

FOOD SELECTION OF A TROPICAL MAMMALIAN FOLIVORE IN RELATION TO LEAF-NUTRIENT CONTENT

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ABSTRACT.—*Kerodon rupestris*, a folivorous rodent endemic to the Caatinga of Brazil, exhibits complex modifications of diet in response to changes in the absolute abundance of 10 food species when their relative abundances remain equal. We evaluated the correlation between a suite of 12 nutrients (energy, ash, carbon, nitrogen, phosphorous, sulphur, zinc, manganese, calcium, magnesium, potassium, and sodium) and the consumption of leaves from 10 different plant species. Regardless of the taxonomic composition of the diet, the proportional representation of all nutrients but sodium was constant during phases of low and high abundance of foods. The uptake of sodium increased by a factor of 2.84, even though total consumption increased only by a factor of 2.04. From multiple stepwise-regression analysis, we suggest that nitrogen, calcium, and potassium contributed significantly to food selection. Carbon and sodium also were correlated with consumption, but excluded from the multiple-regression results because of their intercorrelation with other nutrients. The median-log Levene's test was significant, indicating differences in the relative variation in uptake of the 12 nutrients. At high abundance of resources, sodium exhibited the most consistent daily uptake of all the nutrients, suggesting that it may constrain the maximization of other essential dietary elements. Sodium may play a role in the water balance of this arid-land rodent.

Foraging theory encompasses a wide variety of topics dealing with movement patterns, patch selection, learning, and food selection (Pyke, 1984), each of which includes several hypotheses that attempt to account for patterns of foraging. Herbivores in general, and folivores in particular, are subject to foraging constraints different from those of other predators; as a result, foraging theory frequently deals with herbivores as special cases (Stephens and Krebs, 1986). Prior research on food selection of the tropical folivore *Kerodon rupestris* indicated the manner in which a captive population responded to changes in food abundance (Lacher, 1984; Lacher et al., 1982), but did not provide nutrient analyses of the prey.

Partial consumption characterized periods of low and high abundance of food; specialization or deletion of less-selected foods did not occur as a consequence of elevated resource abundance; and rank order of selection for each food did not remain constant. Early models and empirical tests of foraging theory emphasized the maximization of energy uptake. Recent interest has focused on the role of nutrients in affecting food selection of herbivores (Stephens and Krebs, 1986). Some nutrient-constraint models are univariate and attempt to maximize only one critical nutrient as is the case in models of energy maximization. Recent models of optimal foraging for herbivores generally are based upon the concept of complementarity (Covich, 1972; Rapport, 1980) or maximization under nutrient constraints (Belovsky, 1978, 1981, 1984). In these instances, more than one nutrient is considered in determining foraging rules. Such multivariable models are based upon the assumption that consumption patterns are affected by a suite of food characteristics that include nutrient constraints. Solution of such an optimization problem, generally based on linear programming methods, requires knowledge of the nutrient and caloric requirements of the consumer (Belovsky, 1978, 1981, 1984; Pulliam, 1975; Westoby, 1974, 1978). These data are sometimes available for game or domesticated species, but frequently are lacking for other species, especially those native to tropical areas. In these instances, which comprise the majority of small-mammal species, such optimization techniques cannot be applied. Insights on

determinants of selection must be gleaned from exploratory data analysis. Herein, we present data on the energy and elemental composition of each plant species used in the food-choice experiments to evaluate the correlates of food selection in this tropical folivore.

METHODS

Kerodon rupestris is a large (800 g) saxicolous rodent in the guinea pig family, Caviidae. It is endemic to the Caatinga of northeastern Brazil, a large semiarid region subject to unpredictable periods of extended drought or flooding. *Kerodon* lives in crevices in rocks and boulders, emerges to forage on grasses and leaves, and may be active 24 h/day. It is an acrobatic climber and spends most of its foraging time in trees consuming leaves. During the long dry season typical of the Caatinga, most of the vegetation desiccates and loses its leaves. In contrast, trees that grow in and among the rocks retain their leaves and remain green for long periods during the dry season. *Kerodon* is the only mammal endemic to the Caatinga, in part because it can survive droughts by living in more mesic microhabitats (boulder piles) where it consumes leaves.

Six adult (four males and two females) *K. rupestris* were maintained in a large (250 m²) seminatural enclosure (Lacher, 1980, 1981) and provided with water, corn (*Zea mays*), Brazil nuts (*Bertholletia excelsa*), and pineapple (*Ananas comosus*), ad lib. Although *Kerodon* is largely folivorous, it consumes some seeds and fruits. Because we wished to evaluate differential selection from among a variety of types of leaves, seeds and fruit were provided to guarantee that the animals were not missing certain critical nutrients normally obtained from foliage (Emlen and Emlen, 1975). The effects of the absolute abundance of food were evaluated by a two-phase design in which the total quantity of food was tripled in the second phase. In each phase, equal weights of leaves from 10 common species of Caatinga plants taken from a boulder pile inhabited by *Kerodon* were offered to the colony. The taxa used were: Boraginaceae, *Cordia insignis*; Erythroxylaceae, *Erythroxylum* sp.; Euphorbiaceae, *Croton argyrophylloides* and *C. jacobinensis*; Leguminosae, *Cassia excelsa*; Poaceae, *Brachiaria mutica*; Rhamnaceae, *Rhamnidium* sp. and *Ziziphus joazeiro*; Vitaceae, *Cissus sicyoides* and *C. simstiana*. In phase I, 10 g (wet weight) of each food constituted the daily food offering for each of 10 days (=trials). In phase II, 30 g (wet weight) of each food constituted the daily food offering for each of 10 trials. Daily consumption was adjusted for evaporative water loss and constituted the consumption data. Kruskal-Wallis one-way analysis of variance by ranks (Hollander and Wolfe, 1973) was used to determine if some plant species were consumed in larger quantities than others. A nonparametric simultaneous test procedure for equal sample sizes (Sokal and Rohlf, 1981) was used to establish differential-selection categories based upon statistically distinguishable consumption. Consumption results essentially represent average consumption of the six animals present in the colony.

Samples of leaves from each plant species were dried then ground in a Wiley mill. Subsamples were analyzed for a series of nutritional attributes (reported in mg/g unless stated otherwise) including energy content (kJ/g), ash (percent dry weight), total organic carbon (percent dry weight), phosphorous, sulphur, zinc, manganese, calcium, magnesium, potassium, and sodium. Inorganic cations were evaluated by use of a Perkin Elmer atomic absorption spectrophotometer (Model 2380); sulphur was analyzed by a Klett-Sommerson Turbidimeter; phosphorous was determined with a Zeiss spectrophotometer (Model PM 2DL); and energy content was measured in a plain-jacketed, oxygen bomb calorimeter (Model 1341). Pearson product-moment correlation coefficients (Sokal and Rohlf, 1981) were calculated for all possible pairs of nutrients in the 10 plants. In addition, stepwise multiple-regression analysis (SPSS program REGRESSION—Nie et al., 1975) was performed for each phase to determine which food attributes best predicted consumption patterns based upon the rank sums calculated in the analysis of variance by ranks. We established a set of a priori criteria (Willig and Sandlin, in press; Willig and Selcer, 1989) for identifying plant characteristics that statistically were related to food selection. The characteristic must contribute significantly to the multiple regression and it must change the multiple R^2 (the proportion of variation in rank sums accounted for by all the independent variables in the equation) by $\geq 5\%$.

Nutrient uptake from each plant species was calculated as the product of consumption (dry weight in grams) and the nutrient conversion factor (Table 1) for that species. Daily uptake of a particular nutrient was calculated as the sum of that nutrient's uptake from each of the 10 plant species for that trial. This procedure generates total daily uptake by the population of each nutrient for each phase of the selection experiment. Nutrients that constrain the maximization of other essential dietary elements would be expected to vary to a smaller degree than other less critical elements. We chose to compare variation in daily uptake of each nutrient, independent of differences in sample means or units of measurement, by comparing relative variation of each nutrient in the diet during phase II. We used the median-log Levene's test because it is more powerful than other tests of relative variation, especially when data are skewed in a positive direction (Schultz, 1985). Although less powerful than other multiple-comparison tests, the Games and Howell method

TABLE 1.—Energy and elemental composition* of the 10 plant species (arranged in decreasing phase II rank order) consumed by Kerodon during food-selection trials.

Species	kJ/g	Ash	C	N	P	S	Zn ⁺⁺⁺	Mn ⁺⁺	Ca ⁺⁺	Mg ⁺⁺	K ⁺	Na ⁺
<i>Cassia excelsa</i>	12.76	9.54	33.43	7.66	2.00	0.66	0.02	0.03	26.89	4.49	15.09	0.37
<i>Brachiaria mutica</i>	30.80	9.46	35.09	5.06	3.07	1.43	0.07	0.07	1.54	2.74	25.07	4.32
<i>Croton jacobinensis</i>	28.67	8.33	36.77	5.75	5.05	0.56	0.04	0.08	12.89	2.83	10.28	0.46
<i>Ziziphus joazeira</i>	14.40	8.68	38.29	6.04	1.56	2.30	0.04	0.06	20.90	4.24	13.28	0.36
<i>Rhamnidium</i> sp.	38.46	10.49	34.30	4.30	1.73	1.74	0.03	0.04	26.58	2.79	21.67	0.41
<i>Cordia insignis</i>	29.58	10.33	34.03	4.18	3.58	0.82	0.03	0.08	16.04	4.12	20.64	0.36
<i>Croton argyrophylloloides</i>	9.38	9.17	34.41	3.29	5.22	0.62	0.04	0.11	9.98	3.53	24.00	0.44
<i>Cissus simsiana</i>	15.02	6.95	33.10	3.49	1.79	0.83	0.02	0.03	15.13	3.54	10.24	0.34
<i>Cissus sicyoides</i>	25.54	15.81	34.40	4.88	4.97	2.99	0.06	0.06	39.65	7.32	22.14	0.65
<i>Erythroxylum</i> sp.	17.26	7.07	34.41	4.96	2.70	0.37	0.03	0.09	15.26	2.72	7.30	0.26

* Mean values from two replicate samples reported in all cases, except for ash and P determinations for *C. jacobinensis*, which were each based upon three replicate samples. All elemental values are reported in mg/g dry weight except for N, total organic carbon (C), and ash reported as percent dry weight.

TABLE 2.—Consumption statistics (\bar{Y} = mean) for each plant species by *Kerodon* during phases I and II. The change in consumption from phase I to phase II is indicated by \bar{Y}_{II}/\bar{Y}_I . Consumption values are wet-weight in g.

Species	Phase I			Phase II			\bar{Y}_{II}/\bar{Y}_I
	\bar{Y}	S^2	CV	\bar{Y}	S^2	CV	
<i>Cassia excelsa</i>	9.95	0.00	0.55	29.83	0.08	0.92	3.00
<i>Ziziphus joaziera</i>	9.83	0.31	5.62	27.49	36.68	22.03	2.39
<i>Erythroxylum</i> sp.	1.42	1.17	76.27	1.05	0.54	70.18	0.74
<i>Rhammidium</i> sp.	10.00	0.00	0.00	11.66	90.88	81.76	1.16
<i>Brachiaria mutica</i>	9.03	8.37	32.04	29.07	2.78	5.73	3.22
<i>Cordia insignis</i>	7.75	6.11	31.89	7.01	11.75	48.90	0.90
<i>Croton jacobinensis</i>	10.00	0.00	0.00	24.20	33.27	23.84	2.42
<i>Croton argyrophylloides</i>	6.83	6.03	35.97	7.69	20.65	59.10	1.13
<i>Cissus sicyoides</i>	1.67	8.77	177.34	2.33	6.25	107.29	1.40
<i>Cissus simsiana</i>	1.26	1.15	85.07	2.11	2.61	76.51	1.67
Totals	67.72	15.54	5.82	138.43	159.57	9.13	2.04

(Sokal and Rohlf, 1981) was used to identify significantly different subsets of nutrients because of significant heteroscedasticity.

RESULTS AND DISCUSSION

The nutrient content (Table 1) of the 10 plant species varied considerably for all measured attributes (ratio of highest to lowest content reported for each nutrient—nitrogen, 2.33; total organic carbon, 1.16; phosphorous, 3.35; sulphur, 8.02; ash, 2.27; energy, 4.10; zinc, 3.16; manganese, 3.67; calcium, 25.73; magnesium, 2.70; potassium, 3.44; sodium, 16.83). Although total consumption approximately doubled in phase II as compared to phase I, not all species of food followed this pattern (Table 2). In fact, previous analyses (Lacher, 1984; Lacher et al., 1982) showed that *Kerodon* exhibited distinct food-selection patterns during each phase, and that these patterns changed in response to changes in absolute abundance (Fig. 1). Some foods showed considerable daily fluctuations in consumption within phases (e.g., *Cissus sicyoides* in phase I and phase II), whereas others (e.g., *Cassia excelsa* in phases I and II), exhibited little daily variation in consumption. Moreover, consumption of one food tripled in consumption (*Cassia excelsa*) from phase I to phase II, while others decreased (*Erythroxylum* sp. and *Cordia insignis*) during the same period (Table 2). Clearly, dietary content in terms of species composition differed between phases.

Despite changes in the proportional representation of plant species in the diet, all nutrients except sodium exhibited a nearly constant ratio even though the total uptake of these nutrients doubled (Table 3). In contrast, sodium increased nearly 3-fold. Multiple-regression analysis for phase I indicated that none of the nutrient characteristics significantly accounted for any of the variation in rank among food types. In contrast, the multiple-regression analysis for phase II identified nitrogen, calcium, and potassium that together accounted for 84% of the variation in rank sums. Other characters (total organic carbon, $r = 0.53$; sodium, $r = 0.41$) significantly correlated with selection were not included in the final multiple-regression equation because of their intercorrelation with nitrogen, calcium, and potassium.

The median-log Levene's test detected significant differences in relative variation for the 12 nutrients used to characterize the diet of *Kerodon* ($F = 5.919$, $d.f. = 11, 108$, $P < 0.001$). Unfortunately, the more conservative Games and Howell method failed to identify pair-wise differences. However, sodium exhibited the smallest coefficient of variation in phase II (Table 3), consistent with the idea that it is a determinant of food selection by *Kerodon*.

The ratios comparing mean nutrient uptake from phases II and I (\bar{Y}_{II}/\bar{Y}_I ; Table 3) could be an artifact of combining 10 days of consumption data within each phase, especially if learning occurs. Learning would be suggested by directional changes in the ratios of daily nutrient uptake

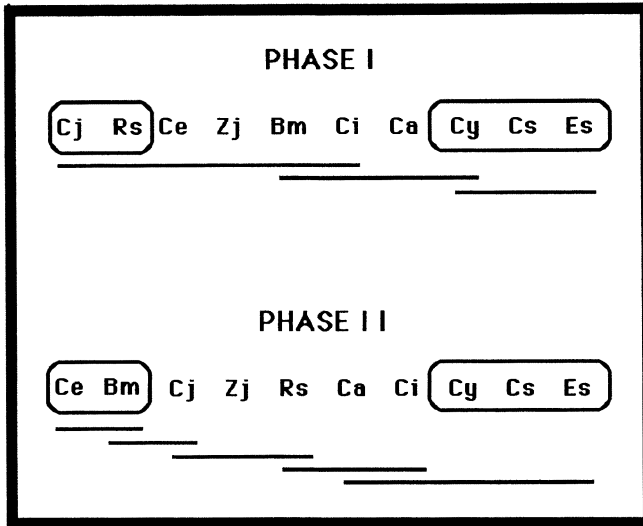


FIG. 1.—Consumption groupings in phases I and II for the 10 experimental foods. Groupings are derived from a posteriori, nonparametric, simultaneous test procedures for equal n conducted on rank sums obtained from a Kruskal-Wallis one-way analysis of variance by ranks (Sokal and Rohlf, 1981). Circles in each phase indicate foods with rank sums either larger (left) or smaller (right) than expected by chance alone ($P < 0.05$: critical end points analysis—Hollander and Wolfe, 1973; McDonald and Thompson, 1967). Abbreviations are: Bm, *Brachiaria mutica*; Ca, *Croton argyrophylloides*; Ce, *Cassia excelsa*; Ci, *Cordia insignis*; Cj, *Croton jacobinensis*; Cs, *Cissus simsiana*; Cy, *Cissus sicyoides*; Es, *Erythroxylum* sp.; Rs, *Rhamnidium* sp.; Zj, *Ziziphus joazeira*.

to mean nutrient uptake during a trial. However, the resultant 10 day by 12 nutrient matrix of daily ratios for phase II did not show perceptible trends. Ratios were variable over the 10 days, but always of similar magnitude to their comparable mean ratios (Table 3). Daily ratios were most variable for energy content ($CV = 14.7$), whereas they were least variable for sodium ($CV = 7.4$). *Kerodon* responded quickly to the increase in absolute abundance of food and elevated its daily uptake of sodium by a ratio of 2.9 on the first day of phase II and maintained that level throughout the balance of the phase (range, 2.5–3.1).

Kerodon clearly responded to changes in overall abundance of food in a manner inconsistent with classical optimal-foraging theory (e.g., the maintenance of partial selections). Lacher et al. (1982) provided several a posteriori explanations for why such behavior might occur: nutrient constraints were presented as a possible explanation. Unfortunately, neither data on the nutrient profile of the foods nor the nutritional requirements of *Kerodon* were available at that time. In the absence of the latter, diet optimization with nutrient constraints cannot be examined rigorously by use of linear-programming methods. Our examination of the nutrient content of the diet of *Kerodon* and the relation between selection and the nutrient attributes of the food types, implicates the critical role of nutrients in determining food selection.

During phase I, when resource abundance was low, selection was indistinct. The ranking of food types changed when resource levels increased in phase II. This suggests that resource levels in phase I were so low that individuals were compelled to consume lower-ranked foods to meet minimum daily requirements. This is consistent with our multiple-regression results from phase I in which none of the food attributes could be combined in a fashion to account for observed consumption rankings. In contrast, during phase II, when rankings were more distinct, the selection of food types was significantly related to their nutrient content. Foods with high nitrogen, high potassium, and low calcium were selected. Remarkably, the ratio of nutrients in the phase I diet was the same as that ratio in phase II, with the exception of sodium (Table 3), despite

TABLE 3.—Consumption statistics for nutrient uptake by Kerodon, regardless of the plant species from which it was obtained, during phases I and II. Nutrient uptake was based upon dry-weight consumption. Units for means are the same as those in Table 1.

Nutrient	Phase I			Phase II			\bar{Y}_{II}/\bar{Y}_I
	\bar{Y}	S ²	CV	\bar{Y}	S ²	CV	
Nitrogen	2.76	0.04	7.22	5.89	0.25	8.54	2.13
Carbon	18.44	1.86	7.39	36.72	14.87	10.50	1.99
Phosphorous	160.20	213.62	9.12	303.04	784.24	9.24	1.89
Sulphur	64.15	63.83	12.45	128.75	317.89	13.85	2.01
Ash	4.97	0.20	8.96	9.74	1.20	11.24	1.96
kJ/g	293.51	664.64	8.78	561.06	6,814.48	14.71	1.91
Zinc	1.99	0.05	10.76	4.24	0.13	8.37	2.13
Manganese	3.34	0.09	8.89	6.30	0.46	10.76	1.87
Calcium	936.48	8,456.85	9.87	1,747.59	54,171.91	13.32	1.87
Magnesium	189.26	335.44	9.68	377.17	1,281.46	9.49	1.99
Potassium	928.34	7,323.97	9.22	1,830.23	59,022.10	13.27	1.97
Sodium	45.44	90.83	20.97	128.77	90.52	7.39	2.84

different proportions of food types in the diet during phases I and II. More or less constant nutrient ratios in phase I and II diets could be a result of similar nutrient profiles in all foods, regardless of their taxonomic identity. This does not appear to be the case here. Of the 66 possible correlations between pairs of nutrients, only seven are significant (ash with Mg [$r = 0.81$], S [$r = 0.74$], Ca [$r = 0.66$], and K [$r = 0.68$]; S with Mg [$r = 0.67$]; Zn with Na [$r = 0.71$]; and Ca with Mg [$r = 0.76$]), as determined from Pearson product-moment correlations (Sokal and Rohlf, 1981). Moreover, approximately 82% of the 66 analyses yielded correlation coefficients <0.50 . The constant nutrient ratios in the diet are not likely mathematical artifacts of high-nutrient correlations among plant taxa.

The failure of the univariable approach to account for the rankings implies that no single prey attribute can be optimized while meeting other minimum daily requirements. Hence, the determinants of selection must include a suite of prey attributes. Despite the pervasive appearance of energy as the currency of optimization in univariable models, we find little evidence of energy playing a dominant role in these analyses. Although energy content (kJ/g dry weight) varied from 38.46 (*Rhamnidium* sp.) to 9.38 (*Croton argyrophylloides*), it did not emerge as a significant predictor of rank in multiple-regression analyses. In fact, energy content was uncorrelated with rank sums in phase II ($r = 0.08$, $n = 10$, $P > 0.05$) and accounted for $<1\%$ of the variation in ranks among foods. Of the 12 food attributes examined, only sulphur content accounted for less variation. Moreover, energy content exhibited the greatest variability in the daily ratios of nutrient uptake in phase II. These results are consistent with other research on generalist herbivores (Belovsky, 1978, 1981, 1984; Stenseth et al., 1977). As Stephens and Krebs (1986) argued, herbivores merit special consideration in foraging theory, and rate-maximizing models may provide only qualitative predictions about herbivore diets. In addition, nutrients other than energy can be expected to play a significant role in shaping herbivore diets. From our results we suggest this to be the case in *Kerodon*. The multiple-regression analysis demonstrated that at least nitrogen, calcium, and potassium were statistical predictors of rank sums during phase II. The most selected foods, *Cassia excelsa* and *B. mutica*, were ranked 1st and 4th with respect to nitrogen, 10th and 1st for calcium (which has a negative coefficient in the regression equation), and 6th and 1st for potassium. Results of stepwise multiple-regression must be interpreted cautiously because independent variables highly correlated with the dependent variable (consumption) may be excluded from the resultant equation if they have high communality with other independent variables already in the equation. From the constant ratio of nutrients (except sodium) in the diet during both phases, we suggest that despite the quantity of food and its taxonomic composition, a particular combination or balance of nutrients is maintained. The potential role of sodium is indicated through its observed increase by a factor of 2.84 (overall consumption only increased

by a factor of 2.04), high correlation with rank sums (it was excluded from the regression equation because of its high correlation with nitrogen), and high concentration in one of the most selected foods (*B. mutica*).

Belovsky (1984) consistently found sodium to be a dietary constraint in generalized herbivores; we expect the same in a tropical, diurnal, arid-land mammal such as *Kerodon*. Guinea pigs (*Cavia porcellus*) cool themselves with saliva; water lost through the saliva during heat stress contains appreciable quantities of sodium. Unless these mammals replace such lost sodium through their diet, water deficits cannot be eliminated, no matter how much water is consumed (Chew, 1965). This is especially critical for *Kerodon*, which has one of the poorest urine-concentrating capacities of any arid-land mammal (Mares et al., 1985). We suspect that sodium does not emerge as the only nutrient affecting consumption because many other nutritional requirements must be satisfied as well. Moreover, interaction among nutrient cations and their effects on altering nutrient requirements are complex in the guinea pig (Navia and Hunt, 1976). Similar processes likely occur in *Kerodon*, if not most rodents.

The aggregate response of six individuals, both males and females, could contribute to the complex results and partial selections. Males may be selecting food based upon a different set of criteria than females. Even individuals of the same sex may have different physiological requirements that could result in the optimization of different dietary attributes. This possibility cannot be examined within the constraints of our experimental design. The analysis of individual, sex-related, and age-specific differences in foraging remains neglected in both empirical and theoretical studies of optimization (Gross, 1986).

In conclusion, the determinants of food selection by *Kerodon* are complex and likely require the maintenance of a constant ratio of nutrients in the diet regardless of the taxonomic identity of the foods. In addition, consumption is related to the presence of nitrogen, calcium, potassium, and sodium in each food type. Models based upon the assumption of optimization of a particular food characteristic, even if constrained by other factors, may need to incorporate these considerations when dealing with polyphagous consumers.

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