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Dietary and foraging strategies of baboons

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SUMMARY

As large-bodied savannah primates, baboons have long been of special interest to students of human evolution: many different populations have been studied and dietary comparisons among them are becoming possible. Baboons' foraging strategies can be shown to combine high degrees of flexibility and breadth with selectivity. In this paper we develop and test multivariate models of the basis of diet selection for populations of montane and savannah baboons. Food selection is positively related to protein and lipid content and negatively to fibre, phenolics and alkaloids. Seasonal changes in dietary criteria predicted by these rules are tested and confirmed. Although nutritional bottlenecks occur at intervals, a comparison between long-term nutrient intakes in four different populations indicates convergence on lower degrees of variation than exist in superficial foodstuff profiles.

1. INTRODUCTION

Partly because of the relevance of the savannah primate niche to human evolution (Peters & O'Brien 1981) and partly for other reasons such as the superior observation conditions this habitat offers, baboon research has been pursued during the last thirty years at numerous locations across Africa (Dunbar 1988). Many studies have quantified the profile of foodstuffs consumed (table 1), so that in baboons more than any other non-human primate, we can start to appreciate the true range of dietary variation.

In recent years primatologists have become more ambitious, attempting to quantify diet not only at the level of foodstuff profile, but in terms of actual nutrient ingestion. However, quite apart from the extensive laboratory analyses this involves, it is an exacting task to follow a focal individual in the field and make a continuous record of the number, size and identity of each bite of food (which can be one per second), even when facilitated by the use of hand-held microcomputers (Whiten & Barton 1988; Byrne *et al.* 1990*b*). Accordingly these 'fine-grain' analyses are still rare in primate research. Barton (1992) found just eight which provided accurate measures of daily dry mass intake.

However, in baboon research we are again uniquely fortunate in that results of such work are becoming available from parallel efforts at five different sites in east and southern Africa. In the main part of this paper we present results from this new work, including our own conducted at two of these sites: one in savannah, the other in a more marginal montane environment.

2. THE FORAGING STRATEGY OF BABOONS: AN OVERVIEW

Characterization of baboons' foraging strategy as adaptably broad, yet selective, may sound paradoxical: yet it is probably the combination that permits a primate like this to succeed in the habitats concerned (Whiten *et al.* 1987; Norton *et al.* 1987). In what follows we summarize the principal dimensions of baboons' approach to foraging.

(*a*) *Adaptability*

Although baboons' modal habitat can be fairly characterized as the band of savannah that sweeps from west, through east, to southern Africa, baboons also exhibit successful invasions of a variety of types of habitat on its margins, including desert, swamp, forest and montane environments. Foraging profiles described even at the level of very gross food types show remarkable variations across these habitats: for the most common food types the ranges are 3–74% (fruit), 1–53% (subterranean items) and 8–53% (leaves) (table 1). At this level of analysis, baboons' foraging strategy can clearly be characterized as highly flexible and adaptable.

(*b*) *Dietary diversity*

The ability to adapt to varying habitats may be a product of flexibility within the foraging strategy

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Table 1. *Local variations in the foraging profiles of baboons*

(Sites are ranked by % fruit in the diet (the most common food type overall).)

1. *Mt Assirik, Senegal (*P. papio*), Sharman (1981); 2. *Gombe, Tanzania (*P. anubis*), J. Oliver; 3. *Suikerbosrand, S. Africa (*P. ursinus*), C. Anderson; 4. Mikumi, Tanzania (*P. cynocephalus*), Norton *et al.* (1987); 5. *Cape Reserve, S. Africa (*P. ursinus*), Davidge (1978); 6. *Bole, Ethiopia (*P. anubis*), Dunbar & Dunbar (1974); 7. *Amboseli, Kenya (*P. anubis*), Post (1978); 8. Laikipia, Kenya (*P. anubis*), Barton (1989); 9. *Ruaha, Tanzania (*P. cynocephalus*), Ramussen (1978); 10. *Gilgil, Kenya (*P. anubis*), Harding (1976); 11. *Drakensberg, S. Africa (*P. ursinus*), Whiten *et al.* (1987). *Data from Dunbar (1988), p. 295.)

food type	percentage of time feeding on item at different study sites (1–11)													
	1	2	3	4	5	6	7	8	9	10	11	range (%)	mean (%)	coefficient (%) of variation
fruits	74	49	43	43	42	41	27	23	16	10	3	3–74	34	61
underground items	3	7	39	12	16	1	33	15	52	27	53	1–53	23	79
leaves	9	14	8	14	25	41	15	27	19	53	26	8–53	23	61
flowers	9	2	7	20	12	12	5	21	1	3	14	1–20	10	72
animals	1	13	3	?	3	4	1	1	9	2	4	1–13	4	103

associated with the modal savannah habitat itself, where baboons exploit an unusual diversity of foods. The most straightforward measure of dietary diversity is the number of different types of food item eaten. Norton *et al.* (1987) expanded their baboon food list in each of five years of study to include 1–6 parts of 185 species of plants.

Another aspect of diversity may be even more important in the maintenance of baboons' particular feeding niche: the ability to extract nutrients from almost all compartments of the environment. At both of our study sites baboons spend the major part of their foraging time ranging through and selecting foods from the seasonally productive herb and shrub layer: but additionally, feeding niche separation from ungulate competitors in this layer is achieved by the capacity to probe the environment in other ways. This includes arboreal foraging which extends the range of leaves, flowers and fruit taken, and also makes available special foods like exudate and birds' eggs; and subterranean foraging, which involves digging up the fleshy bases, roots and storage organs of a variety of herbs, grasses and sedges. Exploitation of the full diversity of these food sources means that baboons can cope with the severe seasonality that typically dries and kills the herb layer for months at a time in these habitats, forcing ungulates into substantial migrations that the baboons can avoid. At our savannah site the arboreal compartment (particularly *Acacia* flowers and seeds) plays an important role (42 % of annual intake by mass), and underground items a more minor one (5.6 % by mass, although 15 % of feeding time; Barton 1989): at our high altitude montane site the reverse is the case and subterranean items account for virtually all the diet in the cold, dry, winter season (Whiten *et al.* 1987).

In a survey of diets in 120 primate species, Harding (1981) found that the typical savannah species, baboons and vervet monkeys, had the most diverse diets (utilizing all nine of the compartments he assessed), followed by woodland – savannah chimpanzees. However, at two sites where baboons and chimpanzees are sympatric, baboons still exhibit the greater diversity of food profile (Peters & O'Brien 1981, 1982).

(*c*) *Selectivity*

Although earlier studies tended to equate baboons' breadth of diet with lack of discrimination, considerable selection can be demonstrated, at a number of levels.

First, baboons utilize only a proportion of the species available. Norton *et al.* (1987) estimated that the 185 species of plant used by Mikumi baboons are selected from among approximately 700. Selection may be expressed at a fine level of discrimination, between species of the same genus which to a human eye appear superficially very similar. Thus, for example, Drakensberg baboons select the corms of just one of three similar species of *Hypoxis* (table 2).

At another level, it is often only one or a few parts of a food species that are consumed. Separating this may

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Table 2. *Selection among corms of related species of Hypoxis*

(All data are percentage of dry mass except water (which is percentage of net mass), starch and alkaloid (both of which are graded on a 3-point scale). Phenol. = total phenolics, tann. = condensed tannins, alk. = alkaloids.)

species	water	protein	lipid	starch	phenol.	tann.	alk.	fibre
H. gerrardii[a]	78.2	3.23	7.0	'3'	0.78	0	0	11.3
H. obtusa	68.6	1.42	6.0	'1'	1.46	0	0	9.8
H. rigidula	70.0	2.46	1.0	'1'	11.26	0	0	12.0

[a] Species consumed.

Table 3. *Composition of selectively processed food parts* (*Acacia*)

		water	protein	lipid	phen.	tann.	alk.	fibre
A. seyal	seed kernel[a]	74.0	49.2	7.5	0.5	0.4	0	4.3
	seed skin	66.7	15.1	3.0	7.5	12.1	0	22.7
	pod	68.2	14.4	5.0	5.6	2.3	0	37.9
A. nilotica	seed kernel[a]	74.5	47.0	11.5	0.6	0.8	0	3.1
	seed skin	59.0	12.0	4.0	7.8	18.0	0	21.8
	pod	—	11.6	12.0	7.2	7.6	'2'	11.5

[a] Denotes parts consumed. Other conventions as for table 2.

be relatively straightforward for a primate like a baboon, as in plucking a flower or fruit. In a number of other cases both hands are used, sometimes in conjunction with the teeth, to process the food, peeling and discarding certain components. For example, in three of six species of *Acacia* used as foods by Laikipia baboons, pods are torn from the tree and, using both hands and teeth together, sliced open and the seeds nibbled out: within the mouth the skins of the seeds are separated and pushed out using the tongue. By such processing the baboons exert considerable control over the composition of the material they finally ingest (table 3), in a fashion simply not open to less dextrous competitors.

3. IDENTIFYING THE BASIS OF DIET SELECTION

The contrasts in composition summarized in tables 2 and 3 suggest some of the reasons why baboons select the species and parts they do. We now tackle the thorny question of how more systematically and comprehensively to specify whatever rules underlie the dietary 'decisions' being made.

(*a*) *Background and rationale*

One of the first nutritional comparisons between selected and discarded food parts in primates was offered by Hamilton *et al.* (1978) for three food types in chacma baboons. Parts chosen for ingestion contained relatively high proportions of protein (also lipid in two cases) and low proportions of fibre (as in table 2).

Aside from this pioneering study, it was primatologists studying arboreal folivores who pursued food versus non-food comparisons extensively (see Milton 1980). The general technique has been the simple one we have already described: foods are compared with non-food control items which appear superficially similar and which present an obvious puzzle as to why they are avoided. A number of constituents may be analysed and, for each one, a food versus non-food difference is tested for statistical significance. Common components examined include potential macronutrients, fibre and secondary compounds. The latter include digestion inhibitors (notably condensed tannins) and toxins such as tannins and alkaloids, which are known to act as anti-herbivory defences in certain contexts (Waterman 1984).

These comparisons show recurring trends, particularly for lower levels of protein and higher levels of fibre in non-foods, implicating these constituents as among the determinants of choice. However, such component-by-component comparisons must ultimately be of limited usefulness. In species like baboons where the diet is so diverse, there is enormous overlap between the proportions of any one component (even protein) when we compare foods with a variety of non-foods. To complicate matters further, several other components differ markedly in some specific food versus non-food contrasts, suggesting a role in these choices at least.

All this suggests what is in any case plausible from first principles: that the basis on which certain items are chosen or even preferred as foods constitutes an equation in which a certain balance of elements is aimed at. Thus, for example, a relatively high proportion of a single nutrient might make an item as attractive as another with lesser proportions of two different nutrients; or an item with a relatively low proportion of nutrient may be acceptable if it has little in the way of negative components like toxins; or given two items with similar nutrient and toxin profiles, it may then be the level of fibre which finally distinguishes one as a food.

We have used discriminant analysis to derive just such multivariate equations expressing the rules of diet selection.

(*b*) *Methods*

Two populations of baboons have been studied. Since 1986 a group of approximately 100 olive baboons

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(*Papio anubis*) has been studied in savannah habitat on the Laikipia plateau, Kenya. Chacma baboons (*P. ursinus*) studied earlier in the Drakensberg mountains on the S. African–Lesotho border sustained relatively low population densities and formed smaller groups: one of approximately nine and another of 14 were studied over an 18-month period.

At each location a variety of standard methods have been used to gather data on behaviour, demography, food availability and nutrient composition (Barton 1989; Barton *et al.* 1992*a*, *b*; Byrne *et al.* 1990*a*, *b*; Whiten *et al.* 1987, 1990).

The principal analyses to be discussed below involve contrasts between plant food and non-food controls. Non-foods included the two types distinguished in the previous section: (i) parts of food plants discarded or avoided; and (ii) parts of species that are not eaten, corresponding to parts of species that are eaten. In the latter case we chose controls that appeared most similar to the item eaten, as in the example already illustrated in table 2. The assay techniques for these samples are described in Whiten *et al.* 1990 and in more detail in Choo (1981). In summary, they included water (air drying at 37 °C to constant mass), total nitrogen (micro-Kjeldahl), lipid (ether extraction), starch (4-point scale based on iodine stain), fibre (acid-detergent), condensed tannins (as quebracho-tannin equivalents, through modified butanol–HCl method), total phenolics (tannic acid equivalents, through Folin-Denis method) and alkaloids (3-point scale utilizing reactions with Dragendorf's reagent). Protein was calculated at $N \times 6.5$, and total carbohydrate was then calculated by subtraction.

Such data from the Drakensberg site have been subjected to a number of stepwise discriminant analyses (SPSS 1983) to establish what components are critical, in combination, for discriminating food from non-food items. For each item, the discriminant procedure computes a function:

$$\text{Food value score} = C + A\cdot x + B\cdot y + D\cdot z\ldots$$

in which C is a constant, A, B are proportional amounts of components (e.g. protein) and x, y are coefficients computed so as to maximize the difference between mean food value scores for foods and non-foods. Coefficients can be positive (valued components) or negative (avoided components).

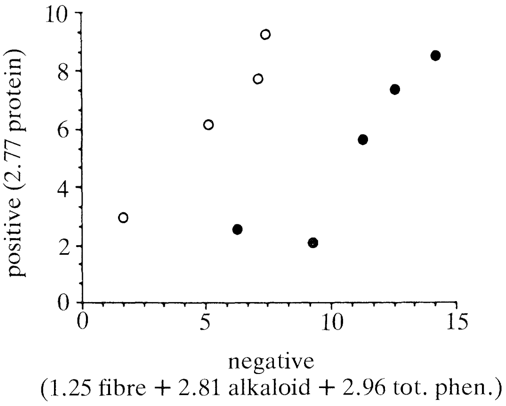

Figure 1. Food and non-food leaves (open circles and closed circles, respectively) plotted against axes separately representing the positively and negatively weighted components contributing to each item's food value score. Coefficients (weightings) are standardized. Note that neither protein alone, nor the negative complex, can differentiate foods from non-foods: only their combined effect achieves this.

(*c*) *Selection rules for major food types*

For four major food items separate comparisons of foods with control non-foods have been done. The end result can be appreciated in an example (figure 1). The sum of the positively-weighted elements in the discriminant function are plotted against those negatively weighted, producing maximal separation between food and non-food leaves. Table 4 shows the weights (coefficients) computed separately for leaves, corms, inflorescences and pale fleshy bases of leaves and stems.

The coefficients indicate that in the selection of different types of foods, different rules apply: only in the case of leaf bases is lipid a significant factor, for example. Just one factor, protein, was important in all cases, although for bases it was outweighed by the coefficients for lipid and fibre content. A number of components consistently failed to contribute to discrimination rules: water content, starch, condensed tannins and total carbohydrate.

(*d*) *Seasonal change in selection rules*

An alternative way of representing graphically such rules is to show in histogram form the relative weights

Table 4. *Standardized discriminant function coefficients distinguishing food types from non-food matched control items*

(Presentation of standardized coefficients here permits direct comparison of the 'importance' of any component within, although not between, analyses. Thus variance in protein, total phenolics and fibre are of roughly equal weight in making discriminations for both leaves and inflorescences.)

	leaves	corms	bases	infloresences
protein	2.8	2.23	0.11	0.67
lipid	—	—	1.12	—
phenolics	−3.0	—	—	—
alkaloid	−2.8	—	—	−0.79
fibre	−1.3	—	−1.2	−0.99
discrimination of foods from non-foods (%)	100	100	100	100
n	9	10	11	10

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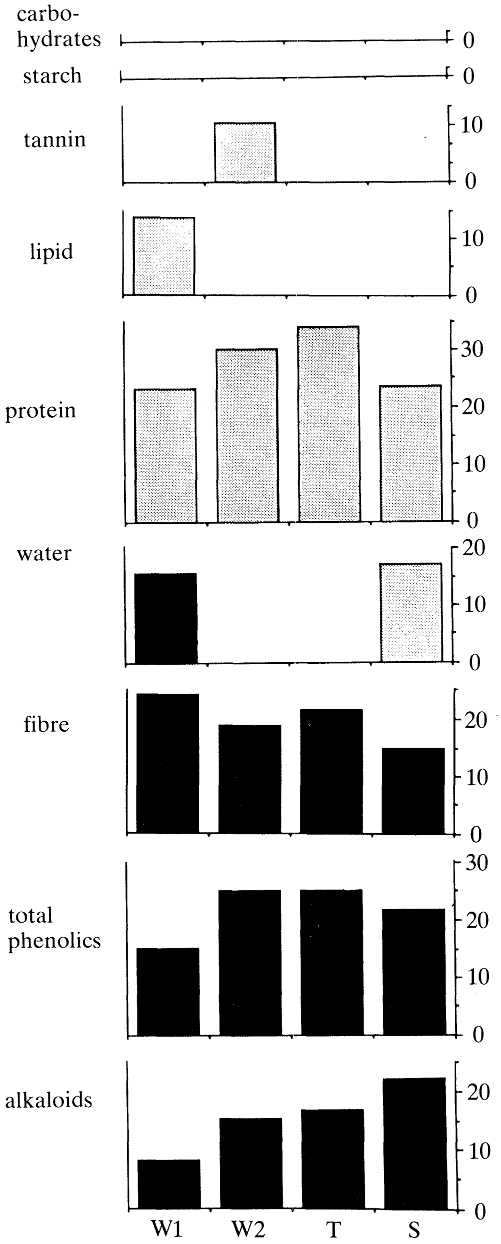

Figure 2. Size of standardized discriminant coefficients, expressed as percentages to show their relative importance in each of four seasons. Because of its inconsistent role, water was dropped from prediction-across-season analyses shown in subsequent figures. Open bars, positive weight; filled bars, negative weight.

attaching to different components. Figure 2 does so for four consecutive periods from winter to spring, during which a flush of fresh leaves and flowers gradually develops (Byrne *et al.* 1990*b*). For each season a separate function has been computed, combining all foods eaten in that season and contrasting them with a sample of appropriate non-food controls. We might expect this more global rule to combine those components significant in the case of the separate comparisons shown in table 3, and indeed this is the case. Of these, four components – protein, fibre, total phenolics and alkaloids – remain significant in all seasons, whereas lipid is picked out only in the winter period, consistent with the fact that underground storage organs are particularly utilized at that time. By contrast, (avoidance of) alkaloids receives progressively heavier weightings as inflorescences and leaves protected in this way become increasingly abundant. This is despite the fact that 'alkaloids' were estimated on only a crude rating scale which did not discriminate the many different specific toxins (and toxicity levels) potentially involved.

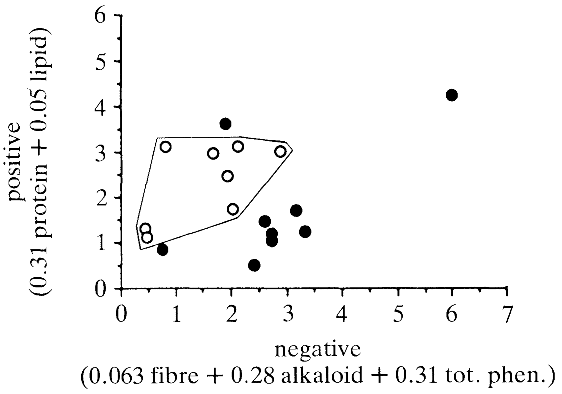

Figure 3. Winter foods (greater than 1 % of diet, open circles) and non-foods (closed circles) plotted on axes showing unstandardized coefficients. The one non-discriminated non-food is an unripe fruit, presumably distinguished from the ripe, eaten fruit by an element we have not yet measured. This item is therefore dropped from analyses shown in subsequent figures.

(*e*) *Testing predictions of the rules*

The status of the 'rules' as we have discussed them so far is essentially descriptive. They simply represent the 'best' overall numerical specification of what distinguishes any particular set of foods and non-foods.

However, we might elevate the rules to the status of a model of the preferences underlying baboons' behaviour if further predictions can be generated and tested. Two ways in which this can be done rely upon the fact that the discriminant procedure works by computing the relative 'attractiveness' of each food and non-food: the food value score. One test of the accuracy of the computed rules is thus that foods with high food value scores should be particularly valued by the baboons, and if monopolizable, they should be the subject of the most intense feeding competition. This test has not yet been applied, although it is apparent that one prediction from these rules derived from plant foods, that vertebrate meat (with high values of protein and lipid and little or no fibre, phenolics or alkaloids) should be highly valued when available, is clearly confirmed (Strum 1981).

Another prediction rests on optimal foraging theory: as food value scores improve seasonally, the threshold of these scores at which the food versus non-food cut-off is made by the animals should rise. To test this, we first show (in figure 3) the general rule describing winter food choice for all analysed foods contributing more than 1 % of feeding records (accounting for 90.3 % of feeding). The polygon describing these points is then preserved in figure 4 and overlaid with the scores for spring foods (each greater than 1 % of the diet and together accounting for 69.9 % of feeding) and non-

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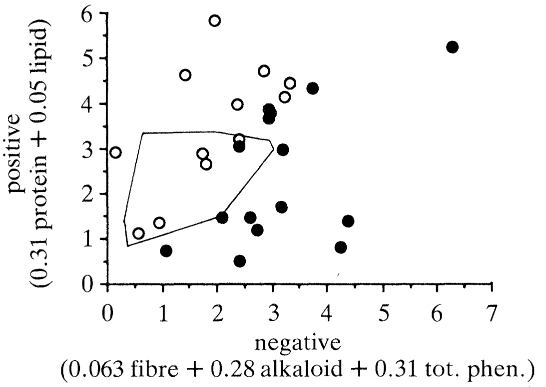

Figure 4. Spring foods (open circles) and non-foods (closed circles; greater than 1 % of diet) superimposed upon polygon for winter foods taken from figure 3. Note the trend in both foods and non-foods to upper left ('attractive') quadrant.

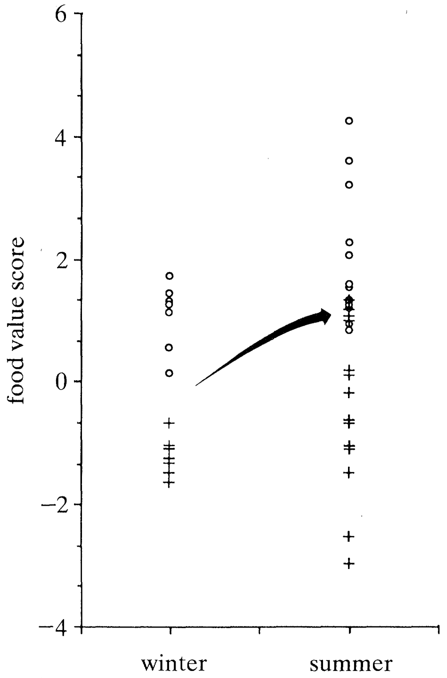

Figure 5. Seasonal change in distribution of food value scores for foods (circles) and non-foods (crosses), using winter coefficients for both seasons. Change in the food versus non-food 'cutoff' is indicated by the arrow.

foods. Both food and non-food scores rise higher in the direction of positive weightings, and the threshold between them appears to rise also, as predicted. This change in cut-off is shown more clearly in a single-dimension plot (figure 5). To check that this effect is robust, Figure 6 repeats the contrast using the coefficients computed from spring data. In this case there is naturally a clearer separation in the spring, (and applying these coefficients to the winter foods and non-foods conversely produces a less clear separation than in figure 5). This result offers strong support for the model because the two low-value foods that drop out of the foraging profile in spring are far from insignificant for the animals in mid-winter: one, a grass base (*Sporobulus congoensis*), accounted for 49.3 % of the foraging records for one group; the other, a sedge base

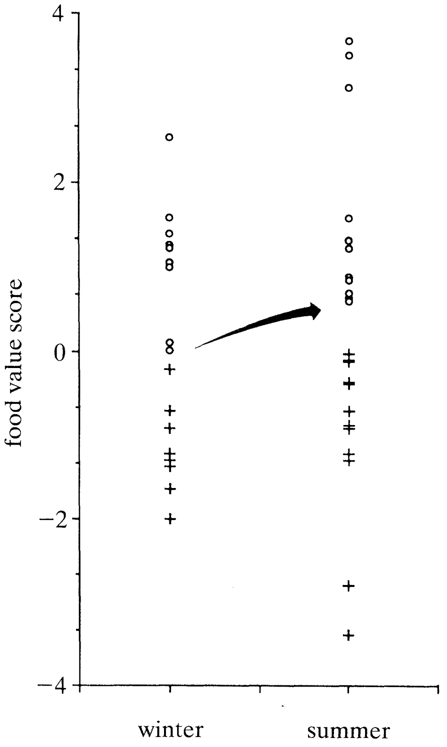

Figure 6. As for figure 5 but using summer coefficients for both seasons.

(*Scirpus falsus*), accounted for 73.2 % of the foraging records of the other group, studied at a high-altitude site.

(*f*) *Dietary correlates of selection ratios in Laikipia baboons*

Although the selection rules described above are derived from only food versus non-food contrasts, the predictions confirmed in the previous section suggests that they may have relevance to preferences among the foods eaten. To test this properly requires the computation for each food of a selection ratio, correcting the proportion of a food in the diet by the availability of it in the environment (at Laikipia the two are correlated, $r = 0.53$, $p = 0.012$). Only for the Laikipia site can we do this well. Discriminant analyses like those outlined above for Drakensberg baboons have not yet been done at Laikipia. We therefore rely on the finding that regular features of the Drakensberg selection rules include positive weightings for protein and negative weightings for fibre of a similar order of magnitude, and have therefore computed protein:fibre ratio that *is* available for Laikipia. Using figures for ten major categories of diet, it was confirmed that selection ratio is well predicted by protein:fibre ratio ($r = 0.829$, $p < 0.001$; Barton 1989).

4. DIETS CONSUMED: INTER-POPULATION COMPARISONS

(*a*) *Proportions of nutrients in the diet*

What dietary profiles result from the selection rules outlined above? Instructive, although as yet far from perfect, comparisons can now be made between four

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Table 5. *Diet composition in four baboon populations*

(Data are mean [and median] percentage of dry mass except water, which is percentage of fresh mass. Laikipia means are for 13 most common foods (Barton *et al.* 1991), accounting for 68 % of feeding time. Drakensberg means are for eight most common foods, accounting for 68 % of feeding time. Amboseli means are for values given in Altmann *et al.* (1987), using eight most common foods, accounting for 68 % of feeding time, given by Post (1978, table 61). Mikumi means are for all plants tested (Johnson 1989, table 4.22). Ranges, rounded to whole numbers, are for all foods tested.)

	Laikipia	Mikumi	Drakensberg	Amboseli
water	70.9 (7–94) [78.7]	—	63.8 (34–93) [77.6]	57.6 [70.4]
protein	21.2 (5–50) [19.1]	13.68 (1–39)	8.44 (2–17) [7.3]	14.4 [15.8]
lipid	6.3 (2–14) [5.0]	5.25 (2–20)	6.3 (1–15) [5.0]	4.4 [4.1]
phenolics	1.7 (0–11) [1.3]	3.20 (0–23)	1.3 (0–13) [1.0]	—
tannin	1.4 (0–15) [0]	2.53 (0–49)	0.6 (0–2) [0]	—
fibre	20.9 (1–56) [24.0]	26.29 (5–55)	21.5 (1–40) [25.3]	22.1[a] [21.8]
n (for range)	66	33–192	39	—

[a] Different method used.

different sites (table 5). These include our Drakensberg and Laikipia sites, together with Amboseli (Kenya) and Mikumi (Tanzania), at both of which long-term studies of yellow baboons (*P. cynocephalus*) have been made. Phytochemical analyses from Amboseli are the most extensive (Altmann *et al.* 1987; Altmann 1990); however, the other three studies, despite covering a restricted range of constituents, offer the advantage of identical methods applied at Waterman's laboratory or directly derived from them.

There are several ways in which dietary comparisons might be attempted. The ideal would be to compute proportions of nutrients based on measures of absolute intake, but opportunities for comparisons on this basis are very restricted as yet (see §4*b*). The approach taken in table 5 is therefore the simpler one of examining the proportional composition of the most common food plants. At all four sites, two thirds of the diet is accounted for by a relatively small number of food types: just 8–13 for the three sites for which information is readily available. For these three sites, mean and median values for nutrient analyses for these items that constitute the bulk of the diet are given in table 5: for the fourth site, only means for the whole sample of foods tested are available. In three cases it is also possible to give the total range of variation.

These figures should therefore be interpreted as 'typical' nutritional profiles, together with the range over which they vary, for baboon foods at the sites concerned, rather than as exact specifications of the overall nutrient intake profile (see §4*b*). As such, they are offered as useful bases for future comparisons with data for other species. In their own right they show at least two important facts.

First, at all sites the range of variation of any one component – whether nutrients, fibre or secondary compounds – is very great. This is likely to be one of the reasons that diet selection rules have to be specified in multivariate terms, because ranges of values for any one component in non-foods can be shown to have a huge overlap with those in foods (Whiten *et al.* 1990). To give just one example, protein in Drakensberg non-foods ranged from 0.9 to 12.7 % compared with 2.1–16.5 % for foods.

Second, although some inter-population differences in the average figures are substantial, they show less variation than at the level of foodstuffs, where variability has already been emphasized. Despite a large difference between the mean protein scores of our Drakensberg and Laikipia baboons, the coefficient of variation across the four samples is 36 %, less than the coefficients of variation for basic foraging strategies shown in table 1. There is thus an indication that through these very variable foraging profiles baboons in different habitats converge on a more limited range of nutrient consumption.

(*b*) *Absolute nutrient intake*

Where data have been collected not only on the relative frequency of items in the diet, but on complete records of amounts ingested, it becomes possible to specify diet in absolute terms. To date, comparisons at this level can be made for protein intake at three of the baboon sites concerned.

This is not a straightforward task and the following must be regarded as a preliminary attempt. A number of differences in methodology are likely to introduce error. One is observational method, which was not identical in the three cases: however, the goal in all was to specify absolute intake and this is probably not the greatest difficulty for comparative purposes. Second, the data are published for focal animals of varying masses: here they are re-expressed in terms of an 'average adult' of 15 kg. Third and perhaps most problematic is the difficulty that in each case data are reported for part of a year, in habitats where we know seasonality can be severe.

Protein intake, in grams per day for a 15 kg baboon, is computed at 69.5 g for Amboseli (based on Stacey

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(1986), table 3) and 88.2 g for Laikipia (based on Barton (1989), table 6.4). As these data are for periods wetter than the average, the fairest comparison in the Drakensberg data appears to be for the spring period (Byrne *et al.* 1990*b*), for which the figure is 75.7 g. The coefficient of variation across these figures for protein intake is then just 22%, consistent with convergence on a more limited range of variation in nutrient intake than exists at the level of foodstuff profile or even at that of the composition of common foods (§4*a*). However, the conclusion that protein intake is consistent across populations in (wet) periods of relatively high availability must be contrasted with the likelihood of significant seasonal fluctuation. This becomes clear when we note that the corresponding protein intake figure for the severe winter and winter–spring transitional periods in the Drakensberg is only 28.2 g (Byrne *et al.* 1990*b*).

These figures are encouragingly consistent with the nutritional requirements in Oftedal's table 5 (p. 166). The winter Drakensberg intake is relatively low by this standard; the other, overall intakes reported above, are relatively high, but we must remember that the natural diets incorporate secondary compounds that are likely to reduce protein digestibility.

5. SUMMARY AND DISCUSSION

We have outlined a number of fundamental respects in which baboons are constrained by, and adapted to, their particular food niche. It seems likely that these would not have been avoided by early hominids in their first invasions of the habitat. Flexibility is observed in the readiness to adopt widely differing dietary profiles with respect both to the severe seasonal changes that characterize savannah, and to a variety of habitats marginal to savannah. Another dimension of dietary flexibility is the breadth of the food profile. Baboons' use of underground storage organs is an important tactic taken to further extremes by present-day savannah hunter-gatherers who can harvest a deeper layer by the use of a simple digging stick (Peters & O'Brien 1981). By contrast with the breadth of diet, precise visually guided reaching and manipulation permit a high degree of selectivity, starting with harvesting and continuing through manual and oral processing of the food.

The computation of rules of diet selection as discriminant functions that express the combined roles of constituents of foods in selection has been shown to be workable and to generate predictions which have been tested and supported. For Drakensberg baboons, protein, fibre, total phenolics and alkaloids were found to play almost equal roles in distinguishing foods from non-foods. The significance of protein and fibre is consistent with the food preferences of Laikipia baboons also, and with previous studies of primates exploiting the superficially very different niche of aboreal folivory (see, for example, Milton (1980); McKey *et al.* (1981)). However, the negative role of tannin found in the latter has been less emphasized in other studies of colobine monkey diet (Waterman *et al.* 1988; Davies *et al.* 1988) and was not found for mountain baboons, for whom phenolics and alkaloids were more important inhibitory influences. Phenolics and alkaloids may be subject to detoxification in the foregut of specialist colobine folivores, a facility probably absent in monogastric primates like baboons.

This analysis of diet selection rules must be regarded as a first approximation for a number of reasons. We have used only a small subset of the components which could in principle be examined, and even the categories we have used are not unitary ('alkaloids' is most obviously a heterogenous category). However, the inclusion of further components in future analyses can be expected essentially to refine an approach which is already justified by its empirical success in discriminating foods and non-foods by using the basic categories of component described here.

The approach draws an important distinction between the compositional basis for choice, and the dietary composition achieved. In the case of Drakensberg baboons, the latter includes significant quantities of starch and lipid, but starch does not figure in the selection rules and lipid does so in only a small way. Whiten *et al.* (1990) noted that this suggests that 'by following certain rules, baboons get, into the bargain as it were, a diet adequately provided with other components (such as starch) which in some foods are associated with the choice element'.

Such dietary 'rules of thumb' represent evolved adaptations to the nutritionally critical components in a certain ecological niche. In the case of baboons (and by extension in ancestral hominids), this niche is characterized by high levels of fibre and, at least in certain habitats and seasons, low levels of protein. It may be that the particular rules shown by our analyses are adaptations to an unusual degree of protein deprivation during the Drakensberg winter (table 5), although the Laikipia selection ratio correlations suggested similar priorities even where foods are richer in protein. Although in principle we might expect the negative weighting of fibre to be nonlinear (a certain amount providing optimal gut passage times), in a dietary environment producing a high input of fibre the rule that evolves might be less sophisticated, and open ended: 'maximize the protein:fibre ratio'. Such a rule should lead to consistent choice of minimal-fibre options if these became available as an evolutionary novelty. This may be what we see in baboons that gain access to food waste tips at African game lodges (and also perhaps in those descendants of savannah primates who frequent the restaurants in those lodges?)

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Discussion

K. Hawkes (*Department of Anthropology, University of Utah, Salt Lake City, U.S.A.*). What about the costs of these foods? Optimal foraging models predict choices based on the nutrient payoff (often measured as calories) per unit of time spent foraging. The 'optimal diet' or 'prey choice' model predicts the inclusion of resources if their profitability (the rate earned for pursuing and handling them after they have been found) is at least as high as the expected rate for passing them by and continuing to search for something better. If the resources exploited by human foragers are evaluated only from the point of view of nutrients per kilogram, many with very low values are exploited whereas many with much higher values are not. When handling costs are considered, and resources are evaluated for nutrients gained per unit time, the economies can be quite clear. Could it be that Dr Whiten's anomalous points are resources with very different handling costs?

A. Whiten. It seems unlikely that the anomalous point in figure 2 can be explained in this way, as this corresponds to an unripe phase of a fruit eaten when ripe and the two thus have similar harvesting and handling properties. However, Dr Hawkes' general point about taking account of costs is an important one. Considering cost–benefit equations is one reason for our multivariate approach, and constituents with negative coefficients can be regarded as one type of cost. The additional costs Dr Hawkes emphasizes can be divided into time-to-find and time-to-process. With respect to the latter, that is something we cannot take precise account of in contrasts of food species with species that are not eaten and therefore not processed at all. However, we took care to make paired contrasts (e.g. eaten deep corm with non-eaten deep corm) that minimize likely handling time differences. In

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contrasts between parts of a plant eaten with those discarded, it is often the part eaten that takes longest to prepare, so the preference cannot be explained by time constraints. However, time-to-process is a variable which it will make sense to include in our further research on dietary preferences within the set of foods consumed.

Time-to-find is a more elusive quantity to measure because nobody has discovered a way to define baboons' search strategy. If we assumed random search, we can at least consider abundance of alternative items. Again, this is automatically taken account of in contrasts between parts discarded or consumed, and in contrasts with species not eaten we have selected items that are far from rare. In examining preferences among the set of food items, abundance is explicitly taken account of in our selection ratios.

E. M. Widdowson (*9 Boot Lane, Barrington, Cambridge, U.K.*). Can Dr Whiten explain how a baboon discriminates for protein and against fibre? Neither has any taste or smell. Does the baboon try the non-food and dislike it, or is the discrimination learned and passed on from generation to generation?

S. A. Altmann (*Department of Ecology and Evolution, University of Chicago, Illinois, U.S.A.*). The characteristics that a discriminant function uses to discriminate between foods and non-foods may not be the ones that the animals use. Much work has been done on the basis for diet selection in mammals. Initially, the research on specific hungers, initiated by Curt Richter (1943), suggested that these inborn physiological mechanisms might provide the basis for selecting nutritionally adequate diet. However, subsequent research has shown that the number of these specific hungers is very limited. They have been documented for sodium, water, energy, oxygen and possibly proteins, but not for any other nutrients (Rozin 1976). Consequently, specific hungers cannot be relied on for obtaining a balanced diet, unless, perchance in a particular habitat, an adequate intake of other nutrients is entailed by their covariance with these basic ones. Considerable research has been done on the behavioural mechanisms by which mammals obtain an adequate diet in the absence of a specific hunger for each nutrient (Barker *et al.* 1977), but many aspects of this complex problem remain to be solved. In this area, we can have a fruitful interchange of ideas between those doing experimental laboratory studies and those studying the natural diets of wild animals.

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K. Milton (*Department of Anthropology, University of California, Berkeley, U.S.A.*). I have an additional comment on Dr Widdowson's question to Dr Whiten. From my work with feeding behaviour of *Hapalemur griseus*, a bamboo-specialist and *Alouatta palliata*, a folivore, I noted that individuals of both species sniffed foliage and then instantly either accepted or rejected it. This suggests that there may be olfactory cues that both prosimians and anthropoids can utilize to differentiate edible from non-edible foliage.

A. Whiten. The answer to Dr Widdowson's specific question about baboons is that we do not know. However, expanding on Professor Altmann's comment, it may be helpful at this stage of research to list the most obvious candidates for proximate mechanisms of selection or avoidance of specific constituents like fibre and protein, and summarize some relevant data which are available for other species. I suggest four alternative mechanisms: (i) direct perception through, for example, taste, smell and texture; (ii) a constituent might instead have after effects (e.g. satiety, relief of symptoms of a particular nutrient deficiency), which the animal learns to associate with immediate perceptual cues of the food concerned (and of course such learning could operate with respect to (i) also, as in learning to recognize by sight a food which tastes good); (iii) animals may evolve an innate liking for the sensations of particular foods or food classes which in their habitat offer a beneficial mixture of constituents; or (iv) young animals may copy the food habits they observe in others (although this last mechanism still begs the question of how such a cultural preference would be established in the first place).

Considering each of these possibilities with respect to protein harvesting, I know of no direct evidence bearing on (iii). By contrast there is a significant literature on possibilities (i) and (ii). This is based mostly on extensive experiments with rats (e.g. Baker *et al.* 1987), but K. Milton has drawn my attention to one experiment by Peregoy *et al.* (1972) which used monkeys. After rearing from 120–210 days old on a low (3.5%) protein diet, rhesus monkeys were allowed to feed from bins of three differently coloured foods with protein contents of 2%, 3% and 25%. Unlike well-nourished control animals, the protein depleted monkeys expressed a preference for the high protein diet within nine minutes of starting to feed. This preference became stronger over succeeding days. When the colours of the 2% and 25% diets were then reversed, the low-protein monkeys at first continued with their (now low-protein) colour preference, but over a period of days learned to switch colour preference, again selecting the 25% protein diet.

Both the rat and monkey experiments have generally been assumed to be evidence for mechanism (ii), although the fact that the monkeys studied by Peregoy *et al.* expressed a preference within nine minutes offers some support for mechanism (i). Mechanism (i) has now been advocated by Deutsch *et al.* (1989), who showed protein-deprived rats' immediate preferences for a number of specific proteins such as gluten and ovalbumin, which could not have been learned before the tests. There is evidence that these unlearned preferences are based on olfactory cues (Heinrichs *et al.* 1990). Wallin (1988) has further examined genetic components in such choice behaviour, artificially selecting for preferences for high protein content or for high energy content through 44 generations of fruitfly larvae. Both lines developed higher preferences in the selected direction.

Although there is evidence that primates readily learn aspects of foraging by watching others (mechanism (iv); Whiten 1989; Whiten & Ham 1992), the work of Peregoy *et al.* suggests that if a monkey was (strangely) led through observation of others initially to select a protein-poor diet, it would be capable of quickly and adaptively adjusting its preferences through individual learning.

I know of no equivalent work on fibre selection, but possibilities (i) and (ii) seem more obviously plausible in this case.

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R. I. M. Dunbar (*Department of Anthropology, University College London, U.K.*). Most of the discussion of dietary nutrients has focused on proteins and secondary compounds, and the role of energy in animals' nutritional budgets has been ignored. Yet, analyses of the time budgets of baboons shows that a significant proportion of the time that animals in a given population have to spend feeding is a function of the habitat's ambient temperature, suggesting that thermoregulatory costs may be important. For a tropical mammal, this in itself is surprising, as it seems that baboons face significant thermoregulatory costs even at altitudes as low as 1000 m above sea level. But it does seem to me to underline the importance of energy as a component of an animal's diet.

A. Whiten. I agree with Dr Dunbar that available energy should be an important 'constituent' to consider and in principle this could be included in the type of multivariate analysis we have advocated. It may turn out to discriminate foods and non-foods even better than the specific nutrients we have considered. However, we have been reluctant to assess overall energy by using calorimetry, because we do not know how much of this energy can be extracted (wood, after all, is a non-food with high energy content). We have preferred to examine specific nutrients, some of which are obvious candidates for selection as energy sources. Of these, fat was shown to be positively valued, particularly in the class of fleshy stem bases which constituted the staple food in the winter period. Starch, by contrast, which was common in some storage organs, did not appear to figure in selection rules: nor did total carbohydrate. However, the latter was estimated crudely, by subtraction. Once we can determine digestibile carbohydrates, it will be possible to compute available energy from this and the protein and fat components, and enter this into the multivariate analyses.