

## Habitat use and resource availability in baboons

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**Abstract.** The behavioural responses of free-living baboons (*Papio*) to temporal and spatial variation in resources is examined. Group foraging effort was related to per caput food availability, both within the study group (*P. anubis*) and across a sample of populations. Group size was positively correlated with both home range size and day range length, indicating ecological costs not predicted by a food defence hypothesis of group living. Furthermore, the tendency for day range length of the study group to increase as resources became scarcer was mirrored by inter-population variation; day range length was correlated negatively with mean annual rainfall, once the positive influence of group size had been partialled out. These relationships, which imply a time minimizing rather than an energy maximizing strategy, may be best explained by increased patchiness of food at lower resource densities, rather than lower average biomass within patches. The study group responded to the inferred decrease in the marginal value of patches in the dry season by increasing patch residency times. Multiple regression analysis of total time spent in each quadrat revealed that apparent preferences for particular vegetation zones were a result of the spatial coincidence of these zones with sleeping sites and waterholes, emphasizing the importance of controlling for confounding factors in studying the determinants of habitat selection. In addition, the mean duration of bouts in each quadrat was related to distance to the nearest waterhole, reflecting the constraints imposed by thermoregulatory water loss in a hot, dry environment. Seasonal shifts in habitat selection tracked spatio-temporal variation in the availability of food and water.

The use of space is an important aspect of the behavioural ecology of a species since it underpins the optimization of resource use. Thus, it is often assumed that patterns of movement and habitat selection are designed to maximize nutrient capture rates relative to time and energy costs (Charnov 1976; Krebs 1978). Optimality models are usually formulated to solve relatively tractable problems of single-resource exploitation, and they have considerable applicability in well-controlled laboratory environments (e.g. Krebs et al. 1977), or in nature when the situation is fairly simple and when only short-term optimization is being considered (Krebs & McCleery 1984), such as in the case of hummingbirds foraging for nectar (De Benedictis et al. 1978). Models of habitat selection, for example, predict that, other things being equal,

habitats should be chosen that yield the highest average rate of energy intake (Stephens & Krebs 1986). Other things are rarely equal, however, and in practice it will be necessary to take account of a number of variables. In the case of omnivorous animals selecting their foraging areas over longer periods, requirements for different nutrients, water, favourable microclimates and safety from predators may complicate optimality principles (Partridge 1978; Belovsky 1984; Post 1984). The use of space in such situations is therefore unlikely to be determined simply by the distribution of a single resource, such as energy, and precise formulations of spatio-temporal decision rules (where to go, when, and for how long), may not be tenable. Under these circumstances a useful approach may be to incorporate several basic categories of resource into broad analyses of the determinants of patterns of home range use and foraging effort, thus

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facilitating the identification of critical ecological constraints.

The ecological determinants of habitat preferences and movement patterns in animals have been much discussed (e.g. primates: Clutton-Brock 1975; Terborgh 1983; Chapman 1988; other mammals: Douglas 1976; Leuthold 1977; Hanski 1989; birds: Balda 1969; Morse 1976; Airola & Barrett 1985). The exact nature of relationships between resource characteristics and the use of space remains somewhat obscure, however (Whelan 1989), owing to imprecision in the methods of evaluating characteristics of the resource base. There have been relatively few attempts to measure and distinguish resource availability and other variables affecting habitat selection. One approach to these issues involves the experimental manipulation of resource variables (Hanski 1989; Whelan 1989), but this procedure is relatively impracticable in the case of large species with large territories or home ranges. The approach we use here is thus to quantify key variables likely to influence foraging decisions, and to use statistical methods to separate likely causal from confounding variables. This is analogous to the approach taken in the past by ecologists attempting to characterize habitat differences between species (e.g. Kikkawa 1968; Green 1971).

The behavioural ecology of *Papio* baboons has been extensively studied, particularly in savannah habitats, and a picture has emerged of animals that are ecologically flexible omnivores, but that are nevertheless highly selective, both in their diet choice and in their home range use (Altmann & Altmann 1970; Hamilton et al. 1978; Post 1978; Rasmussen 1979; Whiten et al. 1987). Savannahs are highly seasonal environments, subject to marked fluctuations in the types and amounts of food that are available (Altmann & Altmann 1970; S. Altmann 1974; Hamilton 1985). Under these varying conditions, animals could either forage for the minimum amount of time necessary in each season to satisfy basic requirements, or attempt to maximize the rate of nutrient acquisition, regardless of changes in food availability (Schoener 1971). In this paper we examine strategies of habitat use and foraging effort in baboons, both in relation to seasonal and spatial resource variation within one population (of *P. anubis*) and in relation to group size and habitat quality across populations.

## METHODS

### Study Area

Fieldwork was conducted by R.A.B. within an area of approximately 50 km<sup>2</sup> at an altitude of 1600–1700 m, situated on the eastern edge of the Laikipia Plateau in central Kenya, East Africa. The site consists of undulating dry woodland and wooded and bushed grassland (following the nomenclature of Pratt et al. 1966), dissected by seasonal watercourses and punctuated by steep granitic inselbergs, or 'kopjes', used by the baboons as sleeping sites. The vegetation is dominated by *Acacia* species, principally *A. etbaica* and *A. mellifera*, but also *A. tortilis* on drier slopes, and stands of *A. xanthophloea* along seasonal watercourses. Stands of the giant spurge *Euphorbia nyikae* occur on the crests of ridges and around other rocky outcrops. The understory is mainly dominated by grasses such as *Cynodon plectostachyus*, *C. dactylon*, *Themeda triandra* and *Eragrostis* spp., and sedges such as *Kyllinga alba*, *K. ulata* and *Cyperus blysmoides* being replaced by more xerophytic species, such as *Sansaviera intermedia*, on drier slopes. Three waterholes have been created by damming gullies, providing water at all times except in the harshest droughts.

Climatically, the study site falls within the category of 'dry savannah' (Delaney & Happold 1979): mean annual rainfall over a 3-year period (1985–1988) was 549 mm (SD = 217.8), with 580 mm during the 12 months of the study (1986). As in many parts of East Africa (Delaney & Happold 1979), much of the rainfall is concentrated in two wet seasons (March–June and November–December; see Fig. 1). Maximum daily temperatures were greatest during the dry seasons, reaching a peak monthly mean for the study year of 37.2°C in February, compared to a low monthly mean of 28.7°C in June. Minimum daily temperatures fluctuated less, the 12-month average being 12.4°C (SD = 1.38). More detailed information about the topography, vegetation and climate of the study site is given in Barton (1989).

### Habitat Sampling Methods

A bipartite system for classifying vegetation zones within the study area was established on the basis of (1) species dominance, and (2) density of trees and shrubs. Four basic density categories were defined: 'open' (grasses and herbs dominant, tree/shrub cover 0–25%); 'light bush' (canopy overlap



rare, tree/shrub cover >25–50%); 'thick bush' (canopy overlap frequent, tree/shrub cover >50–75%); 'forest' (canopy overlap extensive, tree/shrub cover >75–100%). An additional category of 'kopje' was used, but no attempt was made to sub-classify it according to species dominance or tree density, it being comprised essentially of steep rocky slopes and large boulders, with a sparse and distinctive vegetation. This classification system was then used in recording individual habitat use and in compiling a vegetation map of the home range. The map was drawn up by tracing and labelling vegetation boundaries, viewed by walking along ridges and other high points, onto a transparency overlying the topographical map of the area.

Food availability was sampled once per month between May and December of the study year. Three transects were established, two of 2 km and one of 1 km. These contained 28 permanent sampling points. At each sampling point, the number of food items was counted within two 0.25 m<sup>2</sup> quadrats separated by a distance of 2 m. These data were subsequently converted by multiplying the mean dry weight of the items (see below) by their density within quadrats. Thus, biomasses of herb-layer baboon foods were estimated each month from 56 quadrats spaced widely apart, equivalent to a total sample area of 14 m<sup>2</sup>. Biomass of foods obtainable from trees and shrubs was assessed using marked 'focal' plants: four trees and four shrubs at each sampling point (hence 224 plants in total) were marked with coloured tape, and monthly estimates made of the number of food items on each one. These were converted into biomass estimates using species density data obtained from 30-m<sup>2</sup> quadrats at each sample point, plus mean dry weights of items of the different food types. No attempt was made to monitor monthly variation in biomass of subterranean items, which made up 2.4% of mean monthly food intake (Barton 1989). The biomass of the single most important of these foods, the corms of the sedge *Cyperus blysmoides*, was determined in two dry season months, predominantly when corms are eaten. In estimating total baboon food biomass we have assumed that sedge corms were available only in months when they were eaten (August–December), and that, during that time, their biomass did not vary significantly. While these assumptions are unlikely to be wholly realistic, violation of them would have minimal, quantitative rather than qualitative, effects on the overall picture and analyses of seasonality in food availability

(see below). Since phenological sampling points were permanent, biomass could not be measured directly by removing all baboon food items for weighing. Foods were therefore collected at other sites. The number of items harvested were recorded, each 'item' corresponding to an individual baboon bite. Food samples were dried to constant weight and preserved in plastic bags for later chemical analysis. Analysis of protein content was carried out for us by the Pannure Trading Company, Monikie Granary, Dundee, Scotland, using the micro-Kjeldahl method.

In addition to the monthly estimates of baboon food biomass (hereafter 'food biomass'), the total biomass of green vegetation in the herb-layer (hereafter 'green biomass') was measured on grassland plots at 6-weekly intervals, to provide long-term background data for other studies being conducted at the site. These data were collected using the pin-frame method described by McNaughton (1979). They provide a relatively crude index of seasonal variation in food availability over a longer period (January–December) than was possible in the case of food biomass. Green biomass was also estimated at a selection of the food biomass sampling points in 5 months (August–December), to enable direct comparison between the two types of measure.

#### Behavioural Sampling Methods

Behavioural observations were made between January 1986 and January 1987. A previously unstudied group of baboons, numbering about 100 individuals (103 by December 1986) was selected for study because it was frequently seen and because some of its sleeping sites were close to the research base. Each day the baboons were located at their sleeping site around 0700 hours and followed on foot, usually until 1800–1830 hours. Habituation to the observer was rapid, and it was possible to begin collecting basic ranging data within the first month. Using a relief map traced from a 1:25 000 scale ordnance survey map, occupancy of numbered 0.25-km<sup>2</sup> squares was recorded; every 15 min throughout the day, the square occupied by the main part of the troop was recorded on a checksheet. The frequency of use of each quadrat was summed for each month to provide information on the intensity of use of different parts of the home range. Occupancy of different vegetation zones was recorded separately for individual animals at 90-s intervals within

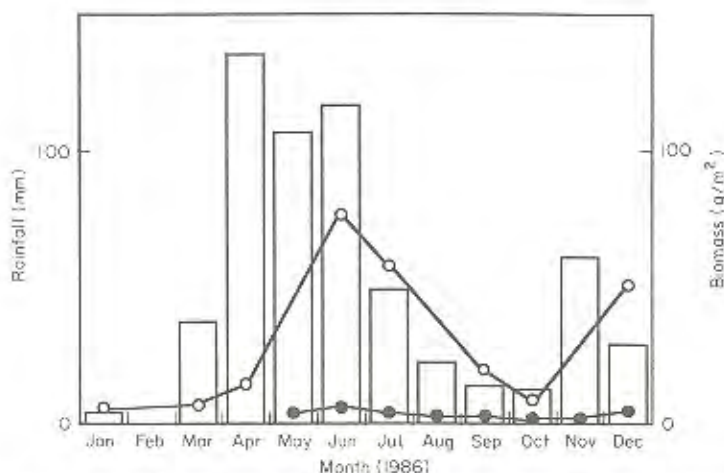


Figure 1. Monthly variation in rainfall and food availability during the study year.  $\square$ : rainfall (data collected at a station 1 km from the nearest boundary of the study group's home range).  $\circ$ : total green biomass in the herb layer, measured by the pin-frame method at approximately 6-weekly intervals.  $\bullet$ : biomass of baboon foods, measured in quadrats once per month. Biomass values in g dry weight per square m.

30-min focal samples (Altmann 1974). Focal animal sampling was carried out on 19 adult females and seven adult males. Habituation, though occurring rapidly, was not sufficient to permit sampling of individual animals until the third month of study (March); accordingly, vegetation zone occupancy data were collected for only 10 months. Five time zones were delineated (0700–0915, >0915–1130, >1130–1345, >1345–1600, >1600–1815), and individuals were sampled for an approximately equal duration within each time zone in each month. All focal animal samples were collected using a handheld Hewlett-Packard HP-71 micro-computer, programmed in BASIC as an event-recorder with two elements (see Whiten & Barton 1988 for further details): continuous recording of feeding and other behaviour, and instantaneous recording of point sample data at 120-s intervals, including activity state and vegetation zone. These data were transferred daily onto magnetic micro-cassettes for storage. Over the 10 months, 479 h of focal sample data were collected, incorporating 12 600 point samples.

#### Analysis

On completion of fieldwork, the focal animal data were transferred directly from microcassettes onto a VAX mainframe computer, and there sorted into a matrix format suitable for analysis by the SPSSX package. In the case of parametric correlation and

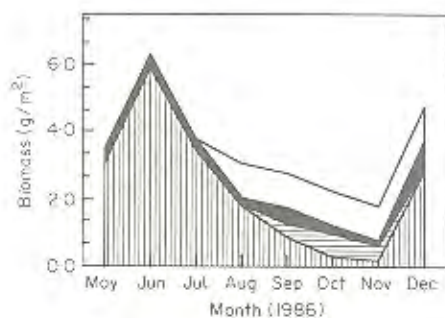
regression analyses, the data were log-transformed to improve linearity. Tests for significance were two-tailed unless otherwise stated. For the purposes of the analyses of inter-population variation, all common baboons (i.e. members of the genus *Papio* excluding the forest-dwelling *leucophaeus* and *mandrillus*) are treated as populations of a single superspecies (see Thorington & Groves 1970; Dunbar 1988).

## RESULTS

#### Seasonal Variation in Food Availability

Fluctuations in food availability during the study period are shown in Figs 1 and 2. Rainfall was evidently a strong influence on food availability: biomass rose steeply from a dry season low to a peak in June, towards the end of the wet season, and thereafter declined gradually through the second dry season, before increasing again in the second wet season at the end of the year. On average, food availability was greater in wet months than in dry months (total biomass:  $t=3.08$ ,  $df=6$ ,  $P=0.022$ ; protein biomass:  $t=4.40$ ,  $df=6$ ,  $P=0.005$ ). There is, however, clearly a time-lag in the effect of rainfall on the biomass estimates: the correlation between baboon food biomass and monthly rainfall ( $r=0.588$ ,  $df=6$ ,  $P=0.069$ , one-





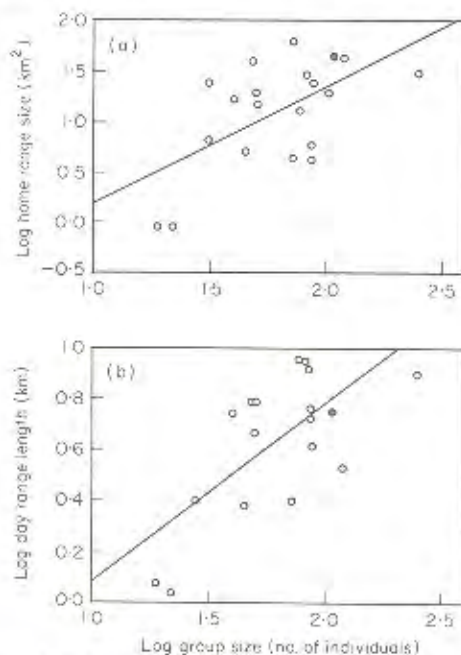
**Figure 2.** Variation in baboon food biomass during the study year, showing the separate contributions of each food type. Fresh herb-layer foods, such as foliage and herb flowers and fruits (▨); dry herb-layer foods, such as loose acacia seeds (▤); tree and shrub foods (■); sedge corms (▧). Biomass values in g dry weight per square m.

tailed) is not as strong as that between the former and rainfall in the previous month ( $r=0.617$ ,  $P=0.05$ , one-tailed), while the correlation between biomass and the rainfall total for the previous 2 months is stronger still ( $r=0.670$ ,  $df=6$ ,  $P=0.035$ , one-tailed).

There is a high correlation between food biomass and green biomass estimates from the same sites ( $r=0.970$ ,  $df=3$ ,  $P=0.003$ ), suggesting that the major factor in the availability of baboon foods is the condition of the herb-layer. This is confirmed by inspection of Fig. 2, which shows that variation in fresh herb-layer foods (grass blades, herb leaves, shoots, flowers and fruits) effectively swamps variation in other foods, resulting in considerably greater food availability in much of the wet season than in the dry season. If the assumption that corms were available only during months in which they were eaten is relaxed, the effect is to increase the wet/dry seasonal disparity. Similarly, if the assumption that corm availability did not decrease through depletion during the dry season is relaxed, this would also increase the disparity.

#### Home Range Size

The size of the home range of the study group was estimated by summing the total number of 0.25-km<sup>2</sup> quadrats entered during the 12-month study period. These formed a coextensive block, enclosing only one quadrat which was never seen to be entered. The home range size given by this method was 43.75 km<sup>2</sup>. Calculation of cumulative



**Figure 3.** Relationships between group size and ranging across populations of baboons (*Papio*). ●: present study population. Other data are from Sharman (1981) and Sharman & Dunbar (1982). (a) Home range size;  $N=19$ ,  $Y = -0.97 + 1.16X$ , with  $r^2=0.36$  (b) Day range length;  $N=18$ ,  $Y = -0.62 + 0.70X$ , with  $r^2=0.48$ .

estimates for each study month revealed that this value is a near asymptote (Barton 1989), and can thus be regarded as the 'true' home range size given the ecological and demographic conditions obtaining at the time of the study.

The home range size of 43.75 km<sup>2</sup> is large compared with other baboon populations, but this appears to be related to group size. Estimates of home range size are available for 20 populations of baboons (Sharman 1981, and this study), and in Fig. 3a these are plotted against group size taken from Sharman & Dunbar 1982: 36% of the variance in home range size is explained by group size, a pattern that is also found in interspecific comparisons (McNab 1963; Clutton-Brock & Harvey 1977). The question then arises as to whether some of the scatter about the regression line in Fig. 3a is related to habitat quality: larger home ranges relative to group size might be expected in comparatively depauperate environments. Direct measures of habitat quality do not exist for these habitats, but mean annual rainfall is thought to be a good indirect measure of primary production and hence

food availability for savannah herbivores (Delany & Hapold 1979). The predicted relationship between rainfall and home range size was, however, not apparent with the effect of group size partialled out (partial  $r = -0.094$ ,  $df = 16$ ,  $P = 0.712$ , data log-transformed).

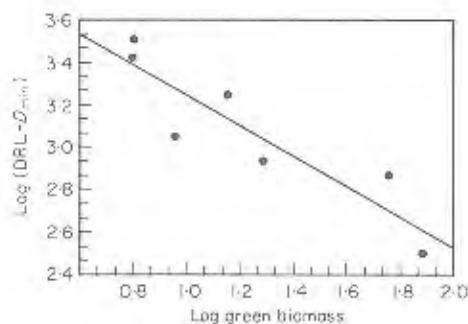
#### Day Range Length and Resource Availability

Mean day range length for the study period, calculated as the mean of the 12 monthly means, was 5.637 km ( $SD = 1.533$ ). Across 18 populations of *Papio* baboons, there is a significant relationship between day range length and group size, with 48% of variance in the former explained (Fig. 3b). Again, the question arises whether any of the residual variation can be ascribed to the influence of resource availability, and in this case, unlike the situation with home range size, mean annual rainfall is indeed significantly (negatively) correlated with day range length with group size partialled out (partial  $r = -0.559$ ,  $df = 16$ ,  $P = 0.016$ ).

Monthly variation in day range length was significant (Kruskal-Wallis  $H = 23.09$ ,  $df = 7$ ,  $P < 0.01$ ). The overall difference between wet months and dry months was not significant ( $t = 1.89$ ,  $df = 7$ ,  $P = 0.103$ ), but, as noted above, the simple wet/dry dichotomy reflects seasonal variation in food availability imperfectly because of time-lags between rainfall and biomass peaks. Reflecting this, the correlation between day range length and monthly rainfall is not significant ( $r = -0.023$ ,  $df = 10$ ,  $P = 0.901$ ), but that between day range length and rainfall for the previous 2 months is significant ( $r = -0.642$ ,  $df = 10$ ,  $P = 0.024$ ).

Biomass estimates can be used to look at the influence of resource availability more directly: as expected, there is an inverse relationship between day range length and green biomass sampled at approximately 6-week intervals ( $r = -0.819$ ,  $df = 6$ ,  $P = 0.024$ ). Baboon food biomass was sampled over a shorter period (8 months rather than 12) with less seasonal variance (missing out the relatively extreme conditions of the first dry season) than is the case with green biomass; its relationship with day range length showed the same trend, but the correlation was not significant ( $r = -0.467$ ,  $df = 6$ ,  $P > 0.05$ ).

The results suggest that the time and energy invested in foraging is inversely proportional to resource density. This, however, may not be a



**Figure 4.** Relationship between day range length (DRL) and food availability, sampled within 6-weekly time blocks. The dependent variable is the average day range length for each time block after subtraction of the estimated minimum day range length (equal to the average distance between sleeping sites), assumed to be constant. Food availability is represented here by the total herb-layer green biomass, measured by the pin-frame method (see text). The equation for the regression line is  $Y = 3.96 - 0.72X$ , with  $r^2 = 0.82$ .

simple inverse relationship, since there is likely to be a minimum day range length (DRL) for any given population, set by the straight-line distance between the previous night's sleeping site and the most distant essential daily resource, such as the next sleeping site. Formally, we can state that

$$DRL = D_{min} + K/b$$

or

$$\log(DRL - D_{min}) = \log K - \log b$$

where  $D_{min}$  is the minimum travel distance,  $b$  is biomass, and  $K$  is the constant relating biomass to the distance travelled in excess of the minimum. This model thus states that the residual quantities  $\log(DRL - D_{min})$  should be linearly related to  $\log b$ , with a regression slope of  $-1.0$ . Estimation of  $D_{min}$  is not straightforward; it may vary seasonally, in line with changes in the spatial distribution of water or other resources, and also on a daily basis, according to whether or not the group returns to the sleeping site occupied the previous night. In the absence of a precise specification for  $D_{min}$ , the mean distance between sleeping sites (4.044 km) provides an approximation. Using this approximation, Fig. 4 shows that the model effectively describes the data: 82% of the variance is explained by the regression, and the 95% confidence limits for the slope range from  $-0.417$  to  $-1.102$ . The slope is of course sensitive to the value for  $D_{min}$ , and given that this has



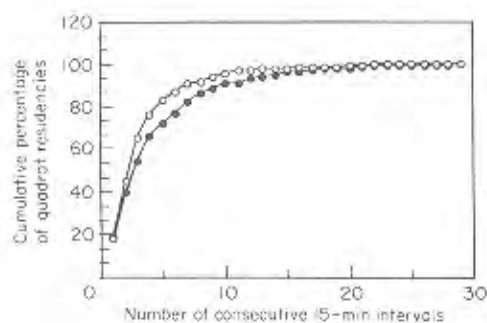


Figure 5. Distribution of quadrat residency times in wet and dry seasons. ●: wet season; ○: dry season.

been somewhat arbitrarily set, the fit to the data is extremely good.

### Patch Residency

Foraging theory predicts that animals should remain in patches longer when the environment is relatively poor or travel times are relatively long or both (Charnov 1976; Stephens & Krebs 1986). We did not evaluate patch residency times directly, owing to the difficulty of defining patch boundaries (see Discussion below), but quadrat residency times may be used to provide an indirect estimate. Here we assume that the longer day ranges and reduced biomass observed in the dry season reflect, respectively, greater between-patch travel times and greater between-patch distances (see Discussion below). We may therefore predict longer quadrat residency times in the dry season than in the wet season. The data do not, however, allow a separation of 'feeding' and 'non-feeding' residencies, and many very short quadrat residencies in both wet and dry season are likely to represent travel, rather than feeding, inasmuch as these are distinct activities in baboons. A refined prediction is therefore that long duration residencies should make up a greater proportion of the total in the dry season than they do in the wet season. The prediction is confirmed: the expected dry/wet season residency distributions are significantly different (Fig. 5; Kolmogorov-Smirnov  $D=0.233$ ,  $N_1=77$ ,  $N_2=68$ ,  $\chi^2=7.836$ ,  $P<0.02$ ). Since successive observations within days are highly unlikely to be independent, using the total number of observations to calculate sample sizes would unduly inflate the chi-squared value. Thus we used a

more conservative procedure, with chi-squared calculated on the basis of the number of days on which observations were made.)

### Determinants of Differential Home Range Use

Using the vegetation map, each 25-ha quadrat in the home range was scored for percentage coverage of each of the three major species types. The amount of time spent in quadrats was positively correlated with *A. etbaica* coverage ( $r=0.219$ ,  $df=75$ ,  $P=0.048$ ; arcsine transformation used on percentages), while correlations with the other two species types were not significant (*A. mellifera*:  $r=-0.089$ ,  $df=75$ ,  $P=0.255$ ; *A. tortilis*:  $r=0.049$ ,  $df=75$ ,  $P=0.361$ ). Quadrats were also scored for percentage cover by the different density types, and these data were combined into single density indices (DI) for each quadrat, using weightings based on rank-order of increasing density (note that the quantitative values of these weightings are proportional to the maximum degree of cover of trees and shrubs within each type: see Methods).

$$DI = \frac{\% \text{ open} + (\% \text{ light bush} \times 2) + (\% \text{ thick bush} \times 3) + (\% \text{ forest} \times 4)}{400}$$

This measure correlates positively with occupancy ( $r=0.351$ ,  $df=75$ ,  $P=0.003$  one-tailed).

The correlations with *A. etbaica* coverage and density could arise either from genuine preferences based on vegetation structure, or because of systematic or coincidental spatial associations between vegetation structure and other important features of the home range, such as sleeping sites and water sources. Accordingly, the distances from the centre of each quadrat to the nearest sleeping site and to the nearest dam were measured in millimetres on the 1:25 000 map. Stepwise multiple regressions were performed to determine the contribution of each variable to differential use of quadrats, over the whole study period, and within each season. Strictly, the independent variables in such an analysis should be statistically independent, since multicollinearities make valid estimation of beta weights and values of  $r^2$  problematic. In the SPSSx program used, however, candidate variables are evaluated for their 'tolerance' (the amount of variance not explained by other independent variables in the regression equation) before qualifying for inclusion. In practice, tolerance levels were not exceeded at any point in these analyses.

Table I. Multiple regression analysis of total quadrat occupancy

Independent variable	Season				
	All	Dry		Wet	
		1	2	1	2
Distance to sleeping site	-0.70***	-0.42**	-0.63***	-0.58***	-0.55***
Distance to waterhole	-0.37**	-0.33*	-0.36***	-0.27*	-0.24*
Coverage of <i>A. etbaica</i>	0.09	0.13	0.22*	-0.08	-0.02
<i>A. mellifera</i>	0.01	-0.08	-0.10	0.01	-0.02
<i>A. tortilis</i>	-0.09	0.03	0.01	-0.07	0.04
Density index (DI)	0.04	0.41**	-0.05	-0.13	-0.10
<i>F</i>	44.33***	10.57***	40.41***	23.28***	18.07***
Adjusted <i>r</i> <sup>2</sup>	0.60	0.35	0.68	0.44	0.40

Values are standardized regression coefficients.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

The regressions are all significant, with between 35 and 68% of the variance in quadrat occupancy explained in each case (Table I). Distance to sleeping sites and distance to waterholes were significantly related to intensity of quadrat use in all seasons; the closer a quadrat was to a sleeping site or to a waterhole, the more intensively it was used. Neither the density index nor percentage coverage by any of the three species types explained significant amounts of the variance over the study period as a whole. Within individual seasons, however, there were significant effects: occupancy was related to density in the first dry season, and to *A. etbaica* coverage in the second dry season. Because the probability of reaching statistical significance by chance alone increases with the number of tests carried out, caution should be exercised in interpreting some of these results. The relatively weak significance of waterhole distance in some seasons is unproblematic because of the consistency of the relationship across the four seasons, but it is possible that the weak effect of *A. etbaica* coverage (dry season 2) is spurious.

Since the dependent variable in the above analyses was the total amount of time spent in each quadrat, the influences of sleeping site and waterhole proximity could have been due either to more frequent use of quadrats or to longer stays in them (or to both). Hence, a stepwise multiple regression analysis was performed using mean quadrat residency as the dependent variable. Insufficient data were available to calculate mean residencies within different

Table II. Multiple regression analysis of mean quadrat occupancy

Independent variable	Beta†	<i>T</i> -value
Distance to waterhole	-0.285	-2.325*
Distance to sleeping site	-0.083	-0.634
<i>A. etbaica</i> coverage	-0.041	-0.249
<i>A. mellifera</i> coverage	0.013	0.180
<i>A. tortilis</i> coverage	-0.097	-0.256
Density index (DI)	0.058	0.437
<i>F</i> = 4.949 <i>P</i> = 0.030 Adjusted <i>r</i> <sup>2</sup> = 0.068		

†Standardized regression coefficient

\* $P < 0.05$ .

seasons, so only the pooled data are analysed. Once again, the regression was significant (Table II), though only 7% of the variance was explained. As with total occupancy, none of the vegetation variables were significant factors, and this time the only variable significantly related to quadrat bout length was distance to the nearest waterhole, indicating that the effect of sleeping site proximity found in the previous analysis was due simply to the higher frequency with which quadrats near the convergence-divergence points of day ranges were entered.

Although the proximity of waterholes continued to be an important influence on range use in wet seasons as well as dry seasons, it does appear that increased water availability somewhat relaxed this constraint; the proportion of time spent within the three 1-km quadrats in which the waterholes were situated was negatively correlated with monthly



rainfall ( $r = -0.602$ ,  $df = 10$ ,  $P < 0.05$ ). This association is not due simply to changing preferences for the relevant vegetation types; *A. ethiopia* predominated in the quadrats surrounding each of the three waterholes, but the percentage of time spent within four other 1-km quadrats where this species predominated, but away from waterholes, was not correlated with rainfall ( $r = -0.386$ ,  $df = 10$ ,  $P > 0.05$ ).

Optimal foragers should track seasonal changes in the profitability of different habitat types: what evidence is there for this? The monthly proportion of time spent in *A. ethiopia* zones (arcsine-transformed) was significantly correlated with the proportion of feeding time devoted to that species ( $r = 0.710$ ,  $df = 6$ ,  $P = 0.024$  one-tailed). This was also true for *A. mellifera* ( $r = 0.733$ ,  $df = 6$ ,  $P = 0.019$  one-tailed), and the correlation for *A. tortilis* was nearly significant ( $r = 0.594$ ,  $df = 6$ ,  $P = 0.054$  one-tailed). As noted, the distribution of *A. ethiopia* zones was correlated with the distribution of waterholes, but the relationship between time spent within them and the proportion of feeding time devoted to the species exists independently of variation in time spent near waterholes (partial  $r = 0.664$ ,  $df = 5$ ,  $P = 0.05$ ). Thus it appears that there is a link between diet and the differential use of vegetation zones. Furthermore, the proportion of time spent in each species zone (arcsine-transformed) was also significantly correlated with the productivity of the given species (*A. ethiopia*;  $r = 0.658$ ,  $P = 0.04$ ; *A. mellifera*;  $r = 0.870$ ,  $P = 0.008$ ; *A. tortilis*;  $r = 0.876$ ,  $P = 0.006$ ;  $df = 6$  in each case), where productivity is biomass of baboon food in g dry weight. Thus it appears that seasonal patterns in the selection of habitats were indeed based on variation in their profitability as foraging areas.

The regression analyses indicated a positive association between quadrat occupancy and density in one of the dry seasons, suggesting, perhaps, that more densely wooded areas are selected when the availability of green herb-layer foods is relatively low. This hypothesis was pursued by examining monthly variation in an index of tree density selection (DSI) analogous to the density index DI

$$DSI = \frac{\text{time open} + (\% \text{ time light bush} \times 2) + (\% \text{ time thick bush} \times 3) + (\% \text{ time forest} \times 4)}{400}$$

where % time is the percentage of time spent in each

density category in a given month. There is a significant negative correlation between DSI and biomass of herb-layer foods ( $r = -0.699$ ,  $df = 6$ ,  $P = 0.042$ ), but no correlation between DSI and biomass of tree foods ( $r = 0.306$ ,  $df = 6$ ,  $P = 0.460$ ). Once the percentage of time near waterholes has been statistically controlled, however, there is no significant correlation between DSI and biomass of herb-layer foods (partial  $r = -0.104$ ,  $P = 0.824$ ).

## DISCUSSION

### Group Size, Foraging Effort and Habitat Quality

Both home range size and day range length were positively correlated with group size across populations, implying that the per caput reduction in resource density brought about by feeding competition within a group leads to an increase in the foraging effort of the group as a whole. Similar relationships for day range length were found in limited samples of populations of long-tailed macaques, *Macaca fascicularis* (van Schaik et al. 1983), and gelada, *Theropithecus gelada* (Iwamoto & Dunbar 1983), and the latter authors suggested that 'each animal has to cover a fairly constant area each day to obtain its daily nutritional requirements' (page 362). Thus, large group size imposes a cost on all individuals, either because the mode of feeding competition is at least in part 'scramble' (each individual suffers approximately equal depression of encountered resource density) rather than purely 'contest' (dominant individuals monopolize resources; see Nicholson 1954; Janson & van Schaik 1988) or because dominant individuals alone do not determine ranging patterns. If competition was purely of the contest variety and dominant individuals determined group movements, the costs would be concentrated exclusively on subordinates' food intake and/or time budgets (assuming that they did not forage separately, as in fission-fusion social organization, which may only be permissible in the relative absence of predators; van Schaik 1989). The monotonic increase in foraging effort with group size suggests that the advantages of group living in baboons are not primarily related to feeding advantages (Wrangham 1980; Krebs & McCleery 1984; see also van Schaik et al. 1983; Stacey 1986). The main alternative hypothesis, that predator pressure underlies group living, could be tested by evaluating predator density in these populations, although it should be



borne in mind that the relationship between predation risk and group size is probably not linear (Krebs & McCleery 1984).

In the present case it is possible to infer an effect of environmental richness, as measured by annual rainfall, on day range length but not on home range size, over and above the group size effect. It is not clear why the effect is found only for day range length: an inverse relationship between habitat quality and home range size has been noted in a variety of reptiles, birds and mammals (e.g. Davies 1978; Jones 1990). The most prosaic explanation is that home range size is harder to estimate than day range length, requiring prolonged observation to obtain the asymptote and therefore that published estimates of the former are less reliable. Furthermore, techniques used to estimate home range size vary (e.g. minimum convex polygon versus quadrat summation techniques), and no attempt has been made to control for the effects of such methodological variation. Certainly, the correlation with group size is better for day range length. Whatever the explanation for this discrepancy, the correlation between day range length and rainfall suggests that baboons respond to variation in resource availability by adjusting their foraging effort. As with seasonal variation in day range length discussed below, this pattern is more consistent with a time minimizing than with an energy maximizing strategy (Schoener 1971), since the latter would predict that foraging effort was maximal, and therefore approximately constant, irrespective of habitat.

#### Environmental Seasonality and Ranging

The results suggest that rainfall-driven variation in food availability has important implications for foraging effort, presumably because the size of the harvesting area needed by each individual to satisfy daily nutritional requirements is inversely related to the average density of food within the home range. The observed seasonal adjustment to day range length corroborates the inference drawn from variation among populations that time minimization is a better model for baboon foraging effort than is energy maximization: the group was apparently able to increase foraging effort in order to maintain nutrient intake when food was less abundant. This notion is further supported by the finding that seasonal fluctuations in feeding rate are offset by adjustments to time spent feeding, resulting in daily intake rates that remain relatively

invariant through the year (Barton 1989). Note, however, that there is no conflict between this conclusion and the possibility that, within the constraints of the daily activity budget, patch residency times are energy maximizing.

Seasonal differences in required harvesting areas could be a function of changes in the density of food items within patches, a reduction in the number or size of patches, or of both types of change. The quantification of 'patches' is notoriously difficult (Wrangham 1983; Krebs & McCleery 1984); it is rare that clear patch boundaries exist in natural situations, especially in the case of terrestrial or semi-terrestrial herbivores and omnivores such as baboons, where patches will tend to be contiguous, overlapping and even concentric. Thus the definition and measurement of patches is always likely to be somewhat arbitrary. Nevertheless, some attempt to evaluate seasonal variation in the spatial heterogeneity of food, as well as in its gross abundance, is clearly desirable. Qualitatively, foods eaten at times of high availability (the middle of the wet season) appeared to be considerably more evenly distributed than 'dry season' foods: the grasses and herbs that provided the foliage, flowers and fruits eaten extensively in the wet season were frequently found in large meadows capable of accommodating the whole group, even with individuals spread widely apart. In contrast, flowering and fruiting *Acacia* trees (80% of the diet in November, the month of minimum average biomass; see Barton 1989) were often clumped in distribution because, while extensive woodlands of the three main food species occurred in many parts of the home range, the production of reproductive parts was to some extent asynchronous. Thus, 'rich pickings' were frequently restricted to relatively small groves within particular areas, and even to individual trees.

A more formal way of examining these trends is to compare the average biomass for the home range with the maximum biomass within patches. The two maximum dry weight biomasses recorded from herb-layer quadrats during the month of peak availability (June) were 40.6 g/m<sup>2</sup> and 32.4 g/m<sup>2</sup>, respectively 6.4 and 5.1 times the average at this time of 6.3 g/m<sup>2</sup>. The maxima for within-patch biomass of *Acacia* flowers (i.e. biomass within a single tree) were 38.0 g/m<sup>2</sup> for *A. etbaica*, and 35.8 g/m<sup>2</sup> for *A. tortilis*, being respectively 16.2 and 13.8 times the average biomasses for the months in which they were recorded. Thus, the dry season decrease in



average biomass appears to be primarily a function of a reduction in patch size and/or number, rather than a reduction in patch quality. The observed seasonal changes in day range length are therefore likely to be principally related to effects on the between-patch travel component, rather than on within-patch harvesting rates. The fact that long quadrat residencies were more frequent in the dry season suggests that the baboons responded to decreases in the marginal value of patches (Charnov 1976), consequent on increases in travel times, by remaining in patches longer.

The hypothesis that variation in day range length is related to patchiness may resolve some apparently contradictory findings in the primate literature: various studies have found negative associations between daily travel and inferred food abundance (Clutton-Brock 1975; Lindburg 1977; Altmann & Muruthi 1988), no associations (Pollock 1977; Waser 1977; Post 1978; Sharman 1981), or even positive associations (Chivers 1977; Richard 1977). These studies lacked direct measurements of food biomass, making interpretation problematic, but other authors have explicitly suggested that travel distance and time devoted to foraging increase in seasons when food is most clumped, independently of marked changes in overall availability (Terborgh 1983; Bennet 1986; Strier 1987; Chapman 1988). Greater understanding of the relative contributions of the within-patch and between-patch travel components to seasonal, inter-population and inter-specific variation in foraging effort will depend on adequate quantification of the overall availability and spatial distribution of resources.

#### Differential Home Range Use

In the main, studies of range use in primates and other mammals have relied on bivariate correlations, or even qualitative descriptions of association with resource distribution (e.g. primates: chapters in Clutton-Brock 1977, but see also Post 1978; Sigg & Stolba 1981; ungulates: Leuthold 1977). We have shown here that bivariate correlations can mislead because habitat variables may be confounded with one another. Using multiple regression, we found that the baboons' ranging patterns were centred on critical resources. The influence of sleeping site proximity is unsurprising, given their limited availability (there were only four regularly used sites within the 44 km<sup>2</sup> home range) and the fact that ranging routes must inevitably

converge on and diverge out from these points. In contrast, the proximity of waterholes was significantly associated with average quadrat bout duration, as well as with total occupancy, indicating a preference to concentrate foraging activities in areas where water could be readily obtained. A causal link between water distribution and home range use is further supported by a 'natural' experiment which occurred with the construction of a new waterhole at the eastern edge of the group's home range in the final month of the present study. As predicted, the group have subsequently developed this area as a stronger focus of their ranging (unpublished data). It appears, therefore, that the need for drinking water influenced the ranging patterns of the group, a conclusion that fits with qualitative observations that water availability determines both what areas savannah animals can survive in, and where they go within their home range (baboons: Altmann & Altmann 1970; S. Altmann 1974; humans: Lee 1976; ungulates: Western 1975; Ginsberg 1989; Taylor 1989).

The importance of water availability for baboons is probably largely a product of their thermoregulatory requirements in a hot, dry environment. While moving about in the open, animals are exposed to intense insolation and radiation of heat from the ground. Mammals vary in their physiological reliance on drinking water; some arid and semi-arid adapted species, such as the oryx, *Oryx beisa*, often drink only once in every 3–4 days (Stanley-Price 1985), but baboons appear to need to drink more frequently than this. Altmann & Altmann (1970), for example, found that yellow baboons, *Papio cynocephalus*, drank on 84% of days when they were observed. As a result, species differ in the distance they can travel away from water, and hence in variables such as home range size. Thus physiological adaptations are an important consideration in comparative behavioural ecology. Baboons maintain core temperatures by sweating and panting (Funkhouser et al. 1967), both of which involve evaporative water loss. Hiley (1976) found that cutaneous water loss in captive baboons subjected to heat exposure at 40°C (a not unknown maximum shade temperature in the present study) increased above baseline by about 360%. Behavioural methods of thermoregulation, principally microhabitat selection, have the advantage that water loss is minimized, and several workers have reported that baboons rest in the shade during the hottest part of the day (Altmann &



Altmann 1970; Stoltz & Saayman 1970; Stelzner 1988). The disadvantage of this strategy is that potential foraging time is lost, and future work might examine whether the extent to which it is used in different populations is related to water availability. Use of shade as a form of behavioural thermoregulation could have implications for differential range use if certain areas provided better cover than others, but, in the only published study addressing this question, Stelzner (1988) found that yellow baboons used shade opportunistically when they encountered it, rather than actively selecting shaded areas of the home range for foraging.

In conclusion, habitat selection by the baboons over an extended period was evidently related to a number of factors, and this complexity reduces the utility of simple optimality principles, such as those based on the maximization of energy yield, in modelling habitat selection. Indeed, much variance in quadrat use remained unexplained in the present analyses, implying that additional factors were operating. Such factors might include herb-layer composition, predation risk and interactions between groups (Altmann & Altmann 1970; Rasmussen 1979); these could profitably be investigated in the future.

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