[a]	0.6987	1,9.79	0.183[a]	0.6780
Indiv. (sp.)	6,21	0.621	0.7115	6,21	0.700	0.6528
Fruit type	6,21	11.832	0.0001	6,21	10.655	0.0001
Fruit × sp.	6,21	0.409	0.8650	6,21	0.427	0.8524

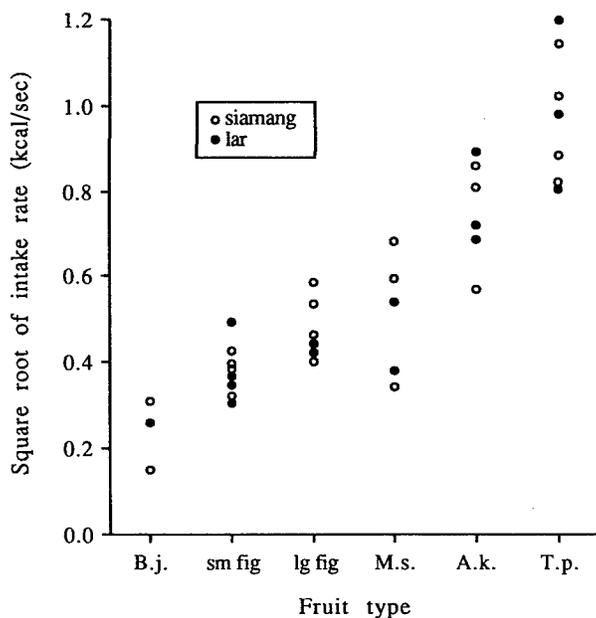[a] Quasi F statistic (Satterthwaite approximation).

Fig. 3. The square root of mean caloric gain rate (kcal/sec) over the last three intervals of feeding sessions for both gibbon species on each of six fruit types. Each point represents the mean exit rate for a particular individual on a particular fruit type averaged over several feeding sessions. Fruit type abbreviations are as in the legend to Fig. 1. Overlapping points were separated slightly for graphical presentation but so as to preserve the original order with respect to the vertical axis.

Association Between Entry and Exit Rates

Across six fruit types, entry and exit caloric gain rates were highly correlated in both lar and siamang (two-tailed Spearman rank correlation, $r_s = 1.0$, $P = 0.005$, $n = 6$ fruit types; Fig. 4). Similar results were obtained using protein and protein/fiber gain as currencies (protein, $r_s = 0.943$, $P = 0.02$, $n = 6$; protein/fiber, $r_s = 1.0$, $P = 0.005$, $n = 6$). These data provide no evidence that gibbons of either species adjusted the time spent feeding in patches so as to compensate for differences between patch types in the initial rates of caloric, protein, or protein/fiber gain. There were no significant correlations between the mean exit gain rate and fruit weight, wet or dry, for siamang (caloric, $r_s = 0.6$, $P > 0.2$; protein, $r_s = 0.657$, $P = 0.2$, $n = 6$; protein/fiber, $r_s = 0.429$, $P > 0.2$, $n = 6$) or
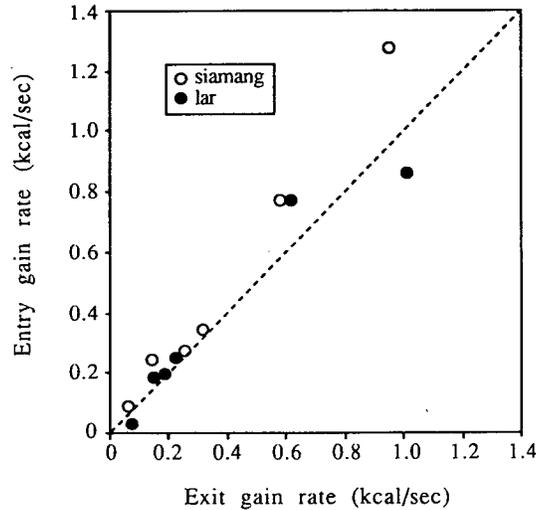
Fig. 4. First quarter (entry) caloric gain rate versus exit caloric gain rate (kcal/sec). Each point represents the mean for one species on one fruit type. The diagonal dashed line has a slope of 1.

for lar (caloric, r_s = 0.6, P > 0.2; protein, r_s = 0.657, P = 0.2, n = 6; protein/fiber, r_s = 0.371, P = 0.5, n = 6).

Weights and Caloric Value

Both the wet weight (weight before drying) and the dry weight of fruit were highly correlated with the caloric value of fruit (in both cases r_s = 0.943, P = 0.02, n = 6). Thus, fruit weight could serve as a reliable indicator of caloric value.

DISCUSSION

Our results suggest that gibbons do not adjust their patch residence times in order to maximize their overall rate of energy intake while foraging. Instead of leaving patches of different types at the same energy intake rate, as predicted by the marginal value model, gibbons systematically leave patches of some types at substantially higher intake rates than others (Table III, Fig. 3). Furthermore, initial and final intake rates are

highly correlated (Fig. 4). This would not be the case if gibbons compensated for differences between initial intake rates in different patch types by adjusting patch residence times. We also investigated the possibility that gibbons maximize the rate of protein intake, or the ratio of protein to fiber intake, in a manner analogous to the MVM. Neither of these currencies removed differences between the exit rates of different fruit types (Table III). Nor did they produce the expected low correlation between entry and exit rates.

Are these results surprising, or was it naive to apply a simple optimal foraging model to a complex system? We think both answers have some validity. Gibbons are clearly not the organisms to which the marginal value model is most likely to apply. While they forage on a patch-by-patch basis, it seems unlikely that they encounter patches at random. Instead, gibbons appear to forage along established travel routes and often visit the same fruit trees on consecutive days. In short, they may know more about alternative patches than just the average travel times and patch productivities. Gibbons usually travel in nuclear family units. Thus, the foraging decisions of individuals are unlikely to be independent of one another. Gibbon fruit patches are also the sites of nonforaging activities, such as social interactions and rest. Although these activities undoubtedly alter the time spent in patches, their effect on the time spent foraging in patches is unclear.

Could gibbons be using a "rule-of-thumb" that approximates an energy-rate maximizing solution? Since gibbons eat a wide array of fruit, leaves, flowers, and invertebrates, it seems unlikely that past selection would have equipped them with "innate" rules for how long to feed in patches of each type. Nor does it seem likely that gibbons possess some mechanism for assessing caloric value directly. Instead, one might expect them to base foraging decisions on some easily perceptible characteristic of fruit that correlates with caloric value, such as fruit weight or consistency. As both wet and dry weights of fruit correlate highly with caloric content, gibbons could approximately maximize the rate of energy intake by maximizing the rates of either wet or dry weight gain. For both currencies, however, exit rates on different fruit types were significantly different (Table III). It therefore seems unlikely that gibbons make even a rough approximation to maximizing energy per unit time feeding, although potentially useful cues appear to be readily available.

Gibbons may be foraging optimally within particular metabolic constraints. Such constraints might include fulfilling certain nutritional requirements and avoiding particular plant toxins (Altmann and Wagner, 1978; Maynard Smith, 1978; Belovsky, 1981; Stephens and Krebs, 1986). For example, gibbons may forage so as to meet minimum daily energetic

and protein requirements while minimizing the ingestion of toxic substances. Further nutritional analyses of gibbon diets are needed. None of the fruit included in this study contained toxic alkaloids (S. Djojosudharmo, unpublished data).

Gibbon foraging decisions may be constrained by factors other than nutritional requirements and plant toxins. Some patch types may consistently involve greater risks of predation than others (Altmann and Wagner, 1978), thereby altering relative patch profitabilities. Alternatively, the need to patrol territorial boundaries may play a major role in determining where gibbon pairs forage. The effect of a benefit to traveling between patches is to reduce the optimal stay time in patches (Kacelnik et al., 1981), but it is less clear how this would have differential effects by patch type. One possibility is that the benefits of feeding are increased in patches that permit greater territorial vigilance. Emergent fig trees, for example, may offer gibbons a better view than fruit trees with crowns within the canopy do. In fact, we know very little about what factors most influence gibbon foraging decisions. An analysis of gibbon foraging patterns in relation to predation hazard and territorial defense would be of value.

Thus far, we have assumed that the declining intake rates we detected (Table I, Fig. 1) were the result of patch depletion instead of satiation. Patch depression would not be expected if fruit were distributed randomly in patches and gibbons searched systematically (Stephens and Krebs, 1986). However, gibbon patches are three-dimensional and movement is restricted along particular routes (i.e., branches). It may be impossible for foraging gibbons to avoid crossing their own or others' paths. The more time a gibbon spends in a patch, the more paths there are to cross. Moreover, if fruit are distributed heterogeneously within patches, gibbons may feed first where intake rates are highest and move to successively poorer regions before finally exiting the tree. Either of these processes alone, or their combination, could lead to patch depression. Unfortunately, our data do not enable us to distinguish between depletion and satiation effects. The gain curve shapes (Fig. 2) are consistent with both mechanisms. We can rule out the influence of certain forms of satiation effects. Increasing satiation may result in (1) progressively longer time intervals between bouts of feeding within sessions, (2) progressive reduction in the length of bouts, and/or (3) declining intake rates between successive bouts (McCleery, 1977). While any combination of these three effects could result in a reduction in the overall rate of intake with time spent in the patch, only the third effect could explain our results since we excluded interbout intervals (i.e., "rests") from the rate calculations.

Table IV. Fraction of Feeding Session Pairs in Which the Fruit Type
on the Vertical Had an Exit Rate Greater than the Fruit Type on
the Horizontal[a]

	sm fig	lg fig	T.P.	A.k.	B.j.	M.s.
sm fig		1/3	0/10	0/19	1/1	1/3
lg fig	11/13		0/2	0/3	—	—
T.P.	22/22	8/8		3/4	6/6	5/7
A.k.	49/50	9/9	2/5		—	1/1
B.j.	0/2	—	0/13			0/3
M.s.	3/5	2/2	3/11	0/1	6/6	

[a] Above the diagonal are pairs of sessions occurring on the same day;
below the diagonal are pairs of sessions from the same or adjacent days.
[b] For abbreviations, see the legend to Fig. 1.

In averaging data collected over 3.3 months, we have assumed that there were no significant changes in the long-term average rate of energy intake in the habitat (R) over this time period. If gibbons track shorter-term fluctuations in resource availability by adjusting patch residence times, then the differences that we detected between the marginal gain rates on different fruit types might reflect temporal phenological variation instead of differences between the fruit types themselves. An examination of the unaveraged data shows that this is not the case. If gibbons foraged as the marginal value model predicts, we would not expect to find systematic differences between the exit rates in patches of different types when the comparison is made between sessions occurring on the same (or adjacent) days (we assume that changes in R are detected on a time scale of greater than 1–2 days). Table IV shows that there are consistent relationships among several fruit type pairs (e.g., in all 19 pairs of small fig and *Aglaia korthalsii* sessions occurring on the same day, the exit rate on *Aglaia korthalsii* was higher). Thus, although R may have changed over the course of the study, differences between the exit rates on different fruit types cannot be attributed to variation in R.

Differences between fruit types in within-patch "search" costs might explain our results if patches left at higher exit rates had proportionally higher search costs. It is interesting in this regard that the three fruit types with the highest exit rates are also the only ones that gibbons husk. But this observation does not help to explain the substantial differences in exit rates among the husked fruit (see Fig. 3). In all other respects, the different fruit types appear to require similar energetic expenditures. It is possible that the consistent differences that we detected between the marginal gain rates on different fruit types were due to systematic errors in the dry weights or caloric values used to calculate the marginal rates. Such errors

might result from weighing and analyzing portions of the fruit that are ingested but not digested. Thus, differences between the marginal gain rates on different fruit might be a consequence of differences between fruits in the proportion actually digested.

This preliminary study reveals that there are a number of important and potentially resolvable issues in primate foraging behavior that have hardly been addressed. Whether or not optimal foraging theory is a suitable framework for investigations of primate foraging behavior remains to be established. We hope that this report encourages further research on the subject.

ACKNOWLEDGMENTS

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