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ORIGINAL ARTICLE

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Day length, latitude and behavioural (in)flexibility in baboons *(Papio cynocephalus ursinus)*

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Abstract Annual cycles in day length are an important consideration in any analysis of seasonal behaviour patterns, since they determine the period within which obligate diurnal or nocturnal animals must conduct all of their essential activities. As a consequence, seasonal variation in day length may represent an ecological constraint on behaviour, since short winter days restrict the length of the time available for foraging in diurnal species (with long summer days, and thus short nights, a potential constraint for nocturnal species). This paper examines monthly variation in activity patterns over a 4-year study of chacma baboons (*Papio cynocephalus ursinus*) at De Hoop Nature Reserve, South Africa. Time spent feeding, moving, grooming and resting are all significant positive functions of day length, even before chance events such as disease epidemics and climatically mediated home range shifts have been accounted for. These results provide strong support for the idea that day length acts as an ecological constraint by limiting the number of daylight hours and thus restricting the active period at certain times of year. Day length variation also has important implications across populations. Interpopulation variation in resting time, and non-foraging activity in general, is a positive function of latitude, with long summer days at temperate latitudes apparently producing an excess of time that cannot profitably be devoted to additional foraging or social activity. However, it is the short winter days that are probably of greatest importance, since diurnal animals must still fulfil their foraging requirements despite the restricted number of daylight hours and elevated thermoregulatory requirements at this time of year. Ultimately this serves to restrict the maximum ecologically tolerable group sizes of baboon populations with increasing distance from the equator. Seasonal variation in day length is thus an important ecological constraint on animal behaviour that has important implications both within and between populations, and future studies at non-equatorial latitudes must clearly be mindful of its importance.

Keywords Behaviour · Ecological constraints · Group size · Seasonality · Time budgets

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Introduction

An analysis of how a species distributes its time among various activities is an essential precursor to understanding the interrelations between its ecology and behaviour (Struhsaker and Leland 1979). Where two activities cannot be performed simultaneously, animals are forced to schedule certain behaviours preferentially, such that costs may be incurred by the reduced opportunities to engage in other biologically important activities (McFarland 1974; Caraco 1979a, 1979b; Dunbar 1992a). As a consequence, determining the ecological and demographic constraints on activity budget allocation and scheduling decisions is a key issue underlying a detailed understanding of mammalian socioecology.

Since the earliest studies, tentative generalisations have been made concerning the relationship between ecological factors (most notably diet and habitat structure) and species' activity budgets (Crook and Gartlan 1966; Crook 1970; Jarman 1974; Clutton-Brock and Harvey 1977). A number of studies have proposed correlations between seasonal variation in activities and food availability (e.g. ungulates: Owen-Smith 1994; carnivores: Williams et al. 1997; primates: Clutton-Brock 1977; Post 1981; Lawes and Piper 1992; Matsumoto-Oda 2002), while others have found direct relationships between activity and climatic variables (rodents: Cox and Hunt 1992; ungulates: Roberts and Dunbar 1991; Owen-Smith 1998; primates: Davidge 1978; Fa 1986; Lawes and Piper 1992; Baldellou and Adan 1997). Furthermore, analyses within species have shown variation in time budgets across primate populations to be related to local climatic conditions (Dunbar 1992a, 1992b; Williamson 1997), although annual variation in baboon time budgets at Amboseli was not easily explained in this way (Bronikowski and Altmann 1996).

While seasonality is undoubtedly important in accounting for intra-annual variation in activity levels, previous studies have almost exclusively focussed on seasonal variation in food availability or climatic parameters. Relatively little attention has been paid to how day length variation at temperate latitudes might itself operate as an ecological constraint. Traditionally, studies of the seasonal importance of day length have tended to focus on photoperiodic influences on hormone levels and reproduction (e.g. Malpaux et al. 1996; O'Brien et al. 1993) or on metabolic rates (Perret et al. 1998), thermoregulation (Aujard and Vasseur 2001) or body weight (Mercer et al. 2000). However, in exclusively diurnal (or nocturnal) species, seasonal variation in day length could represent a significant constraint, since it restricts the length of the active period.

Baboons (*Papio* spp.) are almost exclusively diurnal, and as a consequence are forced to perform most of their essential activities during the daylight hours. Thus where day length varies on a seasonal basis, specific activities may be compressed at certain times of year if the animals are to fulfil their foraging requirements (Dunbar 1988). Furthermore, since short winter days are likely to coincide with periods of lower temperature, energy requirements may also be elevated due to increased thermoregulatory costs, compounding the significance of the day length restrictions. At the other extreme, long summer day length could initially allow for strategic flexibility in foraging (Lawes and Piper 1992), socializing, or thermoregulation (Hill 2003), but may ultimately generate excess time that cannot profitably be used for any active purpose, leading to elevated levels of inactivity. As a consequence, both direct climatic constraints and patterns of day length variation could be important ecological factors underlying seasonal levels of activity allocation at more temperate latitudes. To date, however, few studies have sought to examine their importance.

Since the degree of day length seasonality co-varies with latitude, one implication is that latitude may also be important in accounting for behavioural differences between populations. Previous studies of the importance of latitude have examined relationships at a relatively large scale, and have considered factors such as species geographical ranges and Rapoport's Rule (Cardillo 2002), body size and Bergmann's Rule (Blackmann and Gaston 1996), life history traits (Cardillo 2002) and species richness (Owens et al. 1999). Relatively little attention has focussed on how latitude might account for variation in behaviour between populations of a single species. If day length does operate as an ecological constraint at the population level, then latitude and the degree of day length seasonality is likely to result in observable differences between populations. Again, however, few studies have sought to examine this possibility.

Here we present data on the behavioural patterns of a troop of chacma baboons (*Papio cynocephalus ursinus*) inhabiting a temperate locality to assess the impact of day length and climatic variables on seasonal patterns of activity. In addition, we also address the implications of latitude in accounting for variation in the behavioural ecology of baboons in sub-Saharan Africa.

Methods

Study site

De Hoop Nature Reserve (20°24'E, 34°27'S) is a coastal reserve situated close to Cape Agulhas, Western Cape Province, South Africa. Vegetation is dominated by coastal fynbos, a unique and diverse vegetation type comprising *Proteacae*, *Ericaceae*, *Restionaceae* and geophyte species. The reserve ranges in altitude from 0 to 611 m and has a Mediterranean climate, with a mean annual rainfall of 428 mm and mean annual temperatures of 17.0°C. However, due to its southerly latitude, De Hoop experiences considerable seasonal variation in both rainfall and temperature, as well as day length variation that is more extreme than at any other sub-Saharan African site (range from 9.8 h to 14.2 h). A more detailed description of the ecology of the reserve is given in Hill (1999).

Behavioural data

Data were collected over a 4-year period from March 1997 to February 2001, although no data are available for March 2000. The data are from a single troop of chacma baboons that ranged in size from 33 to 50 individuals, although increases in group size over the course of the study were interrupted by a disease epidemic resulting in large-scale mortality (Barrett and Henzi 1998) and subsequent immigrations into the troop (Henzi et al. 2000). This epidemic coincided with heavy rains in early 1998 that caused a flooding of the vlei, a large land-locked body of brackish water at the centre of the group's ranging area. This resulted in a marked home range shift as access to certain areas of the former range became restricted (Dixon 2001).

The baboons were followed on foot from a distance of a few metres and data were collected by means of instantaneous scan samples (Altmann 1974) at 30-min intervals. At each sample point, information was recorded on the identity and activity state (feeding, moving, grooming or resting) of all visible adult individuals. Analyses are restricted to these four activities since previous studies have shown them to account for over 95% of a baboon's daily activity (Dunbar 1992a). The data set consists 4,187 observation hours (mean of 89.1 h per month) and comprises 11,751 scans with a mean of 3.04 individuals per scan. Following the disease epidemic and home range shift, 2,813 h of data are available (mean of 82.7 h per month), consisting of 9,189 scans and a mean of 2.22 individuals per scan.

In order to ensure that activity budgets were not biased by uneven data collection across the day (since certain activities are performed more often at particular times of day: Clutton-Brock and Harvey 1977), data were averaged for each hour before mean daily time budgets were computed for each month (see also Bronikowski and Altmann 1996). However, seasonal trends in monthly percentage time budgets may disguise, or actually contradict, the underlying patterns of activity (Lawes and Piper 1992; Hill et al., unpublished data). As a consequence, the seasonal analyses presented here use time per day (in hours) spent in each activity as the dependent variable (following Davidge 1978; Lawes and Piper 1992; Agetsuma and Nakagawa 1998; Hill et al., unpublished data). These data were not transformed since none were found to differ significantly from a normal distribution (Kolmogorov-Smirnov: $P>0.05$).

To examine the importance of day length variation and latitude in accounting for population variation in baboon behaviour, we extracted data from the literature on mean annual time budgets from 16 long-term studies of baboons. These data are primarily those utilised by Dunbar (1992a), supplemented with additional data from two populations: De Hoop (feed 42.7%, move 27.1%, groom 15.1%, rest 13.3%) and Mkuzi, South Africa (feed 36.3%, move 30.2%, groom 12.1%, rest 20.6%: Gaynor 1994). Unlike the intrapopulation analyses, percentage time budget data are appropriate here, since for all populations day length is standardised to an approximate 12-h light-dark cycle over the course of the year. The population data were natural log transformed for parametric analysis.

Data analysis

A combination of stepwise and backwards least squares regression analysis was used to determine the environmental factors that best account for seasonal and interpopulation variation in activity patterns. In doing so, a hierarchical order was imposed on the four activities when constructing the equations in order to reflect the biological priorities of each activity to the animals (sensu Dunbar 1992a; but see also Altmann 1980). Feeding time is taken to be of highest priority, such that it is independent of time spent in other activities. Moving time, however, may be partially constrained by time spent feeding, and so feeding time is included as an independent variable. Although grooming is an important activity in social primates, we assume it must in part be constrained by the foraging variables, with time spent feeding and moving thus included as independent variables. Finally, no restrictions were placed upon the independent variables for resting since this is considered of lowest biological priority, with feeding, moving and grooming all included as potential independent variables. All equations were assessed to ensure that the variables incorporated into the final models were both statistically and computationally independent (e.g. no overlapping rainfall variables were included). All tests are two-tailed, with the level for significance set at default levels of $P=0.05$ for inclusion and $P=0.10$ for exclusion from the models.

Results

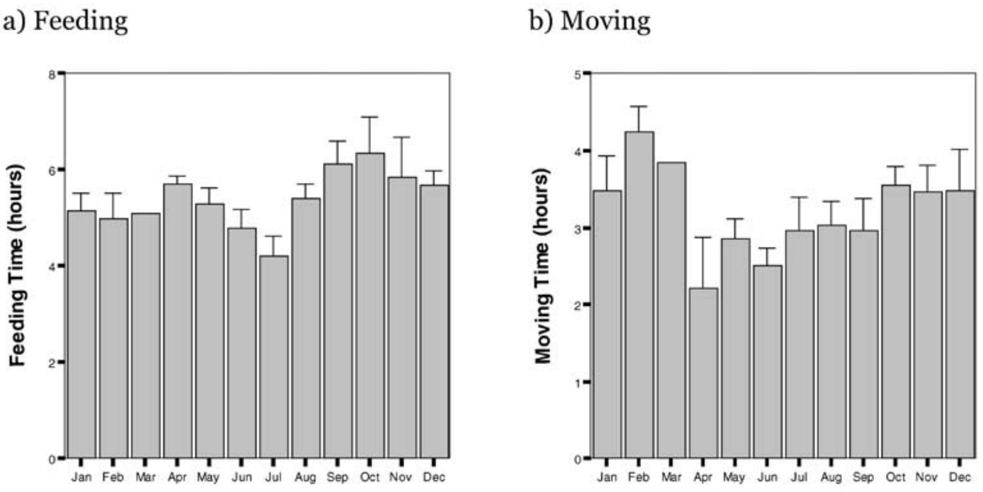
Intrapopulation relationships

Table 1 displays the least square regression equations of ecological and behavioural variables on hours per day spent in the four activities. A consistent feature of the equations is that all contain a significant positive function of day length. However, the equations for feeding, moving and grooming contain negative functions of group size, and although group size is not a significant component of the equation for resting time, a positive coefficient of group size is the first variable stepped into the model before being removed at the final step. These relationships with group size are contrary to almost all of those previously reported in the literature for baboons, where, for example, larger groups spend more time engaged in foraging activity (Slatkin and Hausfater 1976; Stacey 1986; Gaynor 1994).

As stated, a disease epidemic and marked home range shift occurred early in 1998, and these two independent events could significantly affect the behaviour patterns displayed by the study troop. The new ranging areas were of lower quality in terms of food availability (Hill 1999), and thus because the troop was dramatically reduced in size when it started to use these areas more heavily, this could produce spurious relationships with respect to group size. Certainly changes in the nature of the grooming relationships before and after the disease epidemic and home range shift at De Hoop have been reported (Barrett et al. 2002), and different ecological relationships were reported before and after a home range shift at Amboseli (Bronikowski and Altmann 1996). The original analyses were thus re-run for the period following the disease epidemic and home range shift to rule out these confounding effects. This period was selected because it contained the largest amount of available data, and since the primary interest here is in the impact of day length on behaviour patterns, the comparable relationships for the earlier period are not presented. However,

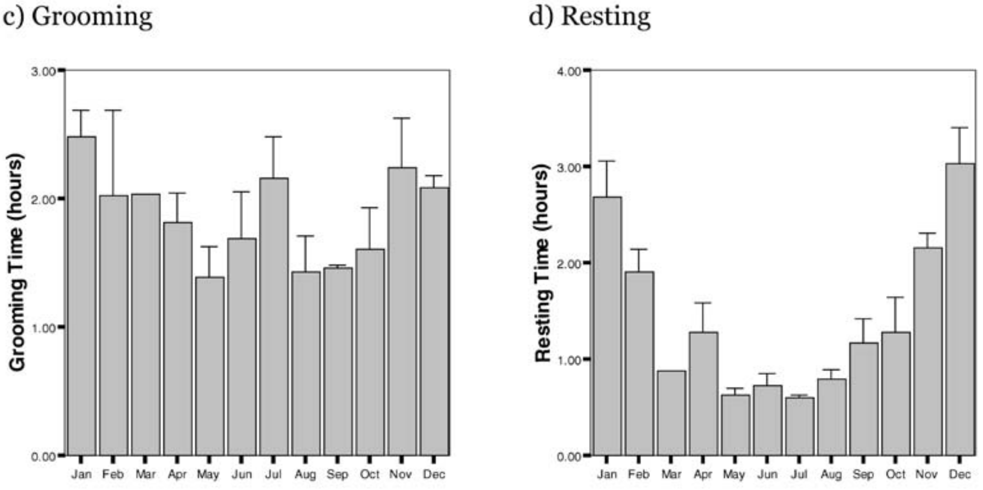
Table 1 Least square regression equations of environmental variables on hours per day spent in activity by chacma baboons (*Papio cynocephalus ursinus*), where D is day length (hours), T is the mean monthly temperature (°C), N is the group size, and RN_{012} is the sum of the rainfall in the study month and preceding 2 months (mm). Variables not included in the final models (but included in the initial list of independent variables) are: MaxT the mean monthly maximum temperature (°C); MinT, the mean monthly minimum temperature (°C); RN_0, the study month rainfall (mm); RN_1, the rainfall in the month preceding the study month (mm); RN_{12}, the sum of the rainfall in the 2 months preceding the study month (mm); and RN_{123}, the sum of the rainfall in the three months preceding the study month (mm). Order of independent variables in equations reflects relative importance as indicated by size of standardised coefficient

Activity	Equation	r^2	*F*	*P*
Feeding	$F=6.12+0.43D-0.17T-0.087\ N$	0.221	$_{(3,43)}$ 4.06	<0.02
Moving	$M=6.91-0.50F-0.0041R_{012}+0.14D-0.060\ N$	0.497	$_{(4,42)}$ 10.37	<0.0001
Grooming	$G=3.78+0.030D-0.46F-0.48\ M-0.043\ N$	0.550	$_{(4.42)}$ 12.84	<0.0001
Resting	$R=-0.59+0.95D-0.89F-0.92\ M-0.91G$	0.979	$_{(4,42)}$ 478.97	<0.0001



a) Feeding

b) Moving



c) Grooming

d) Resting

Fig. 1 Hours per day spent in **a** feeding, **b** moving, **c** grooming and **d** resting by chacma baboons (*Papio cynocephalus ursinus*) for the period following the disease epidemic and home range shift. Data for March are from a single year; n=3 years in all other cases

Table 2 Least square regression equations of environmental variables on hours per day spent in activity for the period following the disease epidemic and home range shift. Initial list of independent variables and abbreviations as for Table 1. Order of independent variables in equations reflects relative importance as indicated by size of standardised coefficient

Activity	Equation	r^2	*F*	*P*
Feeding	$F=1.13+0.61D-0.21T+0.011RN_1$	0.307	$_{(3,30)}$ 4.43	<0.02
Moving	$M=3.41-0.35F+0.19D-0.0030RN_{123}-0.0056RN_0$	0.532	$_{(4,29)}$ 8.25	0.0001
Grooming	$G=2.55+0.34D-0.59F-0.49\ M$	0.713	$_{(3,30)}$ 24.90	<0.0001
Resting	$R=-0.22+1.03D-0.97F-1.00\ M-0.98G-0.031T$	0.986	$_{(5,28)}$ 390.29	<0.0001

the results do remain broadly similar for this earlier period (see also Hill 2003).

The mean numbers of hours per day spent in each activity per month in the period following the disease epidemic and home range shift are displayed in Fig. 1. The new regression equations relating climatic and behavioural variables to hours per day spent in the four activities are in Table 2. All four activities are again significant positive functions of day length, with day length the main effect accounting for the largest proportion explained variance for all but moving behaviour (feeding: partial r^2=0.262, t=3.37, P=0.002; moving: partial r^2=0.078, t=2.21, P=0.035; grooming: partial r^2=0.260, t=7.26, P<0.001; resting: partial r^2=0.731, t=27.10, P<0.001). Feeding time is a significant positive function of day length and of rainfall in the month preceding the study month, as well as a negative function of mean monthly temperature. Moving time is a positive function of day length, a negative function of time spent feeding and negative functions of two measures of rainfall (study month rainfall and the sum of the rainfall in the 3 months preceding the study month). Time spent grooming is a positive function of day length and negative functions of hours per day spent in feeding and moving activity. Similarly, time spent resting is a positive function of day length, negative functions of hours per

Table 3 Least square regression equations of environmental variables on population time budgets, where T is mean annual temperature (°C), N is group size, PPI is the plant productivity index (the number of months per year receiving more rainfall (mm) than twice the mean annual temperature (°C) for that site: le Houérou 1984; see also Hill and Dunbar 2002), and L is the latitude. Independent variables included in the analyses but not incorporated into any of the final models are: RN, the mean annual rainfall (mm); S, Shannons index of rainfall diversity; and A, altitude (m). Order of independent variables in equations reflects relative importance as indicated by size of standardised coefficient

Activity	Equation	r^2	F	P
Feeding	$\ln F=6.23-0.86 \ln T$	0.242	$_{(1,14)}$ 4.47	0.053
Moving	$\ln M=3.75+0.29 \ln N-0.54 \ln T$	0.586	$_{(2,13)}$ 9.18	0.003
Grooming	$\ln G=3.28+0.60 \ln PPI-0.54 \ln F$	0.483	$_{(2,13)}$ 6.07	<0.02
Resting	$\ln R=8.68-1.36 \ln F-0.43 \ln G+0.10 \ln L$	0.825	$_{(3,12)}$ 18.89	<0.0001

day spent feeding, moving and grooming, and also a negative function of mean monthly temperature.

Interpopulation relationships

Since day length is the main factor underlying seasonal variation in activity levels at De Hoop, one obvious implication is that day length variation (and thus latitude) might be an important variable accounting for some of the variation in activity levels between populations. In particular, the proportion of time spent resting, as well as non-foraging time more generally, may show the strongest relationships with latitude, since the long summer days could generate an excess of time that cannot be used strategically for another activity. Although longer days may initially allow for additional or more flexible foraging and social activities, as distance from the equator increases, summer day lengths may become so long that an excess of time is generated that cannot profitably be used for additional essential activities. As a consequence, we would anticipate proportion of time spent inactive (or resting) to increase with latitude across populations, all else held equal. Data on mean annual time budgets from 16 baboon populations are available to test this prediction, with the best-fit equations relating time budget allocations to climatic conditions at each site given in Table 3.

The proportion of time spent feeding decreases as mean annual temperatures increase, with percentage time spent moving increasing with group size and also decreasing as mean annual temperatures increase. Grooming time is a negative function of percentage feeding time and a positive function of the plant productivity index. Finally, resting time is a negative function of both feeding and grooming time, and a positive function of latitude. Interestingly, if the regression is rerun to consider total non-foraging time (percentage time spent grooming and resting combined), then a similar equation is produced (r^2=0.904, $F_{(3,12)}$=37.54, P<0.0001): ln (non-foraging) = 7.53 − 0.86 ln (Feeding) − 0.33 ln (moving) + 0.05 ln (latitude). As predicted, therefore, latitude is an important variable accounting for some of the observed variation between populations in activity patterns, with populations at increasing distance from the equator spending more time in non-foraging activities on an annual basis due to the excess time generated by long summer day lengths.

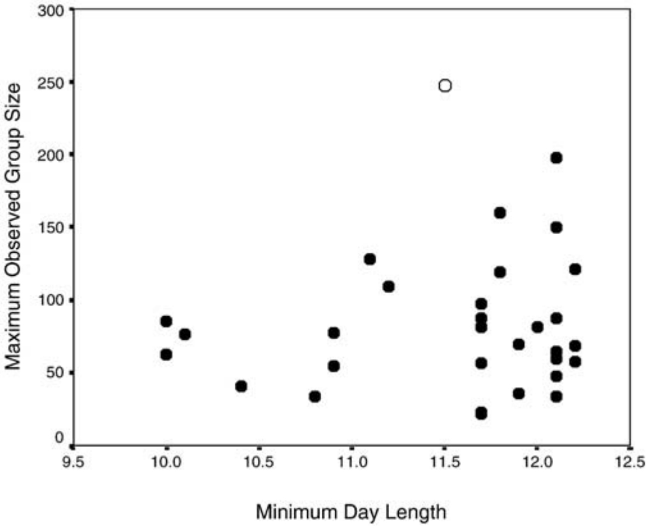


Fig. 2 Observed maximum group sizes across 30 baboon populations (for which a minimum of two groups have been counted) against the minimum day length experienced by that population

The ultimate importance of day length variation in accounting for interpopulation variation in behaviour in diurnal species probably lies in the constraints imposed by short winter days since these could act as a bottleneck within which the animals must nevertheless conduct all of their essential activities. Ultimately, this could constrain populations at temperate latitudes to smaller group sizes than populations experiencing an identical set of ecological parameters at the equator. Fig. 2 plots the maximum group sizes observed for 30 baboon populations, where accurate group counts are available for at least two groups, against the minimum day length for that population. Maximum group size (as opposed to mean group size) is used here since day length should set a ceiling on the maximum possible size of group; although this may impact upon observed population mean group size, it is the maximum possible group size that is ultimately constrained. Fig. 2 illustrates that short winter days do appear to constrain population maximum group sizes, since, with the exception of the Mt. Assirik population (open circle), maximum observed group sizes increase as minimum day lengths increase. Thus day length variation at temperate latitudes does appear to limit an animals behavioural options, such that baboons are constrained to living in smaller groups at these localities.

Discussion

Day length is an important ecological constraint on an individual's behavioural options since it sets the period within which obligate diurnal or nocturnal animals must perform their essential behaviour (Dunbar 1988). However, while a number of studies have suggested relationships between primate behaviour and day length (Hall 1962; Davidge 1978; Fa 1986; Lawes and Piper 1992; Ménard and Vallet 1997; Agetsuma and Nakagawa 1998), none have set out to formally examine its importance. The results presented here confirm that even before random events such as disease epidemics or restricted access to former areas of the home range have been accounted for, day length acts as an ecological constraint by limiting the number of hours within which animals must balance their activity budgets. The importance of day length variation is further reflected in the fact that latitude is important in explaining behavioural variation between populations, since short winter days at more temperate latitudes produce a bottleneck that ultimately limits populations to smaller maximum group sizes as distances from the equator increase.

Day length was a significant factor in all four equations relating activity levels to ecological and behavioural variables. Similar relationships with day length were reported for moving and resting in Japanese macaques (Agetsuma and Nakagawa 1998) and resting in Barbary macaques (Ménard and Vallet 1997), while Lawes and Piper (1992) reported a relationship between feeding and day length for the samango monkeys at Cape Vidal. This suggests that the constraints imposed by day length are generally applicable to diurnal animals (or primates at least) inhabiting temperate environments. However, although day length is the primary parameter underlying seasonal variation in activity levels in most cases, factors other than day length were incorporated into the models such that the equations require some interpretation.

With respect to feeding time, the relationship with day length reflects the constraints imposed by short winter days such that time available for feeding is limited. As the number of daylight hours increases, however, time spent feeding can increase, potentially allowing for a more flexible foraging strategy during the summer months when time is less constrained (Lawes and Piper 1992). However, energetic requirements are likely to be reduced as temperatures rise and the relationship with mean monthly temperature probably reflects these thermoregulatory considerations. Such a trade off is clear from Fig. 1a, where hours per day spent feeding increases either side of mid-winter (July) before levelling off and even declining in the warm summer months. The relationship with rainfall in the month preceding the study month is more problematic. Relationships with rainfall are often taken to reflect seasonal food availability, since rainfall is known to be a reliable predictor of primary productivity in sub-Saharan habitats (Deshmukh 1984; le Houérou 1984). However, if this were the case here we would expect the relationship to be negative, not positive. One possibility is that this relationship may also partially reflect thermoregulatory considerations, since the months following those of highest rainfall are in mid-winter when temperatures are lowest. This relationship could thus reflect the increased nutritional requirements of the cold winter months, although little confidence can be placed in this interpretation.

Moving time is also a positive function of day length, again reflecting the constraints imposed by short winter days and the potential for more flexible foraging strategies in the longer summer months. Within this context, the relationship with feeding time probably reflects the trade-offs that occur between activities when time is limited, since a higher proportion of foraging time (defined as feeding plus moving) is spent feeding when foraging time is constrained (Henzi et al. 1997). Similar trade-offs with feeding were reported by Agetsuma and Nakagawa (1998). Rainfall is also an important determinant of moving time. The relationship with rainfall in the three months preceding the study month is likely to reflect the influence of rainfall on primary productivity, a relationship that has been reported for other studies (Barton 1989; Post 1982). While the relationship with rainfall in the study month might also be related to this, its importance in determining surface water availability is also likely to be important, since this is also a key factor determining baboon ranging patterns (Barton et al. 1992).

Grooming time and resting time are primarily positive functions of day length and negative functions of the other activity categories. This suggests that time allocation to both activities is essentially determined in the light of the time left over after foraging (see Altmann 1980; Dunbar 1992a; Bronikowski and Altmann 1996). Since this 'spare' time increases with day length, time spent grooming and resting also increase accordingly. However, the negative relationship between time spent resting and mean monthly temperature suggests that the relationship with day length is not linear. Indeed, a quadratic component of day length is incorporated into the models if available as an independent variable. Thus due to the correlation between monthly temperatures and day length, the relationship with temperature reflects slightly elevated levels of resting at low temperatures. It is clear from Fig. 1d that resting time levels off at a minimum value of 30 min per day. While it is reasonable to consider resting as a reservoir of 'uncommitted' time that can be drawn of for other activities when required (Dunbar and Sharman 1984), it may still perform specific functions that delimit a minimum time allocation. Certainly a number of previous studies have suggested more 'active' functions for resting, such as energy conservation (Raemakers 1980; Dasilva 1992), a response to heat loading (Stelzner

1988; Hill 2003) or as an interruption of other activities for vigilance (Cowlishaw 1998). Further research is required if we are to understand and identify the proportion of resting time that is committed for specific purposes and that which is uncommitted and free to draw upon for other activities. Nevertheless, it is clear that day length is the primary determinant of time allocated to resting across months at temperate latitudes.

Day length is thus the most important factor accounting for seasonal variation in activity levels at De Hoop. However, similar ecological relationships to those in the intrapopulation analyses are observed across populations. Most importantly, resting time is a positive function of latitude, once the constraints imposed by time allocated to feeding and grooming have been accounted for, although variation in all four activities may be explained on the basis of ecological parameters at each site.

Feeding time is a negative function of mean annual temperature, and there are likely to be two important elements to this relationship. Firstly, the proportion of fruit in the diet increases with temperature (Hill and Dunbar 2002) and this relationship thus reflects the benefits of a high quality diet. However, the negative relationship with temperature is also likely to reflect thermoregulatory considerations, since energetic requirements will decline with temperature. Moving time is also a negative function of temperature, although a positive relationship with group size has the greatest effect within the model. The relationship with group size reflects the importance of intragroup feeding competition in forcing animals to move further to satisfy their nutritional requirements as group size increases, once differences in ecology and diet between sites (reflected in the relationship with temperature) are held constant.

The primary productivity index (which reflects the likely number of growing months in sub-Saharan habitats: Hill and Dunbar 2002) forms a significant component of the equation for grooming time, with populations in more productive habitats (i.e. longer growing seasons) engaged in higher levels of grooming. However, the proportion of time spent feeding also forms a significant component of the equation time, confirming that time spent grooming is primarily determined in the light of time left over from foraging (Altmann 1980; Dunbar 1992a). Similarly time spent resting is a negative function of the time spent feeding and grooming. However, the most important relationship here is that resting time is also significant positive function of latitude, and a similar result is obtained if non-foraging activity is considered as a single behavioural category. Thus, with increasing distance from the equator, populations spend more time resting on an annual basis due to the apparently excess time generated by long summer day lengths. However, the ultimate importance of day length variation appears to lie in the constraints imposed by the short winter days.

Short day lengths during the winter months represent a bottleneck which diurnal species must conduct all of their essential activities, despite the limited number of daylight hours. While animals may be able to compromise on certain activities (e.g. grooming) for a couple of months in order to free up sufficient time for foraging, they must nevertheless live in social contexts that allow them to pass through these bottlenecks without excessive risk of mortality. As a consequence, day length variation at temperate latitudes constrains populations to smaller maximum ecologically tolerable group sizes than would be the case for an identical set of ecological parameters in an equatorial population. The one exception to this appears to be the Guinea baboon (*P. c. papio*) population at Mt Assirik, Senegal. While this is the only Guinea baboon population of in the sample, it is unlikely that phylogenetic effects are important. Rather, groups in this population habitually fragmented into small unstable foraging parties that often ranged and slept alone (Sharman 1981). As a consequence it seems that the maximum observed group size for this population is unlikely to represent the group size that is sustainable as a long-term entity. The constraints imposed by short winter days do thus appear to limit maximum group sizes within populations at non-equatorial latitudes.

Day length is clearly an important ecological constraint at both intra- and interpopulation levels. It is important to note, however, that such constraints are only really significant in species that restrict all of their essential activity to the daylight (or darkness) hours. Cathemeral activity patterns (significant levels of activity during the day and night: Tattersall 1987) are well documented for lemurs (e.g. Andrews and Birkenshaw 1998; Curtis et al. 1999), and other mammals (e.g. Owen-Smith 1998; Rodrigues and Monteiro-Filho 2000; Linnane et al. 2001). As a consequence, these species are unlikely to be constrained in the same way by day length, since any shortfalls in activity during the daylight hours can potentially be made up over the course of the night (or vice versa). Indeed, Curtis and Rasmussen (2002) suggest that the flexibility afforded by cathemerality may have significant adaptive benefits in terms of thermoregulation and avoiding predators, thus making it a highly efficient behavioural strategy. Baboons, however, appear constrained to a diurnal lifestyle, and the nocturnal hunting behaviour of many savannah carnivores may preclude cathemeral strategies in terrestrial primates, and necessitate the use of sleeping sites as predator refuges (Hamilton 1982). The consequence of this, however, is that baboons are restricted in their activity by the length of the daylight period, such that day length is an important constraint on behaviour at non-equatorial latitudes. Day length is clearly an ecological parameter that should be given greater precedence in future studies, and further work on obligate diurnal (or nocturnal) species inhabiting temperate localities is clearly required if we are to fully understand it importance.

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