

FOOD PREFERENCE AS A FUNCTION OF RESOURCE ABUNDANCE
WITH MULTIPLE PREY TYPES: AN EXPERIMENTAL ANALYSIS
OF OPTIMAL FORAGING THEORY

THOMAS E. LACHER, JR.*, MICHAEL R. WILLIG†, AND MICHAEL A. MARES‡

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260 and
Pymatuning Laboratory of Ecology, Linesville, Pennsylvania 16424

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Optimal foraging models are based upon the tenet that natural selection ultimately favors individuals that choose foods that convey the maximum net benefit. Benefit can be variously defined, but normally it is assumed to possess a basis in energetics. Numerous theoretical models have been proposed, most of which are concerned with the maximization of the rate of energy intake in response to a range of available food items (Emlen 1966, 1968; Rapport 1971; Schoener 1971, 1979; Krebs 1973, 1978; Pulliam 1974, 1976; Charnov 1976*a*; Estabrook and Dunham 1976). Other research has emphasized the optimization of patch utilization in a heterogeneous environment (Charnov 1976*b*; Orians and Pearson 1979). Although the number of quantitative experimental studies designed to test these theories has grown dramatically in recent years (e.g., Krebs et al. 1974, 1977; Werner and Hall 1974; Emlen and Emlen 1975; Jenkins 1975; Cowie 1977; Davies 1977; Goss-Custard 1977; Reichman 1977; Stenseth et al. 1977; Stenseth and Hansson 1979; Bond 1980), various aspects of optimal foraging theory remain untested or unsupported by empirical data.

Pyke et al. (1977) summarized the predictions concerning optimal foraging theory made by various authors. If organisms maximize their net rate of energy or mass intake (E_n/T), the optimal diet in a fine-grained environment will exhibit three basic properties. First, the decision to select or reject a particular food item should only depend upon the absolute abundances of other food items which convey greater benefit. If foods of higher value are available, low-value items should be rejected, regardless of their abundance. It follows that increasing the abundances of preferred high-benefit food items will increase consumer specialization on these items. A second prediction states that animals perceive and consume available foods in a rank order of preference. If the abundance of a

Present address: *Huxley College of Environmental Studies, Western Washington University, Bellingham, Washington 98225; †Department of Biological Sciences, Loyola University, 6363 St. Charles Avenue, New Orleans, Louisiana 70118; ‡Stovall Museum and Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019.

high-ranked food increases, then foods of lower rank should be deleted from the diet. Items should be deleted progressively in reverse rank order. A corollary of this is that at infinite abundances, only the highest ranked food should be consumed. The third property of an optimal diet may be considered an extension of the first two. If the optimal diet maximizes E_n/T , food items should be either completely accepted or rejected; no partial consumption should be evident. This specific model of the foraging process was first proposed by Pulliam (1974) and Charnov (1976a).

Charnov (1976a) expressed the foregoing relationships in mathematical terms. Foraging individuals spend time (T) both searching for (T_s) and handling (T_h) prey. For k different prey types,

$$\frac{E_n}{T} = \frac{\lambda_i E_i^* P_i}{1 + \lambda_i h_i^* P_i},$$

where λ_i = the number of prey of type i encountered per unit search time; E_i^* = the expected net energy content of an item of type i ; h_i^* = the expected handling time of an item of type i ; and P_i = the probability that the organism will consume i when it is encountered. For optimal solutions with no nutrient constraints, P_i will assume, by definition, the values 0 or 1. In the Charnov model, the predator has no control over the other variables in the equation. The predator ranks prey according to the ratio E_i^*/h_i^* and the choice to include a given prey type in the optimal diet depends not on the abundance of type i , but only on the abundance of any available prey which ranks above type i .

As recent reviews by Pyke et al. (1977) and Krebs et al. (1980) have noted, many important corollaries of optimal foraging theory have never been substantiated. Much of the previous experimental work on optimal foraging behavior has involved studies in which predators had only limited prey choice (e.g., both Goss-Custard 1977 and Krebs et al. 1977 restricted their observations to predators presented with a two-prey decision). In nature, predators generally have access to a number of alternative prey choices, and dualistic models may therefore offer incomplete insight into the behavior of predators faced with a complex array of nonmobile prey species. Questions concerning the ranking of prey items and the existence of partial consumption have gone largely untested, especially in situations where predators have multiple choices (Pulliam 1980). A controlled experimental analysis of predator choice in response to a number of alternative food types would provide answers to these questions.

We tested the foraging response of a population of consumers to changes in the absolute abundance of an array of food types in a fine-grained environment. Our objective was to evaluate experimentally the value of the three basic hypotheses of a particular optimal foraging model (Pulliam 1974; Charnov 1976a) when examined in light of Charnov's (1976a) mathematical analysis.

MATERIALS AND METHODS

Kerodon rupestris (Caviidae) is an herbivorous rodent, endemic to the Caatinga of northeastern Brazil. Unlike other members of the guinea pig family, it is

TABLE 1

PLANT SPECIES FOUND IN *Kerodon* HABITAT USED IN FOOD PREFERENCE TRIALS

Family	Species	Code
Boraginaceae	<i>Cordia insignis</i> Cham	Ci
Erythroxylaceae	<i>Erythroxylum</i> sp.	Es
Euphorbiaceae	<i>Croton argyrophyloides</i> Muell. Arg.	Ca
	<i>Croton jacobinensis</i> Baill	Cj
Gramineae	<i>Brachiaria mutica</i> (Forsk) Stapf.	Bm
Leguminosae	<i>Cassia excelsa</i> Schrad	Ce
Rhamnaceae	<i>Rhamnidium</i> sp.	Rs
	<i>Ziziphus joazeiro</i> Mart.	Zj
Vitaceae	<i>Cissus sicyoides</i> L.	Cy
	<i>Cissus simsiana</i> R. et S.	Cs

NOTE.—Species are arranged by family and referred to in the text by the species code. All species except *B. mutica* are native. *B. mutica* is introduced but abundant and widespread.

semi-arboreal and leaves constitute the major portion of its diet. A colony of six adults was maintained as part of a comprehensive study of *Kerodon* social behavior (Lacher 1980, 1981), in addition to being utilized to evaluate the effect of resource abundance on food preference. A large room (25 × 10 m) was gridded and contained four different sections modified to simulate the natural habitats of the Caatinga where *Kerodon* is found (rocks, forest, brush, field). The colony room and its seminatural conditions are more extensively described by Lacher (1979, 1980, 1981). *Kerodon* and its general habitat are described in Lacher (1980, 1981), Mares et al. (1981), Streilein (1981), and Mares and Lacher (unpubl. MS). The preference research was conducted in Exu, Pernambuco, Brazil, between April and July 1977.

A critical assumption of the optimal diet model requires consumers to view their habitat as being fine grained. In order to test the equal utilization of the four habitats present in the colony room, we simultaneously placed 10 g of leaves of a domesticated fruit-bearing tree (Annonaceae) at four randomly selected points within each habitat. This procedure was repeated on three consecutive nights. We chose the leaves of this particular tree because they are highly favored by *Kerodon* and would not be used in subsequent food preference trials. The total quantity of leaves consumed per habitat per night was recorded; mean values were calculated and compared using a one-way analysis of variance (Sokal and Rohlf 1969).

Actual food preference testing was conducted in two consecutive 10-trial phases with the basic methodology remaining the same in each phase. Ten different species of leaves were randomly placed at different points within the colony room during each nightly trial. No species was placed at the same position in the room twice; all 10 plant species occur in *Kerodon* habitat (table 1). The array of food types was thus randomly distributed each night, thereby avoiding any complication within the experimental design attributable to consumer spatial learning or conditioning. In addition to the test leaves, 10 samples of control leaves (1 of each test species) were placed in consumer-proof cages in the colony room and used to

TABLE 2

TOTAL AND MEAN QUANTITY (g) OF ANNONACEAE LEAVES CONSUMED PER HABITAT DURING THREE NIGHTS OF TESTING

	MICROHABITAT			
	1	2	3	4
Total	115.3	105.9	107.7	107.2
Mean \pm SD	38.4 \pm 2.7	35.3 \pm 6.3	35.9 \pm 3.6	35.7 \pm 4.7

NOTE.—Since variances were homoscedastic ($F_{\max} = 5.5$, $.10 > P > .05$, NS), differences in mean consumption among habitats were tested via a One-way Analysis of Variance (Sokal and Rohlf 1969); no significant differences were detected ($F = 0.290$; $df = 3,8$; $P \gg .75$).

correct for evaporative water loss in all calculations of ingested plant material. The same 10 species of plants were used during both experimental phases; however, the amount of food presented in each phase varied. Ten grams of leaves of each species were offered in phase 1 and 30 g of leaves per species were offered in phase 2; the relative abundances of each food type remained constant between phases but the absolute quantity of food tripled in phase 2. All 10 trials of phase 1 were conducted first, followed by the 10 replications of phase 2. All six animals were allowed to forage on the experimental foods overnight. The results therefore indicate the sum effect of six solitary foragers. Water, corn, brazil nuts, and pineapple were provided for the animals throughout both phases of experimentation in order to ensure that the nutrient requirements of *Kerodon* were adequately satisfied; preferences among leaves should therefore be maximally exhibited (Emlen and Emlen 1975).

Throughout optimal foraging literature, terms like preference, consumption, and rank are often used indiscriminately, inaccurately, or imprecisely. We here assign formal definitions to certain terms which are critical to a coherent treatment of the implications of optimal foraging theory: consumption—grams ingested; preference—ordering of consumption for a particular food type with respect to the consumption of all other food types taken individually; rank—numerical symbol (1– K) for preference where 1 represents the highest preference and K the lowest; the dietary proportion—consumption of a particular food type divided by total consumption.

RESULTS

All Annonaceae leaves had an equal probability of being found and consumed by *Kerodon*, regardless of their location within a particular habitat (table 2). This supports our assumption that the colony room was perceived by the animals in a fine-grained manner.

Total per species consumption for phase 1 reveals that some species were consumed more than others, thus suggesting the existence of preferences (tables 3, 4). During phase 2, the threefold increase in food availability resulted in approximately a twofold increase in total consumption (677.17 g vs. 1384.32 g).

TABLE 3
 QUANTITY OF FOOD SPECIES (grams of leaves) CONSUMED BY THE *Kerodon* POPULATION DURING PHASE I

PLANT SPECIES	TRIAL										TOTAL
	1	2	3	4	5	6	7	8	9	10	
Ci	10.00	5.32	4.18	10.00	10.00	10.00	10.00	6.54	4.88	6.60	77.52
Ca	6.02	9.00	7.76	9.28	8.80	7.71	2.55	4.31	3.92	8.90	68.25
Ce	10.00	9.87	9.88	9.88	10.00	9.94	10.00	10.00	10.00	9.94	99.51
Cy	1.59	.35	.45	1.06	.70	.87	0	10.00	.57	1.07	16.66
Cs	0	2.05	0	.08	1.34	1.18	1.35	1.58	3.49	1.49	12.56
Cj	10.00	10.00	10.00	10.00	10.00	10.00	10.00	10.00	10.00	10.00	100.00
Rs	10.00	10.00	10.00	10.00	10.00	10.00	10.00	10.00	10.00	10.00	100.00
Zj	10.00	10.00	8.25	10.00	10.00	10.00	10.00	10.00	10.00	10.00	98.25
Es	4.07	2.03	1.34	1.00	1.44	.49	1.70	.91	1.02	.15	14.15
Bm	10.00	9.64	10.00	10.00	.80	10.00	10.00	9.83	10.00	10.00	90.27
Total	71.68	68.26	61.86	71.30	63.08	70.19	65.60	73.17	63.88	68.15	677.17

NOTE.—Consumption is tabulated by food species and trial; reported values are corrected for evaporative water loss.

TABLE 4
 QUANTITY OF FOOD SPECIES (grams of leaves) CONSUMED BY THE *Kerodon* POPULATION DURING PHASE 2

PLANT SPECIES	TRIAL										TOTAL
	1	2	3	4	5	6	7	8	9	10	
Ci	9.77	8.91	9.02	4.16	4.33	10.87	1.68	7.56	2.91	10.85	70.06
Ca	7.50	10.28	0	5.12	7.36	10.82	10.92	4.90	3.90	16.11	76.91
Ce	29.48	29.87	29.19	30.00	30.00	29.88	30.00	30.00	29.86	30.00	298.28
Cy	2.77	.71	6.87	2.58	5.82	.42	0	3.81	0	.34	23.32
Cs	1.59	2.21	3.08	3.95	1.88	0	1.20	0	5.12	2.04	21.07
Cj	17.77	15.92	29.86	25.89	16.52	29.69	25.86	29.84	29.09	21.54	241.98
Rs	29.02	26.97	3.93	7.49	7.18	17.30	6.13	1.60	9.32	7.68	116.62
Zj	23.33	22.70	11.94	17.47	27.46	30.00	17.50	28.08	27.97	28.46	234.91
Es	.63	.37	1.63	2.57	1.53	1.19	.26	.54	1.32	.42	10.46
Bm	29.73	30.00	29.14	29.76	29.48	29.74	29.17	24.40	29.42	29.87	290.71
Total	151.59	147.94	124.66	128.99	131.56	159.91	122.72	130.73	138.91	147.31	1,384.32

NOTE.—Consumption is tabulated by food species and trials; reported values are corrected for evaporative water loss.

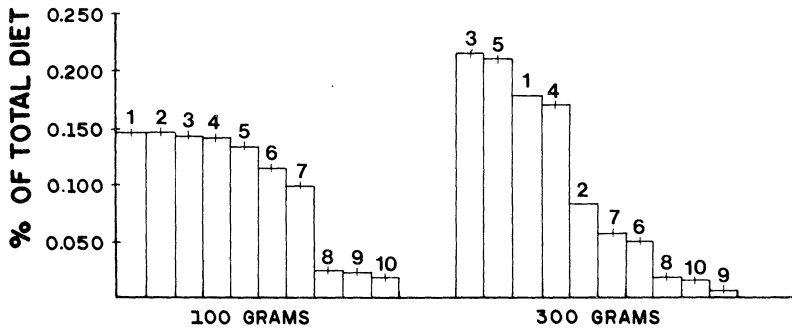


FIG. 1.—Proportional representation of each food item in the diet, for both the 100 and 300 g phases. When the abundance is increased, the differences in preference become more accentuated. Numbers represent plant species (see table 7).

Our interest, however, was not in comparing total consumption, but rather in determining whether the predators selected prey types in equal proportions during both phases. Figure 1 represents the proportional changes in dietary composition as a result of the increase in total food availability. This overall difference in diet composition appears to result from both an increased consumption of preferred food types and a decreased consumption of less preferred types.

If predators do not increase their specialization on preferred foods when the abundance of these foods increases, changes in the consumption of each food type should be proportional to the increase in total consumption. This was statistically tested by a series of *t*-tests (Sokal and Rohlf 1969) on the food consumption data for each species (table 5). Only four plant species were consumed in quantities not significantly different from the proportional increase in total consumption, while six species evidenced statistically altered dietary proportions. Four species (Ci, Ca, Rs, and Es) were consumed in lower proportions, while two species (Ce and Bm) exhibited increased dietary proportions. As proposed by the theory of optimal foraging, our results indicate that the degree of specialization exhibited is altered when the absolute abundance of resources increases. However, the expected concomitant decrease in the partial consumption of low rank food items did not occur; partial consumption was as evident at high abundances as at low abundances.

Optimal foraging theory also predicts that preference should remain constant when resources increase. Spearman Rank Correlation Analysis (Siegel 1956) indicates that plant species preference ranks based upon mean consumption were highly correlated from phase 1 to phase 2 ($r_s = 0.809$, $t = 3.89$, $P < .005$). However, the situation is more complicated than the correlation analysis suggests. Bartlett's test (Sokal and Rohlf 1969) indicated high heteroscedasticity among variances for plant species consumption (table 6) which precluded further parametric statistical analyses. We therefore performed the Kruskal-Wallis Analysis of Variance by Ranks (Siegel 1956) to see if different species received significantly different ranks in phases 1 and 2. The correlation does not consider the variation in ranks within phases, whereas the AOV is actually based upon

TABLE 5
 QUANTITY OF EACH FOOD SPECIES (grams of leaves) CONSUMED IN PHASE 1, PHASE 2, AND THE TOTAL OF BOTH PHASES

PLANT SPECIES	PHASE		t_s^\dagger	P	SIGNIFICANCE
	1	2			
Ci	77.52 (.114)	70.06 (.051)	4.578	.001 < P < .01	**
Ca	68.25 (.101)	76.91 (.056)	2.924	.01 < P < .02	*
Ce	99.51 (.147)	298.28 (.215)	98.600	P < .001	***
Cy	16.66 (.025)	23.32 (.017)	.518	.50 < P < .90	NS
Cs	12.56 (.019)	21.07 (.015)	.534	.10 < P < .20	NS
Cj	100.00 (.148)	241.98 (.175)	2.059	.05 < P < .10	NS
Rs	100.00 (.148)	116.62 (.084)	2.913	.01 < P < .02	*
Zj	98.25 (.145)	234.91 (.170)	1.748	.10 < P < .20	NS
Es	14.15 (.021)	10.46 (.008)	2.506	.02 < P < .05	*
Bm	90.27 (.133)	290.71 (.210)	5.464	P < .001	***
Total	677.17	1,384.32

NOTE.—Values in parentheses indicate the proportional representation of food type in the diet during a particular phase. Probability levels (P) show the results of the individual *t*-tests comparing Phase 1 and Phase 2 means, assuming that dietary consumption remains proportional in both phases but that the total food consumed per species will increase proportionately to the increased level of total food consumption (1384.32/677.17 = 2.044).

$$\dagger \text{ where } t_s = \frac{[(2.044)\bar{X}_1 - \bar{X}_2] - 0}{\left[\frac{(2.044)^2 S_1^2}{n_1} + \frac{S_2^2}{n_2} \right]^{1/2}}$$

- NS = Not significant.
- * = Significant.
- ** = Very significant.
- *** = Highly significant.

TABLE 6
CONSUMPTION STATISTICS FOR FOOD SPECIES DURING PHASES 1 AND 2

SPECIES CODE	PHASE 1		PHASE 2	
	Mean	SD	Mean	SD
Ci.....	7.75	2.47	7.01	3.43
Ca.....	6.82	2.46	7.69	4.54
Ce.....	9.95	.06	29.83	.28
Cy.....	1.67	2.96	2.33	2.50
Cs.....	1.26	1.17	2.11	1.61
Cj.....	10.00	.00	24.20	5.77
Rs.....	10.00	.00	11.66	9.53
Zj.....	9.83	.55	23.49	6.06
Es.....	1.42	1.08	1.05	.74
Bm.....	9.03	2.89	29.07	1.67

NOTE.—Bartlett's test (Sokal and Rohlf 1969) reveals that the variances are highly heteroscedastic, indicating that parametric comparisons of mean consumption are inappropriate.

Bartlett's Test for Homogeneity of Variance was calculated using groups with nonzero variances. Phase 1: $M = 112.5$, $F = 12.2$, $df = 9,6627$, $P \ll .001$; Phase 2: $M = 89.0$, $F = 12.4$, $df = 7,5184$, $P \ll .001$.

them (i.e., means usually behave less erratically than trial values). Although the correlation analysis is simpler, we favor the AOV because it takes into account the among-trials variation within a phase and relies upon this variability to ascertain differences between phases. The results reveal that at least one plant species within each phase has a significantly different rank from the others (table 7, bottom). To further elucidate differences among species ranks, we performed nonparametric distribution-free multiple range tests on the consumption data. Dunn's Multiple Comparison Procedure (Hollander and Wolfe 1973) indicates the existence of five mutually exclusive groups in phase 1 and seven such groups in phase 2 (table 7). Each of these groups contains plant species which have statistically indistinguishable preferences based upon rank sums. The number of groups within each phase represents the within-phase preference; each group can now be assigned a preference rank, since the food types within each groups are not statistically different in preference.

The determination of within-phase preferences using Dunn's Multiple Range Test (Hollander and Wolfe 1973) showed that preference rankings changed dramatically from phase 1 to phase 2. These changes occurred primarily with the higher ranked foods in phase 1. The group containing Cy, Cs, and Es split into two groups, but remained the three least preferred foods. Likewise, Ci and Ca combined into one group in phase 2, but overall, both fell in rank. The greatest problem concerns the phase 1 groups Zj-Rs-Cj and Bm-Ce. All three foods in the Zj-Rs-Cj group fell in within-phase preference, whereas Ce rose in within-phase preference (table 7). In our experiment, preference for types is not a complete or consistent phenomenon. This is a serious empirical contradiction to optimal foraging theory. Furthermore, five groups were formed in phase 1 and seven in phase 2. In order for a consumer to be completely satiated, it may need to finish all the items in one type, and begin to feed on the next ranked type (or statistically

TABLE 7
NONPARAMETRIC ANALYSIS OF LEAF CONSUMPTION BY RANKS

PREFERENCE	PHASE 1			PHASE 2			CHANGE IN DIETARY PROPORTION
	Species Code	Rank Sum	Grouping	Species Code	Rank Sum	Grouping	
Least	Cs	171.5		Es	138.5		*
	Cy	181.0		Cy	198.5		NS
	Es	181.5		Cs	207.5		NS
	Ca	390.0		Ca	415.5		*
	Ci	566.0		Ci	421.0		**
	Ce	640.0		Rs	482.0		*
	Bm	645.0		Zj	706.0		NS
	Zj	735.0		Cj	724.5		NS
Most	Rs	770.0	Bm	835.0	***		
	Cj	770.0	Ce	921.5	***		

NOTE.—During both phases 1 and 2, consumption statistically varied among plant species. Dunn's Multiple Comparison Procedure (Hollander and Wolfe 1973) indicates preference groupings. Species adjacent to the same vertical grouping line are statistically indistinguishable, with the experimentwise error rate set at .05.

Kruskal-Wallis One-way Analysis of Variance by Ranks (Siegel 1956). Phase 1: $H = 75.36$, $df = 2$, $P << .001$; Phase 2: $H = 83.60$, $df = 2$, $P << .001$.

NS = Not significant.

* = Significant.

** = Very significant.

*** = Highly significant.

indistinguishable group of types) until full. At the end of a feeding trial, however, there should never be more than three groups: a group with all completely consumed types, a group with partially consumed types, and a group of uneaten types. We exceeded this maximum in both phases.

Three important conclusions may be drawn from these results. First, tripling available food resources has a statistical and biological effect upon preference such that groups of statistically indistinguishable food types tend to become subdivided into their component species. Second, within-phase preference is not consistent from phase to phase because some reordering of rank occurs. However, our analysis is unable to distinguish the actual biological causes for this rank shifting from the possible results of using nonparametric tests based upon ranks rather than parametric analyses of the actual consumption values. Third, the number of statistically distinguishable groups formed in either phase exceeded the maximum number possible under the expectations of optimal foraging theory.

DISCUSSION

Support for Optimal Foraging Theory

Little experimental evidence has been presented to support the prediction that a consumer is capable of perceiving mean food value and subsequently ordering these values into a consistent ranking, yet this assumption is essential to all optimal foraging models. Gill (1977) observed that individual voles (*Microtus californicus*) show consistent preferences for a variety of grasses and herbs, consuming the most preferred species first. However, his among-trial comparisons were qualitative and lacked statistical control.

Our data showed that plant species ranks based upon mean consumption were significantly correlated between experimental phases. Increasing absolute abundance did not significantly alter the ranking of mean consumption but had two major effects. First, dietary proportions were altered significantly (table 5). In general, foods of high rank were consumed in greater proportions as a response to increasing overall abundance while foods of low rank were consumed in lower proportions. Second, within-phase preference was statistically altered (table 7). With an increase in abundance, the animals subdivided what had previously been statistically indistinguishable food groupings into their constituent species. These results are consistent with the expectations of the energy-maximization model of optimal foraging theory.

Some of our results are theoretically problematic. Certain foods of low rank were consumed in equal proportions during both trials (table 5). In addition, even though ranks of mean consumption were correlated between phases, preferences did not remain consistent from phase to phase. Neither the existence of partial preferences nor the shifting of ranks is expected under optimal foraging theory, and both present major contradictions to the three basic postulates discussed in Pyke et al. (1977).

What to Maximize?

The exhibition of partial consumption of foods of low rank creates difficulties with respect to optimal foraging theory. Virtually all theoretical models, especially those most widely accepted, predict that partial consumption should not occur if animals are energy maximizers. This prompts us to ask exactly what leaf-eating rodents do maximize. Leaves, within a given major habitat type, are extremely consistent in calories/gram dry weight (Golley 1969). It is unlikely that folivores exhibit preferences based upon caloric differences. Because *Kerodon rupestris* occurs only in the semiarid Caatinga of Brazil, we first tested the hypothesis that preference rank is correlated with the moisture content of leaves. There was, however, no relation between preference rank during phase 2 and rank in relative water content of the plant species ($r_s = 0.139$; $t = 0.397$; $.9 > P > .5$).

If neither energy nor water intake is being maximized, what is? One possibility is that folivores maximize E_n/T based on available caloric density (NcNab 1978). Species of leaves which have a low fiber and cellulose content would effectively be of higher energy content relative to the bulk they occupy in the digestive tract. Although we did not quantitatively determine fiber content in the 10 species of leaves utilized, qualitatively there was no perceptible relation between preference rank and degree of fibrousness.

Estabrook and Dunham (1976) in their model of optimal diet stated that the value of a given food item must be independent of the nutritional history of the predator. This assumption is applicable to virtually all energy optimization models. For folivores selecting leaf "prey," it is unlikely that this assumption holds true. We doubt that each leaf species represents a balanced diet to the leaf eater. Folivores may therefore represent a classic example of dietary optimization with nutrient constraints (Pulliam 1975) and as such would be expected to demonstrate partial consumption.

Leaves have been shown to contain numerous compounds of high nutritive value (Hladik 1978). In general, young leaves tend to be higher in protein content than mature leaves. In this study, only mature leaves collected immediately before the initiation of the trial were presented to the rodents. However, among species variability is quite high, not only in protein content, but also in lipid and micronutrient composition (Hladik 1978). There is little doubt that certain species of leaves may offer a close to optimal mixture of carbohydrates, protein, lipids, and minerals, but it is probably necessary, nevertheless, to supplement the diet with smaller amounts of less preferred foods. *Kerodon* demonstrated partial consumption for two species of the genus *Cissus*. Although no data are present for nutrient composition of these particular species, the leaves of *Cissus dinklagei* in Gabon have an extremely high lipid content (Hladik 1978). The consistent partial consumption of both *Cissus* species observed during our experimentation may have occurred in response to an increased level of lipids in the leaves.

Leaves which contain secondary compounds, such as alkaloids and tannins, may account for the lack of preference for some species. This has previously been demonstrated as a mechanism for the protection of seeds from seed predators (Janzen 1971). The least-preferred plant species used in our trials, *Erythroxylum*

sp., belongs to a genus (which includes cocaine) known to contain relatively high concentrations of alkaloids.

How Fast Can a Predator Window Shop?

Although observed partial consumption may well be related to nutrient constraints (Pulliam 1975, 1976; Davies 1977; Reichman 1977), another possibility is that the partial consumption represents a stochastic phenomenon related to sampling behavior. The number of prey of type i encountered per unit time (λ_i) was assumed by Charnov (1976a) as being beyond the predator's control. For predators feeding on mobile prey, this is probably true, although Hughes (1979) has presented a model demonstrating that, by learning, predators can alter their optimal diet. By learning to decrease recognition time, increase ranking efficiency, and increase handling efficiency, none of which are intrinsic prey properties, predators can not only change λ_i , but can transpose the rank of prey items.

Cornell (1976) has also incorporated a predator's learning capacity into a model predicting that generalist predators which feed on patchy resources should demonstrate a flexible learned search image. This flexible search image would require a high ability on the part of the predator to distinguish the relative rank of available prey items, and would involve a certain degree of sampling behavior, enabling the predator to evaluate novel prey and to estimate prey abundances. Cornell's (1976) observations apply particularly to nonmobile prey, and coincide quite well with conclusions drawn by Pulliam (1974) in his model for optimal foraging by mobile predators on sessile prey.

Pulliam (1974) mentions a number of possible ways that predators can modify λ_i , often resulting in the appearance of partial consumption. One argument particularly applicable to our data is the effect of satiation on the predator's assessment of prey density. Encounter frequency is the predator's only estimation of prey density. Hungry predators are, by definition, encountering prey at low densities, and when initiating a foraging bout should forage as if preferred prey are rare. As the predator becomes satiated it will begin to forage more selectively, thus changing its foraging strategy from that of a generalist to that of a specialist. Animals subjected to overnight feeding trials may well forage in this manner. At the beginning of a trial, all individuals are hungry. As the trial progresses, the level of satiation increases, and the foraging behavior of each individual approaches the optimal model. This could explain the lack of a significant decrease in the dietary proportions of the third and fourth ranked prey types during phase 2. If a *Kerodon* does not encounter one of the top ranked species within a limited period of foraging, it may underestimate the abundance of these species and consume the number three and four species in much the same proportions as it did during phase 1. This phenomenon would be accentuated by the random-distribution of prey types, so that predators may incorrectly evaluate the abundance of preferred foods because of the random nature of encounter. This was, in fact, observed during the initial two trials of phase 2. It took the predator population two trials to reassess the available abundance of high-preference foods and reduce the relative consumption of Rs from its phase 1 levels (tables 3, 4). The dietary composition

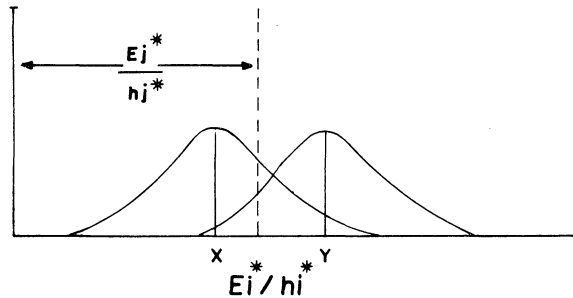


FIG. 2.—The optimal diet (E_j^*/h_j^*) in relation to the range of available food items (E_i/h_i^*). Value decreases as one moves away from the origin. The mean value of food type X falls within the optimal diet; the mean value of food type Y does not. Because of an inherent variability in the quality of items within a food type, however, numerous items of food type Y are included in the optimal diet at the expense of less valuable items of food type X .

during trial ten of phase 1 (table 3) and trial one of phase 2 (table 4) was quite similar as opposed to the highly significant differences reported in the results for the overall values for the two phases (table 5). We emphasize, however, that at any one time the consumer may be foraging optimally with regard to its perception of abundance and occurrence. The appearance of partial consumption in the diet would then be an artifact of the accumulation of a sequence of different phases of foraging, each of which, independently, was optimal. This kind of behavior may be interpreted as sampling (Jenkins 1975; Krebs et al. 1977) but would actually be an ephemeral readjustment of optimal foraging behavior based upon modifications in the predator's state of knowledge of his nutritional environment.

Items, Types, and Changes in Rank

Hughes (1979), in an enlightening reevaluation of certain aspects of optimal foraging theory, pointed out the difficulties present in ranking prey. The concept of prey rank as a continuum of multivariate properties probably applies, at least in part, to all prey species, and is probably most applicable to plants. Plants are extremely dependent upon the patch of soil on which they grow, and once established, cannot move to another site. Micronutrient concentrations, and subsequently prey rank, might vary among individual plants more so than among animals. The predator that can select the best items, rather than having a fixed search image on the type, will benefit from this ability to discriminate. It is therefore easy to visualize a situation wherein individual items of a species with high mean rank are rejected in favor of individual items of a species with a lower mean rank, but with a high variability in the nutritional value of individual items (fig. 2).

The contrast of item versus type can be taken to the extreme, and preference for an item can become semantic. Selection of items based on relative value assumes an exceptionally highly developed ability on the predator's part, and conflicts with previous behavioral observations of the existence of search images. Nevertheless,

it offers possible explanations for the observed persistence of the partial consumption of low preference foods.

The distribution of value within prey-types can have a marked effect on the structure of the optimal diet. In nature, consumers are presented with a number of alternative food types. Variability exists both within and between types. In general, between-type variation should be much greater than within-type variation. We expect that consumers monitor all acceptable food items and assess their relative value. When the within-type variation in nutritional value of these items is small, the consumer may idealize these types; the energy and effort expended to separate and select individual items which differ little in value is probably not worth the associated costs. The consumer should then only consume the highest ranked type, but should continue to sample other highly ranked foods when encountered, to check both their abundance and their value. The need to consume minimum quantities of certain micronutrients should play an important role in sampling.

When the items of the highest ranked food have been exhausted the consumer, based upon his assessment of other available types, switches to the type next in rank order. We expect that this kind of behavior is most common in animals such as granivores and carnivores which obtain a nearly complete diet from each food item. Consumers that are well acquainted with their foraging area would also be expected to sample less and forage in a type-by-type manner.

When within-type variation in nutritional value is very large, we would expect a different kind of foraging behavior. Again, the consumer should begin a foraging bout accepting only items of the highest ranked type. Eventually most of the best items in the highest rank food type would be consumed such that the mean value of the remaining high-ranked type becomes less than the mean value of the best items (or some subset, see fig. 2) of the second most highly ranked food. A smart consumer would then switch from the most preferred type to the second ranked type; it should continue to consume the best items of rank two and leave the worst items of rank one alone until the value of the uneaten rank two type becomes less than the value of the previously uneaten species of higher rank. Even this requires the predator to be an extremely patient and accurate window shopper and the prey to be nonmobile and obvious. We expect to see this behavior in folivores and frugivores (Farentinos et al. 1981), as well as in hungry or inexperienced predators which show little selectivity or sample frequently (fig. 3).

Additional Complicating Factors

We believe that optimal foraging theory has a certain heuristic value in that it presents a simple, testable hypothesis which is amenable to experimentation. Many authors have recently discussed faults in this inherent simplicity (Hughes 1979; Krebs et al. 1980; Pulliam 1980), and our results have shown the situation to be complex indeed. Much of the confusion might be resolved by a more rigorous experimental design. Our results examined the sum response of six adult individuals to changes in resource abundance; we assumed that all individuals foraged optimally, and that there would be no interference among individuals. Lacher

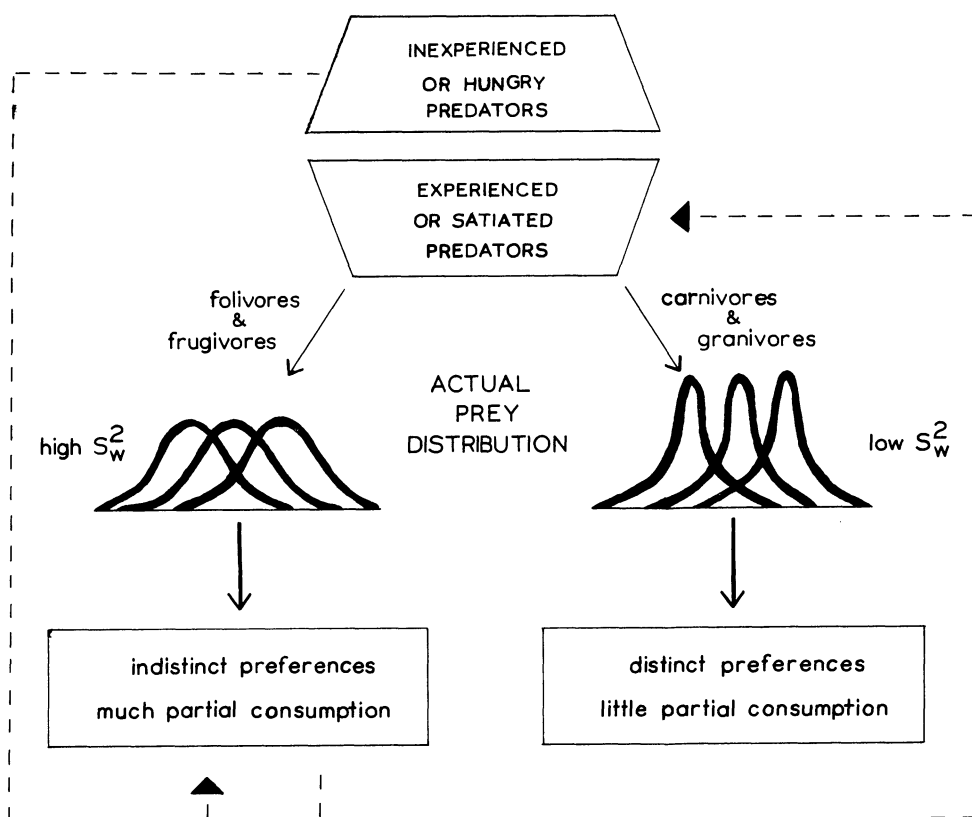


FIG. 3.—Diagrammatic representation of the effect of the within-type variability of prey value on the structure of optimal diet. The prey of carnivores and granivores should show a relatively low within-type variability, and the prey of frugivores and folivores should show a relatively high within-type variability and an associated overlap of their distribution. The dotted line shows the pathway expected for hungry or inexperienced predators, regardless of their feeding habits. As animals become more satiated, or learn the location of all available prey types, they will follow the pathway indicated by the solid lines. Their optimal diet will then reflect the actual distributions of prey value, and will not be colored by the predator's perception of the available resources.

(1980, 1981) demonstrated that *Kerodon* foraged in short sallies, consuming small quantities of leaves during each sally. Observations indicated that one animal would not monopolize a given feeding tray for any period of time and that 10 g of food probably would not be consumed by an individual at one sitting. The random placement of food trays eliminated the chance that one animal would learn the location of the best food and defend it against other animals. Nevertheless, the possibility exists that our complex results may be related to differential foraging by individuals; an individual-per-individual analysis would have been more valuable.

First, not all animals may have the same perception of optimal. Males and

females may have different nutrient requirements, for example, and not all individuals have the same nutritional history or physiological status. Optimal foraging behavior might exhibit individual variation intrinsic to certain other characters which vary individually. Second, social status may influence optimal foraging behavior; dominant animals may gain first access to preferred foods, especially when those foods are nonmobile. We have recently initiated research along these lines with a small, granivorous rodent. Aside from our work, this is virgin territory, sorely in need of further investigation.

Optimal foraging models are, in general, powerful theoretical tools for our understanding of the way animals procure their nutrition, especially when utilized with a full understanding of their restrictions and limitations. A great deal more experimental work with real predators and real prey is required to clarify how well our models correspond to nature.

SUMMARY

Data were collected on the response of a small population of folivores (*Kerodon rupestris*: Caviidae) to changes in the absolute abundance of 10 different species of leaves. When absolute abundances were tripled (relative abundances were held constant) the folivore population significantly altered its proportional consumption of food types. In general, preferred foods were consumed in greater relative proportions when abundance was increased and the relative utilization of less preferred foods declined.

Otherwise, our results were problematic in relation to the assumptions and predictions of the energy maximization model of optimal foraging theory. First, not all foods of low rank decreased in consumption when we increased the abundance of high-ranked foods. The partial consumption of low-ranked foods (or partial preferences as referred to in the literature) is contrary to the tenets of energy maximization. Second, preferences did not remain consistent from phase to phase. In fact, ranks shifted considerably, especially with respect to high-ranked foods.

A number of factors may have been responsible for these contradictions to optimal foraging theory. Folivores may represent an example of the special case of optimal foraging with nutrient constraints (Pulliam 1980). The partial consumption of low-ranked foods would then be expected in this situation. Also, the encounter rate for a given item or type is probably not constant in time or space; the rate of encounter is an ephemeral value, affected by an animal's degree of satiation, and dependent upon its degree of familiarity with the distribution of food items within its foraging area. This suggests that animals are optimal foragers, *sensu* Charnov, only in the short term. The probability of accepting an item when it is encountered will be either zero or one in the short term, but in the long term (hours, days, seasons, years) it will assume an average value between zero and one. Finally, consumers should evolve search images for types or species, when within-type variability is very small and overlap among types minimal. When within-type variability is large, and distributions of food value overlap a great deal, natural

selection should favor consumers that select high value items and do not generalize on a type's average values. We present a scenario which proposes that feeding habits may influence the way a consumer optimizes its foraging behavior.

Empirical tests of optimal foraging models based upon energy maximization have upheld theoretical predictions when predators were presented with limited prey choices (e.g., Goss-Custard 1977; Krebs et al. 1977). Tests which have examined more complex situations (Zach and Smith 1980; this paper) suggest that models which include considerations of nutrient constraints (Pulliam 1975) or predator learning (Hughes 1979; Stenseth and Hansson 1979; Pulliam 1980) may, in fact, be more appropriate.

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