Evolutionary Ecology **16:** 579–593, 2002.

Research article

Climatic determinants of diet and foraging behaviour in baboons

R.A. HILL[†,*] and R.I.M. DUNBAR
Population and Evolutionary Biology Research Group, School of Biological Sciences, Nicholson Building, University of Liverpool, Brownlow Street, Liverpool L69 3GS UK; [†]Evolutionary Anthropology Research Group, Department of Anthropology, University of Durham, 43 Old Elvet, Durham DH1 3HN UK
*(*author for correspondence, tel.: +44-191-374-7525; fax: +44-191-374-2870;*
e-mail: r.a.hill@durham.ac.uk)

Received 20 November 2001; accepted 19 September 2002

Co-ordinating editor: P. Harvey

Abstract. Baboons (*Papio* spp.) are characterised by a large degree of variation in foraging behaviour and dietary composition. Previous analyses have suggested that much of this can be traced to differences in ecological conditions between sites. The proximate mechanism underlying these relationships is assumed to be mediated via the impact of climatic conditions on food availability, and ultimately the impact that this has on dietary composition. This paper examines these relationships more explicitly. Data from 15 baboon populations were used to assess the relationship between foraging variables and dietary composition. Only feeding time showed significant relationships with dietary composition, with percentage of time spent feeding decreasing with proportion of fruit in the diet, and increasing with the proportion of subterranean items. No relationships were found between diet composition and moving time or day journey length, although significant relationships were found between these variables and group size. The proportions of feeding time spent feeding on fruit, subterranean items and leaves were functions of the ecological conditions experienced by that population, although no relationships were found for the percentage of feeding time devoted to flowers or animal material. The relationships between the proportion feeding time spent on fruits, leaves and subterranean items and ecological variables could be best explained through understanding the way in which bush and tree level vegetation respond to the climatic environment and the impact this has on fruit availability. In this respect, temperature and seasonality are the key climatic parameters. This provides good support for the idea that the proximate mechanism underlying the relationship between foraging time and ecological variables is mediated via the impact of the climatic environment on vegetation structure and food availability. Similar factors have been proposed to explain much of the geographic variation in species diversity, suggesting that these relationships have far wider relevance and may account for much of the observed geographical variation in mammalian behaviour.

Key words: climate, feeding, fruit, primates, seeds, subterranean items, vegetation

Introduction

Relationships between intraspecific variation in foraging behaviour and environmental variables have been reported for a variety of primate species (baboons, *Papio* spp.: Dunbar, 1992a, 1996; gelada, *Theropithecus gelada*: Dunbar, 1992b; chimpanzees, *Pan* spp.: Williamson, 1997; gibbons, *Hylobates* spp.: Lan *et al.*, submitted). For example, in an analysis of the time budgets of 14 baboon populations, Dunbar (1992a, 1996) found the proportion of time spent feeding to be a negative function of mean annual temperature, a positive function of day journey length, and functions of two measures of rainfall seasonality (the number of dry months and Simpson's index of rainfall diversity). Day journey length was itself found to be a function of mean annual rainfall and of group size. These relationships were interpreted as reflecting the climatic constraints on food availability. Rainfall, and the degree of seasonality, were taken to represent important constraints on resource availability through their impact on the distribution of bush-level vegetation (within which the majority of preferred baboon foods are found: Dunbar, 1992a). Similar conclusions were drawn with respect to percentage time spent moving, where group size and the number of dry months were selected as the key variables in Dunbar's (1992a) analysis. Vegetation dispersion, and thus food availability, as well as social factors, were again proposed to be the key factors underlying much of the interpopulation variation in baboon moving behaviour. Baboon foraging behaviour thus appears to be closely linked to the ecological conditions experienced by each population, although the proximate link mediating the impact of climatic factors on foraging behaviour is suggested to operate via its impact on food availability (Dunbar, 1992a).

Similar relationships have been proposed between other elements of baboon behavioural ecology and the prevailing ecological conditions. While Dunbar (1992a) showed that baboon time budgets (and their underlying climatic determinants) could be used to predict maximum group sizes across populations, Barton *et al.* (1996) went on to formalise how food distribution could explain the variation observed in social structure within baboon groups. Although predation pressure was taken to be a key factor determining group size, the spatial distribution of food determined the potential for within group contest competition, and this in turn determined female social relationships and the internal structure of the group (Barton *et al.*, 1996; see also van Schaik, 1989).

In a more recent study, Hill *et al.* (2000) showed that variation in interbirth intervals of baboons across 14 populations could also be traced to differences in ecological (as well as demographic) conditions. Hill *et al.* (2000) suggested that these relationships could be explained, at least in part, through the impact of climatic conditions on food availability, with long interbirth intervals associated with small group sizes reflecting low food availability in these populations. Thus food availability appears to be the primary factor suggested to underlie much of the observed variation in behaviour and life history between baboon populations. To date, however, little attention has been paid to how ecological conditions influence food availability and constrain a species' diet and foraging strategy.

An effective foraging strategy is an essential element of any animal's behaviour, since without access to adequate energy reserves the ability of an individual to reproduce successfully might be significantly compromised. Altmann (1991, 1998) provided compelling evidence to support this and showed that the diet of yearling primates can predict quite accurately the future survival and reproductive success of these individuals. As a consequence, knowledge of how ecological conditions constrain a species' foraging strategy has far reaching implications for the understanding of a species' demographic and life history variation. Baboons represent an ideal species with which to examine the ecological determinants of diets and foraging behaviour, since there is a wealth of data available on not only their ecological and behavioural flexibility (Barton *et al.*, 1996), but also on their dietary diversity (Dunbar, 1988; Whiten *et al.*, 1991). This paper explores the possibility that differential food availability might be the link underlying much of the behavioural and ecological variation in baboons.

Methods

The foraging profiles for 15 populations of baboons are given in Table 1, along with climatic data for each site. Populations were only included if a minimum of 10 months data were available on diet composition. Baboon diets were indexed by the percentage of feeding time that is spent feeding on fruits, leaves, subterranean items, flowers and animal matter (following Dunbar, 1988; Whiten *et al.*, 1991). In this context, fruits are taken to include both fleshy fruits and seeds, with no further distinction made between these food types since these data are not available for the majority of sites. Data on percentage time spent feeding and moving, as well as day journey length, are also available for the majority of populations with dietary data (see Table 1). Although slightly different methodological procedures may have been used in data collection at each site, it is unlikely that this will lead to significant errors in the diet and behavioural data, particularly since only long-term data sets are included in this analysis. Following convention with primate field studies, we use the term diet to refer to the proportional distribution of time spent feeding on different dietary categories (with all categories summing to unity); this is not necessarily the same thing as dietary intake. Our concern here, however, is principally with the costs the animals incur in meeting their nutritional requirements and this is more appropriately indexed by the proportion of feeding time devoted to the different dietary items.

Previous cross-populational analyses of baboon behavioural ecology have utilised a number of indices to quantify rainfall seasonality and the length of the growing season (e.g. Dunbar, 1992a, 1996). Following analyses by

Table 1. Foraging profile for 15 populations of baboons with relevant behavioural, climatic and topographic data for that site

Site	*F*	*M*	*DJL*	*N*	*Fr*	*Sub*	*Le*	*Fl*	*An*	*T*	*R*	*S*	*PPI*	*A*	*L*	Ref
Papio cynocephalus anubis																
Bole, Ethiopia	20.5	25.4	1.2	19	41	1	41	12	4	19.5	1105	0.84	8	1700	9°25N	Dunbar and Dunbar (1974)
Chololo, Kenya	40.2	35.8	6.6	102	23	15	27	21	1	22.9	549	0.86	5	1661	0°30'S	Barton (1989)
Gilgil, Kenya	50.7	30.4	4.6	57	10	27	53	3	2	18.1	595	0.83	5	1768	0°30'S	Harding (1976)
Gombe, Tanzania	25.8	19.4	–	23.5	49	7	14	2	13	23.5	1417	0.82	8	680	4°40'S	Oliver, ers. comm. to RIMD
Masai Mara, Kenya	–	–	–	–	46	8	44	1	1	20.5	1025	0.99	12	1700	1°05'S	Popp (1978)
Shai Hills, Ghana	20.3	18.2	1.3	38.8	59	17	8	5	0	25.9	1065	0.87	8	1000	5°55'N	Depew (1983)
Papio cynocephalus cynocephalus																
Amboseli, Kenya	46.4	26.1	5.0	59.2	27	33	15	5	1	23.4	335	0.67	3	1127	2°40'S	Post (1978); Bronikowski and Altmann (1996)
Mikumi, Tanzania	36.5	26.1	3.4	120	43	12	14	20	–	25.3	866	0.87	6	550	7°15S	Norton *et al.* (1987); Rasmussen, pers. comm. to RIMD
Ruaha, Tanzania	47.7	24.2	–	72	16	52	19	1	9	21.7	298	0.58	3	1230	7°40'S	Rasmussen (1978); Sigg and Stolba (1981)
Papio cynocephalus hamadryas																
Erer-Gota, Ethiopia	–	–	9.5	83	45	2	28	22	0	24.2	665	0.87	5	1200	8°51'N	Kummer (1968)
Papio cynocephalus papio																
Mt Assirik, Senegal	23.5	36.9	7.9	247	74	3	9	9	1	29.4	941	0.69	5	150	13°00'S	Sharman (1981)
Papio cynocephalus ursinus																
Cape Point, South Africa	33.5	29.0	7.9	85	42	16	25	12	4	17.9	631	0.91	6	10	34°15'S	Davidge (1978)
Drakensberg, South Africa	56.6	17.7	4.6	11.8	3	53	26	14	4	14.6	1197	0.87	9	2045	29°00'S	Whiten *et al.* (1987, 1991)
Mkuzi, South Africa	36.3	30.2	4.5	47.3	90	1	6	3	1	22.4	630	0.78	6	125	32°38'S	Gaynor (1994)
Suikerbosrand, South Africa	–	–	4.1	78	43	39	8	7	3	16.0	732	–	–	1600	27°00'S	Anderson, pers. comm. to RIMD

F – mean annual feeding time (%), *M* – mean annual moving time (%), *DJL* – day journey length (km), N – group size, Fr – fruits (%), *Sub* – subterranean foods (%), Le – leaves (%), *Fl* – flowers (%), *An* – animal matter (%), *T* – mean annual temperature (°C), *R* – mean annual rainfall (mm), *S* – Shannon's index of rainfall diversity, *PPI* – plant productivity index (months), *A* – altitude (m), *L* – latitude.

Bronikowski and Webb (1996) and Williamson (1997) evaluating a range of diversity indices for describing rainfall seasonality, we utilise the Shannon index (which ranges from 0 (highly seasonal) to 1 (no seasonality)) and the plant productivity index (PPI: the number of months per year receiving more rainfall (in millimetres) than twice the mean annual temperature for that site (in °Celcius): le Houérou, 1984) in place of the Simpson index and V (the number of months receiving less than 50 mm rainfall) utilised in previous analyses (e.g. Dunbar, 1992a, 1996).

Backwards multiple regression analysis was used to determine the best-fit regression equations relating diet components to the climatic and topographic variables, since this method utilises the most favourable inclusion criteria given the sample sizes involved. However, since backward regression can sometimes incorporate variables purely on the basis of their interrelationships with other variables, each equation was assessed to ensure that it was biologically realistic, and that it was not statistically dependent on the initial list of independent variables. Data were not transformed since none were found to deviate significantly from a normal distribution (Kolmogorov–Smirnov: $p > 0.25$ in all cases). Values for Shannon's index and PPI were not available for Suikerbosrand, and thus this site could not be incorporated into the original models.

However, if these measures of rainfall seasonality did not form a significant component of the initial model, then the analysis was rerun with these variables excluded, thus allowing Suikerbosrand to be included in the data set. Sample sizes may thus differ between models and only the final equations are presented here. Since sample sizes are relatively small, we conduct power analysis using GPOWER (Faul and Erdfelder, 1992) to evaluate non-significant results and to assess the potential biological significance of these relationships, as suggested by Thomas and Juanes (1996). Following Cohen (1988) we take a value of 0.8 to indicate a high power for any given effect. As with previous analyses (Dunbar, 1992a, 1996; Hill *et al.*, 2000) this paper follows convention in considering all five *Papio* species as subspecies of a single superspecies *Papio cynocephalus* (e.g. Jolly, 1993), and thus no restrictions are placed on the analyses on the basis of phylogeny.

Results

It is clear from Table 1 that baboon diets are dominated by fruits, leaves and subterranean items, with flowers and animal matter constituting a much smaller proportion of the diet. However, it is also evident that even with foraging profiles described at this very gross level, considerable variation is observed across habitats (Whiten *et al.*, 1991). Since both feeding and moving time, as well as day journey length also differ significantly between baboon populations (Dunbar, 1992a), it might be anticipated that dietary differences could go some way to explaining differences in foraging time across populations.

Diet composition and time budget components

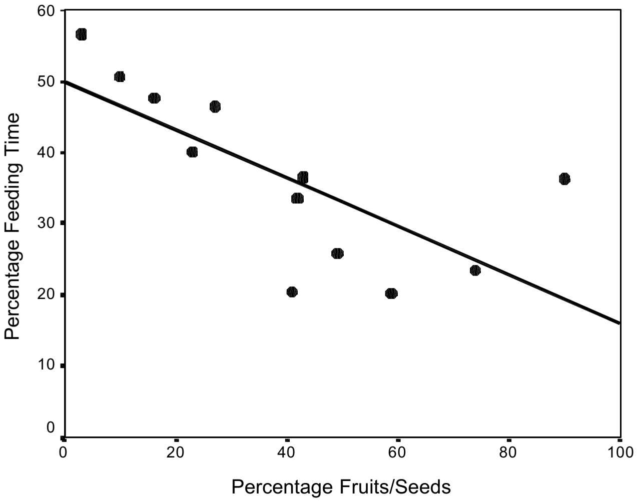
Table 2 displays the relationships between diet composition and percentage time spent feeding and moving and day journey length. Only feeding time shows significant relationships with diet composition across populations, with time spent feeding correlated with both the proportion of fruits and subterranean food items in the diet (see Figure 1). No significant relationships exist for moving time or day journey length, although moving time shows a significant positive relationship with group size and the relationship between group size and day journey length approaches significance. However, the potential biological significance of some of the non-significant relationships with diet composition cannot be dismissed since small sample sizes result in low statistical power of the tests (range 0.05–0.33). Sample sizes of 21 populations would be required to detect even large effects ($r \geq 0.5$) at an acceptable power (Cohen, 1988). Nevertheless, those relationships with diet that are significant show high statistical power (fruits and seeds – 0.89; subterranean items – 0.99). Applying Bonferroni's correction for multiple comparisons (Rice, 1989; Haccou and Meelis, 1992) does little to affect these findings, since for six comparisons per dependent variable the level of rejection for a significant correlation is set at $p = 0.0083$. The relationship between feeding time and the proportion of diet devoted to fruits ($p = 0.0088$) only just exceeds this critical value, while the other two significant relationships remain significant.

Feeding time increases as the proportion of subterranean food items in the diet increases ($r^2 = 0.632$, $F_{(1,11)} = 18.88$, $p = 0.001$), and decreases with increasing proportion of fruits in the diet ($r^2 = 0.514$, $F_{(1,11)} = 11.62$, $p = 0.006$),

Table 2. Pearson's correlations between feeding time, moving time and day journey length and the proportion of feeding time devoted to the five dietary categories

Diet component	Feeding		Moving		Day journey length	
	r	*p*	*r*	*p*	*r*	*p*
Fruits/seeds $_{(n = 12)}$	−0.716	0.009	0.242	ns	0.028	ns
Subterranean $_{(n = 12)}$	0.816	0.001	−0.329	ns	−0.129	ns
Leaves $_{(n = 12)}$	0.320	ns	0.114	ns	0.013	ns
Flowers $_{(n = 12)}$	0.022	ns	0.268	ns	0.388	ns
Animals $_{(n = 11)}$	−0.004	ns	−0.458	ns	−0.301	ns
Group size $_{(n = 12,12,11)}$	−0.214	ns	0.720	0.008	0.590	0.09

(a) Fruit



(b) Subterranean items

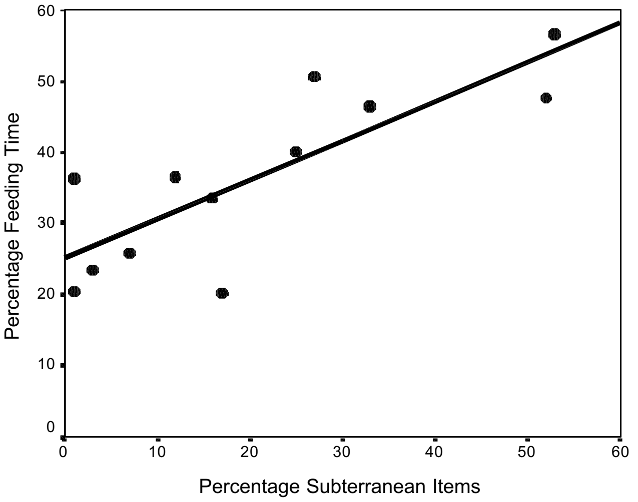


Figure 1. Relationships between feeding time and (a) percentage of feeding time constituting fruits and (b) percentage of feeding time constituting subterranean items.

although a quadratic equation is the best fit for this relationship ($r^2 = 0.793$, $F_{(2,10)} = 19.20$, $p < 0.001$) since feeding time asymptotes at a minimum value of about 20%. The variability in feeding time across baboon populations can be attributed primarily to the extent to which they concentrate on these two dietary categories. Hence, it is the variance in these two that we principally need to explain. There is also a significant quadratic relationship between the proportion of feeding time spent on subterranean food items and the proportion of time on fruits (Figure 2: $r^2 = 0.627$, $F_{(2,12)} = 10.09$, $p = 0.003$). This suggests that subterranean food items are only exploited when higher quality food items such as fruits and seeds are not available. In turn this implies that differential food availability, at least in terms of gross dietary types, might be the link underlying the relationships with feeding time. However, an alternative explanation might simply be that percentage time spent feeding increases with the proportion of subterranean items in the diet due to the increased processing time associated with this food type. A more complete understanding of cross-populational variability in feeding time and diet choice may thus only come from a consideration of how the dietary composition relates directly to the climatic conditions at any given site.

Environmental correlates of diet composition

The relationships between the proportion of feeding time devoted to each of the five dietary categories and the ecological conditions for that population are given in Table 3. Significant regression equations are produced for the percentage of feeding time devoted to fruits, subterranean items and leaves. No significant relationships exist between the proportions of flowers or animal matter in the diet and any environmental variables, although, again, small sample sizes contribute to the low power of these analyses.

Temperature was found to be a component of the equations for all three significant relationships, although the sign of the relationship differs between

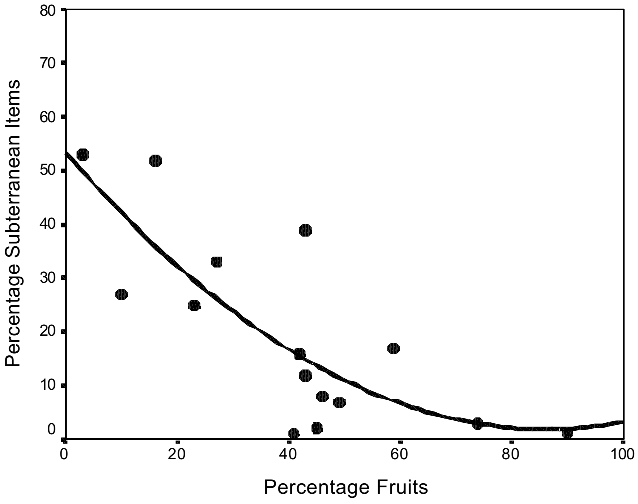


Figure 2. The relationship between percentage of feeding time spent feeding on fruit and on subterranean food items for 15 baboon populations.

Table 3. Relationships between environmental variables and the percentage of feeding time devoted to the five food types

Food type	Equation	r^2	*F*	*p*
Fruits/seeds	$\mathrm{Fr} = 30.55 + 2.63\ \mathrm{T} - 0.023\ \mathrm{A} + 4.23\ \mathrm{PPI}$	0.776	$_{(3,10)}11.552$	0.001
Subterranean items	$\mathrm{Sub} = 164.45 - 3.06\ \mathrm{T} - 97.07\ \mathrm{P_S}$	0.530	$_{(2,11)}6.202$	0.016
Leaves	$\mathrm{Le} = 90.86 - 2.69\ \mathrm{T} - 0.83\ \mathrm{L}$	0.572	$_{(2,12)}8.004$	0.006
Flowers	–	–	–	–
Animal matter	–	–	–	–

T – mean annual temperature (°C), *A* – altitude (m), *PPI* – plant productivity index (months), P_S – Shannon's index of rainfall diversity, *L* – latitude. Independent variable included in the analysis but not incorporated in the final models is *P* – mean annual rainfall (mm).

the dietary categories. The proportion of feeding time devoted to fruit is a positive function of temperature, although there is also a negative relationship with altitude that serves to further modify this overall relationship. In addition, the proportion of fruit-feeding increases as the number of productive months (indexed by PPI) increases. The proportion of feeding time devoted to subterranean items declines as mean annual temperatures increase and rainfall becomes less seasonal (Shannon's index of rainfall diversity increases). Although no correlations were found between the proportion of feeding time devoted to leaves and total feeding time, significant relationships are found between leaf consumption and climatic variables: The proportion of feeding time spent on leaves is a negative function of both temperature and latitude.

Discussion

Baboon foraging is characterised by a large degree of behavioural and dietary flexibility that can be traced to differences in the ecological environment (Dunbar, 1992a; Barton *et al*., 1996). Time spent feeding by baboons is negatively related to the proportion of feeding time devoted to fruits, and a positive function of the proportion of time spent on subterranean items. No relationships were found between diet composition and percentage time spent moving or day journey length. This is perhaps surprising, since different food types might be anticipated to have different distributions (i.e. different patch sizes and inter-patch distances) and these would be expected to affect the ranging behaviour of the baboons. However, small sample sizes leading to low statistical power for small and medium effects may restrict the possibility of detecting anything but strong biological effects. Nevertheless, other factors confound the relationships between moving and day journey length with diet composition.

The most obvious explanation for the lack of relationship between moving time and day journey length with diet composition relates to the fact that both of the factors correlate with group size. Similar relationships with group size have been reported both within (van Schaik *et al.*, 1983; Stacey, 1986) and between populations (Dunbar, 1992a; Bronikowski and Altmann, 1996; Hill, 1999). These relationships are likely to reflect the fact that each animal must forage over roughly a constant area of its own each day such that total travel distances increase with group size, although the effects of feeding disruption due to increased intragroup competition may also be important with respect to moving time (Dunbar, 1992a). Barton *et al.* (1992) showed that sleeping site availability set the minimum distance travelled daily by baboons, although access to water sources was also important. Since these factors are as much a feature of the topographical environment (e.g. cliffs, rivers) as the ecological environment (e.g. trees, rainfall), they may further obscure any relationship between diet composition and day journey length or moving time. As a consequence, we would predict that the impact of dietary composition on foraging behaviour should be mediated primarily through its influence on feeding time, although data from further populations are required to rule out small sample size effects and confirm the absence of relationships between diet and moving and day journey length.

The relationships between percentage time spent feeding by baboons and the proportion of this time devoted to fruits and subterranean items almost certainly reflects the nutritional benefits of feeding upon higher quality food items. However, the increased processing time of subterranean items must at least partially account for these trends. Previous studies of diet choice in baboons have shown that a number of food constituents determine patterns of diet selection, and these include protein, fibre, phenolics and alkaloids (Whiten *et al.*, 1991; Barton and Whiten, 1994), as well as water (Barton, 1989) and micronutrients (Gaynor, 1994). Of these, the protein to fibre ratio is cited most frequently as the primary factor governing diet choice in primates (Hamilton *et al.*, 1978; McKey *et al.*, 1981; Whiten *et al.*, 1990; Wrangham *et al.*, 1991; Barton and Whiten, 1994). Foraging strategies would thus be expected to incorporate a high proportion of foods that are high in protein and low in fibre. However, Altmann (1998) concluded that energy was of primary importance (at least for the Amboseli population) and thus baboons would be expected to select foods on the basis of energy or carbohydrate levels. Both protein and carbohydrate levels are thus significant factors underpinning baboon diet selection, and the availability of high quality food items in any environment may therefore go some way to accounting for differences in time spent feeding between populations.

Since fruits and seeds are generally high in carbohydrates and protein respectively (Altmann *et al.*, 1987; Barton *et al.*, 1993; Gaynor, 1994), the negative relationship between feeding time and the proportion of fruits and seeds almost certainly reflects the fact that less time is required to satisfy an individuals' nutritional requirements when higher quality food is available. However, the relationship with subterranean food items is perhaps less obvious, since these too are known to be relatively high in nutrients, at least in terms of carbohydrate composition (e.g. Altmann *et al.*, 1987; Barton *et al.*, 1993; Gaynor, 1994). The energetic and time costs associated with excavating and processing subterranean food items must go some way to explaining this relationship (Whiten *et al.*, 1990), although it is also important to remember that dietary composition will also reflect the availability of various food types at the different sites. Since the different dietary guilds respond in varying ways to the ecological environment, it might be that subterranean food items are only exploited when higher quality foods (e.g. fruits and seeds) are not available (Post, 1978; Whiten *et al.*, 1987). The strong negative relationship between the proportion of feeding time devoted to fruits and that spent on subterranean items suggests that this might be the case. However, to fully elucidate the factors contributing to variation in feeding time across baboon populations we need to understand how the availability of the different food types responds to ecological conditions.

Significant regression equations with ecological variables are produced for the percentage of feeding time devoted to fruits, subterranean items and leaves. Temperature is a component of all three equations, although the signs of the relationships differ between the dietary components. The proportion of feeding time spent on fruits is a positive function of temperature, a fact that probably reflects the way in which bush cover responds to temperature across sub-Saharan Africa. Since bush cover is a positive function of temperature (Dunbar, 1992a, 1996; Hill, 1999), the increased proportion of fruits and seeds in the diet must be due to the increased availability of these food items as bush-level cover increases. The negative relationship with altitude probably serves to modify this overall relationship since temperatures decline with altitude. However, these results suggest that fruits and seeds are selected preferentially as their availability increases (see Altmann and Altmann, 1970; Hamilton *et al.*, 1978; Barton, 1989). This suggestion is further supported by the negative relationships with temperature for the proportions of feeding time spent on both subterranean items and leaves, since it suggests that these items constitute 'fall-back' foods as bush cover, and thus the availability of preferred foods, declines (Post, 1978; Whiten *et al.*, 1987).

The positive relationship between the proportion of feeding time spent on fruit and the number of productive months further suggests that fruits and seeds are being selected preferentially when they become available. The proportion of tree cover (the other vegetation level likely to contain a significant proportion of fruits and seeds) declines as the number of non-productive months increases (Dunbar, 1996; Hill, 1999). Thus it again appears that fruits form a larger proportion of the diet when they are available. However, seasonality is also an important factor influencing diet composition. Shannon's index of rainfall diversity and latitude were incorporated into the equations for the proportion of feeding time devoted to subterranean items and leaves, respectively. These relationships probably reflect the fact that in more seasonal environments, periods of food shortage are likely to occur at certain times of year. Since fruits and seeds, as the most preferred food items, might be scarce at such times, diets are likely to shift to other food sources as seasonality, and thus food scarcity, increases (e.g. Post, 1978; Whiten *et al*., 1987; Byrne *et al*., 1993).

Diet composition is thus constrained by the impact of climatic conditions on vegetation structure, and most notably on the availability of fruits and seeds, with subterranean food items, as well as leaves, primarily exploited when higher quality food is not available (Post, 1978; Whiten *et al*., 1987; Byrne *et al*., 1993). It should be noted though, that the preceding analyses have considered fruits and seeds to be a single dietary category. The possibility that the availability of fruits and seeds might respond in different ways to climatic conditions cannot be discounted, although the data are not currently available to test this further. Nevertheless, the variation in diet composition between populations need not necessarily reflect differences in nutritional intake. Byrne *et al*. (1993) showed that despite major differences in diet composition between two troops of baboons separated climatically by an altitude range of 400 m in the Drakensberg mountains, there was no difference in nutrient gain. Thus while specific populations may vary in their absolute nutritional requirements (due to such factors as thermoregulatory costs), variation in diet and feeding time alone is unlikely to lead to a significant divergence in energy intake between sites.

The finding that temperature is the key climatic parameter underpinning the relationships between diet and ecological conditions is significant, since temperature is not often considered an important constraint on tropical animal ecology. However, similar relationships have been found with respect to mammal species richness in southern Africa (Andrews and O'Brien, 2000). Andrews and O'Brien (2000) found mean annual temperatures to be a significant influence on large (>45 kg) mammal ecology. However, although plant species richness was the best factor accounting for variability in mammal species richness across all species (although especially in small (<45 kg) species), with 75% of the variance explained, thermal seasonality did explain 69% of the variance. Mammal species richness is greatest where seasonal variability in water, temperature and energy regimes are least, since this leads to greater plant species diversity where food production and productivity of the environment are greatest. Since plant diversity is itself a function of climate

(O'Brien, 1993), mammal richness is therefore an indirect function of climate (Andrews and O'Brien, 2000). Similar relationships have been reported for North American species richness (Currie, 1991). Although mammal species richness is a far broader dependent variable than that considered in this study, the ultimate conclusions are largely similar. Thus it is clear that much of the variation in mammalian behaviour, from fine-grained analyses of species diet selection to the composition of faunal assemblages, can be traced to the way in which vegetation structure is constrained by the climatic environment.

Acknowledgement

We thank two anonymous referees for constructive comments on earlier drafts of this manuscript.

References

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

Altmann, S.A. (1998) *Foraging for Survival: Yearling Baboons in Africa*. University of Chicago Press, Chicago.

Altmann, S.A. and Altmann, J. (1970) *Baboon Ecology*. University of Chicago Press, Chicago.

Altmann, S.A., Post, D.G. and Klein, D.F. (1987) Nutrients and toxins of plants in Amboseli, Kenya. *Afr. J. Ecol.* **25**, 279–293.

Andrews, P. and O'Brien, E.M. (2000) Climate, vegetation, and predictable gradients in mammal species richness in Southern Africa. *J. Zool. Lond.* **251**, 205–231.

Barton, R.A. (1989) Foraging strategies, diet and competition in olive baboons. *Ph.D. Thesis*, University of St. Andrews.

Barton, R.A., Byrne, R.W. and Whiten, A. (1996) Ecology, feeding competition and social structure in baboons. *Behav. Ecol. Sociobiol.* **38**, 321–329.

Barton, R.A. and Whiten, A. (1994) Reducing complex diets to simple rules: food selection by olive baboons. *Behav. Ecol. Sociobiol.* **35**, 283–293.

Barton, R.A., Whiten, A., Byrne, R.W. and English, M. (1993) Chemical composition of baboon plant foods: implications for the interpretation of intra- and interspecific differences in diet. *Folia Primatol.* **61**, 1–20.

Barton, R.A., Whiten, A., Strum, S.C., Byrne, R.W. and Simpson, A.J. (1992) Habitat use and resource availability in baboons. *Anim. Behav.* **43**, 831–844.

Bronikowski, A.M. and Altmann, J. (1996) Foraging in a variable environment: weather patterns and the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.* **39**, 11–25.

Bronikowski, A.M. and Webb, C. (1996) Appendix: a critical examination of rainfall variability measures used in behavioural ecology studies. *Behav. Ecol. Sociobiol.* **39**, 27–30.

Byrne, R.W., Whiten, A., Henzi, S.P. and McCulloch, F.M. (1993) Nutritional constraints on mountain baboons (*Papio ursinus*): implications for baboon socioecology. *Behav. Ecol. Sociobiol.* **33**, 233–246.

Cohen, J. (1988) *Statistical Power Analysis for the Behavioural Sciences*. 2nd edn. Lawrence Erlbaum, Hillsdale.

Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.* **137**, 27–49.

Davidge, C. (1978) Ecology of baboons (*Papio ursinus*) at Cape Point. *Zool. Afr.* **13**, 329–350.

Depew, L.A. (1983) Ecology and behaviour of baboons (*Papio anubis*) in the Shai Hills Game Production Reserve, Ghana. *M.Sc. Thesis*, Cape Coast University.

Dunbar, R.I.M. and Dunbar, P. (1974) Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. *Folia Primatol.* **21**, 36–60.

Dunbar, R.I.M. (1988) *Primate Social Systems*. Chapman and Hall, London.

Dunbar, R.I.M. (1992a) Time: a hidden constraint on the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.* **31**, 35–49.

Dunbar, R.I.M. (1992b) A model of the gelada socio-ecological system. *Primates* **33**, 69–83.

Dunbar, R.I.M. (1996) Determinants of group size in primates: a general model. In W.G. Runciman, J. Maynard Smith and R.I.M. Dunbar, (eds) *Evolution of Social Behaviour Patterns in Primates and Man*. Oxford University Press, Oxford, pp. 33–57.

Faul, F. and Erdfelder, E. (1992) GPOWER: A priori, post-hoc and compromise power analysis for MS-DOS [Computer program]. Bonn, FRG: Bonn University, Department of Psychology.

Gaynor, D. (1994) Foraging and feeding behaviour of chacma baboons in a woodland habitat. *Ph.D. Thesis*, University of Natal.

Haccou, P. and Meelis, E. (1992) *Statistical Analysis of Behavioural Data*. Oxford University Press, Oxford.

Hamilton, W.J. III, Buskirk, R.E.R. and Buskirk, W.H. (1978) Omnivory and the utilization of food resources by chacma baboons, *Papio ursinus*. *Am. Nat.* **112**, 911–924.

Harding, R.S.O. (1976) Ranging patterns of a group of baboons (*Papio anubis*) in Kenya. *Folia Primatol.* **25**, 143–185.

Hill, R.A. (1999) Ecological and demographic determinants of time budgets in baboons: implications for cross-populational models of baboon socioecology. *Ph.D. Thesis*, University of Liverpool.

Hill, R.A., Lycett, J.E. and Dunbar, R.I.M. (2000) Ecological and social determinants of birth intervals in baboons. *Behav. Ecol.* **11**, 560–564.

Jolly, C.J. (1993) Species, subspecies, and baboon systematics. In W.H. Kimbel and L.B. Martin (eds) *Species, Species Concepts, and Primate Evolution*. Plenum Press, New York, pp. 67–107.

Kummer, H. (1968) *Social Organisation of Hamadryas Baboons*. Karger, Basel.

le Houérou, H.N. (1984) Rain use efficiency: a unifying concept in arid-land ecology. *J. Arid. Environment*. **7**, 213–247.

McKey, D.B., Gartlan, J.S., Waterman, P.G. and Choo, G.M. (1981) Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biol. J. Linn. Soc.* **16**, 115–146.

Norton, G.W., Rhine, R.J., Wynn, G.W. and Wynn, R.D. (1987) Baboon diet: a five-year study of stability and variability of the plant feeding and habitat of the yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *Foila Primatol.* **48**, 78–120.

O'Brien, E.M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *J. Biogeogr.* **20**, 181–198.

Popp, J.L. (1978) Male baboons and evolutionary principles. *Ph.D. Thesis*, University of Harvard.

Post, D.G. (1978) Feeding and ranging behaviour of the yellow baboon (*Papio cynocephalus*). *Ph.D. Thesis*, Yale University.

Rasmussen, D.R. (1978) Environmental and behavioural correlates of changes in range use in a troop of yellow (*Papio cynocephalus*) and a troop of olive (*Papio anubis*) baboons. *Ph.D. Thesis*, University of California, Riverside.

Rice, W.R. (1989) Analysing tables of statistical tests. *Evolution* **43**, 223–225.

Sharman, M. (1981) Feeding, ranging and social organisation of the guinea baboon. *Ph.D. Thesis*, Yale University.

Sigg, H. and Stolba, A. (1981) Home range and daily march in a hamadryas baboon troop. *Folia Primatol.* **36**, 40–75.

Stacey, P.B. (1986) Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol.* **18**, 175–187.

Thomas, L. and Juanes, F. (1996) The importance of statistical power analysis: an example from Animal Behaviour. *Anim. Behav.* **52**, 856–859.

van Schaik, C.P. (1989) The ecology of social relationships among female primates. In V. Standen, and R.A. Foley, (eds) *Comparative Socioecology: The Behavioural Ecology of Humans and Other Animals*. Blackwell Scientific publications, Oxford, pp. 195–218.

van Schaik, C.P., Noordwijk, M.A., de Boer, R.J. and den Tonkelaar, I. (1983) The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.* **13**, 173–181.

Whiten, A., Byrne, R.W., Barton, R.A., Waterman, P.G. and Henzi, S.P. (1991) Dietary and foraging strategies of baboons. *Phil. Trans. R. Soc. Lond. B* **334**, 187–197.

Whiten, A., Byrne, R.W. and Henzi, S.P. (1987) The behavioural ecology of mountain baboons. *Int. J. Primatol.* **8**, 367–387.

Whiten, A., Byrne, R.W., Waterman, P.G., Henzi, S.P. and McCullough, F.M. (1990) Specifying the rules underlying selective foraging in wild mountain baboons, *P. ursinus*. In M.T. De Mello, A. Whiten and R.W. Byrne (eds) *Baboons: Behaviour and Ecology, Use and Care*. University of Brasilia Press, Brasilia, pp. 5–22.

Williamson, D.K. (1997) Primate socioecology: development of a conceptual model for the early hominids. *Ph.D. Thesis*, University College, London.

Wrangham, R.W., Conklin, N.L., Chapman, C.A. and Hunt, K.D. (1991) The significance of fibrous foods for Kibale forest chimpanzees. *Phil. Trans. Roy. Soc. B* **334**, 171–178.