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Nutritional constraints on mountain baboons *(Papio ursinus)*: implications for baboon socioecology

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Summary. Populations of baboon (*Papio* sp.) at geographic and climatic extremes for the genus show a tendency to one-male organization, whereas most baboons live in multimale social groups; this effect has been attributed largely to limitation of food supply, but baboons' complex diet has hindered proper nutritional analyses. To test these optimal-diet explanations of social variation, we quantified intake and used phytochemical analysis of foods to compare the nutrition, during seasonal changes, of two groups of mountain baboons *(P. ursinus)* living at different altitudes of a continuous grassland habitat. The majority of plant foods were eaten uniquely by one or other group, though their altitudinal separation was only 400 m, and the time budget of feeding choices varied with age-sex class as well as season. Converting to a common currency of nutrients reveals that baboons gained the same yield from a unit time spent foraging (whether this is measured in edible dry weight, or simply protein) in both groups, despite their differing mean altitude, whereas seasonal variation was large and statistically significant. Increased feeding time at the winter "bottleneck" made no effective compensation for the poorer food yields: in late winter there was a minimum for daily nutrient gain at both altitudes. Apparently this population is already at an extreme for the time animals devote to foraging in winter, when they rely on inconspicuous and slow-to-harvest swollen shoot bases and underground plant storage organs. Since an individual's nutrient yield does not vary with altitude, we conclude that socioecological parameters are effectively optimized for feeding. Since contest competition is absent, this adjustment of foraging efficiency is largely through the effect of differential density on scramble competition. Differences in social structure are considered to be a secondray consequence of optimal foraging, mediated through altitudinal variation in either population density or in day range limits.

Key words: Baboon – Socioecology – Diet – Altitude – Seasonality

Introduction

Socioecological explanations for primate behaviour routinely make use of diet as an intervening variable between the environment and a population's distribution, abundance and social organization (e.g. Crook and Gartlan 1964; Altmann 1974; Wrangham 1979, 1987). These population parameters are assumed to result from adaptations to optimize dietary intake and other factors such as avoiding predation. However, given the complexity of primate diets, actual food intake has seldom been quantified – an obvious problem in testing socioecological models.

Only in the case of animals with very simple diets has it generally been possible to back optimality theorizing by measurement of the diet obtained, in units that make sense for an individual's reproductive success. This approach has been used successfully for species that eat homogeneous foods [e.g. insects eaten by starlings *Sturnus vulgarus* (Kacelnik 1984), or by sticklebacks *Gasterosteus aculeatus* (Milinski and Heller 1978); nectar eaten by sunbirds *Nectarina reichenowi* (Gill and Wolf 1975), or by bees (Schmid-Hempel et al. 1985)]. Varied diets in herbivores are more difficult to quantify, but species with compound stomachs nevertheless often eat a restricted range of plants and some quantification has been possible [e.g. moose *Alces alces* (Belovski 1984); antelope (Jarman 1974); langurs *Presbytis* spp., (Hladik 1977)].

Primates which lack gut specializations to ferment leaves, however, often have very complex diets. This complexity applies especially to some of the more terrestrial species [e.g. chimpanzees *Pan troglodytes* of Mahale, Tanzania, have been recorded eating 328 plant foods from 198 species (Nishida and Uehara 1983); baboons *Papio cynocephalus* of Mikumi, Tanzania, utilize between

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one and six parts from each of 185 species of plant (Norton et al. 1987); and yearling baboons of Amboseli, Kenya, ate 277 foods in total (Altmann 1991); a single group of mountain gorillas *Gorilla g. beringei* was recorded to eat 75 foods from 38 plant species (Watts 1984)]. Each food contains a different balance of nutrients and digestion inhibitors, and each needs to be treated separately to measure its value to the animal. This has made proper assessment of the nutritional constraints on the behaviour of most primates a demanding matter, and consequently rarer (but see Hladik 1973; Watts 1984; Altmann 1991; Wrangham et al. 1991; and references in Barton 1992).

The African and Arabian baboons *Papio* spp. are of particular interest for primate socioecology, since their adaptability and wide habitat tolerance are accompanied by striking variations in social organization (see Kummer 1968, 1984; Altmann 1974; Anderson 1982, 1983; Byrne et al. 1987, 1990). At the north-eastern and southern extremes of the genus' range, small groups led by one or two males occur, routinely in *P. hamadryas* and at times in several montane populations of *P. ursinus*. In between, the typical baboon organization is a large multi-male, multi-female troop. Differences of this kind have clear implications for the sociobiological strategies of individuals. The occurrence of one-male groups has been explained as a consequence of low population densities, which themselves result from very sparse food supplies [in desert habitats of north-west Africa and Arabia (Kummer 1984); in subalpine habitats of South Africa (Byrne et al. 1987)]. Although these attempts to explain variations in social organization rely on postulation of food supply limitations, their assumptions have not been tested at any of the sites where one-male groups are regularly found.

The chacma baboons *Papio ursinus* of the Drakensberg mountains, South Africa, are of especial relevance to the hypothesis that sparse food is limiting, since the altitudinal gradient of the mountains has striking effects on the habitat within the same baboon population, and one-male groups have been recorded in the higher zones (Whiten et al. 1987; Byrne et al. 1987). In addition, the climate at this latitude is seasonal, with a long, dry winter presumably imposing extra nutritional stress before the spring allows plant growth to resume. In other ways, the site is conveniently "simple" in its ecology, with abundant water, essentially no shade and no serious threat of predation on baboons (Whiten et al. 1987; Byrne et al. 1987). Baboons at this site are thus ideal for testing optimality models of nutrient intake.

This paper examines the diet of two groups of these "mountain baboons" living at different altitudes in the Drakensberg. The period of study, from the middle of winter to the middle of summer, spanned the range of possibilities for a nutritional "bottleneck"; after midsummer, food becomes visibly more abundant for the baboons, and this plenty is then gradually eroded during the winter. In support of this claim, Henzi et al. (1992) showed that day journey length increased with decreasing food availability, and showed a sharp increase in length for both groups in late winter; this is also the period of greatest mortality for antelope in the same area (Scotcher 1982). In principle, ambient temperature differences at the differing altitudes of the two groups' ranges could complicate comparisons of nutrition, since below a critical level (which depends on body weight) homeothermic animals increase metabolic heat production, thus requiring more energy for warmth alone (Peters 1983). However, in practice the mean daily maxima at the two sites are above the critical temperatures for chacma baboons (rising to 15–16 °C even in midwinter), and the mean daily minima do not differ significantly (correlated *t*-test, $t = 1.83$, $P > 0.05$) and are actually slightly lower at the lower altitude in midwinter.

To test the adequacy of current socioecological theories for baboons, nutritional comparisons are required, both within this study and ultimately with other populations in the rest of the range of the genus. For this to be possible, it is essential to go beyond description in terms of food lists (which may vary even on a scale of a few kilometers or a few weeks), to the timebudgets of individuals' feeding choices, and finally to the currency of actual nutrients obtained from foraging. Only then is it possible to ask whether nutrition differs between groups living at different altitudes, or between different seasons; whether equivalent nutrition can be obtained at the expense of greater effort at higher altitudes and harsher times of year; and whether any nutritional bottleneck (not necessarily at the same time at different altitudes) occurs for these animals.

Methods

Details of the Giants Castle study site are given in Whiten et al. (1987), and the study animals are described fully in Byrne et al. (1990). In this paper, data from two groups (9 of "High group", whose range centred on 2250 m, and 13 of "Low group", whose range centred on 1835 m) is analysed over the 6-month period from 19 July 1983 to 10 January 1984.

The order in which subjects were selected for focal animal sampling was opportunistic within each group, because of constraints on observation caused by steep terrain, extreme group dispersion and difficulties of habituation. However, selection was guided by an attempt to obtain similar amounts of data from each independently moving individual in each month. Focal samples were of 15 min duration, since pilot observation showed that the risk of losing track of a subject became severe with longer samples; within focal periods, instantaneous samples were made of activity at 2-min intervals, since almost all foods were processed in less than 2 min. If the subject was feeding, the species and part was noted.

We collected samples for phytochemical analysis of the commoner plant foods in the diet of either group, over the same period as we observed the baboons eating them. We processed these items in as close a fashion as possible to that used by the baboons, so that food samples consisted of only the portion of the plant normally ingested. (Control items, and discarded material from foods, were also collected, and the baboons' selection criteria have been analyses elsewhere: see Whiten et al. 1990, 1991). Samples of approximately 10 g wet weight were accumulated, noting the number of estimated "baboon handfuls" each sample represented. Duplicates, up to ten samples per food, were collected in most cases. Each was weighed accurately and then dried in an open low-temperature oven to constant weight. Samples were then sealed in individual plastic bags and stored in a dry, dark environment to await transport to the United Kingdom for chemical analysis.

Phytochemical analysis was carried out in the Department of Psychology, University of St Andrews, except for the protein assay which was done by the Panmure Trading Company, Monikie Granary, and simple sugar content determination for a few foods which was done by Scottish Grain Distillers. Each sample was analysed for fibre content [acid-detergent fibre (ADF) assay (Goering and van Soest 1970) divided by 1.2 to give percentage dry weight], and phenolics and tannins were extracted in 80% aqueous methanol. Total phenolics, as tannic acid (Folin-Denis assay, divided by 7.5 to give percentage dry weight), and condensed tannins (proanthocyanidin method) were then measured; see Mole and Waterman (1987) for both methods. Nitrogen content was analysed by the micro-Kjeldahl method (Allen et al. 1974) and multiplied by 6.25 to give crude protein. Lipids were determined with the Soxhlet method, extracting the sample for 5 h in petroleum ether. Simple sugars were determined by high-performance liquid chromatography. Starch was tested with iodine reaction, with the strength of reaction graded on an arbitrary scale of 0 to 3. Dry weight of a typical "baboon handful" of each food was obtained by division of the samples' final dry weight by the estimated number of handfuls involved, and water content calculated from the wet weight recorded in the field. An estimate of the total edible fraction of each food was obtained by subtraction of the percentages of both fibre and whichever is the larger of condensed tannin and total phenolics. (Despite the terms, condensed tannin is not necessarily included within total phenolics and these measures overlap to an unknown extent in any given case). Note that this is a *maximum* estimate; it is likely in practice that a baboon fails to digest more fibre than is estimated with an ADF test, and digestion inhibitors will further lower effective utilization of nutrients. Results from duplicate samples were averaged, since in general they agreed closely.

Separate periods of focal observation were used to estimate processing rates for different foods. A hand-held portable computer (Hewlett Packard HP41) was programmed to calculate feeding times and rates. Button presses were used to indicate starts and ends of feeding bouts, handfuls of food ingested within a bout, and the times at which items were eaten singly while "travel feeding". The computer prompted for the plant name and part eaten after each feeding bout. Thus the time to process an average baboon handful of the food could be calculated.

Throughout the study, regular scan samples were also taken at 30-min intervals of the activity of each visible animal (including whether it was "feeding" or "moving", which normally meant movement as part of foraging). The baboons were categorized into adult males, adult females, juveniles and infants.

Results

To study seasonal changes in the diet of each group in more detail, the data were divided into three periods: 19 July to 3 September "late winter", 4 September to 10 October "spring", and 11 October to 10 January "early summer". Focal data for some of the animals were insufficient to carry out all statistical analyses at the level of individuals. Instead, individuals were grouped into four age-sex classes: adult male (High group: JG; Low group: DV, HL, ME), adult female (High group: PK, SP, ML; Low group: JA, ST, CH), older juvenile (High group: JM, SK; Low group: SZ, TR, CA, PL) and younger juvenile (High group: PA, DR, RO; Low group: SF, SY, SO); see Byrne et al. (1990) for further details of these individuals. Data were pooled within these four classes in each group, enabling statistical comparison between groups and seasons to be carried out systematically, with age-sex classes as the replicates.

Diet diversity

All items recorded as eaten by either study group over this period are given by species and part consumed in Table 1. Where the food was also recorded during focal samples, its percentage contribution to each group's diet is given for each of the three seasons (in terms of time spent eating).

The summed totals for the number of different food types utilized in each season, and the totals for more major items that make up more than 1% of feeding time at each season, were first examined (see Table 1). These simple parameters might be expected to reflect the facts that (i) population density is much lower at the higher altitude (Whiten et al. 1987), presumably as a result of food limitations, and (ii) late winter is the time when green plants are least visible in the Drakensberg. Low group indeed proved to have a greater range of diet items available than High group in late winter and spring, and each group had more items available in spring than winter. However, other effects are less straighforward. In early summer, High group ate a wider range of foods than Low group, and both groups' diets included a similar number of "major foods" (≥1% of feeding time). Furthermore, none of the effects is large, except the relative impoverishment in range of major foods used by High group in late winter. But in any case, these frequencies tell us only how a baboon's feeding time is spread over the available foods, not what it obtains thereby; for instance, even High group in late winter *may* be obtaining an excellent diet, depending on exactly what their feeding time yields.

The lack of diet overlap between the two groups is striking given the proximity of the two groups. Again taking 1% of feeding time as the criterion for a major food, few foods which are major foods for either group in a season are major ones for both. Discounting foods not identified specifically, 2 out of 16 major foods in late winter are shared between the groups, 4 out of 13 in spring, and 5 out of 21 in early summer. In late winter, these two groups only share 6 plant foods in all, out of the 27 species they were recorded as eating; as spring advances, many plants naturally appear at first low then high altitude, yet over the whole study 42 plant items were recorded uniquely in one group, against 19 in both. Most plants, therefore, are important only to one of the two groups, despite their altitudinal separation of only around 400 m and horizontal distance apart of only 8 km.

Each group's diet also shows strong seasonality in plant species eaten. Not only is a wider range of plants eaten as the spring progresses, but only three plants for High group and three for Low Group are major items in all three periods, apart from unidentified forbs and grasses.

Age-sex differences in feeding

It is evident from these preliminary analyses that feeding behaviour in each group differs according to season and

Table 1. Foods eaten by mountain baboons during the study

Code	Species name	[a] part	Winter		Spring		Summer	
			High	Low	High	Low	High	Low
acai	*Acalypha punctata*	fl	0.00	0.00	0.00	0.00	0.00	3.98
acal	*Acalypha punctata*	lf	0.00	0.00	0.00	0.00	0.88	0.00
sygl	*Alepidea woodii*	lf	0.47	0.00	0.00	0.00	0.58	0.00
aloi	*Aloe saponaria*	fl	1.18	0.42	0.00	0.00	0.00	0.00
alol	*Aloe saponaria*	lf	0.00	0.00	0.00	0.00	0.00	0.00
fanb	*Aristea ecklonii*	lb	0.16	0.00	0.00	0.00	0.00	0.00
asci	*Asclepias stellifera*	fl	0.00	0.00	0.00	0.17	0.00	0.00
carb	*Carex zuluensis*	lb	8.37	0.00	11.90	0.00	1.11	0.00
carl	*Carex zuluensis*	lf	0.24	0.00	0.51	0.00	0.00	0.00
cled	*Clematis brachiata*	st	0.00	0.00	0.00	0.00	0.47	0.27
cusf	*Cussonia paniculata*	fr	0.00	4.75	0.00	0.43	0.00	0.00
cyri	*Cyrtanthus tuckii*	fl	0.00	0.00	0.00	0.35	0.00	0.00
diei	*Dierama dracomontanum*	fl	0.00	0.00	0.00	0.00	2.17	0.00
diec	*Dierama robusta*	cm	0.16	0.00	0.16	0.00	0.19	0.00
dieb	*Dierama robusta*	lb	0.00	0.00	0.00	0.00	0.00	0.00
grai	*Elionurus muticus*	fl	0.00	0.00	0.27	1.41	16.68	2.02
ceri	*Erica cerinthoides*	fl	0.00	0.76	0.00	0.00	0.00	0.00
eucb	*Eucomis bicolor*	lb	0.00	0.00	0.00	0.00	0.00	0.00
opbb	*Eulophia foliosa*	lb	0.00	0.00	0.00	0.00	0.24	9.37
opbc	*Eulophia foliosa*	cm	0.00	7.70	0.24	9.67	0.27	9.51
opbi	*Eulophia foliosa*	fl	0.00	0.00	0.00	0.14	0.00	0.00
clal	*Euphorbia clavarioides*	lf	0.00	0.00	0.00	0.00	0.00	0.00
spui	*Euphorbia natalensis*	fl	0.00	0.00	0.00	0.17	0.00	2.31
fesi	*Festuca costata*	fl	0.00	0.00	0.00	0.00	0.19	0.00
gazi	*Gazania krebsiana*	fl	0.75	0.00	0.31	1.31	0.51	0.00
glai	*Gladiolus longicollis*	fl	0.00	0.00	0.00	0.29	0.24	0.00
yeld	*Haplocarpha scaposa*	st	0.00	0.00	0.00	0.00	1.29	0.49
whed	*Helichrysum ecklonis*	st	0.00	0.00	0.00	0.00	2.31	0.00
whei	*Helichrysum ecklonis*	fl	0.00	0.00	0.00	0.00	0.58	0.00
heli	*Helichrysum vernum*	fl	0.59	0.00	0.76	0.00	0.39	0.00
heri	*Herschelia baurii*	fl	0.00	0.00	0.00	0.41	0.00	0.20
whgd	*Hirpicium armeroides*	st	0.00	0.00	0.00	0.00	0.24	0.00
hypb	*Hypoxis gerrardii*	lb	0.00	0.00	0.00	0.00	0.00	0.17
hypi	*Hypoxis gerrardii*	fl	0.00	0.00	0.00	0.14	0.00	4.10
hypc	*Hypoxis gerrardii*	cm	0.16	7.14	0.81	5.02	3.33	1.37
kohi	*Kohautia amatymbica*	fl	0.00	0.00	0.62	17.50	0.44	6.41
sawb	*Kniphofia sp.*	lb	0.00	0.00	0.00	0.00	9.16	0.00
irii	*Moraea ardesiaca*	fl	0.00	0.00	0.00	0.00	0.47	0.00
mori	*Moraea stricta*	fl	0.00	0.63	7.62	0.00	0.00	0.00
morc	*Moraea stricta*	cm	25.91	0.63	27.60	4.92	3.33	1.02
oxai	*Oxalis obliquifolia*	fl	0.00	0.00	0.00	0.00	0.00	0.00
peli	*Pelargonium luridum*	fl	0.00	0.00	0.00	0.00	0.00	0.00
caft	*Protea caffra*	sd	0.00	1.67	0.00	0.69	0.00	0.38
rups	*Protea roupelliae*	sd	0.00	4.47	0.00	0.78	0.00	0.79
cafs	*Protea subvestita*	sd	0.94	0.00	0.47	0.00	0.00	0.00
nasl	*Ranunculus baurii*	lf	0.00	0.00	0.00	0.00	0.19	0.20
sori	*Rumex woodii*	fl	0.00	0.00	0.00	0.00	2.14	0.00
scib	*Scilla natalensis*	lb	0.00	0.00	0.00	0.00	0.00	1.10
gwsb	*Scirpus falsus*	lb	30.85	9.90	14.61	9.15	0.47	0.00
gwsl	*Scirpus falsus*	lf	0.32	0.00	1.35	0.00	0.00	0.00
sesd	*Senecio macrocephalus*	st	0.00	0.42	0.00	0.79	0.51	0.35
trib	*Sporobulus congoensis*	lb	0.00	22.24	0.00	2.58	0.00	0.00
gari	*Tulbaghia natalensis*	fl	0.00	1.67	0.00	0.22	0.00	0.00
grsb	*Tetraria cuspidata*	lb	0.00	2.72	0.00	0.00	0.00	0.00
grsi	*Tetraria cuspidata*	fl	0.00	0.00	0.00	0.00	0.00	0.20
velb	*Vellozia viscosa*	lb	0.00	0.00	0.00	0.00	0.00	0.00
beli	*Wahlenbergia grandiflora*	fl	0.00	0.00	0.00	0.00	0.00	0.31
watc	*Watsonia lepida*	cm	4.89	5.47	6.64	7.77	9.76	4.28
watb	*Watsonia lepida*	lb	0.32	4.31	1.14	2.74	2.46	0.96
wati	*Watsonia lepida*	fl	0.00	0.00	0.00	0.22	1.81	3.86
meri	*Watsonia socium*	fl	0.00	0.00	0.00	0.00	0.00	0.68
merc	*Watsonia socium*	cm	0.00	6.47	0.00	0.00	0.00	0.52
merb	*Watsonia socium*	lb	0.00	0.00	0.00	0.22	0.00	0.00
inva	invertebrate	tt	4.09	2.86	6.33	4.20	4.06	2.60
musa	field mushroom	tt	0.00	0.00	0.00	0.00	0.00	0.98
pufa	puffball	tt	0.00	0.00	0.00	0.17	0.70	0.20

Table 1. Continued

Code	Species name	ᵃ part	Winter		Spring		Summer	
			High	Low	High	Low	High	Low
psfl	forb-1	lf	0.63	0.00	0.00	0.00	0.00	0.00
pkgi	forb-2	fl	0.00	0.00	0.00	0.00	0.19	0.00
plsb	sedge-1	lb	0.00	1.90	0.00	0.00	0.00	0.00
forl	unidentified forb sp.	lf	2.06	0.76	12.42	10.49	27.49	17.01
gral	unidentified grass sp.	lf	17.91	13.12	6.02	16.84	1.95	7.88
fori	unidentified forb sp.	fl	0.00	0.00	0.24	1.03	0.90	0.31
ford	unidentified forb sp.	st	0.00	0.00	0.00	0.00	0.94	1.23
forb	unidentified forb sp.	lb	0.00	0.00	0.00	0.14	1.33	0.86
Total eaten			19	21	20	30	37	33
Total forming over 1% diet			8	15	10	14	16	16

Percentage time spent eating each food type during each season (winter, spring, summer) by the two study groups (High, Low), is given for foods recorded during focal-sample observations

[a] Parts eaten: fl, inflorescence; lf, leaf; st, stem; lb, swollen base of leaf or shoot; fr, fleshy fruit; sd, dry seed; cm, underground storage organ; tt, entive item

Table 2A. Percentage time that each age-sex class spent eating each food type in High group during each season

Food	Male			Female			Older juvenile			Younger juvenile		
	Winter	Spring	Summer	Winter	Spring	Summer	Winter	Spring	Summer	Winter	Spring	Summer
acai	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
acal	0.00	0.00	3.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sygl	0.00	0.00	0.00	0.00	0.00	2.33	1.89	0.00	0.00	0.00	0.00	0.00
aloi	2.82	0.00	0.00	0.00	0.00	0.00	1.89	0.00	0.00	0.00	0.00	0.00
fanb	0.00	0.00	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
asci	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
carb	7.04	16.19	3.51	6.41	10.05	0.00	14.15	13.04	0.00	5.88	8.33	0.94
carl	0.00	0.95	0.00	0.00	0.48	0.00	0.94	0.62	0.00	0.00	0.00	0.00
cled	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.89
cusf	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cyri	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
diei	0.00	0.00	0.00	0.00	0.00	7.75	0.00	0.00	0.00	0.00	0.00	0.94
diec	0.00	0.00	0.00	0.64	0.00	0.78	0.00	0.62	0.00	0.00	0.00	0.00
grai	0.00	0.00	26.32	0.00	0.48	19.38	0.00	0.62	16.30	0.00	0.00	4.72
ceri	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
opbb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94
opbc	0.00	0.00	0.00	0.00	0.96	0.00	0.00	0.00	1.09	0.00	0.00	0.00
opbi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
spui	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
fesi	0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.00	0.00	0.00	0.00	0.00
gazi	1.41	0.00	0.00	0.64	0.00	0.00	0.94	1.24	1.09	0.00	0.00	0.94
glai	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94
yeld	0.00	0.00	1.75	0.00	0.00	2.33	0.00	0.00	1.09	0.00	0.00	0.00
whed	0.00	0.00	1.75	0.00	0.00	1.55	0.00	0.00	2.17	0.00	0.00	3.77
whei	0.00	0.00	0.00	0.00	0.00	2.33	0.00	0.00	0.00	0.00	0.00	0.00
heli	0.00	0.00	0.00	0.00	0.96	1.55	0.00	0.00	0.00	2.35	2.08	0.00
heri	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
whgd	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94
hypb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
hypi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
hypc	0.00	1.90	10.53	0.64	0.00	0.78	0.00	0.62	1.09	0.00	0.69	0.94
kohi	0.00	0.00	1.75	0.00	0.00	0.00	0.00	2.48	0.00	0.00	0.00	0.00
sawb	0.00	0.00	3.51	0.00	0.00	2.33	0.00	0.00	11.96	0.00	0.00	18.87
irii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.89
mori	0.00	4.76	0.00	0.00	6.22	0.00	0.00	5.59	0.00	0.00	13.89	0.00
morc	36.62	32.38	1.75	17.31	25.84	0.78	27.36	28.57	3.26	22.35	23.61	7.55
caft	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rups	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cafs	0.00	0.00	0.00	0.00	0.00	0.00	3.77	1.86	0.00	0.00	0.00	0.00
nasl	0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.00	0.00	0.00	0.00	0.00
sori	0.00	0.00	0.00	0.00	0.00	2.33	0.00	0.00	4.35	0.00	0.00	1.89
scib	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
gwsb	26.76	7.62	0.00	38.46	18.66	0.00	21.70	9.94	0.00	36.47	22.22	1.89
gwsl	0.00	0.00	0.00	1.28	1.91	0.00	0.00	0.00	0.00	0.00	3.47	0.00

Table 2A. Continued

Food	Male			Female			Older juvenile			Younger juvenile		
	Winter	Spring	Summer	Winter	Spring	Summer	Winter	Spring	Summer	Winter	Spring	Summer
sesd	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.94
trib	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
gari	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
grsb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
grsi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
beli	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
watc	8.45	16.19	21.05	1.92	4.78	3.88	5.66	5.59	14.13	3.53	0.00	0.00
watb	0.00	0.95	1.75	1.28	0.96	0.78	0.00	1.24	5.43	0.00	1.39	1.89
wati	0.00	0.00	3.51	0.00	0.00	0.78	0.00	0.00	1.09	0.00	0.00	1.89
meri	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
merc	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
merb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
inva	1.41	6.67	7.02	3.21	4.78	2.33	0.00	6.21	2.17	11.76	7.64	4.72
musa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pufa	0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.00	1.09	0.00	0.00	0.94
forl	2.82	8.57	12.28	4.49	17.70	37.98	0.94	13.66	30.43	0.00	9.72	29.25
gral	12.68	2.86	0.00	22.44	6.22	3.88	18.87	8.07	1.09	17.65	6.94	2.83
psfl	0.00	0.00	0.00	0.64	0.00	0.00	1.89	0.00	0.00	0.00	0.00	0.00
fori	0.00	0.95	0.00	0.00	0.00	1.55	0.00	0.00	1.09	0.00	0.00	0.94
pkgi	0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.00	0.00	0.00	0.00	0.00
ford	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.77
forb	0.00	0.00	0.00	0.00	0.00	1.55	0.00	0.00	0.00	0.00	0.00	3.77
plsb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 2B. Percentage time that each age-sex class spent eating each food type in Low group during each season

Food	Male			Female			Older juvenile			Younger juvenile		
	Winter	Spring	Summer	Winter	Spring	Summer	Winter	Spring	Summer	Winter	Spring	Summer
acai	0.00	0.00	7.53	0.00	0.00	1.25	0.00	0.00	5.74	0.00	0.00	1.39
acal	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sygl	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
aloi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.69	0.00	0.00
fanb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
asci	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.00
carb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
carl	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cled	0.00	0.00	1.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cusf	7.50	1.74	0.00	3.03	0.00	0.00	0.00	0.00	0.00	8.47	0.00	0.00
cyri	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.39	0.00
diei	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
diec	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
grai	0.00	0.00	1.08	0.00	2.86	0.00	0.00	0.00	4.92	0.00	2.78	2.08
ceri	0.00	0.00	0.00	3.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
opbb	0.00	0.00	8.60	0.00	0.00	16.25	0.00	0.00	9.84	0.00	0.00	2.78
opbc	2.50	6.96	13.98	18.18	8.57	8.75	3.33	12.72	13.93	6.78	10.42	1.39
opbi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.58	0.00	0.00	0.00	0.00
spui	0.00	0.00	1.08	0.00	0.00	3.75	0.00	0.00	1.64	0.00	0.69	2.78
fesi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
gazi	0.00	1.74	0.00	0.00	0.95	0.00	0.00	1.16	0.00	0.00	1.39	0.00
glai	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.16	0.00	0.00	0.00	0.00
yeld	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00	0.00	0.00	0.00	0.69
whed	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
whei	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
heli	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
heri	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.82	0.00	0.69	0.00
whgd	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
hypb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69
hypi	0.00	0.00	5.38	0.00	0.00	2.50	0.00	0.58	5.74	0.00	0.00	2.78
hypc	0.00	5.22	1.08	15.15	6.67	1.25	8.33	4.05	2.46	5.08	4.17	0.69
kohi	0.00	13.91	6.45	0.00	28.57	11.25	0.00	15.03	6.56	0.00	12.50	1.39
sawb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 2B. Continued

Food	Male			Female			Older juvenile			Younger juvenile		
	Winter	Spring	Summer	Winter	Spring	Summer	Winter	Spring	Summer	Winter	Spring	Summer
irii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
mori	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
morc	2.50	4.35	2.15	0.00	2.86	1.25	0.00	6.94	0.00	0.00	5.56	0.69
caft	5.00	0.00	0.00	0.00	0.00	0.00	1.67	0.00	0.82	0.00	2.78	0.69
rups	0.00	1.74	0.00	6.06	0.00	0.00	3.33	0.00	2.46	8.47	1.39	0.69
cafs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nasl	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.82	0.00	0.00	0.00
sori	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
scib	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00	2.46	0.00	0.00	0.69
gwsb	10.00	10.43	0.00	6.06	4.76	0.00	10.00	7.51	0.00	13.56	13.89	0.00
gwsl	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sesd	0.00	0.00	0.00	0.00	1.90	0.00	0.00	0.58	0.00	1.69	0.69	1.39
trib	15.00	1.74	0.00	15.15	0.00	0.00	30.00	2.31	0.00	28.81	6.25	0.00
gari	0.00	0.87	0.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00	0.00	0.00
grsb	7.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.39	0.00	0.00
grsi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.82	0.00	0.00	0.00
beli	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00	0.00	0.00	0.00	0.00
watc	2.50	18.26	9.68	6.06	7.62	1.25	13.33	1.73	4.10	0.00	3.47	2.08
watb	12.50	2.61	1.08	3.03	0.95	1.25	0.00	4.62	0.82	1.69	2.78	0.69
wati	0.00	0.87	4.30	0.00	0.00	2.50	0.00	0.00	6.56	0.00	0.00	2.08
meri	0.00	0.00	1.08	0.00	0.00	0.00	0.00	0.00	1.64	0.00	0.00	0.00
merc	22.50	0.00	0.00	0.00	0.00	0.00	1.67	0.00	0.00	1.69	0.00	2.08
merb	0.00	0.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
inva	0.00	7.83	3.23	3.03	2.86	2.50	3.33	4.05	3.28	5.08	2.08	1.39
musa	0.00	0.00	3.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69
pufa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.82	0.00	0.69	0.00
forl	0.00	6.09	17.20	3.03	9.52	22.50	0.00	17.34	17.21	0.00	9.03	11.11
gral	7.50	13.91	9.68	18.18	20.00	16.25	18.33	16.76	4.92	8.47	16.67	0.69
psfl	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
fori	0.00	0.87	0.00	0.00	0.95	1.25	0.00	2.31	0.00	0.00	0.00	0.00
pkgi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ford	0.00	0.00	2.15	0.00	0.00	1.25	0.00	0.00	0.82	0.00	0.00	0.69
forb	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.58	0.82	0.00	0.00	1.39
plsb	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.08	0.00	0.00

altitude. Do age-sex classes also differ significantly from each other, regardless of group of residence? To examine differences in feeding pattern in more detail, the percentages of time that each age-sex class spends feeding on each food type were calculated (Table 2A for High group, 2B for Low group), for each season.

For statistical comparisons, raw frequencies were examined with the χ^2 test. The data were aggregated into categories according to the parts of the plant that were eaten (leaves, stems and stem bases, inflorescences and seeds, and corms), in order to examine seasonal changes and differences between age-sex classes. (In the tests below, unidentified insects were excluded; the data were also examined with insect food kept as a category, and the results were essentially the same.)

Within each age-sex class, seasonal variation in the pattern of eating different plant parts was highly significant in all cases (High group: males $\chi^2 = 35.1$, $P \leq 0.001$; females $\chi^2 = 149.2$, $P \leq 0.001$; older juveniles $\chi^2 = 22.4$, $P \leq 0.001$; younger juveniles $\chi^2 = 25.8$, $P \leq 0.001$; Low group: males $\chi^2 = 25.4$, $P \leq 0.001$; females $\chi^2 = 24.0$, $P \leq 0.001$; older juveniles $\chi^2 = 35.3$, $P \leq 0.001$; younger juveniles $\chi^2 = 33.8$, $P \leq 0.001$; $df = 6$ in all cases). This result is a predictable one, since the above-ground portions of plants are severely limited in late winter in this habitat: animals of all ages and sexes are naturally forced to rely more on underground storage organs, leaves and stem bases in this harsh time than in early summer, by which time inflorescences and seeds are available.

Within each season, however, differences persist *between* age-sex classes in most cases (High group: late winter $\chi^2 = 23.2$, $P \leq 0.01$; spring $\chi^2 = 30.0$, $P \leq 0.01$; early summer $\chi^2 = 71.2$, $P \leq 0.001$; Low group: late winter $\chi^2 = 16.7$, $P \leq 0.05$; spring $\chi^2 = 26.3$, $P \leq 0.01$; early summer $\chi^2 = 15.7$, ns; $df = 9$ in all cases). Clearly, in further analyses the age-sex classes as well as seasons must be kept separate.

These effects appear to have rather different origins in the two groups (see Fig. 1). In High group, adult male reliance upon undergroup storage organs at all seasons is striking; females spend more time eating leaves than do other animals, especially in early summer; and young juveniles seem to rely more than other animals on shoot bases and especially insects, even when a wider range of food is available in summer. In Low group, all these

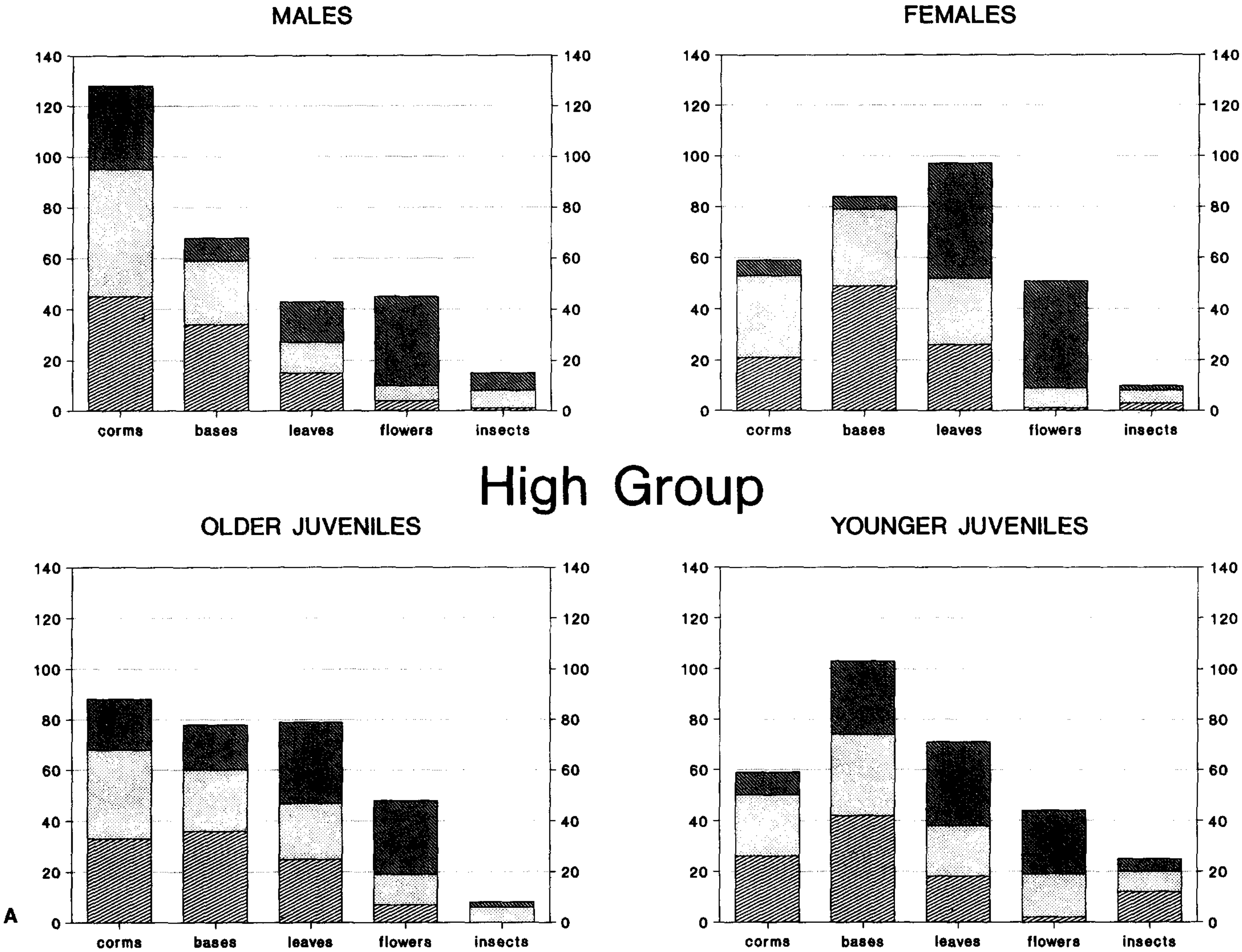

Fig. 1A, B. Seasonal variation in usage of food types for **A** High group and **B** Low group. In each season, usage is expressed as a percentage of overall feeding time budget. In each column, late winter feeding time is at the base *(broad stripes)*, then spring *(stippling)*, with early summer at the top *(close stripes)*

effects are less obvious, though the importance of underground storage organs for males is still clear, as is the use of shoot bases by young juveniles. The latter effect is likely partly to reflect the lack of processing necessary to exploit the soft bases of various monocotyledons available in spring and summer. However, in late winter shoot bases are important for all age-sex classes, and at that season the only bases available are those of grasses and sedges. These are inconspicuous and slow to process, and the large amount of time devoted to their exploitation must therefore reflect the lack of alternative foods for Low group at this time.

Nutritive yield of time spent feeding

To evaluate what a baboon obtains from its actual distribution of time spent in consumption of different foods, the nutritive gain obtained in unit time is required.

Table 3 gives chemical analyses of the main foods used by mountain baboons during this study. Dry weight is used rather than wet weight; since water was not limited in the study area, whether animals gained water by drinking or by the moisture content of foods was of little relevance. The high food value of underground storage organs, in terms of their high proportion of edible matter, lack of digestion inhibitors and high starch content is immediately apparent. However, in comparison to these storage organs, protein is higher in leaves, inflorescences, stems and leaf bases, and even in *Cussonia paniculata,* the one fleshy fruit that is available to some of the population. In addition, this fruit is high in simple sugars (10.4% fructose, 11.8% glucose and 1% sucrose); however, it does not occur in the range of High group. The dry seeds of *Protea* spp. appear low in both the proportion edible and in protein, and high in fibre; it is however quite possible that our *Protea* samples included some material that baboons are able to spit out while chewing these seeds.

Table 4 shows the variation in the rates of acquisition

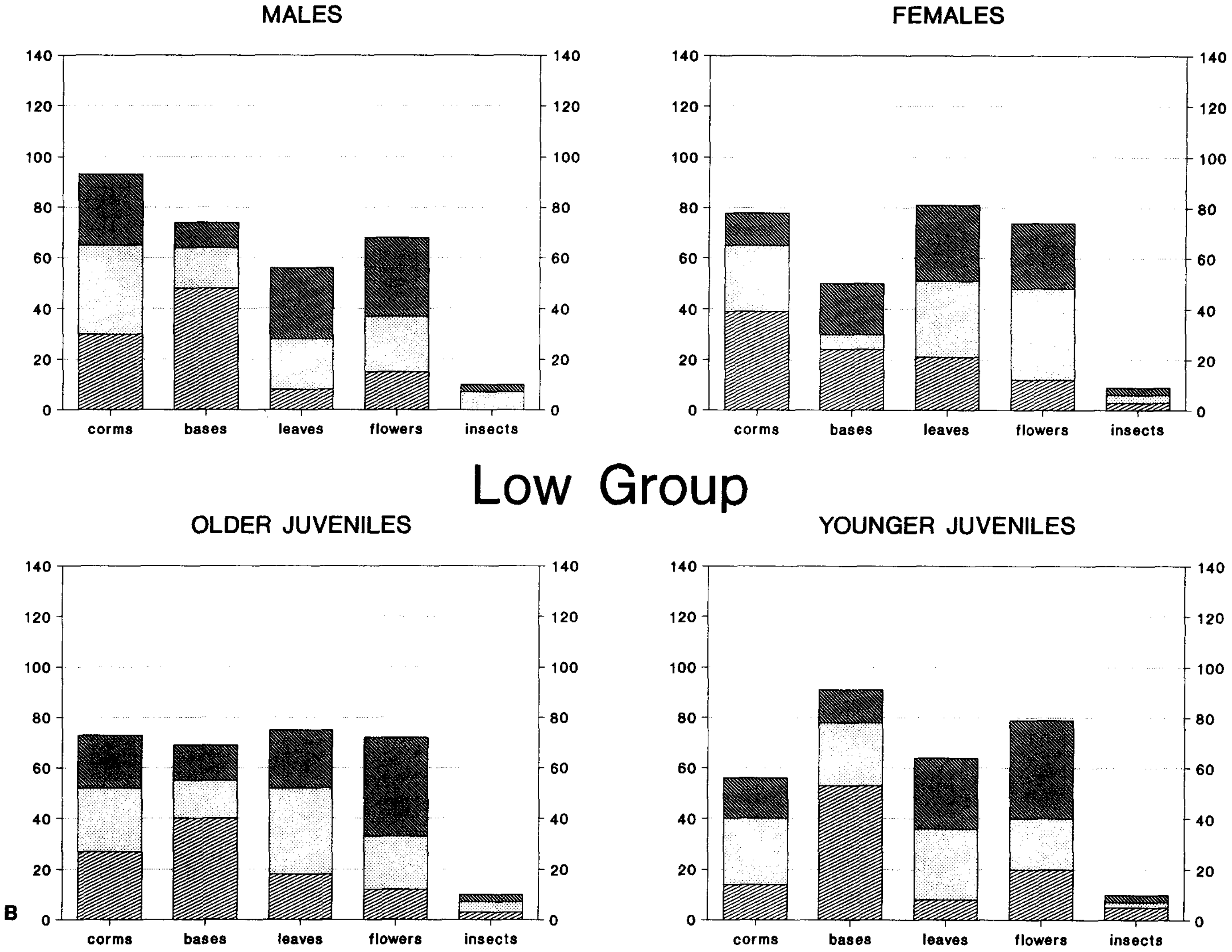

Fig. 1 (continued)

of diet items. These data were then multiplied by (i) the dry weights of items, (ii) the maximum edible content of each food, and (iii) its protein content, to give three different measures of the gain per unit time feeding on that food. Where a food had not specifically been collected for chemical analysis, the average values of nutrients for other examples of that plant part was used; where no individual measure of the dry weight of a typical baboon handful was available, the known weight of the item whose physical appearance was most similar was used. Finally, in order to estimate the actual foraging efficiency of each group at each season, the three estimates of gain per unit time on each food were each multiplied by the actual proportion of time recorded for feeding on each food. Summing over all foods then gives the gain per unit time of foraging (100 min is the period used), and enables direct comparisons to be made between different areas and different seasons in the same currency.

To examine the reliability of any differences, the consistency of differences across age-sex classes was used: thus, mean gains were computed separately for each age-sex class, for each group, for each season. Analyses of variance were then performed with the age-sex classes as the replicator variable; since the individuals were different across groups, "groups" was a between-subjects variable while "seasons" was a repeated measure variable within subjects.

These analyses were performed with each of the measures of gain, as follows. (i) Dry weight yield in 100 min foraging: the effect of seasons is significant ($F = 10.89$, $df = 12,2$, $P < = 0.002$) whereas neither groups ($F = 0.99$, $df = 6,1$) nor the interaction ($F = 0.20$, $df = 12,2$) is near significance (Table 5 shows the mean yields of each age-sex class). (ii) Maximum edible dry weight yield in 100 min foraging: a similar pattern is found with this presumably better measure of yield (Fig. 2 depicts the yield on this second measure). Here again seasons is significant ($F = 12.75$, $df = 12,2$, $P \leq 0.001$) whereas neither groups ($F = 0.40$, $df = 6,1$) nor the interaction ($F = 0.71$, $df = 12,2$) remotely approaches significance. As can be seen from Fig. 2, the superficial appearance of a difference between groups in the season of greatest food shortage (spring for Low group, late winter for High

Table 3. Chemical analyses of main foods

	WT	H_2O	ADF	CT	TP	EDIB	PROT	FAT	ST
a) Leaves									
alol	0.43	96.0	7.7	0.00	0.71	91.6	4.46	5.0	0
clal	0.75	82.0	19.0	0.00	0.64	80.4	6.08	11.5	0
forl	0.03	75.0	26.3	1.15	5.25	73.6	14.55	7.0	0
gral	0.03	80.0	28.2	0.73	2.52	69.2	11.76	6.0	0
gwsl	0.03	58.0	40.2	3.77	2.04	56.0	9.78	1.0	0
nasl	0.43	93.1	21.7	0.00	0.95	77.4	13.77	9.5	0
sygl	0.26	80.4	24.4	0.00	4.34	71.3	9.04	6.5	0
Mean nutrient value:						74.2	9.92		
b) Inflorescences									
acai	0.21	76.5	25.1	0.97	12.65	62.3	14.00	3.0	0
aloi	0.07	80.0	13.2	0.00	0.00	86.8	9.18	0.0	0
ceri	0.14	80.3	35.5	21.33	4.47	43.2	6.24	11.5	0
grai	0.02	54.4	45.3	0.00	0.33	54.4	12.12	0.0	0
gazi	0.11	82.5	27.7	0.59	3.33	69.0	8.92	9.5	0
heli	0.08	82.3	28.0	0.00	3.73	68.3	10.43	5.0	0
kohi	0.04	80.3	25.4	0.00	2.25	72.4	14.70	5.0	1
mori	0.07	73.3	19.3	0.00	1.47	79.2	13.88	5.0	0
sori	0.21	85.1	30.7	19.60	4.48	49.7	12.99	5.0	2
wati	0.46	88.2	16.3	1.19	1.44	82.3	8.45	1.0	0
whei	0.08	77.9	34.7	0.00	1.80	63.5	8.04	8.5	1
Mean nutrient value:						66.5	10.81		
c) Stems									
cled	0.26	81.7	39.5	2.47	3.40	57.1	16.44	5.0	0
sesd	0.14	89.0	21.6	0.00	2.91	75.5	7.35	6.0	0
whgd	0.06	83.6	28.4	0.00	1.84	69.8	5.42	6.0	0
yeld	0.20	85.4	31.1	0.00	1.66	67.2	8.88	11.0	0
Mean nutrient value:						67.4	9.52		
d) Underground storage organs									
diec	4.22	79.6	8.7	0.88	4.08	87.2	8.70	2.5	3
hypc	0.39	78.2	11.3	0.00	0.78	87.9	3.23	7.0	3
morc	0.21	57.9	3.8	0.00	0.32	95.9	5.54	3.0	3
opbc	0.90	86.2	25.8	0.00	0.58	73.6	3.66	3.5	0
watc	2.97	50.7	2.5	2.88	1.03	96.5	2.92	3.0	3
Mean nutrient value:						88.2	4.81		
e) Swollen leaf bases									
carb	0.11	78.3	32.9	0.00	0.98	66.1	6.91	13.0	1
fanb	0.08	67.0	26.5	2.28	1.44	71.2	7.96	2.0	0
grsb	0.02	13.2	41.4	0.00	0.40	58.2	3.49	2.0	0
gwsb	0.02	76.8	33.3	0.57	1.35	65.4	7.66	16.0	0
scib	0.54	90.5	19.3	0.00	0.75	80.0	14.40	2.0	0
sawb	0.08	87.4	27.8	0.00	0.73	71.5	16.48	13.0	0
trib	0.01	36.0	21.6	0.00	0.43	78.0	5.90	5.0	0
watb	0.20	83.8	32.8	1.15	0.96	66.1	10.68	13.0	0
Mean nutrient value:						69.6	9.19		
f) Fleshy fruits									
cusf	10.25	63.6	20.8	0.53	1.23	78.0	8.07	11.0	0
g) Dry seeds									
caft	5.65	43.0	51.1	1.80	1.21	47.1	5.20	3.0	0
rups	6.22	0.0	64.1	4.25	2.58	31.7	3.30	2.0	0
Mean nutrient value:						39.4	4.25		

Food abbreviations as in Table 1

WT, dry weight of average baboon handful; H_2O, water; other measures as % dry weight: ADF, fibre; CT, condensed tannins; TP, total phenolics; EDIB, estimated maximum % edible; PROT, protein; FAT, lipid; ST, starch, arbitrary units

Table 4. Rates of acquisition for items of different types

Type of item	Rate (min^{-1})	*n*
Watsonia (spp.) corm	0.70	12
Dierama robusta corm	0.88	7
Hypoxis gerrardii corm	1.63	5
Eulophia foliosa corm	1.45	14
Moraea stricta corm	3.03	21
Inconspicuous leaf bases[a]	8.57	20
Easy-to-find, easy-to-process items[b]	14.85	17
Protea (spp.) and *Cussonia paniculata*	0.33	estimated

[a] *Scirpus falsus, Tetraria cuspidata, Sporobulus congoensis* and "pale sedge"

[b] All other leaf bases, all inflorescences, all leaves and stems, insects and fungi

Table 5. Food yield for an average baboon in different groups and at different seasons (dry weight, g, gained in 100 min foraging time)

	Winter	Spring	Summer
High group			
Adult male	70.6	109.7	142.0
Adult female	56.7	77.4	144.1
Older juvenile	90.5	92.3	185.1
Younger juvenile	60.3	70.8	179.1
Low group			
Adult male	139.3	110.0	349.6
Adult female	98.9	77.2	109.2
Older juvenile	70.7	78.1	226.0
Younger juvenile	87.2	117.6	107.7

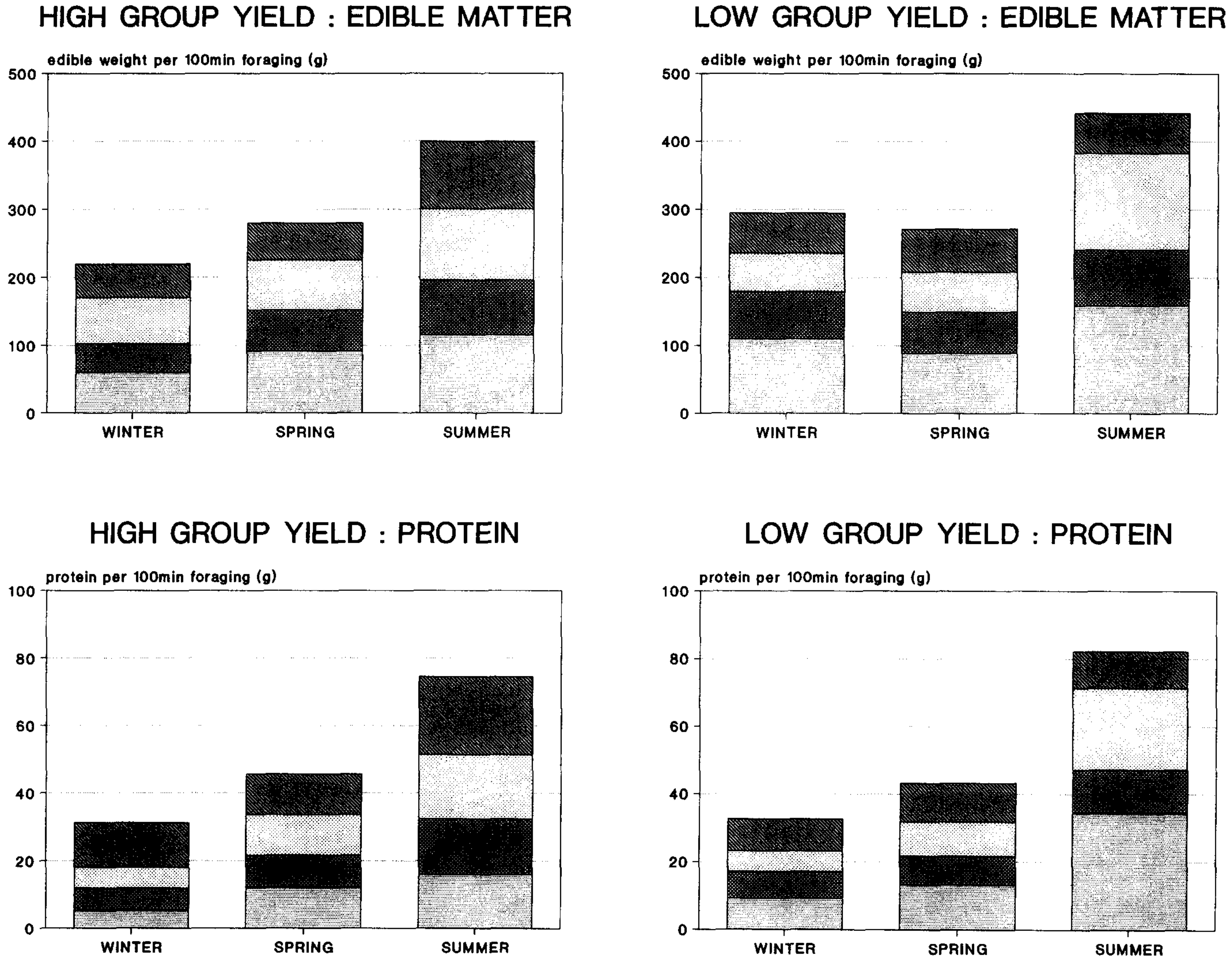

Fig. 2. Foraging efficiency of High group and Low group, measured as average yield from 100 min foraging time, in terms of edible dry weight *(upper histograms)* and protein dry weight *(lower histograms)*. Yields by each age-sex class are stacked, with males at the base *(spotting)*, then females *(fine cross-hatch)*, then older juveniles *(stippling)*, and younger juveniles at the top *(close stripes)*

Table 6. Percentage of time spent foraging at different seasons

	Late winter	Spring	Early summer
High group			
Male	73.0	71.2	66.4
Female	76.3	75.3	69.0
Juvenile	77.8	79.6	77.4
Low group			
Male	68.1	66.8	67.9
Female	73.4	79.1	70.8
Juvenile	77.7	70.8	75.7

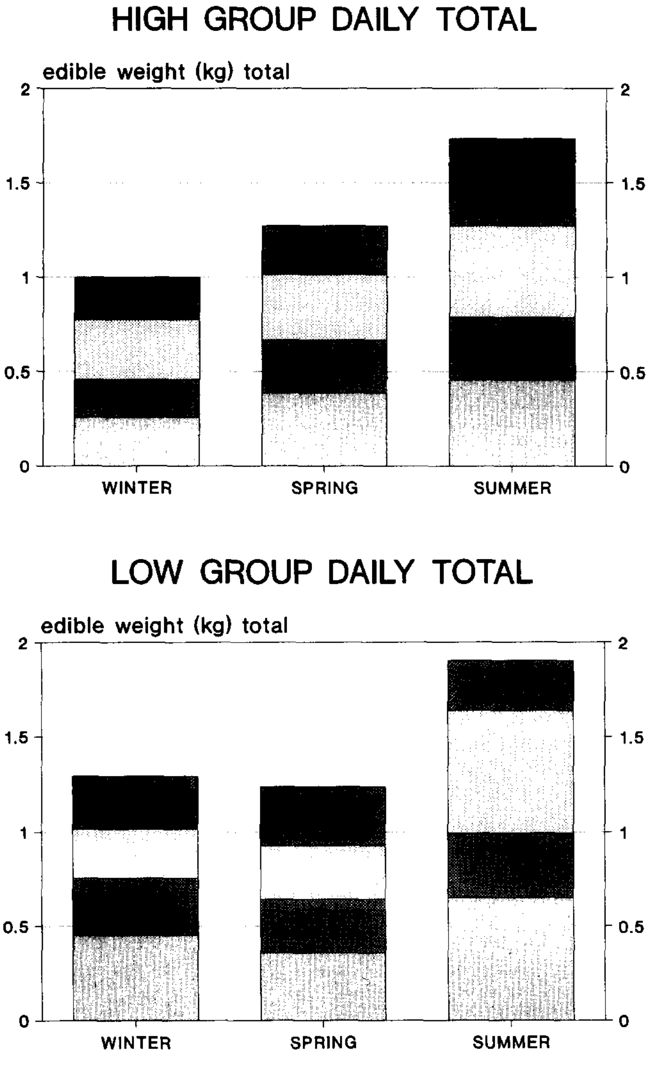

Fig. 3. Daily yield of edible dry weight food. Codes as Fig. 2

group), is largely due to the better diets of adult males and females in Low group in winter, and it does not generalize to juveniles. (iii) Protein dry weight yield in 100 min foraging: very similar results are obtained (see Fig. 2). Seasons is again significant ($F = 14.3$, $df = 12{,}2$) whereas neither groups ($F = 0.06$, $df = 6{,}1$) nor the interaction ($F = 0.15$, $df = 12{,}2$) remotely approaches significance. The consistency of the three measures and the reliable effects of seasonal difference give us confidence that the apparent absence of a difference in nutritive gain per unit time foraging, between baboons living in High and Low groups, is real.

Nutritive intake

Baboons could potentially compensate for the strong seasonal differences in the yield of their time spent feeding, by feeding longer each day at the times of poorest yield; Barton (1989, p. 205) showed just such an increase in feeding time during times of low intake rate at Chololo, Kenya, although the compensation achieved was only partial. To test this possibility, the proportion of time foraging (i.e. "feeding" plus "moving", since baboons normally feed while moving continually) was calculated in each season (Table 6). Inspection of these data shows that foraging time is indeed slightly greater in the harsh late winter than the more clement early summer. However, an analysis of variance carried out on the edible dry weight yield, corrected with these data for foraging time variations, showed no effective compensation. As before, groups was a between-subjects variable and seasons a repeated measure between subjects, again with age-sex classes as replicator variable. Seasons once more emerges as a significant variable ($F = 9.79$, $df = 12{,}2$, $P < = 0.003$) while neither groups nor the interaction approach significance (respectively $F = 0.48$, $df = 6{,}1$, ns; $F = 0.50$, $df = 12{,}2$, ns). In terms of daily food yield as well as intake rate, mountain baboons experience a strong effect of the time of year but no effect of altitude of residence (see Fig. 3).

Discussion

Baboons in the Drakensberg mountains experience strong effects of climate on their diet. Through the year, the items which form major foods at each season largely change; the range of items they eat expands from the harsh late winter to the more clement early summer; and the range of food types eaten expands, from a winter reliance on underground storage organs and the swollen bases of inconspicuous and slow-to-process shoots, to a wider range including many plant leaves, flowers and seeds. Altitudinal effects of climate are also striking, even between two groups whose ranges differed by only 400 m in average height, and whose ranges centred on points only 8 km apart in the continuous grassland habitat. Most plant foods are only of importance to one group or the other, and the majority of recorded foods are eaten uniquely by one group. Also, a wider range of items is eaten in late winter and spring by the lower group, although this effect reverses in early summer, and each group relies on a similar number of major foods at any given season. Seasonal and altitudinal effects interact in their effects on food choice; for instance at the higher altitude in late winter, males rely especially on underground storage organs and females on leaves, whereas at the lower altitude both sexes are more dependent on swollen shoot bases.

These findings emphasize the need for comparisons in the common currency of nutritional gains. Moving to this level of analysis, a much simpler picture emerges. A consistent result is found, whether the currency used is that of dry weight of food, the maximum edible fraction of that dry weight, or only the protein gained (protein content has been found to be the only nutrient that consistently predicted diet choice for all classes of plant food for these baboons: Whiten et al. 1991). Mountain baboons gain significantly less nutrition from the same time invested in foraging during the late winter than the early summer. They are not able effectively to compensate for this by feeding for longer when the rate of gain of nutrients is lower. This is presumably because animals in this population are *already* at the extreme for the amount of time they invest in foraging, among populations on which data are available (Whiten et al. 1987); any greater proportion of time feeding would thus be expected to cut damagingly into time needed to warm up on cold mornings, rest, and service relationships by social grooming (see Dunbar 1988).

By contrast, the group (and hence the altitude) of residence has no effect on nutrient gain, despite the major altitudinal differences in specific dietary composition noted above and the natural expectation that plant yields should decrease with altitude. This result is just what would be predicted by any theory that assumes the animals' distribution and behaviour is an optimal solution to ecological problems, given a population at little risk from predation or other threats.

What is the behavioural mechanism of this nice balance, whereby the effect of altitude on diet is removed? Mediation could in principle be through either or both of the two possible forms of competition, "contest" or "scramble" (Janson and van Schaik 1988). That is, baboons could be living in smaller groups at higher altitude, thus facing less direct competition; or baboons could be living at an overall lower density at higher altitude, such that each quadrat of food is depleted by fewer animals. (Ranges of these baboons overlap massively, so scramble competition would include within-group and between-group components). Group size did decline with altitude at the time of the study (Whiten et al. 1987; Henzi et al. 1990); however, group size differences cannot be the origin of the lack of difference found in this study, since both High and Low groups were selected for study because of their similar size (i.e. Low group was atypically small for its altitude). In any case, contests were very rare and occurred at a similar rate in both groups (the rate of displacement by another baboon was, on average, 0.77 per animal per 100 h in Low group, against 0.80 per animal per 100 h in High group: Byrne et al. 1990). Whether contest competition becomes significant in larger groups of this population is unknown, but two considerations suggest not. Firstly, inter-adult spacing is so large, in the range 30–60 m (Byrne et al. 1990), as to make contest competition only an occasional risk. Secondly, at another Drakensberg site, the number of items eaten per meter of travel has been found not to vary with group size at a given altitude (Henzi and Lycett, in prep.), supporting the hypothesis that contest competition is of relatively small importance for all mountain baboons. Scramble competition is, however, a plausible cause of altitudinal difference. The population density of baboons is lower at higher altitude: in this study site, we estimate 0.95 animals per km^2 at the altitude of High group, 1.87 animals per km^2 at that of Low group (Whiten et al. 1987). We therefore conclude that adjustment of foraging efficiency is largely through effects of differential density on scramble competition.

The social effects we observed – small, functionally one-male groups – are most straightforwardly explained as a consequence of variation in *total food supply,* in two possible ways. Low population density, resulting from limited food supply, might *permit* small, one-male groups despite the high costs to females of the herding which accompanies intergroup encounters, because in a sufficiently sparse population encounters are infrequent; one-male groups are advantageous for successful males since they allow reproductive exclusivity, and for female members since they minimize feeding competition (as argued by Byrne et al. 1987). Alternatively, sparse food might *constrain* group size, through stress incurred from the long day ranges need to obtain adequate nutrition; and smaller groups will be monopolizable by single males (as argued by Dunbar 1992). The latter account must assume some additional pressure for groups to form at all, most likely to minimize any predation, but it treats feeding stress as the direct cause of any variations in group size. Less plausible are models that invoke *patch size* rather than food yield (e.g. Wrangham 1980, 1987): displacements of one group by another at feeding patches would presumably then be expected, and we observed none in 2 years. Indeed, the habitat appeared strikingly devoid of the rich patches of food that would accommodate different sizes of group at different altitudes. Finally, explanations that treat group size as a *compromise* between food supply and some other ecological parameter that might be correlated with altitude (e.g. variations in predator density, or in birth rate), would predict some resulting trade-off in food yield rates, yet we found no such compromises.

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References

Allen SE, Grimshaw HM, Parkinson JA, Quarnby C (1974) Chemical analysis of ecological materials. Blackwell Scientific, Oxford

Altmann SA (1974) Baboons, space, time and energy. In: Sussman RW (ed) Primate ecology: problem-oriented field studies. John Wiley, New York, pp 243–280

Altmann SA (1991) Diets of yearling female primates *(Papio cynocephalus)* predict lifetime fitness. Proc Natl Acad Sci USA 88:420–423

Anderson CM (1982) Baboons below the tropic of Capricorn. J Hum Evol 11:205–217

Anderson CM (1983) Levels of social organization and male-female bonding in the genus *Papio*. Am J Phys Anthropol 60:15–22

Barton RA (1989) Foraging strategies, diet and competition in olive baboons. Unpublished PhD thesis, University of St Andrews

Barton RA (1992) Allometry of food intake in free-ranging primates. Folia Primatol 58:56–59

Byrne RW, Whiten A, Henzi SP (1987) One-male groups and intergroup interactions of mountain baboons *(Papio ursinus)*. Int J Primatol 8:615–633

Byrne RW, Whiten A, Henzi SP (1990) Social relationships in mountain baboons: leadership and affiliation in a non-female-bonded monkey. Am J Primatol 20:313–329

Belovski GE (1984) Herbivore optimal foraging: a comparative test of three models. Am Nat 124:97–115

Crook JH, Gartlan JS (1966) Evolution of primate societies. Nature 210:1200–1203

Dunbar RIM (1988) Primate social systems. Croom Helm, London

Dunbar RIM (1992) Time: a hidden constraint on the behavioral ecology of baboons. Behav Ecol Sociobiol 31:35–49

Gill FB, Wolf LL (1975) Economics of feeding territoriality in the golden-winged sunbird. Ecology 56:333–345

Goering HK, Soest PJ van (1970) Forage fibre analysis: apparatus, reagents, procedures and some applications (US Department of Agriculture Handbook No. 379). ARS, USDA, Washington DC

Henzi SP, Dyson ML, Deenik A (1990) On the relationship between group size and altitude in mountain baboons *(Papio ursinus)*. Int J Primatol 11:319–325

Henzi SP, Byrne RW, Whiten A (1992) Patterns of movement by baboons in the Drakensberg Mountains: Primary responses to the environment. Int J Primatol 13:601–628

Hladik CM (1973) Alimentation et activité d'un groupe de chimpanzés reintroduit en forêt gabonaise. Terre Vie 27:343–413

Hladik CM (1977) A comparative study of the feeding strategies of two sympatric species of leaf monkey: *Presbytis senex* and *Presbytis entellus*. In: Clutton-Brock TH (ed) Primate ecology. Academic, London, pp 324–353

Janson CH, Schaik CP van (1988) Recognizing the many faces of food competition in primates: methods. Behaviour 105:165–186

Jarman PJ (1974) The social organisation of antelope in relation to their ecology. Behaviour 48, 21–267

Kacelnik A (1984) Central place foraging in starlings *(Sturnus vulgaris)*. I Patch residence time. J Anim Ecol 53:283–299

Kummer H (1968) Social organization of hamadryas baboons. University of Chicago Press, Chicago

Kummer H (1984) From laboratory to desert and back: a social system of hamadryas baboons. Anim Behav 32:965–971

Milinski M, Heller R (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks *(Gasterosteus aculeatus)*. Nature 275:642–644

Mole S, Waterman PG (1987) A critical analysis of techniques for measuring tannins in ecological studies, I. Techniques for chemically defining tannins. Oecologia 72:137–147

Nishida T, Uehara S (1983) Natural diet of chimpanzees *(Pan troglodytes schweinfurthii)*: long-term record from the Mahale Mountains, Tanzania. Afr Stud Monogr 3:109–130

Norton GW, Rhine RJ, Wyn GW, Wynn RD (1987) Baboon diet: a five-year study of stability and variability in the plant feeding and habitat of Mikumi National Park, Tanzania. Folia Primatol 48:78–120

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Schmid-Hempel P, Kacelnik A, Houston AI (1985) Honeybees maximise efficiency by not filling their crop. Behav Ecol Sociobiol 17:61–66

Scotcher JSB (1982) Interrelations of vegetation and eland (*Taurotragus oryx* Pallas) in Giant's Castle Game Reserve, Natal. PhD Thesis, Witwatersrand University

Watts DP (1984) Composition and variability of mountain gorilla diets in the Central Virungas. Am J Primatol 7:323–356

Whiten A, Byrne RW, Henzi SP (1987) The behavioural ecology of mountain baboons. Int J Primatol 8:367–388

Whiten A, Byrne RW, Waterman P, Henzi SP, McCulloch FM (1990) Specifying the rules underlying selective foraging in wild mountain baboons, *P. ursinus*. In: Mello MT de, Whiten A, Byrne RW (eds) Baboons: behaviour and ecology, use and care. Brasilia University Press, Brasilia, pp 5–22

Whiten A, Byrne RW, Barton RA, Waterman PG, Henzi SP (1991) Dietary and foraging strategies of baboons. Philos Trans R Soc London B 334:187–197

Wrangham RW (1979) On the evolution of ape social systems. Soc Sci Inform 18:335–368

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–300

Wrangham RW (1987) The evolution of social structure. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. Chicago University Press, Chicago, pp 282–296

Wrangham RW, Conklin NL, Chapman CA, Hunt K (1991) The significance of fibrous foods for Kibale Forest chimpanzees. In: Whiten A, Widdowson EM (eds) Foraging strategies and natural diet of monkeys, apes and humans. Clarendon, Oxford, pp 11–18