Feeding Behavior of Yellow Baboons
(Papio cynocephalus) in the Amboseli
National Park, Kenya

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The results of an 11-month field study of the feeding behavior of adult yellow baboons (Papio cynocephalus) *are presented. Although catholic feeders, the baboons are not unselective in their choice of foods, and a small number of foods account for the bulk of their feeding time and are significant determinants of their home-range utilization patterns. These preferred foods are consumed throughout the year, a response, perhaps, to relatively minor fluctuations in their availability. Seasonal changes in food abundance are, however, reflected in other aspects of the baboons' feeding behavior, including a tendency to show greater day-to-day dietary variability during periods of higher rainfall and greater overall food availability. It is suggested that this, and other, aspects of baboon feeding behavior can be understood only in the context of the extremely "patchy" distribution of their food supplies.*

INTRODUCTION

Despite both the recent increase in interest in the feeding of nonhuman primates (e.g., Clutton-Brock, 1977; Sussman, 1979) and the proliferation of research on various aspects of baboon social organization and ecology,

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few studies to date have focused specifically on a quantitative documentation of baboon food habits (although see Aldrich-Blake *et al.,* 1971; Crook and Aldrich-Blake, 1968; Davidge, 1978; Hamilton *et al.,* 1978; Harding, 1976). As Schoener (1971, p. 384) has noted, the distinction between generalists and specialists can be drawn in several different ways [e.g., dietary breadth or diversity (Morse, 1971), extent of behavioral flexibility during foraging (Homewood, 1978), and degree of dietary overlap with sympatric competitors (Struhsaker, 1978)]; baboons appear to be true generalists along virtually any axis. It is, however, the extraordinary breadth of their diet that has occasioned the most comment (see, e.g., Altmann and Altmann, 1970; DeVore and Hall, 1965; Demment, 1978; Hamilton *et al.,* 1978; Harding, 1976; Rowell, 1966), and it is the adaptive significance of this dietary diversity that merits closer scrutiny (see Discussion).

In this report I present quantitative data, collected between September 1974 and August 1975, on the feeding behavior and diet of adult yellow baboons *(Papio cynocephalus)* in the Amboseli National Park, Kenya. A separate report (Post, 1981a) examines the nature and extent of dietary differentiation between males and females in this population, and other results from this study are presented in detail elsewhere (Post, 1978, 1981b).

METHODS

Study Site and Population

The study animals were members of a free-ranging social group of yellow baboons in the Amboseli National Park of southern Kenya. Detailed descriptions of the Amboseli ecosystem are given by Western (1972) and Western and Van Praet (1973). General ecological characteristics of the area, particularly as they pertain to the resident primate species, are discussed by Altmann and Altmann (1970), Post (1978), and Struhsaker (1967). The area is primarily semiarid short-grass savannah, with pronounced rainfall seasonality and little annual variation in average temperature (Fig. 1). Following Altmann and Altmann (1970), four seasons can be identified: the short rains (November–January), the interrains (February), the long rains (March–May), and the long dry season (June–October).

The study area is a complex mosaic of woodland and grassland vegetation types, with a small number of species dominating each stratum. Soils are highly alkaline and calcareous. In the woodlands, the fever tree *(Acacia*
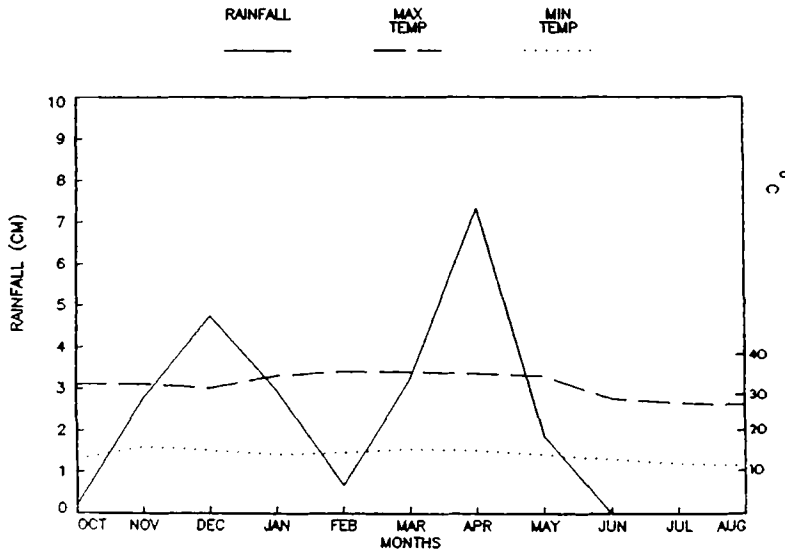
RAINFALL   MAX   MIN
TEMP   TEMP

Fig. 1. Rainfall and mean daily maximum and minimum temperatures for the 11 study months.

xanthophloea) is distributed primarily in low-lying areas surrounding permanent swamps and waterholes; the umbrella tree *(A. tortilis)* is dominant in areas with less soil moisture. These are the only tree species in the study area. The most common shrubs in the woodlands are *Azima tetracantha, Salvadora persica,* and *Sueda monoica;* other abundant species are the forbs *Trianthema ceratosepala* and *Dicliptera albicaula* and the grasses *Cynodon dactylon* and *Sporobolus consimilis (= S. robustus).* The grasslands are dominated by perennial species of the genus *Sporobolus,* notably *S. kentrophyllus, S. africanus,* and *S. marginatus* [recently split into two species, *S. iocladus* and *S. cordofanus* (P. Lee and S. Altmann, personal communication)]. In recent years there has been a substantial reduction in the number of standing fever trees and a transformation of the plant community into a xeromorphic, halophytic one (Western, 1972; Western and Van Praet, 1973).

During 1974-1975, when this study was undertaken, the study area was inhabited by approximately 200 baboons in five social groups (see Altmann *et al.,* 1977). Intensive data collection focused on members of a single social group (Alto's group) numbering 46 individuals at the start of the study and 50 at its termination (see Post, 1978; Altmann *et al.,* 1977).

Behavior Sampling

Two males (Stubby and Peter) and two females (Preg and Brush) were chosen initially for intensive behavioral sampling; a third male (Chip) was selected as a "backup" in case of the death or emigration of either or both of the males (which did not occur). Individuals were chosen for day-long focal-animal samples (J. Altmann, 1974) in the following manner: starting at the beginning of each month I chose each day's focal animal at random from among the four main focal animals. After each animal had been sampled for 2 days, 1 day was then spent with Chip as the focal animal. During any remaining days in a given month, animals were chosen at random from among the entire subset of five animals.

The focal-animal samples were of the following form [see Post (1978) for a more complete description of sampling methods]: the focal individual was continuously observed during one 15-min interval during each of the 11 hr (0700–1800) constituting a sample day. The following information was dictated into a portable tape recorder and subsequently transcribed onto coding sheets.

(a) Activity State Occupied. Five activity states (feeding, moving, resting, socializing, and drinking) were defined so as to form a mutually exclusive and exhaustive set. Complete descriptions of the identifying criteria for each state are given elsewhere (Post, 1981b). Of particular relevance for this report, feeding began when the subject first made contact with any part of a food plant, excluding contact with the plant as a locomotor substrate, and terminated when the subject either moved more than one full stride or stopped orienting visually toward the food plant.

(b) Transition Times Between Activities. A "split-action" stopwatch was used to record the time at which the focal animal left one activity state and entered another.

(c) Food. All ingested items were identified as to species and plant part (see below) whenever possible.

These data thus provide information on the proportion of time spent in each activity state, the proportion of time spent feeding on different foods, and the duration of individual activity "bouts" (defined as un-interrupted periods within a single activity state). Other data recorded duting these samples, such as the occurrence of spatial supplantations at feeding sites, are not discussed below. The amount of sample time for each individual is shown in Table I.

Habitat Sampling

To gain an overview of the distribution of food resources within Alto's group's home range, three types of information were collected.

Table I. Number of Minutes of Focal Sample Time

Animal	1974			1975							
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Stubby (male)	98	184	135	349	265	234	322	291	431	337	146
Peter (male)	66	246	126	243	250	175	249	190	241	274	231
Chip (male)	0	0	0	142	126	271	154	154	128	207	0
Preg (female)	136	173	117	372	269	423	346	292	346	395	169
Brush (female)	126	214	202	183	393	264	308	308	328	451	250

(a) Delineation of Habitat Types. During August–September, 1974, 24 vegetation zones were defined on the basis of the dominant species in each of the four vegetation strata [detailed vegetation-zone protocols are described elsewhere (Post, 1978)]. The locations of over 300 individual "patches" of these vegetation zones were then mapped directly onto an aerial photograph of the study area (see Post, 1978, Fig. 27). Although techniques for the more accurate *post facto* ordination and classification of plant communities exist (see McIntosh, 1967; Pielou, 1969; Whittaker, 1970), they require detailed quantitative data on the density of individual species that I was unable to gather owing to the large size of the group's home range [over 40 km² (Post, 1978)]. A subjective vegetation zonation scheme of this kind was successfully utilized in a study of the entire Amboseli ecosystem (Western, 1972).

(b) Plant Species Density. In order to understand the differential abundance of plant species within vegetation zones, approximately 5 days per month were spent collecting species density data by means of the "point-centered quarter" method (Cottam and Curtis, 1956; Grieg-Smith, 1965). A location within the group's home range and a compass bearing were chosen at random; at the starting location, and at every 100 m along the specified compass bearing, a vertical stake was placed in the ground. Four quadrants were defined by two lines, one parallel and one perpendicular to the compass bearing, intersecting at the stake. Within each quadrant I recorded the following:

(1) the distance to, and species of, the nearest grass, forb, shrub, and tree; and

(2) the vegetation zone (see above) within which the point was located. The species density can be estimated from these data (see Cottam and Curtis, 1956; Penfound, 1963; Pielou, 1969).

(c) *Plant Phenology.* For each grass plant identified in b, I recorded the approximate proportion of fresh, green blades (0–25, 25–50, 50–75, or 75–100%). For forbs, shrubs, and trees, I recorded the approximate abundance (absent, light, medium, or heavy) of flowers, fruits, and leaves.

The following conventions are observed below.

(1) A significance level of 0.05 is utilized throughout.

(2) All results are expressed in units of feeding *time,* rather than the number or volume of items ingested.

(3) Three different classifications of baboon foods are used. A "food type" refers to a specific plant part irrespective of species (e.g., floral buds, grass blades). A list of food types identified in this study is given in Table II. A "food species" refers to a plant species irrespective of food type (e.g., the fever tree, *Acacia xanthophloea*), while a "food item" refers to a combination of food type and food species (e.g., the gum of *A. xanthophloea).*

Table II. List of Food Types

1. Grass blades
2. Fresh pods, plucked from tree
3. Dried pods from ground
4. Shrub or vine fruits
5. Forb fruits
6. Tree flowers
7. Shrub leaves
8. Forb flowers
9. Grass corms
10. Tree exudate (gum)
11. Forb floral buds
12. Tree leaves
13. Forb leaves
14. Shrub leaves
15. Grass seedheads/stems
16. Grass blade bases
17. Tree cambium
18. Mushrooms
19. Forb or shrub roots
20. Vertebrate prey
21. Animal feces
22. Insects

RESULTS

Diet Composition: Annual Proportions

The species composition of the baboons' diet is shown in Fig. 2, which shows the relative proportions of time spent feeding on any parts of the 16 most heavily utilized species. These proportions were computed by summing all data from all focal samples for a given month, computing the proportion of time spent feeding that month on each species, and then calculating the mean proportion for each species over the 11 months of the study. An alternative method, whereby each month's estimate was obtained by averaging each of the daily estimates for that month, gave substantially similar results (for comparable figures, see Post, 1978). Table III lists the plant parts most commonly eaten from these 16 species.

The baboons were observed feeding on over 30 identified species. Given the relatively low plant species diversity in this savanna ecosystem, their reputation as generalist consumers appears well-founded; however, it is also apparent that a relatively small number of species account for a disproportionate share of the baboons' diet in Amboseli. Over 60% of the animals' feeding time was spent on just five species (Fig. 2), and two of
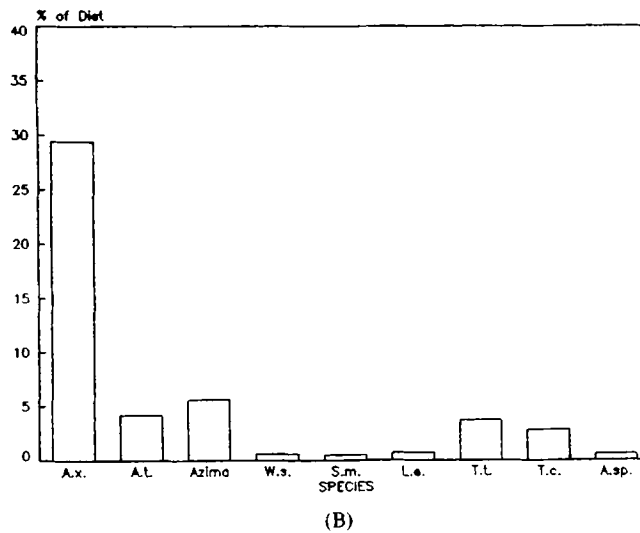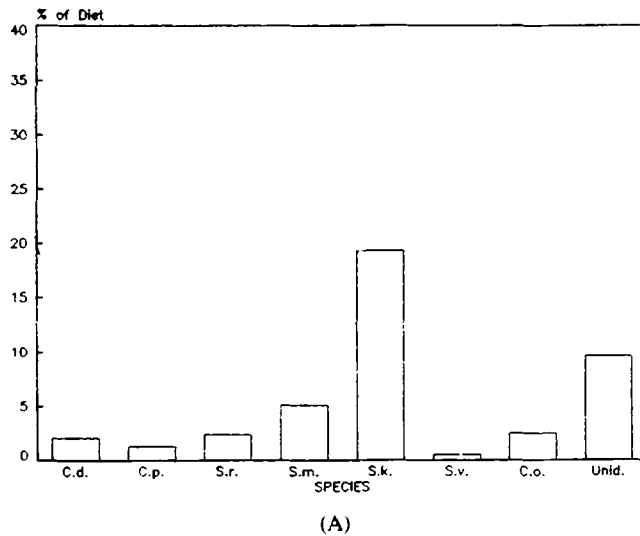
(A)

(B)

Fig. 2. Percentage of time spent feeding on each of eight grasses (A) and nine nongrasses (B). Abbreviations are as follows: (A) C.d., *Cynodon dactylon;* C.p., *C. plectostachyus;* S.r., *Sporobolus robustus;* S.m., *S. marginatus;* S.k., *S. kentrophyllus;* S.v., *Setaria verticullata;* C.o., *Cyperus obtusiflorus;* Unid., unidentified grass or sedge. (B) A.x., *Acacia xanthophloea;* A.t., *A. tortilis;* Azima, *Azima tetracantha;* W.s., *Withania somnifera;* S.m., *Sueda monoica;* L.e., *Lycium europaeum;* T.t., *Tribulus terrestris;* T.c., *Trianthema ceratosepala;* A.sp., *Abutilon* sp.

Table III. (A) List of Major Food Species, with Principal Parts Consumed from Each, and (B) Common Species Not Eaten by the Baboons

(A)	
Species	Parts consumed
Trees	
Acacia xanthophloea	Seeds, gum, cambium, flowers
A. tortilis	Seeds, flowers
Shrubs	
Azima tetracantha	Fruits
Withania somnifera	Fruits
Lycium europeum	Leaves, flowers
Salvadora persica	Fruit, leaves
Sueda monoica	Leaves
Cordia gharaf	Leaves
Forbs	
Trianthema ceratosepala	Floral buds
Tribulus terrestris	Fruits, leaves
Commicarpus plumbagineus	Fruits
Abutilon sp.	Flowers
Rhamphicarpa heuglinii	Flowers
Grasses and sedges	
Sporobolus kentrophyllus	Corms
S. marginatus	Corms, blades
S. robustus (= consimilis)	Pithy stems, corms
S. spicatus	Blades, seedheads
Cynodon dactylon	Blades, seedheads
C. plectostachyus	Corms, blades
Cyperus obtusiflorus	Corms
C. laervigatus	Blades, stems
Setaria verticullata	Blades

(B)	
	Species
Shrubs	*Solanum incanum*
	Maerua sp.
Forbs	*Dasyphaera prostrata*
	Dicliptera albicaula
	Kochia indica
	Trianthema triquetra
	Leucas stricta
	Aerva lanata
	Seriocomopsis hildebrandtii
Grasses and sedges	*Odyssea jaegeri (= paucinerva?)*
	Sporobolus africanus
	Dactyloctenium bogdanii

these species, the fever tree *Acacia xanthophloea* and the grass *Sporobolus kentrophyllus,* accounted for just under one-half of all feeding time.

Given the small number of major food species, it is not surprising that the baboons' preference for certain vegetation zones can be predicted by the relative abundance of a small number of plant species within those zones. The relative proportion of time spent in each of 12 grassland vegetation zones, corrected for their differential availability, was significantly correlated with the summed density of two grass species, *Sporobolus kentrophyllus* and *S. marginatus* (r_s = 0.724, N = 12, P < 0.01). Similarly, occupancy of the eight nongrassland vegetation zones was significantly correlated with the summed density of the fever tree and the shrub *Azima tetracantha* (r_s = 0.848, N = 8, P < 0.05) (Post, 1978). The relative abundance of "patches" of these vegetation zones within different areas of the home range is, in turn, a significant predictor of the overall area occupancy (Post, 1978).

The baboons' heavy reliance on the fever tree is apparent from the data in Fig. 2. The baboons also sleep exclusively in fever tree groves, conspicuously avoiding the other common tree in the area, *Acacia tortilis* (Altmann and Altmann, 1970; S. A. Altmann, 1974). The marked decline in the number of baboons in the study area between 1964 and 1971 is presumably related, at least in part, to the equally substantial decline in the fever tree population (Western, 1972; Western and Van Praet, 1973; see also Altmann, 1980; Struhsaker, 1973, 1976).

Little is known at present concerning the determinants of food choice by the Amboseli baboons, although work on this problem is underway (S. A. Altmann, in preparation; see also Altmann and Wagner, 1978; Hausfater and Bearce, 1976). Several observations may be relevant to this question. First, a substantial number of relatively common species were never observed being eaten; these species are listed in Table III. Furthermore, selectivity on the part of the baboons apparently extends to those plant species that are included in the diet. I examined the data in Fig. 2 for a relationship between relative species densities over the home range as a whole and consumption by the baboons. The density of any species (d_i) can be approximated by

$$d_i = \sum_j d_{ij} \cdot a_j,$$

where d_{ij} = the density of species i in vegetation zone j and a_j = the proportion of the home range made up of vegetation zone j. The relative densities of all grass and forb species making up at least 0.5% of the diet were computed in this manner (for data see Post, 1978, Table 62). Correlations between relative densities and dietary percentages are not significant for

these two classes ($r_s = 0.580$, $N = 7$, $P > 0.10$ for grasses; $r_s = 0.600$, $N = 5$, $P > 0.10$ for forbs), although both were in the predicted direction (i.e., positive). That is, the amount of time that baboons devoted to feeding on species in each of these classes was not merely a reflection of the differential abundance of those species. This analysis was not undertaken for trees or shrubs since, on the one hand, there are only two tree species in the area and, on the other, shrub density is clearly a poor indicator of food abundance owing to marked interspecific variability in shrub size, number of berries or leaves per individual, etc.

Figure 3 gives the overall dietary composition by food type (i.e., irrespective of species; see Methods). Grass and sedge corms, the swollen underground stem bases used as storage organs for nutrients and moisture (Fritsch and Salisbury, 1965; Esau, 1965), are the baboons' major food, as has been previously noted (Altmann and Altmann, 1970; Harding, 1976; Rose, 1976). The ability to extract these corms, a process requiring considerable dexterity and extensive digging and handling (see Rhine and Westlund, 1978; Rose, 1976), may be a major component of the differentiation of the baboons' feeding niche from that of sympatric vertebrates in the area, particularly the vervet monkeys and the grazing and browsing ungulates.

Tree gum, exclusively from the fever tree (see Hausfater and Bearce, 1976), is the second most heavily utilized food type (Fig. 3). The Amboseli
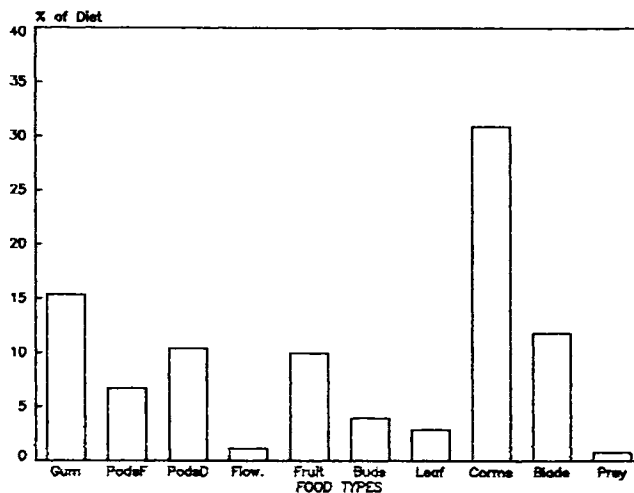

Fig. 3. Percentage of time spent feeding on each of 10 food types. Pods F, fresh pods; Pods D, dried pods (see text); Flow., flowers; Blade, grass or sedge blades; Prey, vertebrate or invertebrate prey.

baboons may be unique among the Old World anthropoids in their reliance upon this food type, which forms a major part of the diet of several prosimians and callithricids (see Discussion). The distribution of gum sources may be an important determinant of baboon ranging patterns [see Post (1978) and Discussion].

Animal prey, including both vertebrates and invertebrates (primarily grasshoppers), accounts for just over 1% of the animals' feeding time. Despite its relatively small contribution to the diet (at least when expressed as a proportion of time spent feeding), animal matter may be a critical source of various nutrients, especially protein and vitamin B_{12} (see Hausfater, 1976). Baboon predation on vertebrates is discussed in detail elsewhere, as is the tendency for this behavior to be engaged in primarily by adult males (e.g., Harding 1973; Hausfater 1976; Strum 1975).

Baboons feed upon the seeds of both species of *Acacia* in Amboseli; I have distinguished feeding on fresh seed pods (pods F) and dried seed pods (pods D). In the former case, green seed pods are plucked directly from the tree; in the majority of feeding bouts the pods are opened using the incisors and individual seeds removed from their seed coats and ingested. Occasionally, however, the pod itself, along with enclosed seeds, is consumed. Dried seed pods of both species (although primarily of *A. xanthophloea;* see below and Fig. 4) are picked from the ground and ingested in much the same manner as the fresh pods, except that the brown, dried-out pod itself is never consumed. The ability of the baboons to feed upon these dried seeds furnishes them with a dependable year-round supply of food (see below).

Diet Composition: Monthly Variability

Both the wide limits of the baboons' food tolerance and the highly seasonal nature of the Amboseli environment (Fig. 1) lead us to expect marked monthly and seasonal variations in diet, at least insofar as rainfall fluctuations affect the relative abundance of baboon foods. In this section I examine both the extent of dietary variability and its relationship to food availability.

Figures 4 and 5 show the extent of monthly dietary variability (food items and food types, respectively). Two relatively distinct classes of food items can be distinguished in Fig. 4. Certain food items (e.g., the gum and dried seeds of *Acacia xanthophloea,* the corms of *Sporobolus kentrophyllus*) show high consumption in virtually all months; others (e.g., the fruits of *Azima tetracantha* and *Tribulus terrestris,* the fresh pods of *Acacia xanthophloea* and *A. tortilis)* show more distinct peaks in consumption
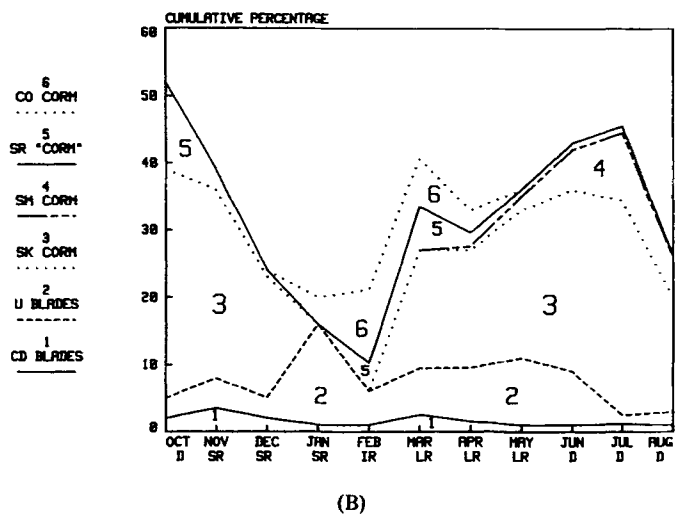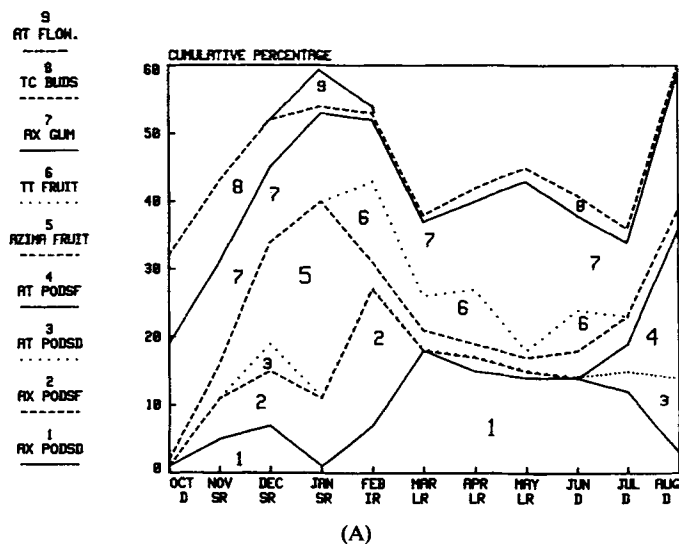
Fig. 4. Proportion of total time spent feeding each month on each of nine nongrass food items (A) and six grass food items (B). Species abbreviations as for Fig. 2; food-type abbreviations as for Fig. 3. Vertical scales are cumulative, such that the total height of the curve represents the proportion of total feeding time spent on those nine (A) or six (B) food items each month. Symbols beneath each month represent the season in which that month occurred: D, dry season; SR, short rains; LR, long rains; and IR, interrains.
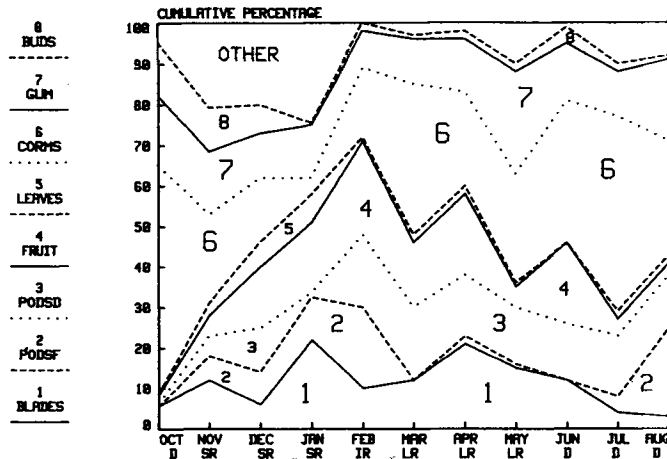
Fig. 5. Proportion of total time spent feeding each month on each of eight food types. See the legend to Fig. 4.

(Fig. 4). Whether this distinction is due to differences in the magnitude of monthly fluctuations in the availability of these foods is examined below.

The baboons' diet during the short rains (November-January) was unusual in several respects. In particular, the baboons consumed large quantities of the fruits of *Azima tetracantha,* the floral buds of *Trianthema ceratosepala,* and the flowers of *Acacia tortilis* relative to other periods, with a correspondingly low consumption of grass corms (Figs. 4 and 5). During this period the baboons' activity profile was distinct as well, with animals spending less time feeding, spending more time moving, and traveling greater distances each day [(Post, 1978, 1981b); similar results were obtained in a later study of this group by Altmann (1980)]. The nature of the underlying relationships is not immediately apparent. Lowered consumption of corms may directly lower the proportion of time feeding; corms require extensive processing and handling (Harding, 1976; Altmann and Altmann, 1970; Rhine and Westlund, 1978) and thus probably yield less energy per unit of feeding time. In addition, utilization of patchily distributed food sources such as *Azima tetracantha* shrubs and *Acacia tortilis* trees, at the expense of the more abundant and uniformly distributed grass corms, may require more traveling between food patches and longer day-journeys.

The relationships between the monthly fluctuations in food abundance and the baboons' diet are summarized in Fig. 6 and Table IV. Figure 6 was constructed by plotting, for each food item, the proportion of plants containing that food item in medium or heavy abundance (or, in the
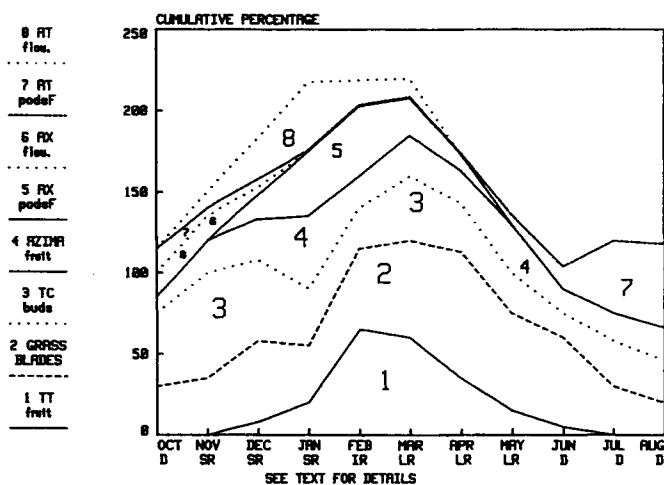
Fig. 6. Summed proportions of sampled plants containing each of eight food items "medium" or "heavy" in abundance. See text for details. For example, in February approximately 60% of all sampled *Tribulus terrestris* (TT) plants had fruit medium or heavy in abundance, approximately 50% of all sampled grasses had leaves 50% green, etc. Species abbreviations as for Fig. 2; food types as for Fig. 3.

case of grass blades, with blades 50–100% green). Only food items whose phenology was adequately sampled (at least 10 individuals sampled each month) are included in Fig. 6. Note that several important foods (*Acacia xanthophloea* gum and dried seeds, grass corms) are not included in this figure due to the absence of information concerning monthly fluctuations in abundance (see below). Also, the vertical scale is cumulative but is *not* normalized to reflect intermonthly differences in *total* food availability. Thus, while we can directly compare the abundance of any single food item in different months by examining the width of any particular segment, the total amount of these eight foods available in any month is represented only schematically by the overall height of the curve. Nonetheless, the general

Table IV. Correlations Between Relative Food Item Abundance and Utilization (See Text)

Food item	r_s	Significance
Acacia xanthophloea, fresh seed pods	0.889	< 0.01
Grass blades, all species	0.841	< 0.01
Azima tetracantha, fruits	0.575	< 0.05
Tribulus terrestris, fruits	0.852	< 0.01
Trianthema ceratosepala, floral buds	0.364	NS

decline in food availability during the dry season (June-October), with the exception of *Acacia tortilis* pods, is apparent; this decline is likely to intensify interindividual competition for food at this time (Post *et al.,* 1980). Also noteworthy is the alternation of fruiting/flowering cycles for the area's two tree species, *Acacia tortilis* and *A. xanthophloea.*

Correlations between relative abundance (Fig. 6) and monthly utilization (Fig. 4) are shown for five food types in Table IV. Correlations were computed only for those items constituting at least 0.5% of the baboon's diet in 6 or more months. With one exception, the baboons appear to respond to increases in availability with increased utilization (Table IV). For two other food items (fresh pods and flowers of *A. tortilis*) the periods of availability are quite limited (June–October for pods, December–March for flowers); the peak periods of consumption of these food items (July–August for pods, February for flowers) are even more restricted. This discrepancy may be due either to changes in the nutritional characteristics of these food items through time or to the highly patchy distribution of the *A. tortilis* trees (see Discussion).

As expected, grass blades are eaten in the greatest amounts during the two rainy seasons (Figs. 4 and 5); the mean monthly utilization of grass blades is significantly correlated with the monthly rainfall ($r_s = 0.693, N = 11, P < 0.05$), as is the proportion of grasses showing fresh growth ($r_s = 0.648, N = 11, P < 0.05$). This pattern, whereby baboons prefer to feed on new grass growth stimulated by the onset of the rains, has been noted in other baboon studies in Amboseli and elsewhere (Altmann and Altmann, 1970; Harding, 1976; Rose, 1976).

No data could be collected on the relative availability of three major baboon foods: grass corms, fever tree gum, and dried seed pods of the fever tree. As discussed above, all show relatively intensive utilization throughout the year (Figs. 4 and 5). Corms form a higher proportion of the animals' diet during the long dry season (Fig. 5), and their function as an underground storage organ suggests that both the amount of stored material and its nutritive value are inversely proportional to the amount of new growth in stems and blades and hence should increase during periods of little or no growth (i.e., the long dry season). The seasonal increase in corm feeding may be due to this factor alone; an additional influence might be the general decline in the availability of alternative plant foods during this period (Fig. 6).

The determinants of gum production by trees are not well understood (Smith and Montgomery, 1959; Zimmerman, 1961), and, if seasonal fluctuations exist, they are unlikely to be severe (Coimbra-Filho and Mittermeier, 1977; Ramirez *et al.,* 1977). Circumstantial evidence points to an increase in gum production during the dry season (see also Charles-

Dominique, 1974); commercial gum collection (primarily from *Acacia drepanolobium* and *A. senegal*) takes place almost exclusively during the dry season in Tanzania and the Sudan (Howes, 1949), and there is evidence that gum production is inhibited during periods of high water availability due to the trees' greater ability to withstand bacterial infection at those times (Howes, 1949; Theysen and Bunker, 1927). Both the year-round consumption of fever tree gum and the slight increases during the rainy seasons (Figs. 4 and 5) are difficult to account for if this is the case.

Fever tree pods began appearing on the trees early in the short rains (December) and had largely disappeared from the branches by the middle of the long rains (April) (Fig. 6). The fresh pods are eaten throughout this period (Fig. 4). However, no information is available concerning the amount of time pods can be expected to remain on the ground prior to germination or disappearance due to other causes (including their consumption by baboons). Dried pods were consumed during all months; the apparent peak in consumption during the long rains (Fig. 4) may be a response to an increase in availability at this time as the production of new pods tapers off and the pods produced during earlier months accumulate on the ground. It should be noted that the consumption of dried pods declines as the dry season (May–October) progresses (Fig. 4), which may also reflect this declining availability.

In summary, a small number of food items (the corms of several species of grasses and sedges, the gum and dried seeds of the fever trees) are consumed throughout the year; the availability of these items apparently shows relatively minor fluctuations. The baboons superimpose an "opportunistic" strategy onto this pattern, taking advantage of peak periods of production of foods showing more restricted availability [see Hamilton *et al.* (1978) and Discussion].

Diet Diversity and Overlap

Diet diversity was calculated using the Shannon-Wiener statistic, H (see Struhsaker, 1974, 1975; Harvey, 1977):

$$H = -\sum_i p_i \cdot \log_e p_i,$$

where p_i = the proportion of feeding time spent on food type i. The data collected each month can be used to compute two different diet diversities. One (monthly diversity) uses p_i values calculated from the *pooled* sample data from all days within a given month. The second (mean daily diversity) uses the p_i values from each day within a given month to calculate a diet

diversity for each individual day; a monthly figure is then calculated by taking the mean of these daily diversities for all days within a given month. These two statistics have been calculated for each of the 11 study months (Table V). It can shown (see Post, 1978, Appendix) that these two statistics need not be equal for any given month, even if the total feeding time for all days within that month is the same. Moreover, the difference between the two diversities may yield information concerning the extent of within-month feeding variability.

Thus, we see (Table V) that monthly feeding diversity is higher during the months with higher rainfall, reflecting, perhaps, the wider array of foods available at those times (see Fig. 6). That is, monthly feeding diversity is correlated with monthly rainfall and is higher during the 6 rainy-season months than the 5 months of the interrains and dry season (Table V). However, mean daily diversity shows no such relationship with rainfall (Table V). Thus, in wetter months, monthly feeding diversity is higher relative to mean daily feeding diversity, and the *difference* between these two statistics increases (see Table V).

I interpret these results as follows: high monthly feeding diversity, such as is observed during the months with higher rainfall (Table V), can be achieved either by a broad but unchanging diet each day or by a narrow daily diet accompanied by day-to-day dietary shifts. The evidence in Table V suggests that the baboons take the latter course, for the higher monthly diversities are *not* accompanied by higher mean daily diversities. A hypothesis to account for this increase in day-to-day feeding variability is presented in the Discussion.

This interpretation is supported by data on dietary overlap within and between months. The dietary overlap statistic (see Holmes and Pitelka, 1968; Struhsaker, 1974, 1975; Waser, 1975) is defined as

$$O(x,y) = 1 - \tfrac{1}{2} \left(\sum_i |p_{ix} - p_{iy}| \right),$$

where $O(x,y)$ = the overlap between days (or months) x and y, p_{ix} = the proportion of time spent feeding on food type i during day (or month) x, and p_{iy} = the proportion of time spent feeding on food type i during day (or month) y. Within-month dietary overlap can be calculated as the mean overlap between all pairs of days within a given month. This statistic is significantly correlated both with rainfall (see Table V) and with the difference between monthly and daily feeding diversity ($r_s = -0.866$, $P < 0.05$). Thus, within-month dietary overlap is lower (i.e., day-to-day feeding variability is *higher*) in months with higher rainfall. This higher variability "produces" the more diverse rainy-season diets when data from all days within a given month are pooled.

Table V. Indices of Dietary Diversity and Within-Month Dietary Overlap

Month	Monthly diversity (H)	Mean daily diversity ($\bar{H}$)	$H - \bar{H}$	Mean within-month dietary overlap
Oct.	1.17	0.99	0.18	0.52
Nov.	1.88	1.17	0.71	0.40
Dec.	2.05	1.56	0.49	0.44
Jan.	1.98	1.33	0.65	0.43
Feb.	2.03	1.54	0.49	0.44
Mar.	1.83	1.34	0.50	0.40
Apr.	2.01	1.47	0.54	0.45
May	1.91	1.49	0.43	0.49
June	1.95	1.52	0.42	0.49
July	1.72	1.35	0.37	0.53
Aug.	1.78	1.44	0.35	0.51
Mean				
Rainy seasons	1.94	1.39	0.55	0.43
Dry seasons	1.73	1.37	0.36	0.50
Mann-Whitney U, rainy vs dry	8 ($P = 0.08$)	14 ($P > 0.20$)	1.5 ($P < 0.02$)	3 ($P < 0.05$)
r_s with rainfall	0.572 ($P < 0.05$)	0.063 (NS)	0.752 ($P < 0.01$)	-0.618 ($P < 0.05$)

Seasonal Dietary Patterns

These overlap data can also be used to support the notion that environmental seasonality is reflected in gross patterns of baboon food choice. Mean within- and between-season dietary overlap is tabulated in Table VI. For all seasons, the mean within-season dietary overlap is greater than any of the between-season overlaps for that season (see Struhsaker, 1975). The "significance" of this result is difficult to assess: the sampling distribution of this overlap statistic is, to my knowledge, not known and, in addition, individual values on which these means are based are not independent of one another. Furthermore, we would expect, even in the absence of any marked environmental seasonality, that the diets in adjacent months would show higher overlap than the diets in nonadjacent months. Relatively high within-season dietary overlap may be due to nothing more than the general similarity of diets in adjacent months rather than to any independent "seasonal" effects.

However, further analysis suggests that this "adjacent month" effect is not responsible for the apparent seasonal clustering of baboon diets. Mean dietary overlap between days in adjacent months is 0.420 (899 day-pairs) compared to a value of 0.408 ($N = 4545$) for mean overlap between days in different but nonadjacent months. However, mean overlap between days in adjacent months that fall within the same season (e.g., March and April) ($\bar{X} = 0.451$, $N = 525$) is appreciably higher than mean overlap between days in adjacent months falling in different seasons (e.g., May and June) ($\bar{X} = 0.377$, $N = 364$). Thus, diets in adjacent months show substantially greater overlap if those months fall within the same season, strengthening the argument that seasonal climatic events are accompanied by discernible shifts in the baboons' diet.

In summary, this section has shown the following.

(a) Rainy-season diets are more diverse overall than dry-season diets.

(b) This is accomplished by higher day-to-day variability in food choice during the rainy-season months, rather than by more diverse diets on individual days within those months.

Table VI. Within- and Between-Season Dietary Overlap

	Short rains	Interrains	Long rains	Dry season
Short rains	0.375	0.331	0.354	0.338
Interrains	—	0.437	0.388	0.400
Long rains	—	—	0.460	0.450
Dry season	—	—	—	0.501

(c) Diets from any pair of days show greater similarity if those days fall within a given season than if they do not, and this is not simply the result of pooling together adjacent months into seasons.

DISCUSSION

Diet and Home-Range Utilization

For animals feeding on patchily distributed foods, the problems of home-range utilization and food choice are closely linked; that is, dietary patterns are not independent of the more general problem of "scheduling" activities in time and space (S. A. Altmann, 1974; Hockett, 1964). Figure 7 (modified from Post, 1978, Fig. 27), which depicts the spatial distribution of three of the vegetation zones within Alto group's home range along with the location of the group's sleeping groves, illustrates this "patchiness" clearly. The large size of this home range [over 40 km²; see Post (1978)], relative to the locomotor capacities of the animals themselves, exacerbates

Fig. 7. Spatial distribution of "patches" of three vegetation zones over the home range of Alto's group. A, *Acacia tortilis* Woodland; B, regenerating *A. xanthophloea* woodland; C, bare "pans" of "black-cotton" soil and little vegetation. Filled circles represent sleeping groves, and the horizontal bar represents a distance of 1 km.

the problems imposed on the baboons by this resource patchiness. Thus, the decision to forage in the *A. tortilis* woodland ("A" in Fig. 7), located primarily in the southern and southeastern portions of the home range, makes the resources in the northwestern portion of the range, in particular the *A. xanthophloea* saplings in habitat type "B," virtually unavailable that day (see Fig. 7).

How does this pattern of resource clumping affect the baboons' food choices? First, it seems apparent that our analysis of the constraints on the baboons' diet must include a consideration of a "risk" factor (see Post, 1981a). That is, consider a situation in which there is some uncertainty about the availability of food in the *tortilis* woodland (e.g., toward the beginning or end of the flowering or fruiting season for *A. tortilis*). The decision to forage in the *tortilis* woodland is "risky" not only because less food than expected (or no food) may be present, but also because that foraging decision severely restricts the range of other habitat types the animals can visit that day. An alternative course of action (i.e., foraging elsewhere for foods known to be abundant) may be preferable at such times [although, as I argue elsewhere (Post, 1981a), our understanding of how animals actually evaluate such risky options, as well as our ability to predict how they *should* make such an evaluation, is limited at present]. I would suggest that the observation (Post, 1981a) that the periods during which *A. tortilis* flowers and pods were consumed were considerably more restricted than the periods during which these items were available may be related to the avoidance of this risky foraging option. It should be noted that the pods of the mature fever trees (*A. xanthophloea*), which show considerably less "clumping" (Post, 1978), are consumed throughout the period during which they are available (Figs. 4 and 6).

These considerations may be related to a second observation noted above. The baboons responded to increased food supplies during the rainy season with increased day-to-day variability in food choice (Table V). The same pattern was evident in their utilization of both vegetation zones and quadrants within their home range; that is, quadrant and vegetation-zone utilization was more variable on a daily basis (i.e., showed lower overlap between days), and more diverse on a monthly basis, during the rainy seasons (Post, 1978). Considering Fig. 7, if we envision a period of relatively high food availability during which some food is available in all three vegetation zones, but a different range of food items is available in each, the baboons can utilize all available food by either (a) visiting patches of *all* vegetation zones each day or (b) concentrating their foraging within a small range of vegetation zones on a daily basis, switching to new vegetation zones (and new areas of the home range) on successive days. That the baboons choose the second strategy, of daily "specialization" within a more

generalized monthly pattern, may be a direct response to the patchy distribution of vegetation zones; the first strategy would, in these circumstances, entail extensive between-patch "traveling" costs in terms of both time and energy.

Gum Feeding by the Amboseli Baboons

Although the consumption of *Acacia xanthophloea* gum by the Amboseli baboons had been noted previously (Altmann and Altmann, 1970; Hausfater and Bearce, 1976), the extent of that consumption (see Figs. 3-5) is nonetheless surprising. Gumivory is pronounced in many primate species, primarily prosimians and callithricids (reviewed by Charles-Dominique, 1974; Coimbra-Filho, 1977; Ramirez *et al.*, 1977), but the Amboseli baboons appear to be the only Old World anthropoid, and the only large-bodied species, utilizing tree gum to such a great extent.

Hausfater and Bearce (1976) have shown that the baboons' preference for the gum of *Acacia xanthophloea* over that of *A. tortilis* is probably a function of the substantially larger soluble carbohydrate fraction in the former. However, the nutritional characteristics of fever tree gum may be only one of the components of the role played by this food item within the socioecology of the Amboseli baboons. A baboon would frequently leave a group progression if a gum ooze were sighted (Altmann and Altmann, 1970, p. 144). For unknown reasons, the baboons appeared to prefer gum from younger trees, belts of which were found toward the periphery of the group's range (Fig. 7). Thus the distribution of this food source may have an important influence on the overall ranging patterns of Alto's group (Post, 1978). The identification of individual trees was difficult due to the large home-range size of Alto's group; while some individual trees were frequently revisited, it is not clear whether the baboons systematically reopen bark wounds to stimulate gum production, as reported for other species (see Ramirez *et al.*, 1977).

In addition, fever tree gum shares with vertebrate prey the characteristic of being distributed in relatively large, mobile "packages" capable of sustaining continuous feeding for considerable periods of time. Largely for this reason, interindividual competition for gum often takes unusual forms. Such competition is, in general, quite common within the baboon group (see Altmann and Altmann, 1970; S. A. Altmann, 1974; Post *et al.*, 1980); its most overt manifestation is frequent supplantations at feeding sites. While supplantations at gum sites themselves were not uncommon, individuals that could dislodge a sizable portion for themselves

would often leave the vicinity of the site to feed undisturbed by other group members. Individuals were never observed actually taking food already in another animal's possession (cf. Dittus, 1977); however, on several occasions I observed "scrap feeders" (see Hausfater, 1976) congregating in the vicinity of an individual feeding on a particularly large gum bolus. This is reminiscent of the behavior of animals around a prey carcass (Hausfater, 1976; Harding, 1973; Strum, 1975) and these incidents were the only occasions when this behavior was observed outside of predatory episodes.

Baboons as Generalist Consumers

The baboons' relatively large body size is presumably related to their generalist feeding strategy: decreasing dietary selectivity with increasing size is a general characteristic of primates (Gaulin, 1979) and other mammals (e.g., Jarman, 1974). Within that general constraint, the degree of omnivory can vary in response to a variety of factors. On the basis of their study of a population of chacma baboons *(Papio ursinus)*, Hamilton *et al.* (1978) argue that the selective advantages of such a generalized diet are enhanced by (a) increased interspecific and intragroup competition, (b) resource patchiness and reduced food availability, and (c) the tendency to form large multimale social groups. Two of their conclusions are particularly relevant to the results presented above.

(a) "Omnivory enables low-ranking individuals to reduce competition with higher-ranking individuals while still living in close proximity to them... the potential to utilize alternative foods effectively is particularly advantageous to low-ranking animals" (Hamilton *et al.,* 1978, p. 922). Intragroup competition for food may indeed place a selective premium on a generalized diet; however, this need not necessarily be achieved via the mechanism of intragroup dietary differentiation organized by rank (or any other criterion). Omnivory, of course, is not a condition that exists apart from the behavior of the animals themselves, and it can be achieved by increasing *either* the within- *or* the between-individuals component of the population's feeding niche (Roughgarden, 1972, 1974); it is not necessarily accompanied by increases in the latter, as implied by the quotation above. Furthermore, the data from Amboseli do not support the notion that a greater fraction of the diet of low-ranking individuals consists of "alternative foods." On the contrary, it may be the animals of high rank that can most efficiently exploit these alternative food sources. Thus, while food choice among the Amboseli baboons is a function of both sex (Post, 1978) and rank (Post *et al.,* 1980), we have suggested that adult males, the

highest-ranking age–sex class (Hausfater, 1975), have diets that are more variable (Post, 1978, Tables 29 and 30) and that overlap less with those of other members of their own age–sex class (Post *et al.,* 1980) than do members of other age–sex classes. High rank may enable these males to feed on less abundant, more patchily distributed and unpredictable foods (Post, 1978) as a consequence of their lower probability of being supplanted from feeding sites.

(b) "Omnivory allows baboons to choose alternative foods when certain items are depleted" (Hamilton *et al.,* 1978, p. 918). This suggests a more diverse diet during periods of decreased food availability, a prediction in accordance with most optimal foraging models (see Krebs, 1978; Pyke *et al.,* 1977). However, the Amboseli baboons are *most* specialized during just such a period (i.e., dietary diversity is *lowest* during the dry season). Of course, this apparent contradiction may be more terminological than substantive: the baboons may be less *selective* during the dry season, with the low diversity of their diet at that time a reflection more of the extreme dearth of available food types than of any specialization on their part. Nonetheless, the results from this study suggest that the baboons' omnivorous habits allow them to expand their dietary range during periods of increased abundance: that is, they have the ability to take advantage of intermittent peaks in the availability of certain foods during the rainy season, which may in turn ensure adequate supplies of less variable foods (e.g., corms, gum) during less favorable periods.

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