Time: a hidden constraint on the behavioural ecology of baboons

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Summary. Data from wild populations of baboons are used to derive functional equations relating time budget components, day journey length and group size to environmental variables. This set of equations predicts both time budgets in an independent sample of populations and the geographical distribution of baboon populations extremely well. I then use these equations to examine the maximum ecologically tolerable group size for baboons occupying different habitats. Groups which exceed this value exhibit signs of ecological stress: they spend less time resting and in social activity than would be expected for their size and environment, they are more likely to fragment during foraging and they travel faster. Populations living in poor quality (low rainfall) habitats are more likely to live in groups that are stressed in this way.

Introduction

When two activities cannot be scheduled simultaneously, animals who are forced to choose between them incur costs in terms of reduced opportunities to engage in other biologically important activities (McFarland 1974; McFarland and Houston 1981). Despite the considerable attention given to the relationship between the environmental factors and time budget structure in the optimal foraging literature (e.g. Schoener 1971; see Stephens and Krebs 1986), rather little consideration has been given to the more general (especially social) consequences of animals' decisions about how to schedule their activities.

Altmann (1980) and Dunbar and Dunbar (1988) have examined female time budgets in relation to the energetic demands of lactation in baboons and gelada, respectively. These studies have suggested that, as the energetic demands on it rise, an animal finds that its time budget becomes increasingly compressed until it is forced to give up time from one or more other activity categories. Ultimately, the animal may be forced to give up social time. Doing so can be expected to have serious implica-

tions for the stability of the animal's social relationships, and thus ultimately both for its personal fitness and for group cohesion (Dunbar 1988). Dunbar and Dunbar (1988) show that gelada females engage in a number of strategies designed to buffer their social relationships against time budgeting problems of this kind.

In this paper, I analyse data from the time budgets of a number of baboon populations in an attempt to determine the intrinsic and extrinsic determinants of time budget structure. I use the regression equations obtained from this analysis to examine the extent to which populations are under ecological stress and the extent to which time budgeting problems impose a constraint on group size. I conclude by asking how populations avoid a serious time budget crisis in habitats where other considerations demand that they live in larger groups than the analysis would consider optimal for that habitat.

Methods

The data derive from 18 populations of baboons (genus *Papio*) distributed throughout sub-Saharan Africa (Fig. 1). The original studies at these sites all provide data on time budgets, group size and key environmental variables, while most provide data on day journey length. In addition, a further five studies provide data on day journey length and relevant environmental and demographic variables, but not time budgets. Studies carried out on the same population were considered to be independent samples provided they were undertaken at least 5 years apart and there had been a significant change in group size or climate between the two studies.

Among the environmental variables that are likely to be of most interest as determinants of behavioural ecology are rainfall, temperature and the density of vegetation cover. In sub-Saharan African habitats, rainfall is known to be a reliable index of both plant biomass and net plant productivity not only between habitats (Coe et al. 1976; Le Houeron and Hoste 1977; Deshmukh 1984) but also within habitats (McNaughton 1985). Whenever possible, mean annual rainfall recorded at the site at the time of the study is used in the present analyses. Where this was not available, mean annual rainfall was determined from the longitudinal records for the nearest weather station.
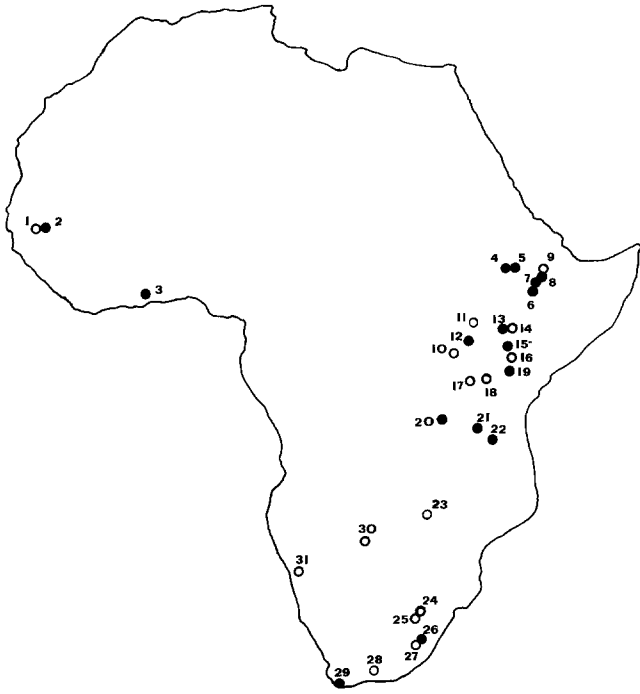
Fig. 1. Location of sampled populations. Sites and sources for data are as follows: *Papio papio*: 1. Badi, Senegal (Dunbar and Nathan 1972; R. Dunbar, unpublished data); 2. Mt. Assirik, Senegal (Sharman 1981); *P. anubis*: 2. Shai Hills, Ghana (Depew 1983); 4. Bole Valley and 5. Mulu, Ethiopia (Dunbar and Dunbar 1974a; R. Dunbar, unpublished data); 6. Metahara, Ethiopia (Aldrich-Blake et al. 1971); 7. Awash Falls, Ethiopia (Nagel 1973 and pers. commun.); 10. Ishasha, Uganda, 1965 (Rowell 1966); 11. Murchison, Uganda (Hall 1965); 12. Budongo Forest, Uganda (Patterson 1976); 13. Chololo, Kenya (Barton 1989); 14. Laikipia, Kenya (Berger 1972); 15. Gilgil, Kenya, 1973 (Harding 1976) and 1984 (Eley et al. 1989); 16. Nairobi NP (DeVore and Hall 1965); 17. Manyara, Tanzania (Altmann and Altmann 1970); 18. Serengeti NP, Tanzania (Altmann and Altmann 1970); *P. hamadryas*: 8. Awash Station, Ethiopia (Nagel 1973 and pers. commun.); 9. Erer-Gota, Ethiopia (H. Sigg, pers. commun.); *P. cynocephalus*: 19. Amboseli, Kenya, 1969 (Altmann and Altmann 1970) and 1975 (Post 1978); 20. Gombe, Tanzania (J. Oliver, pers. commun.); 21. Ruaha, Tanzania (J. Oliver and A. Collins, pers. Commun.); 22. Mikumi, Tanzania (D. Rasmussen 1978 and pers. commun.); 23. Kariba, Zimbabwe (Hall 1963); *P. ursinus*: 24. Honnet, S. Africa (Stoltz and Saayman 1970); 25. Suikersbosrand, S. Africa (Anderson 1981 and pers. commun.); 26. Giants Castle, S. Africa (Whiten et al. 1987, A. Whiten, pers. commun.); 27. Drakensberg, S. Africa (Hall 1963); 28. Mt. Zebra NP, S. Africa (R. Seyfarth, pers. commun.); 29. Cape Point, S. Africa, 1959 (Hall 1963) and 1975 (Davidge 1978; C. Bielert, pers. commun.); 30. Okavango, Botswana (Hamilton et al. 1975, 1976); 31. Kuiseb, Namibia (Hamilton et al. 1975, 1976)

In addition to total annual rainfall, the evenness with which rainfall is distributed across the year plays an important part in determining the type of vegetation cover. Forests are more likely to occur in those habitats where rainfall is more evenly distributed as well as being substantial in volume, whereas grassland and scrub habitats are more likely to result where rainfall is seasonal. Two indices of the dispersion of rainfall across the year were derived. One is the number of months in the year which received less than 50 mm of rainfall. The other is Simpson's index of the proportional distribution of total rainfall across the 12 months of the year. Simpson's index of diversity, Z, is calculated as:

$$Z = 1 - \sum_i p_i^2$$

where p_i is the proportion of the annual rainfall falling in the ith month (Peet 1974). This index varies from $Z=0$ (completely uneven) to $Z=1$ (completely even).

For the main sample of habitats, the number of months with less than 50 mm of rainfall, V, correlates with total annual rainfall:

$$V = 7.96 - 3.02\,P \tag{1}$$

($r^2 = 0.455$, $F = 8.35$, $df = 1,10$, $P < 0.02$) where P is the mean annual rainfall (in mm). The diversity of rainfall across the months of the year, Z, is given by:

$$Z = 0.48 + 0.041\,T - 0.00101\,T^2 \tag{2}$$

($r^2 = 0.680$, $F = 9.58$, $df = 2,9$, $P < 0.02$) where T is the mean ambient temperature (in °C). These relationships will be used to simplify some of the later analyses for convenience of graphical presentation.

Most studies do not provide data on ambient (shade) temperature, but such data are almost always available from nearby weather stations. In tropical habitats, the diurnal variation in temperature is often considerable. Ideally, we need to determine the proportion of time that temperatures are above or below critical maximum and minimum thresholds. In most cases, data on which to calculate such values are not readily available. Instead, I have calculated the mean annual temperature by averaging the monthly mean temperatures (these in turn being calculated as the average of the monthly minimum and maximum temperatures). Although the mean annual temperature will tend to underestimate the number of degree-days below a specific threshold, the variance in mean temperature across the sampled range of altitudes and latitudes is considerable, making it less likely that this lack of precision will swamp any underlying functional relationships that might exist.

Baboons are omnivores with a strong preference for soft-bodied fruits and, to a lesser extent perhaps, seeds (see Dunbar 1988). Much of their diet is thus to be found above ground in the shrub and tree layers. These vegation layers are also important in providing shade during the heat of the day. Although data on the density of tree and shrub layer vegetation are not available for most of these habitats, there seems to be a reasonable correlation between these two variables and the environmental variables which are available. For a sample of 8 East African habitats (Table 1), a stepwise multiple regression analysis yielded the following equation for the density of tree cover:

$$\ln(E) = 17.28 - 2.82\,\ln(A) - 23.18\,\ln(Z) \tag{3}$$

($r^2 = 0.365$), where E is the percentage of ground surface shaded by trees, A the altitude (in m) and Z is rainfall diversity. The density of shrub and bush layer cover was given by:

$$\ln(B) = 2.57 + 1.86\,\ln(T) - 2.76\,\ln(V) \tag{4}$$

Table 1. Vegetation cover in East African habitats

Habitat	Cover (%)[a]		Altitude (m)	Rainfall (mm)	Temperature (°C)
	Tree	Bush			
Tsavo, Kenya	2.1	26.3	1100	750	24.0
Gilgil, Kenya	1.0	30.6	2000	690	21.6
Metahara, Ethiopia	10.6	16.3	950	639	24.5
Sendafe, Ethiopia	0.0	28.6	2600	1105	14.4
Bole, Ethiopia	25.0	67.1	1700	1105	19.5
Mulu, Ethiopia	0.0	12.0	2200	1105	15.9
Sankaber, Ethiopia	6.7	42.0	3300	1385	9.8
Gich, Ethiopia	0.0	1.0	3900	1515	7.7

[a] Percentage of ground surface covered by vegetation at specified level; all samples based on line transects using either point samples or 1 m² quadrats

$(r^2 = 0.409)$, where B is the percentage of ground surface shaded by vegetation in the bush and shrub layers (i.e. 1–5 m in height), T is mean temperature and V the number of dry months. Essentially, the more even the rainfall distribution, the more extensive the tree cover, but the less extensive the bush level cover in the habitat. The remaining unexplained variance in each case is, of course, made up from the effects of relative humidity, soil type and fertility as well as other geophysical aspects of the local environment, all of which are known to be important determinants of the degree of vegetation cover (Dye and Spear 1982; Bell 1982).

Although definitions of activity categories vary somewhat from one study to another, the amount of variance is unlikely to be too great given the limited number of activity categories under consideration. In general, *feeding* is the active searching, handling or consuming of food items; *moving* is quadrupedal progression; *social activity* is any friendly interaction (in baboons, about 95% of this involves social grooming); and *resting* is sitting or lying inactive. These four categories generally account for more than 95% of the activity budgets of free-living populations. The remaining time (*other activities*) is accounted for by a variety of minor categories like agonistic interactions, drinking and sexual behaviour. For present purposes, these have been ignored.

The data used in this paper are summarised in Table 2. Populations are included in the sample only if the authors state that their activity data were obtained by some recognised bias-free sampling procedure (usually instantaneous scan sampling or focal animal sampling: see Altmann 1974). Most African habitats are markedly seasonal, with a major (and sometimes a second minor) wet season. Activity budget data are therefore average values for the year as a whole (obtained by averaging the separate values for wet and dry periods). Only those 14 populations for which there are data on all variables and estimates of activity budgets based on both wet and dry seasons were used in the main analysis. Four other populations provide activity budgets from a single season only (wet season: Badi, Metahara; dry season: Gilgil 1975, Awash Station). I use these populations to test the validity of the equations derived from the main sample.

In addition to annual time budgets, time spent feeding during the dry season is also listed where these data are available: a similar analysis was carried out on dry season feeding time in order to examine the effect of seasonal variation in food availability on feeding time (see Dunbar and Sharman 1984).

In order to determine which factors influence baboon time budgets, I used a stepwise multiple regression procedure to find the set of variables that accounted for the highest proportion of the observed variance in the data. Additional variables were added into the regression equation only so long as they continued to explain a significant proportion of the variance. In all cases, the data were log-transformed to ensure normality, although in most cases doing so does not have a significant effect on the coefficient of determination. Time allocations to activity categories are interrelated because the amount of daytime is fixed and animals have to make decisions about how to apportion their available time. As a result, time allocations to different categories will be traded against each other. This is likely to be especially true of resting time, since this appears to be used as a reserve of uncommitted

Table 2. Behavioural ecology data on baboon populations

Population	Time budget (%)				Dry season Feed (%)	Group size	Day journey (km)[a]	Mean annual rainfall (mm)	Months <50 mm rain (V)	Rainfall diversity (Z)	Mean annual temperature (°C)
	Feed	Move	Rest	Soc							
A. Main sample:											
2. Mt. Assirik	23.5	36.9	20.7	18.9	33.1	247	7.9	941	7	0.803	29.4
3. Shai Hills	20.3	18.2	61.4	22.7	22.3	23.7	1.3	1065	4	0.855	25.9
4. Bole Valley	20.5	25.4	35.4	15.9	30.5	19	1.2	1105	5	0.849	19.5
5. Mulu	40.8	25.0	22.4	14.7	–	22	1.1	1105	5	0.849	15.9
7. Awash Falls	30.9	25.0	30.5	12.2	35.3	71	5.3	639	6	0.856	24.5
12. Budongo	59.3	17.6	5.9	16.9	–	37.5	3.8	1500	2	0.886	22.0
13. Chololo	40.2	33.1	17.4	7.8	39.0	102	5.6	549	8	0.857	22.9
15b. Gilgil (1984)	50.7	30.4	9.6	9.3	–	57	(4.3)	642	5	0.908	18.1
19b. Amboseli (1975)	48.0	24.1	20.9	6.7	51.0	46.5	6.1	225	5	0.861	20.0
20. Gombe	25.8	19.4	30.2	10.6	28.1	43	(2.4)	1380	4	0.862	24.5
21. Ruaha	47.4	24.2	16.7	4.5	–	72	(6.8)	354	9	0.917	21.7
22. Mikumi	36.5	26.1	25.0	5.9	38.6	120	3.4	734	5	0.862	24.5
25. Giants Castle	56.6	17.7	16.8	7.7	57.6	11.8	(0.9)	1197	5	0.866	14.6
28b. Cape (1975)	33.5	29.0	26.3	11.3	31.5	85	8.2	631	7	0.884	17.9
B. Subsidiary sample:											
1. Badi[b]	26.1	9.1	46.6	15.8	–	83	–	941	7	0.803	29.4
6. Metahara[b]	38.9	26.3	23.7	9.9	–	87	5.8	639	6	0.856	24.5
8. Awash Station[c]	29.7	25.4	31.4	13.5	–	51	6.1	666	8	0.841	24.8
15a. Gilgil (1973)[c]	47.1	20.4	21.4	10.1	–	50	4.6	595	5	0.908	18.1
C. Day journey sample:											
9. Erer-Gota	–	–	–	–	–	83	8.9	665	7	0.858	24.2
10. Ishasha	–	–	–	–	–	45	2.4	1292	2	0.906	22.0
19a. Amboseli (1969)	–	–	–	–	–	40	5.5	380	5	0.861	20.0
23. Honnet	–	–	–	–	–	77	9.0	307	9	0.846	24.1
24. Suikersbosrand	–	–	–	–	–	78	4.1	700	–	–	16.0

Sources: as given in Fig. 1
[a] Values in parentheses estimated using the equation given in Table 3
[b] Activity budget data for wet season only
[c] Activity budget data for dry season only

free time that can be converted into other activity categories when required (see Dunbar and Sharman 1984; Dunbar and Dunbar 1988). Although we are ultimately interested in the way animals trade time between activity categories, we can only study this process if we can first determine how much time animals *ought* to devote to each activity in the absence of any time-budgeting constraints. I assume that this will largely be a consequence of factors extrinsic to the activity budget itself (i.e. environmental and demographic parameters).

In order to try to circumvent this problem, I imposed a hierarchical causal order that was intended to reflect the biological priorities for the animals. I assumed that time spent feeding was an absolute priority and was therefore independent of time devoted to any other activity; moving, resting and social time were therefore excluded as possible independent variables. Time spent feeding was then assumed to be a possible determinant of time spent moving. No restrictions were placed on the determinants of time spent resting or engaged in social interaction, however, since it was assumed (at least initially) that the time available for these two activities was limited by the amount of time that had to be devoted to foraging in order to survive.

One final issue needs to be clarified, and this concerns the problem of phylogenetic inertia that has so dogged comparative analyses (see for example Harvey and Mace 1982; Harvey and Pagel 1991). I argue here that time budgets are not species-typical variables, but vary between populations within a species in relation to local habitat conditions. Furthermore, although the data in this analysis derive from the five nominal species of baboons (*Papio hamadryas, P. anubis, P. cyncephalus, P. papio* and *P. ursinus*), I follow the consensus among taxonomists in arguing that these are better considered as subspecies (see for example Smuts et al. 1987). Analyses of *Papio* blood proteins by Shotake et al. (1977), for example, suggest that the taxa assigned to this genus may be only sub-specifically differentiated. Indeed, Kawamuto et al. (1982) have shown that Nei's genetic distance between the cercopithecoid primates as a whole is no greater than that for congeneric species in most other taxa.

Results

Determinants of the time budget

The regression equations that account for a significant proportion of the variance in the four time budget variables and day journey length are given in Table 3.

Analysis of the data for the nine populations with day journey length as well as activity budgets indicated that only group size and annual rainfall were significantly related to day journey length. The analysis was therefore repeated for the full sample of 21 studies that give data on day journey length; this yielded an equation that was virtually identical to that for the main subsample, so this second equation is given in Table 3. Note

that day journey length is a positive function of group size (as might be expected on the grounds that each individual will have to forage a roughly constant area of its own each day) and a negative function of rainfall. There are two ways in which this second variable might influence day journey length. One is that, assuming that the length of the day journey is determined by the distance individuals have to move from one patch to another, rainfall provides an index of resource density (or, alternatively, resource patchiness), and hence inter-patch distance. The other is that, assuming that day journey length is dependent on the distance that animals have to travel between feeding sites and water sources, rainfall provides an approximate measure of the availability of surface water. The available data do not allow us to distinguish between these two possibilities. However, Altmann and Altmann (1970), Sigg and Stolba (1981) and Barton (1989) have all shown that water is an important limiting factor influencing baboon ranging patterns.

The equation for day journey length given in Table 3 was then used to estimate day journey lengths for the five populations in the main sample for which this variable had not been determined. These interpolated values are given in parentheses in Table 2.

The feeding time requirement is determined primarily by the diversity of rainfall and the mean ambient temperature (these two variables between them account for 43% of the variance). The number of low-rainfall months and the length of the day journey were also found to make small further contributions (explaining about 7% of the total variance each). Note that because the sign of the logarithm of a probability is negative, the effect due to rainfall diversity is in fact negative not positive: the less even the distribution of rainfall across the year (i.e. the more seasonal it is), the more time is devoted to feeding.

The fact that the regression coefficient for temperature is close to unity suggests that the effect in this case is due entirely to the costs of thermoregulation, which rise linearly with declining temperatures (Kleiber 1961; Tokura et al. 1975; Mount 1979). In fact, given that ambient temperature predicts rainfall diversity (Eq. 2), it is not surprising to find that temperature alone gives a reasonable estimate of time spent feeding:

$$\ln(F) = 7.049 - 1.156 \ln(T) \tag{5}$$

$(r^2 = 0.307, F[1,12] = 5.32, P < 0.05)$. Although the costs of thermoregulation are a linear function of temperature, the best-fit equation is a logarithmic function of

Table 3. Regression equations for time budget

Dependent variable	Best-fit equation[a]	r^2	F	df	P
Day journey (km)	$\ln(J) = 1.344 + 0.784\ln(N) - 0.4731\ln(P)$	0.691	18.87	2,18	<0.001
Feeding time (%)	$\ln(F) = 7.408 + 4.439\ln(Z) - 0.883\ln(T) - 0.447\ln(V) + 0.158\ln(J)$	0.584	3.15	4,9	~0.06
Moving time (%)	$\ln(M) = 2.201 + 0.163\ln(N) + 0.219\ln(V)$	0.660	10.68	2,11	<0.01
Resting time (%)	$\ln(R) = 10.550 - 1.333\ln(F) - 0.323\ln(N) - 0.282\ln(P)$	0.782	11.98	3,10	<0.01
Social time (%)	$\ln(S) = -1.599 + 0.488\ln(P) - 4.965\ln(Z)$	0.534	6.31	2,11	<0.02

[a] T = mean ambient temperature (°C); P = mean annual rainfall (mm); V = number of months with <50 mm rainfall per year; Z = Simpson's index of monthly rainfall diversity; N = group size
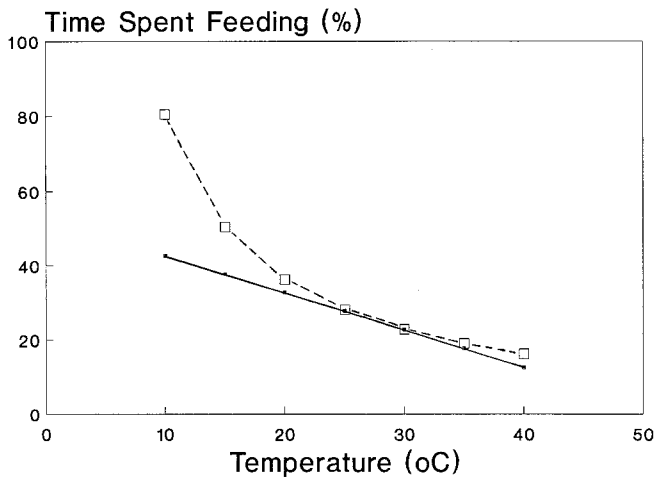
Time Spent Feeding (%)

Fig. 2. Percentage of time spent feeding plotted against ambient temperature. *Dashed line* plots the graph for Eq. 5. The *solid line* indicates approximately the slope that would be expected from Kleiber's relationship between ambient temperature and thermoregulation. (The graph has been standardised to 30° C, with a slope of $b=1$ on either side.) The additional feeding time above this line at low and high temperatures suggests that the animals are compensating for declining forage quality as habitats becomes increasingle extreme

temperature with a scaling coefficient greater than 1 (Fig. 2). The most likely explanation for this difference is that forage quality declines at low and high temperatures, thereby forcing the animals to spend more time feeding in order to obtain a given nutrient intake. The protein content of grasses, at least, is known to be a quadratic function of ambient temperature in these habitats (Dunbar 1991a).

The same effect is almost certainly responsible for the influence of the number of dry months (V) on time spent feeding. At first sight, the negative regression coefficient seems puzzling. However, the number of dry months is negatively related to the density of bush cover (Eq. 4); hence, the relationship can be interpreted as implying that the more dry months there are, the less bush layer cover is available, and (since the bulk of the baboons' preferred food sources are in this layer) the more time they have to spend feeding. Much of this extra feeding time is probably due to higher harvesting costs rather than the ingestion of larger quantities of food: the lower density of food items both within and between patches probably means that non-travel search times are much higher.

The main variables selected as determinants of time spent moving are group size and the number of months with less than 50 mm of rainfall. The relationship between group size and moving time invites either of two interpretations: namely, (1) that it reflects the fact that larger groups have longer day journeys (and hence spend more time travelling) or (2) that it reflects a disturbance effect due to group size (as group size increases, so animals' feeding bouts are disrupted more frequently, and they are forced to move short distances to new sites more often, even though the group as a whole does not travel a significant distance forwards: see van Schaik

et al. 1983; Stacey 1986, Altmann 1987). The latter seems the more likely. The significance of rainfall dispersion as a determinant of moving time is probably related to this effect: rainfall dispersion is an index of the quantity of bush level cover in the habitat (see Eq. 4 above), and hence this determines the distance animals have to move between feeding patches within a given area. This suggests that a significant proportion of the time spent moving by animals is a consequence of changes in feeding site rather than major episodes of travel (as reflected in the day journey length).

The analyses suggest that actual social time is determined by two key environmental variables (total rainfall and the diversity of rainfall), with the first of these accounting for most of the variance. Essentially, this suggests that animals can afford to spend more time in social interaction in richer habitats.

Previous analyses of baboon time budgets suggested that resting time might act as a source of spare time that could be converted into additional feeding time whenever this was required (Dunbar and Sharman 1984; Dunbar and Dunbar 1988). The latter study, in particular, suggested that ultimately resting time is inelastic in response to demands placed on it by feeding time: that is to say, it becomes harder to surrender resting time as the residual quantity approaches zero. This is confirmed by the present analysis, which shows that 68% of the variance in resting time is accounted for by feeding time on its own:

$$\ln(R) = 7.25 - 1.17 \ln(F) \qquad (6)$$

$(r^2 = 0.675,\ F[1,12] = 24.92,\ P < 0.001)$. Since this relationship is logarithmic, it follows that resting time reaches an asymptotic value. Equation 6 indicates that this occurs in the region of 5–10% of time spent resting.

Resting time is also negatively related to the amount of cover in the environment, and this can be interpreted in terms of heat load. In open habitats, high radiation loads (especially at midday) appear to force the animals to rest rather than forage (see for example Altmann and Altmann 1970; Stoltz and Saayman 1970; Stelzner 1988; see also Wheeler 1984). In habitats where there is significant tree cover, however, it seems that this effect is ameliorated because the animals are able to continue with their normal activities in the shade. The import of this is quite serious from the animals' point of view: climatically enforced resting time is apparently "time out" that cannot be used for any other purpose (including grooming). As a result, the animals' active day is shorter in open high-temperature habitats: their essential activities have to be crammed into a shorter period with less opportunity to rest between activity bouts.

Dry season time budget

In tropical habitats, vegetation often dies off during the dry season due to a combination of lack of water and high radiation loads under cloudless skies. Such conditions are usually associated with an increase in the fibre content of plants and a consequent decline in digestibi-

lity (Braun 1973; van Soest 1982). This ought to be translated into an increased demand for feeding time since the animals will have to eat more to achieve the same nutrient intake.

Ten of the studies listed in Table 2 provide data that allow us to separate wet and dry season time budgets. Five of these give data on day journey lengths during the dry season. I included temperature, rainfall, the two indices of rainfall dispersion and day journey length as potential independent variables. Since there is no consistent tendency for day journey lengths to be longer in the dry season than during the wet season (two studies show an increase, two a decrease and one no change), I have used annual day journey length rather than dry season day journey for this analysis.

Stepwise multiple regression analysis of the amount of time spent feeding yields an equation that is generally similar in form to that for the annual time budget, except that the indices of rainfall now play no part at all:

$$\ln(F_{Dry}) = 5.732 - 0.800 \ln(T) + 0.233 \ln(J)$$

($r^2 = 0.681$; $F[2,7] = 8.529$, $P < 0.05$). The reduced importance of the rainfall indices in this case might reflect the small sample size for this analysis.

However, rainfall diversity turns out to be the only factor that influences the change in feeding time requirement from wet to dry seasons. Because of negative values of the dependent variable, I used only raw data in this analysis. The best-fit equation was:

$$\Delta F = 197.78 - 226.21 \, Z \tag{7}$$

($r^2 = 0.693$, $F = 18.039$, $df = 1,8$, $P < 0.025$) where ΔF is the difference between dry and wet season feeding time ($\Delta F = F_{dry} - F_{wet}$). This suggests that as rainfall becomes more seasonal in its distribution, so the animals are obliged to spend proportionately more time feeding during the dry season (presumably reflecting the increased dessication of plants). Conversely, in habitats where $Z > 0.875$, the reverse is true: animals spend proportionately more time feeding during the wet season as rainfall becomes more evenly distributed across the year. Such habitats are likely to lie in the extremes of the temperature distribution (see Eq. 2) where either desert or heavily forested habitats tend to prevail (see Eq. 3). In these habitats, evaporative cooling from wet coats may have an important impact on thermoregulation during the wet season.

Equation 7 also suggests that there will be limits to baboons' abilities to colonise certain habitats. If the maximum tolerable change in feeding time in the dry season is approximately $\Delta F = 25$ percentage points, then baboons will not be able to balance their time budgets in habitats where $Z < 0.764$. Similarly, there will be an upper limit at $Z = 0.985$. (Maximum permissable ΔF will, of course, vary across habitats depending on the environmentally-imposed baseline value for F_{wet}.)

Testing the equations

The time budget equations given in Table 3 can be tested using the data from the four subsidiary study sites. The

Table 4. Comparison of observed time budget with values predicted by the equations given in Table 3

Population	Percentage of time					
	Feeding			Moving	Resting	Social
	O	E	SD	SD	SD	SD
Metahara, Ethiopia	38.9	36.0	0.22	0.22	0.28	0.08
Gilgil, Kenya (1973)	47.1	56.0	0.68	0.13	0.71	0.51
Awash Stn, Ethiopia	29.7	28.5	0.09	0.02	0.01	0.40
Badi, Senegal	26.1	20.3	0.45	2.62	0.38	0.23
Population standard deviation[a]	13.03			5.35	13.22	5.25

[a] From main sample populations given in Table 3

relatively small differences between wet and dry season data (see preceeding section) means that we can use the equations given in Table 3 even though the data themselves derive from only one season.

Table 4 compares the observed and predicted values for the four activity categories for each of the four populations. Both the observed and expected values, as well as the number of standard deviations separating these two values, are given for time spent feeding, but only the number of standard deviations are given for the other three activities. The sample standard deviation for each activity (calculated from the data for the main sample populations in Table 2) is given in the final row of the table. In general, the fit between observed and predicted values is remarkably close. The observed values are, on average, only 0.44 standard deviations from the predicted ones. In only one of the 16 cases (moving time at Badi, Senegal) do the two values differ by more than 1 standard deviation. Since observation conditions in this habitat made it especially difficult to see animals on the ground (see Dunbar and Nathan 1972), it is likely that moving animals were under-represented, while animals resting, feeding or socialising in trees were over-represented in this particular sample.

By converting the z-scores in Table 4 to two-tailed probabilities of the deviation of observed from predicted, we can use Fisher's procedure for pooling independent tests (Sokal and Rohlf 1969, p. 623) to determine whether the observed distribution of z-scores is larger than we would expect by chance alone if there was no relationship between observed and expected values. With $\chi^2 = 17.884$ and $df = 2k = 32$, it is clear that the observed values are significantly more similar to the predicted values than would be expected by chance ($P > 0.95$). Over half of the total value of χ^2 is due to the single aberrant point (Badi moving time). Discounting this point gives $\chi^2 = 8.419$ ($df = 30$, $P > 0.995$).

Ecologically tolerable zone

I define the *ecologically tolerable zone* as that range of environmental parameters within which the animals are able to meet their time budget requirements while living

in groups of at least a certain minimum size. That minimum size is set by the species' anti-predator strategies, and may vary from one habitat to another depending on the density of predators and the availability of trees and other refuges (see Dunbar 1988). The range of environmental parameters between the minimum and maximum values is the ecologically tolerable zone. At present, we cannot specify what the minimum group size for survival is, but we can at least examine the way in which the maximum value imposed by time budget constraints varies with habitat conditions.

Three points need to be resolved first, however. One is that the regression equations given in Table 3 for resting and social time are conditional equations: that is to say, they take into account those cases where animals under ecological stress have already adjusted their time budgets to make survival possible. Our purpose here is to determine how the animals *should* behave in the constraint-free situation. In other words, if the animals had infinite time available to them, what is the minimum time they *ought* to devote to resting and social interaction? The second problem concerns the functions these two activity categories serve for the animals, since it is these that will determine their minimum time allocations. The final problem is that body weight is known to vary across habitats (Dunbar 1990) and, since body weight is known to affect many ecological variables (Peters 1983), its effect on time budgets needs to be evaluated.

For present purposes, I assume that social time largely functions as the "glue" that maintains the social cohesion of groups through time, and that, subject to any purely environmental constraints, resting time is a pool of free time that can be drawn on when additional time is required in one of the other biologically more essential categories (see Dunbar 1988; Dunbar and Dunbar 1988).

If social time acts as the "glue" to maintain the cohesion of groups, then it ought to be directly related to group size. Table 3 suggests that this may not necessarily be the case for this sample of baboon populations (through it is the case, for example, in gelada: see Iwamoto and Dunbar 1983; Dunbar 1992). This could be either because group size is genuinely irrelevant in the case of *Papio* baboons or because the effects of group size are masked by the ecologically more pressing demands of environmental conditions within the wide range of habitats occupied by this sample of baboons. Some evidence to support the second suggestion is given by the fact that grooming time does correlate with group size in *Papio* when these are analysed as species averages (which tends to cancel out the effects of environmental variables) (see Dunbar 1991 b). A comparative analysis of time spent grooming and group size in a number of primate species indicates that, generally speaking, these two variables are closely correlated (Dunbar 1991 b). I therefore assume that the second is the more likely explanation, and use the comparative data to generate a relationship between group size and required grooming time. Since there are significant differences between major taxonomic groupings, I considered only

the data from Old World monkeys given by Dunbar (1991 b). A least-squares regression yields the following equation:

$$S = 4.533 + 0.0764\,N \tag{8}$$

($r^2 = 0.490$, $N = 20$ species, $F[1,18] = 17.262$, $P < 0.001$).

The most likely constraint on resting time would seem to be the heat load that animals face during the day. High radiant head loads in open habitats during the middle of the day may force animals to take shelter (see Wheeler 1984). I therefore reran the stepwise regression analysis with resting time as the dependent variable and only group size, rainfall, ambient temperature, day journey length and the two rainfall dispersion indices as independent variables. The best-fit equation turned out to be:

$$R = 0.970 - 7.923\,\ln(Z) + 0.601\,\ln(V) \tag{9}$$

($r^2 = 0.347$). (Recall that Z is mainly a function of temperature: see Eq. 2.)

Feeding requirements will be influenced by body weight in two distinct respects: (1) absolute energy requirements scale to the 0.75 power of body weight (Kleiber 1961; Peters 1983) and (2) throughput is slower in larger guts, so that larger animals are able to extract a higher proportion of nutrients from their ingesta. Since gut throughput rate (and hence nutrient extraction rates) scale to the 0.346 power of body size (Demment and van Soest 1985), the net effect will be to scale feeding time by a ratio of the $0.75 - 0.356 = 0.404$ power of body weight (assuming that harvesting rates remain constant).

Unfortunately, body weights are not known for most of the study sites in the sample. I have therefore used the equations for male and female body weight given in Dunbar (1990) to estimate body weights for each population. I then determined the mean body weight for adults from this (as a simple average of male and female weight) and scaled this for metabolic requirements and digestive efficiency. The feeding time requirement for each site was adjusted for the influence of body weight by scaling against the sample mean body weight of $W_x = 17.58$ kg to give:

$$F_W = F \times W^{0.404}/3.184$$

where F_W is the weight-adjusted feeding time. If the original feeding time for each population is scaled to a standard body weight using the inverse of this scalar, the best-fit stepwise regression equation for feeding time is:

$$\ln(F) = 6.866 + 4.077\,\ln(Z) - 0.950\,\ln(T) - 0.290\,\ln(V) + 0.155\,\ln(J) \tag{10}$$

($r^2 = 0.532$).

Since stride length scales to the 0.333 power of body mass (Peters 1983), the time required to travel a given distance needs to be scaled by the ratio:

$$M_W = M \times 2.598/W^{0.333}$$

where M_W is the moving time requirement adjusted for the effects of body size.

Using the equations given in Table 3 for moving time and for day journey length, and Eqs. 8, 9 and 10 for

Table 5. Maximum ecologically tolerable group sizes for different habitats predicted by the simulation

Rainfall (mm)	Maximum Ecologically Tolerable Group Size at: Mean annual temperature (°C)								
	0	5	10	15	20	25	30	35	40
100	0	0	0	69	151	176	27	0	0
300	0	0	0	73	156	187	41	0	0
500	0	0	0	77	160	197	59	0	0
700	0	0	0	81	164	208	80	0	0
900	0	0	0	84	166	218	105	0	0
1100	0	0	0	85	167	228	132	0	0
1300	0	0	0	83	166	237	162	0	0
1500	0	0	1	79	161	244	195	0	0
1700	0	0	1	69	151	248	231	0	0
1900	0	0	1	51	132	246	268	0	0
2100	0	0	0	22	96	232	304	0	0
2300	0	0	0	0	29	188	333	27	0
2500	0	0	0	0	0	31	305	272	0
2700	0	0	0	0	0	0	46	419	0
2900	0	0	0	0	0	0	46	419	0

the minimum social, resting and feeding time requirements, together with the above scalars for body weight, I then determined by iteration the maximum group size that a population could sustain in a given habitat if the animals converted all their spare resting time into feeding and moving and social time, subject to the constraint of a minimum resting time allocation of 5% under all conditions (as implied by Eq. 6). In order to simplify the presentation, I have used Eqs. 1 and 2 to derive values for V and Z for each habitat from annual rainfall and temperature and, then, Eqs. 3 and 4 to derive values for E and B so that the results can be given as a simple two-dimensional array.

The results of the simulation are given in Table 5. Four points should be noted.

First, whether or not we impose a minimum group size, baboons are clearly likely to be found only in habitats of moderate temperature and moderate to high rainfall. The distribution suggests that baboons find it hard to survive in dry habitats under very cold or very hot temperature regimes or in very wet habitats. Indeed, it seems that they can only cope with high rainfall habitats when ambient temperatures are proportionately higher. This reinforces the implications of Eq. 7.

In Africa, habitats with more than 1500 mm of rainfall per year are normally forested (unless they lie at altitudes above about 2500 m asl) and, in general, these habitats are not occupied by baboons (who generally prefer forest-edge or woodland habitats). The simulation thus suggests that, except under very high-temperature regimes, baboons would generally experience considerable difficulty in meeting their time budget requirements in forested habitats. The main problem seems to be the amount of time they have to spend feeding. Given that the amount of bush layer cover declines as rainfall increases (and habitats become more forested: see Eqs. 3 and 4), and given that this is the layer in which most of the baboon's preferred foods occur, then feeding time

may be expected to increase (mainly as a consequence of the time taken to search for food items).

Second, the maximum tolerable group size is never very large. Although maximum group sizes can approach 400 animals under the wettest conditions, few African habitats receive more than 2000 mm of rainfall a year and this would reduce the maximum tolerable group size to about 280 animals. No population of baboons for which censuses exist has group sizes larger than this: the largest recorded individual group sizes are 247 for one exceptional group of *Papio papio* studied by Sharman (1981) and 198 for one of the *P. cynocephalus* groups censussed by Altmann and Altmann (1970) at Amboseli. It is perhaps significant that, as predicted by the model, the West African forest baboons (genus *Mandrillus*) do seem to form larger group sizes (at least as temporary herds) in their high rainfall ($P > 2000$ mm), high temperature ($T > 30°$ C) habitats than the woodland/savannah *Papio*: herd sizes of 175–250 have been repeatedly observed among mandrills in particular (Jouventin 1975; H. Kudo, personal commun.) Nonetheless, it is clear that baboons could never achieve the massive herd sizes typical of many of the open-country antelope.

Third, note that time budget constraints would prevent *Papio* baboons occupying habitats where ambient temperatures were lower than 10° C or higher than 35° C. I shall use this result to test the validity of these analyses and, by implication, to provide a second test of the original time budget equations (see below).

Finally, the correction for body mass has only a marginal impact on maximum group size within the range of body weights for extant baboons. Recalculation using the original feeding time equation given in Table 3 with no correction for body weight results in group sizes that are slightly smaller (by ca. 5–10 animals) at the lowest rainfall range, and slightly larger (by c. 10–20 animals) at the highest rainfall end of the range.

One way to test the model is to see how well it predicts the geographical distribution of baboons over a relatively confined area that has a marked variation in temperature and rainfall. The Simen Mountains in northern Ethiopia provide us with such an opportunity: they have a steep altitudinal gradient rising from approximately 1700 m to 4500 m with a deep east-west rain shadow. A second site is available at Mt Menegasha, an extinct volcanic cone that lies due west of Addis Ababa some 500 km to the south of the Simen.

Table 6 gives the relevant environmental parameters for seven locations in the Simen and two locations on Mt Menegasha. For each locality, the maximum group size predicted by the model and the occurrence of baboons of this genus is noted. *Papio* do not live at altitudes above 3000 m where predicted maximum group sizes would be less than about 10 animals. *Papio hamadryas* were, however, seasonal visitors to Sankaber (where the predicted maximum tolerable group size is just 6), but rarely stayed for more than 2 days at a time (Dunbar and Dunbar 1974b). Unfortunately, actual group sizes are not known for the Simen habitats, although in no cases were they large by *Papio* standards. However, the observed size of one group of *Papio anubis* censussed

Table 6. Test of predictions of the simulation model: Maximum ecologically tolerable group size predicted by the model for various sites in the Simen Mountains and Mt Menegasha, Ethiopia, compared to the observed distribution of baboons

Site	Altitude[a] (m)	Temp (°C)	Rainfall (mm)	N_{max}[b]	Baboons present?[c]
A. Simen Mountains:					
Tissisat Falls	1695	18.3[d]	950[e]	61	yes
Flasha Amba	2000	16.5[f]	1400[f]	47	yes
Wolkefit Pass	2770	12.5[g]	993[g]	20	yes
Sankaber	3250	9.8[g]	1385[g]	6	(no)[e]
Gich	3900	7.7[g]	1515[g]	0	no
Chennek	4000	7.0[d]	1515[h]	0	no
Ras Dedjen	4660	3.9[d]	1515[h]	0	no
B. Mt Menegasha:					
Juniper forest zone	2750	13.6[d]	1105[i]	30	20[j]
Upper moorland zone	4180	6.8[d]	1105[i]	0	no

[a] All altitude values for Simen taken from 1:25000 maps from Messerli and Aerni (1977) and from 1:500000 East Africa series for Mt Menegasha
[b] Maximum ecologically tolerable group size predicted by the equations given in Table 3
[c] Based on personal surveys or reports from other biologists
[d] estimated from the equation for temperature given by Dunbar (1992): $T = 28.4 - 0.00476 A - 0.176 L$ where A = altitude and L = distance from equator (in degrees latitude) ($r^2 = 0.803$)
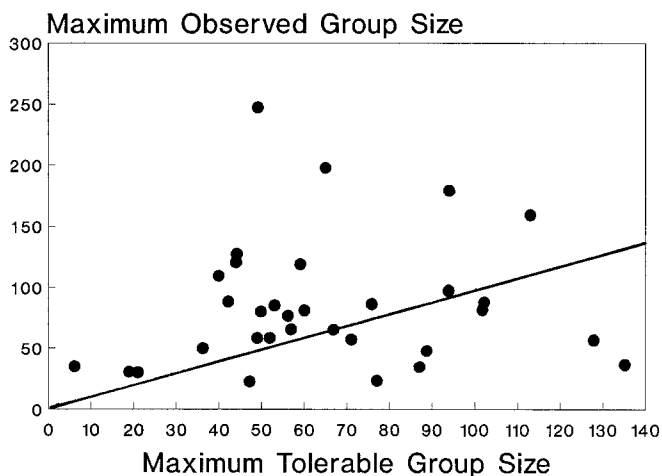[e] value for Zarema 20 km to west given by Hurni (1982)
[f] estimated as Makseguit (from Hurni 1982)
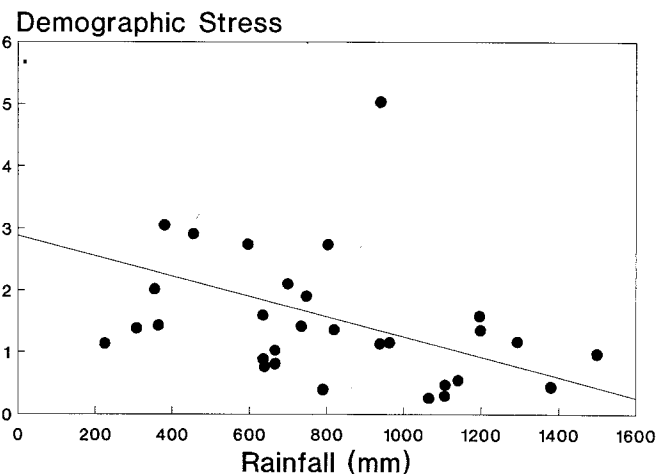[g] from Hurni (1982)
[h] estimated as Gich (from Hurni 1982)
[i] estimated as for Addis Ababa (20 km to east); altitude taken as altitude of baboon sightings for lower zone
[j] observed group size ($n = 1$ group)

Fig. 3. Observed maximum group size for each population, plotted against the maximum ecologically tolerable group size predicted for that population by the model

Fig. 4. Demographic stress on maximum observed group size for each population, plotted against mean annual rainfall (see text for details)

on the lower slopes of Mt Menegasha was within the predicted maximum.

This test thus offers considerable support for the model.

Ecological stress

Data on mean and maximum group sizes are available for a total of 32 populations (15 of the populations included in the main analysis, with separate data for two altitudinal levels in one of these, plus a further 16 sites for which only demographic data are available: see Ta-

ble 7). Figure 3 plots the maximum observed group size for each population against the maximum ecologically tolerable size predicted by the model, while Fig. 5 does the same for the mean group size for each population.

In 22 of the 32 cases, the maximum observed group size exceeds the predicted value (Fig. 3). If we use the ratio of observed/predicted group sizes as an index of demographic stress, a stepwise regression with rainfall and temperature as independent variables indicates that only rainfall contributes significantly to the variance in demographic stress (Fig. 4):

$$\ln(X_{max}) = 3.510 - 0.514 \ln(P)$$

Table 7. Demographic data for baboon populations

Population	Group size		Max (N)[a]	Z	V	Rain	Temp
	Mean	Max					
2. Mt Assirik, Senegal	94.5	247	49	0.803	7	941	24.9
3. Shai Reserve, Ghana	19.1	36	135	0.855	4	1065	25.9
4. Bole, Ethiopia	19.5	23	77	0.849	5	1105	19.5
5. Mulu, Ethiopia	22.0	22	47	0.849	5	1105	15.9
6. Metahara, Ethiopia	47.8	87	102	0.856	6	639	24.5
7. Awash Falls, Ethiopia	55.8	81	102	0.856	6	639	24.5
8. Awash Station, Ethiopia	54.0	57	71	0.841	8	666	24.8
9. Erer Gota, Ethiopia	83.0	97	94	0.858	7	665	24.2
10. Ishasha, Uganda	45.0	58	49	0.906	2	1292	22.0
11. Murchison NP, Uganda	27.6	48	89	0.894	3	1140	23.3
12. Budongo, Uganda	41.3	65	67	0.886	2	1500	22.0
14. Laikipia, Kenya	101.0	179	94	0.900	8	747	22.9
15. Gilgil, Kenya (1973)	65.0	121	44	0.908	5	595	18.1
16. Nairobi NP, Kenya	42.1	87	76	0.871	5	963	19.6
17. Manyara NP, Tanzania	66.0	81	60	0.856	5	818	17.9
18. Serengeti NP, Tanzania	22.0	34	87	0.897	5	792	22.0
19a. Amboseli, Kenya (1969)	50.8	198	65	0.861	5	380	20.0
19b. Amboseli, Kenya (1978)	28.0	65	57	0.861	5	225	20.0
20. Gombe NP, Tanzania	43.5	56	128	0.862	4	1380	24.5
21. Ruaha NP, Tanzania	71.5	119	59	0.862	9	354	21.7
22. Mikumi NP, Tanzania	80.2	160	113	0.862	5	734	24.5
23. Kariba, Zimbabwe	46.0	109	40	0.805	7	804	25.1
24. Honnet, S. Africa	47.2	77	56	0.846	9	307	24.1
25. Suikerbosrand, S. Africa	78.0	88	42	–	–	700	16.0
26a. Giants Castle (High)	18.6	30	19	0.866	5	1197	12.1
26b. Giants Castle (Low)	31.3	49	36	0.866	5	1197	14.5
27. Drakensberg, S. Africa	30.6	58	52	0.867	5	941	16.8
28. Mt Zebra NP, S. Africa	28.0	30	21	0.881	10	364	14.0
29a. Cape Point, S. Africa (1959)	45.0	80	50	0.883	7	633	17.3
29b. Cape Point (1975)	55.3	85	53	0.884	7	631	17.9
30. Okavango, Botswana	79.4	128	44	0.825	8	457	23.6
31. Kuiseb, Namibia	26.3	34	6	0.967	12	18	15.0

Sources: see Fig. 1

[a] Maximum ecologically tolerable group size predicted by the simulation model

($r^2 = 0.285$, $F_{1,30} = 11.979$, $P < 0.01$; $t[\text{slope} = 0] = -3.461$, $P < 0.01$ two-tailed), where X_{max} is the stress on maximum group size (defined as observed maximum group size divided by the predicted maximum).

In contrast, although the population *mean* group size exceeds the maximum tolerable predicted for that habitat by the model in 14 out of 32 cases (Fig. 5), the deviations from the maximum value are absolutely much smaller for populations that exceed the maximum than is the case for those that do not (mean absolute deviation = 1.64 SD for populations below the predicted maximum vs 0.83 SD for populations above). In only one of the 14 cases that lie above the diagonal is the difference between observed and predicted values large enough to be statistically significant in its own right ($P \le 0.05$ one-tailed), whereas this is true for seven of the 18 cases that lie below the diagonal. The difference is statistically significant ($\chi^2 = 4.270$, $df = 1$, $P < 0.05$). This suggests that, despite the crudeness of the model, the constraint imposed by the maximum ecologically tolerable group size is a real one: population average values do not often exceed this value by a very large margin, even though individual groups within a population may do so.
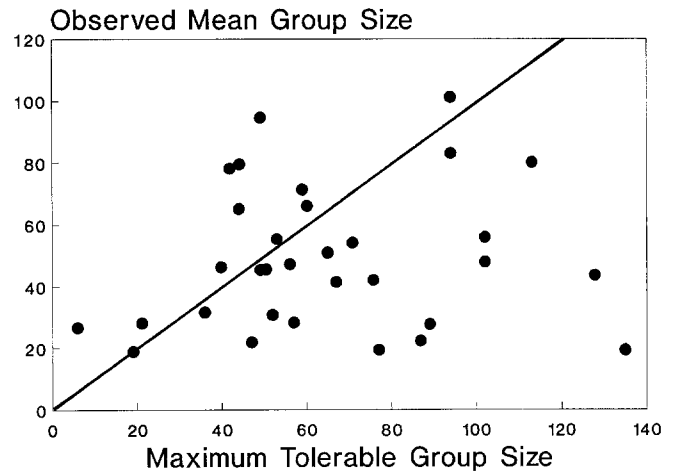
Fig. 5. Observed mean population group size, plotted against the maximum ecologically tolerable group size predicted for that population by the model
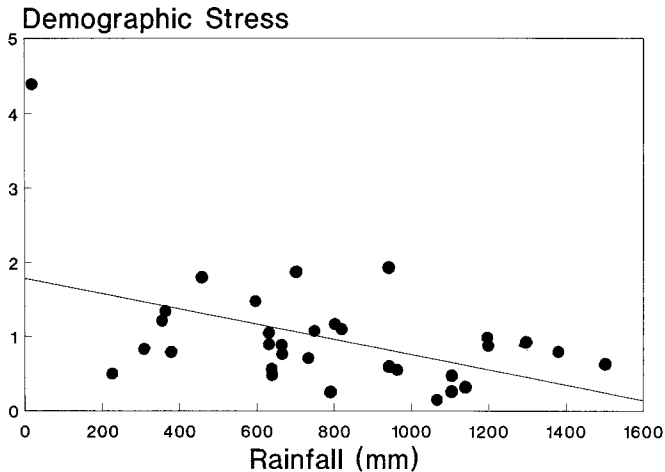
Demographic Stress

Fig. 6. Demographic stress on mean population group size, plotted against mean annual rainfall (see text for details)

Given the constraints imposed by small maximum group size, we might expect the demographic stress to be greatest in more marginal environments. This seems to be so: stepwise regression analysis reveals that demographic stress on the population mean group size, X_{mean}, is negatively related to rainfall (but not to temperature):

$$\ln(X_{mean}) = 2.792 - 0.473 \ln(P)$$

(Fig. 6: $r^2 = 0.309$, $F_{1,30} = 13.395$, $P < 0.01$; $t[\text{slope} = 0] = -3.660$, $P < 0.01$ two-tailed), suggesting that animals come under increasing time budget stress as habitats become drier. This probably means that maximum tolerable group sizes approach the minimum size required for survival in these habitats, with the result that the animals have very little freedom of movement in their time budgets and are forced to exploit every time-saving device they can to ensure that group size is above the minimum required for survival.

If this interpretation is correct, then groups experiencing demographic stress should have larger net deficits on their resting and social time budgets. I have used the equivalent deficit on feeding time as the baseline against which to compare this. In principle, feeding time should be under much greater constraint and should show little difference between the two categories.

Figure 7 shows that the prediction is upheld. The median deficit (observed minus predicted) on feeding time is -0.05 percentage points for stressed groups and -3.30 percentage points for unstressed groups (Mann-Whitney test: $P > 0.10$ one-tailed), whereas the median deficit on resting-plus-social time is -4.60 percentage points for stressed groups and $+5.25$ percentage points for unstressed groups ($p < 0.02$ one-tailed). Stressed groups tend to maintain feeding at the expense of resting and social time.

Given this, we might expect groups that devote less time than they should to social interaction to be less socially cohesive. There is some evidence to support this prediction: the median demographic stress for groups which were known to fragment regularly into smaller parties during foraging or which subsequently under-
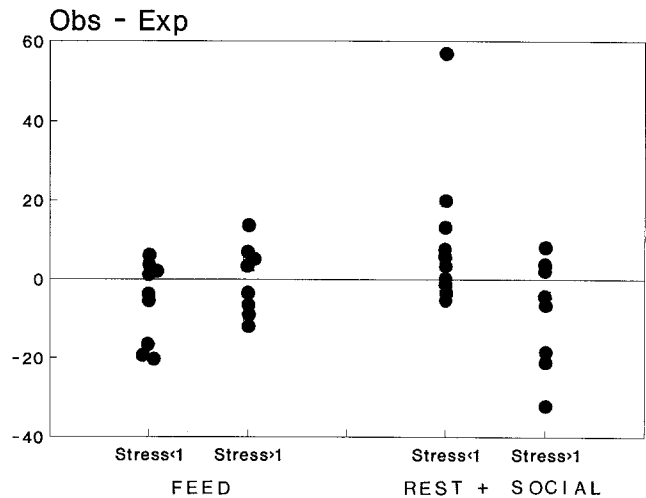
Obs - Exp

Fig. 7. Difference between observed and predicted values for time spent feeding and for time spent resting plus social, for stressed and unstressed groups. Stressed groups are those in which the observed group size exceeds the maximum ecologically tolerable size predicted by the model
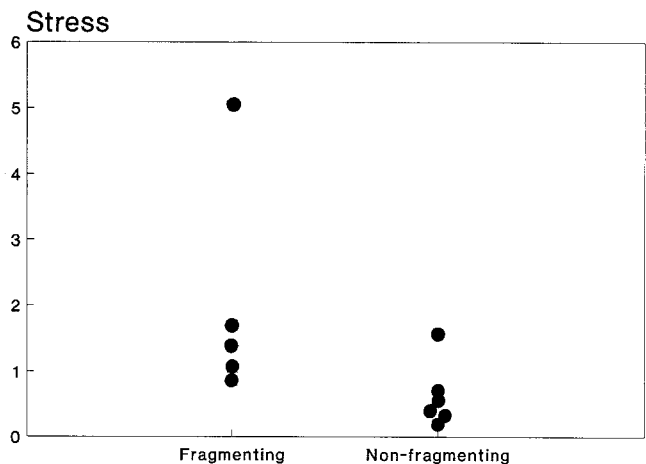
Stress

Fig. 8. Demographic stress for individual groups that habitually fragmented during foraging (or underwent fission), compared with the stress in groups that did not

went fission was 1.378, compared to 0.402 for groups which were not described as fragmenting in this way (Fig. 8: Mann Whitney test, $P = 0.015$ one-tailed).

We should expect groups under time budget stress to pursue strategies designed to make more time available for essential activities. One of the few ways in which animals can make effective time savings is to increase the rate of travel during the day. This would enable them to minimise the amount of time that has to be devoted to travel in order to cover the distance they need to if they are to meet the group's daily foraging requirements. Although there are energetic costs to travelling faster (Taylor et al. 1982), it is likely that these are considerable less than the short term fatigue effects due to lactic acid build-up in muscle tissue and mechanical stress on joints. The additional feeding time required to fuel a higher rate of travel is thus likely to be considerably less than the time saved by travelling faster.

Speed (km/hr)
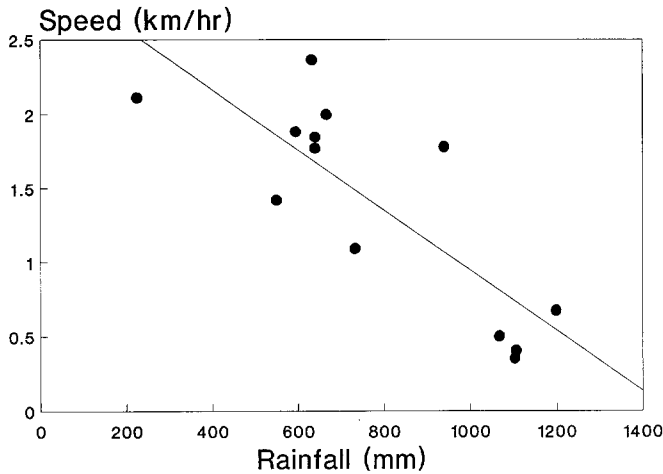
Fig. 9. Mean rate of travel for individual groups, plotted against mean annual rainfall. Mean rate of travel is calculated from day journey length and time spent moving (assuming a 12-h day)

Mean speeds of travel vary by a factor of six over the sampled populations and correlate significantly with both demographic stress ($r_s = 0.626$, $n = 13$, $P < 0.05$ two-tailed) and rainfall (Fig. 9: $r_s = -0.658$, $P < 0.05$ two-tailed), but not with ambient temperature ($r_s = 0.133$, NS). A stepwise regression with demographic stress, rainfall and temperature as independent variables yielded the following best-fit equation:

$$\ln(K) = 4.895 + 0.451 \ln(X) - 0.700 \ln(P)$$

($r^2 = 0.715$, $F_{2,10} = 12.527$, $P < 0.01$), where K is the speed of travel when moving (km/h) and X the demographic stress index for the group. Demographic stress alone accounts for 50.4% of the variance. Rate of travel is calculated from day journey length and the number of hours spent moving (determined from the time budget, assuming a 12-h day).

While the extreme populations in Fig. 9 may be exceptional, it is clear that a doubling of travel speed is well within the animals' normal capacities and this would represent a saving of around half the time spent moving. With moving time accounting for around 25% of time on average (Table 2), this would represent a saving of some 12%. In contrast, the cost of doubling travelling speed from 1-2 km/h (close to the upper limit for baboons) would add an additional 70.5% to the metabolic costs of moving for a 20-kg animal (Peters 1983, Eq. 6.3). This would add about 17.6% to the total feeding time requirement. With feeding time accounting for an average of 34.7% of the day, this would represent only an additional 6.1% of time devoted to feeding. The time savings from faster travel thus exceed the cost incurred in terms of extra feeding, such that there is a net gain of 6 percentage points that can be devoted to other activities.

I interpret this as evidence that baboons in marginal habitats attempt to alleviate an impending time-budget crisis by increasing their rate of travel proportionately. Note that this effect has already been incorporated into the equations for moving time given in Table 3. This

may explain why day journey length does not appear as a determinant of moving time, as might have been expected. In effect, it does, but the animals compensate by stepping up travel rate in direct proportion, as is indicated by the regression coefficient close to unity when speed of travel is regressed on day journey length:

$$\ln(K) = -0.996 + 0.927 \ln(J)$$

($r^2 = 0.96$, $n = 12$, $F = 239.592$, $P \ll 0.001$). (Note that the definition of travel speed is only circular in this context if moving time is *a priori* constrained to be the same in all populations for some reason; but this would seem to be implausible given the observed variation in moving time.) One alternative explanation here is that the apparent correlation is due to populations with small measured day journeys spending more time milling around within the same general area without the group as a whole moving forwards (see above). Better measures of travel speed are clearly required to exclude this possibility.

Discussion

I have tried to show that time acts as a constraint on group size in baboons. This constraint arises from a combination of environmental factors influencing basic time budget variables (for example, as a result of nutrient intake requirements) and the fact that the length of the active day is limited. The analyses have shown (1) that populations do not often exceed this constraint on group size, (2) that the severity of this constraint is directly related to environmental conditions, (3) that this constraint explains at least part of the genus' geographical distribution and (4) that groups under demographic stress as a result of this effect tend to exhibit other signs of social and ecological stress (e.g. increased risk of fragmentation, increased rates of travel). What is perhaps most surprising about the results is the extent to which the equations can account for the variation in the behavioural ecology of baboons. In most cases, the range in values on these variables across baboon populations is considerable (a factor of 2–4 on most time budget variables, and a full order of magnitude on resting time, day journey length and group size). To be able to explain 50–70% of the variance in these cases is no small feat.

There are two possible interpretations of the regression equations obtained in these analyses. One is that they reflect direct causal relationships; the other is that they are simply predictive correlations that reflect independent covariance with some third variable. Thus, ambient temperature may influence time spent feeding either (a) by determining the energy required for thermoregulation and by influencing forage quality (and so determining the gross rate of energy intake) or (b) because temperature and feeding time both happen to covary independently with the same third variable (such as rainfall). It seems most likely in this particular case that a real causal effect exists: temperature is reflecting thermoregulatory requirements. In other cases, such as the relationship between feeding time and rainfall diversity,

it seems likely that a more complex causal chain is involved: rainfall diversity influences forage quality, and this in turn influences the quantity of food that has to be eaten to balance the animal's nutrient budget.

The main lesson here, perhaps, is that although the analyses provide us with a very clear guide as to what factors are involved, more detailed field studies are needed to elucidate the precise nature of the mechanisms involved. In particular, we need to determine just which aspects of forage quality are relevant to the animals' time budgets. Barton (1989) found that food density in the herb layer was the most important factor influencing baboons' foraging patterns in a relatively poor quality habitat at Chololo. The present analyses, however, suggest that it is the availability of food in the bush/shrub layer that is generally more critical. Clearly, in poorer habitats with limited bush cover, other vegetation layers will be more prominent. A closer examination of the way animals trade time in different habitats would be especially valuable.

The importance of ambient temperature as a determinant of baboon behavioural ecology is striking. Temperature is not usually taken to be of great significance in tropical environments, except insofar as high heat loads may result in reduced forage quality. It is clear from the present results that baboons encounter significant problems related to thermoregulation even at moderate mean annual temperatures (15–20° C). Such habitats are, of course, likely to have rather cold nights (minimum temperatures as low as 5° C, well below the animals' thermoneutral zone).

Some of the relationships, on the other hand, are similar to those obtained in other studies. The influence of habitat quality on time budgets, for example, has been demonstrated directly in at least two baboon populations. Altmann and Muruthi (1988) and Eley et al. (1989) have shown that groups with access to human settlements (invariably a source of high quality foods) spend significantly less time feeding and more time resting than wild groups. Likewise, Singh and Vinathe (1990) found that urban and rural populations of Indian bonnet macaques spent less time foraging than forest-living populations.

Similarly, Stelzner (1988) has shown that the Amboseli baboons respond to the heat load generated by high ambient temperatures around midday by resting in shade whenever they encounter it. Stelzner's data show that baboons do not actively seek out areas with high bush cover, but rather exploit cover opportunistically as they encounter it during foraging. This suggests that these baboons face a conflict of interest in which the demands of feeding time often outweigh the costs of heat loading, especially in more marginal habitats like Amboseli where their time budgets are tightly constrained.

Van Schaik et al. (1983) found that day journey length and time spent travelling increased monotonically with group size in longtailed macaques, while resting time decreased. They also found that the amount of time spent searching for dispersed food items and the amount of social tension (number of agonistic interactions per day per individual) increased with group size, and suggested that this provided a proximate mechanism underlying some of the above effects. Van Schaik et al. (1983) argued that this was evidence for a "pushing forward" effect during foraging rather than evidence to suggest that food patches were of limited size. Until we have more detailed data on baboon foraging strategies, we cannot say which of these two effects might underlie the observed baboon behaviour. In addition, the present results suggest that a third factor (namely, the increased search-time costs of foraging within low-quality patches in poor environments) may play an important role in the case of baboons. This point merits detailed study.

One other point of interest is the fact that the results imply that travel is less costly to the animals than time itself. This tends to confirm Altmann's (1987) conclusion that the primary locomotor advantage of increased body size in mammals may in fact be conservation of time rather than energy. Altmann suggested that this gain might come through either reduced risk from predators (through less time being spent active) or increased access to better food sources (through being able to traverse a larger area during a given time). The present analyses do not allow us to comment on the particular mechanism in this case, but the fact that baboons can dramatically increase their rate of travel under poor habitat conditions tends to suggest that they are not energy-limited.

Perhaps the most significant question concerns the mechanism that maintains group size below the upper limit. It is likely that actual group size is a function of a number of considerations affecting the animals, one of which will be the minimum size required to reduce predation risk to an acceptable level. In some populations, this may lie well below the maximum that is ecologically tolerable (in time budget terms). As group size grows through natural recruitment, it will approach this upper limit, and groups will be forced to split into smaller groups. However, predation risk will make it difficult for groups to split into units below a certain size. Hence, we may expect to observe a frictional effect whereby groups have to increase some way beyond the maximum group size before they can undergo fission. This effect may be exacerbated if fission can only occur providing there are enough adult males and females in the group to produce two demographically viable subgroups. This may explain why the maximum group size often exceeds the maximum ecologically tolerable (Fig. 3). Given that the extent to which the maximum observed group size exceeds the predicted value (the stress on maximum group size) increases as habitat quality declines (Fig. 5), it seems likely that these problems may become especially intrusive for animals living in poor quality habitats where maximum group sizes tend to be small. Finally, it is clear that increased demographic stress on a group causes it to become dispersed and fragmented, and that it is this that probably precipitates fission.

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