# Day length variation and seasonal analysis of behaviour

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**Annual cycles in day length are an important consideration in seasonal analyses of behaviour. Seasonal variation in day length not only represents an ecological constraint on activity, but also imposes methodological restrictions on analyses. This paper examines the implications of monthly variation in day length using data from a troop of chacma baboons (*Papio cynocephalus ursinus*) at De Hoop Nature Reserve, South Africa. Time spent feeding, moving, grooming and resting each month were all significant positive functions of day length, confirming its importance as an ecological constraint. More importantly, the results highlighted the necessity of including day length as an independent variable in this form of analysis. Where day length is excluded, there are problems interpreting relationships, since it is impossible to separate out the independent effects of temperature and day length. The analyses also confirmed that percentage time budgets, which have sometimes been used in this form of analysis, are subject to significant biases where data are from populations experiencing substantial degrees of day length variation. Future research must be aware of the methodological constraints imposed by seasonal variation in day length, and further work is clearly required to fully determine its importance.**

**Key words**: activity, day length, latitude, photoperiod, primate, seasonality.

## INTRODUCTION

The general relationship between ecological factors (most notably diet and habitat structure) and species' activity budgets has had a long history in behavioural ecology (Crook & Gartlan 1966; Jarman 1974; Clutton-Brock & Harvey 1977). Many studies have proposed correlations between seasonal variation in activities and food availability (Post 1981; Lawes & Piper 1992; Williams *et al.* 1997; Owen-Smith 1998), while others have reported direct relationships between activity and climatic variables (Davidge 1978; Fa 1986; Lawes & Piper 1992; Roberts & Dunbar 1991). Seasonality is an important element in many of these relationships, although previous studies have almost exclusively focused on seasonal variation in food or climatic parameters. Recently though, Hill *et al.* (2003) illustrated that day length variation at temperate latitudes could in itself operate as an ecological constraint. These analyses also suggested that day length variation might have a number of methodological implications.

The problem is illustrated if we consider an animal that engages in a notional activity that ranges from 25 to 30% of its time budget over the course of the year (Fig. 1). At the equator, with an approximate 12 h light–dark cycle, this translates to an identical activity pattern ranging from 3 to 3½ h over the course at the year. However, at a latitude of 35°S (the approximate latitude of the study site in this paper) the patterns of activity are completely reversed. Percentage time budgets may thus not only confound the relationships under investigation, but could also produce opposite and misleading results simply because the time budgets are not computed over the same length of day across the year. Nevertheless, time budgets have formed the basis of a number of studies of seasonal variation in animal behaviour at non-equatorial latitudes (*e.g.* Engel & Young 1992; Henzi *et al.* 1997; Tieleman & Williams 2002; Shi *et al.* 2003). While certain studies have utilized hours per day spent in activity to overcome this problem (Davidge 1978; Lawes & Piper 1992; Agetsuma & Nakagawa 1998; Hill *et al.* 2003), none have set out to formally examine its effects. Here we present data

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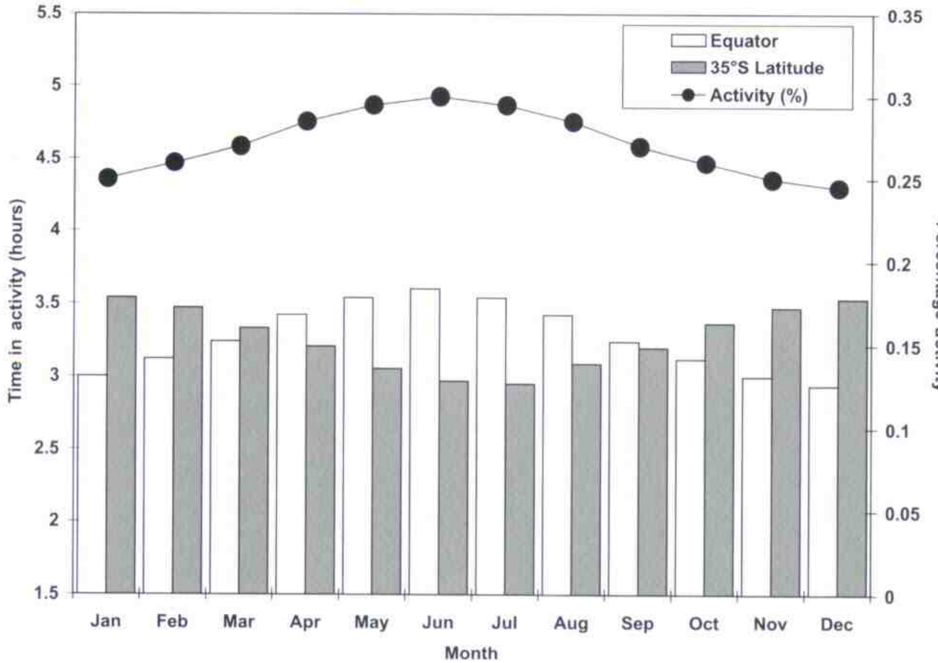


**Fig. 1**. Behaviour patterns in hours per day for a notional animal that engages in an activity that varies seasonally from 25 to 30% of its time budget at the equator (open bars) and at a latitude of 35°S (shaded bars).

on the behavioural patterns of a troop of chacma baboons (*Papio cynocephalus ursinus*) from a temperate locality to examine the implications of day length variation on seasonal analyses and to provide a framework for future studies.

## METHODS

### *Study area*

De Hoop Nature Reserve (20°24′E, 34°27′S) is a coastal reserve close to Cape Agulhas, the southern tip of South Africa. The reserve ranges in altitude from 0 to 611 m and has a Mediterranean climate: mean annual rainfall is 428 mm, with mean annual temperatures of 17.0°C. Owing to its southerly latitude, De Hoop experiences considerable seasonal variation in both rainfall and temperature, as well as day length variation unparalleled at any sub-Saharan African site (range: 9.8–14.2 h). A more detailed description of the ecology of the reserve is given in Hill (1999).

### *Data collection and analysis*

The chacma baboons at De Hoop have been under observation since 1996. The data presented here are from a single troop (VT) and are restricted to a two-year-period from May 1998 to April 2000 (excluding March 2000). Data are confined to this period since it followed a significant home range shift (Dixon 2001) which could have disrupted the behavioural patterns under investigation; changes in the nature of grooming relationships before and after the home range shift have been reported (Barrett *et al.* 2003). Group size ranged from 33 to 41 individuals over this period. The baboons were followed on foot from a distance of a few metres, with data collected by means of instantaneous scan samples (Altmann 1974) at 30-minute 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 were restricted to these four activities since previous studies have shown them to account for over 95% of baboon daily activity (Dunbar 1992). To ensure that the data were evenly spread across the day (since certain activities are performed more often at particular times of day (Clutton-Brock & Harvey 1977)), data were averaged for each hour before monthly time budgets and mean monthly hours per day in each activity were computed.

A combination of stepwise and backwards least squares regression analysis was used to determine the environmental factors that best accounted for seasonal variation in activity levels. In constructing the equations, a hierarchical order was imposed

**Table 1**. Least square regression equations of environmental variables on hours per day in activity, where T is the mean monthly temperature (°C), $RN_1$ is the rainfall in the month preceding the study month (mm), D is day length (hours), and $RN_{123}$ is the sum of the rainfall in the three months preceding the study month (mm). Independent variables not included in the models are MaxT, the mean monthly maximum temperature (°C), MinT, the mean monthly minimum temperature (°C), $RN_0$ study month rainfall (mm), $RN_{12}$, the sum of the rainfall in the two months preceding the study month (mm), $RN_{012}$, the sum of the rainfall in the study month and preceding two months (mm), and N, the group size. Order of variables in each equation reflects relative importance as indicated by size of standardized coefficient.

| Activity | Equation | $r^2$ | $F$ | $P$ |
|---|---|---|---|---|
| Feeding | $F = 0.12 + 0.85\ D - 0.32\ T + 0.011\ RN_1$ | 0.453 | $_{(3,19)}5.24$ | 0.008 |
| Moving | $M = 3.10 - 0.35\ F + 0.20\ D - 0.0033\ RN_{123}$ | 0.526 | $_{(3,19)}7.04$ | 0.002 |
| Grooming | $G = 2.23 - 0.57\ F + 0.33\ D - 0.39\ M$ | 0.760 | $_{(3,19)}20.10$ | <0.0001 |
| Resting | $R = -0.17 + 0.98\ D - 0.96\ F - 1.02\ M - 0.98\ G$ | 0.985 | $_{(4,18)}291.24$ | <0.0001 |

on the four activities to reflect the biological priorities of each activity to the animals (see Dunbar 1992; Hill *et al.* 2003). All equations were assessed to ensure that the variables incorporated were both statistically and computationally independent (*e.g.*, no overlapping rainfall variables), and backwards regression was used where no equation was generated by the stepwise procedure. All tests are two-tailed with the level of rejection set at $P = 0.05$ for inclusion and $P = 0.10$ for exclusion from the models.

## RESULTS

Table 1 displays the least square regression equations of ecological and behavioural variables on hours per day spent in the four activities. Feeding time is a 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 and negative functions of time spent feeding and a composite measure of rainfall (sum of the rainfall in the three 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 and negative functions of hours per day spent feeding, moving and grooming. All four activities are thus significant positive functions of mean monthly day length.

The equations relating environmental variables to percentage time budgets for the four activities are given in Table 2. Interestingly, most of the equations are similar to those in Table 1, although differences exist in the equation for grooming time. However, the most significant discrepancies from Table 1 are in relation with day length. Day length does not form a significant component of the equations for either grooming or resting time, and the sign of the relationship is reversed for percentage moving time. This suggests that computing percentage time budgets over days of unequal length may result in a lack of sensitivity to day length variation, even though certain variables may produce ostensibly identical relationships to those for hours per day in activity. Nevertheless, the fact that differences exist for most of the equations suggests that the potential for errors in using time budgets may be considerable.

As a final analysis, we further examined the importance of day length in understanding seasonal relationships by excluding it as an independent variable (Table 3). The precise equations are not

**Table 2**. Least square regression equations of environmental variables on the percentage time budgets. Independent variables and abbreviations as for Table 1. Order of variables in each equation reflects relative importance as indicated by size of standardized coefficient.

| Activity | Equation | $r^2$ | $F$ | $P$ |
|---|---|---|---|---|
| Feeding | $F = 0.44 - 0.026\,T + 0.033\,D + 0.0010\,RN_1$ | 0.519 | $_{(3,19)}6.83$ | 0.003 |
| Moving | $M = 0.70 - 0.019\,D - 0.38\,F + 0.00030\,RN_{123}$ | 0.455 | $_{(3,19)}5.28$ | 0.008 |
| Grooming | $G = 0.32 - 0.42\,F - 0.00024\,RN_{123}$ | 0.541 | $_{(2,20)}11.79$ | <0.0001 |
| Resting | $R = 0.99 - 0.98\,F - 1.02\,M - 1.03\,G$ | 0.975 | $_{(3,19)}246.68$ | <0.0001 |

**Table 3**. Least square regression equations of environmental variables on hours per day spent in activity with day length excluded from the analysis. Other independent variables and abbreviations as for Table 1. Order of variables in each equation reflects relative importance as indicated by size of standardized coefficient.

| Activity | Equation | $r^2$ | $F$ | $P$ |
|---|---|---|---|---|
| Feeding | – | – | – | – |
| Moving | $M = 3.77 - 0.0041\ RN_{123} - 0.27\ F - 0.079\ T$ | 0.513 | $_{(3,19)}6.67$ | 0.003 |
| Grooming | $G = 2.17 - 0.32\ F + 0.090\ T$ | 0.533 | $_{(2,20)}11.42$ | <0.0001 |
| Resting | $R = -1.86 + 0.20\ T$ | 0.544 | $_{(1,21)}25.10$ | <0.0001 |

important here, but Table 3 does highlight two key points. The first is that day length is essential in understanding time allocations to the four behavioural categories, since not only is no statistically significant model generated for feeding time, but the amount of variance explained by the models for the other three behaviours is greatly reduced. Secondly, in the absence of day length as an independent variable, a positive coefficient of mean monthly temperature enters the equations for grooming and resting time. This is understandable, since the two variables are highly correlated (Pearsons $r = 0.856$, $n = 24$, $P < 0.0001$), but it nevertheless complicates the interpretation of previously reported relationships between seasonal activity levels and temperature where day length has not been considered as an independent variable.

## DISCUSSION

Day length is an important ecological constraint on an individual's behavioural options since it sets the period within which an animal must perform its 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 & Piper 1992), only one has set out to formally examine its importance (Hill *et al.* 2003). As a consequence, many studies have failed to control for its effects.

The data presented here confirm that seasonal analyses of behaviour at latitudes with significant day length variation must be conducted using hours per day spent in activity as the dependent variable. Percentage time budgets, which have sometimes been used in this type of analysis (Engel & Young 1992; Henzi *et al.* 1997; Tieleman & Williams 2002; Shi *et al.* 2003), are subject to significant biases when data are from populations where day length varies seasonally. The problems stem from the fact that percentage values are not scaled to the same length of day. As a consequence there is a need to treat with caution any relationships previously reported in the literature that have utilized percentage time budgets, since many of these may be subject not only to statistical errors, but also to problems in interpretation.

Even if hours per day spent in activity is used as the dependent variable, there may be problems in interpreting relationships with mean monthly temperature where day length is excluded as an independent variable. This problem stems from the interrelationship between monthly temperatures and day length. The results in Table 3 clearly illustrate that if day length is excluded as an independent variable, then time spent grooming and resting are strong positive functions of mean monthly temperature. As a consequence, where day length has been omitted in previous analyses, it is impossible to separate out the independent effects of temperature and day length. Thus, thermoregulatory or temperature-related explanations cannot be proposed with any certainty where relationships were found between temperature and levels of activity.

These results suggest that seasonal analyses of behaviour at non-equatorial latitudes must be conducted using hours per day spent in activity as the dependent variable, and should include day length as an independent variable. However, there is a potential problem with this approach if the other activity states are included as independent variables, since there is then a sense of statistical inevitability about the relationships. If day length and the three other activities, which together with the dependent variable account for at least 95% of that day, are included as independent variables, then their inclusion in the models is perhaps not surprising and it tells us little about the biological trade-offs involved. It is also important to note that an analogous problem exists for time budgets anyway, since all activities must sum to 100%. For the analyses presented here, however, this does not appear to be the primary explanation, since if we take the case of hours per day spent resting and re-run the equation in Table 1 with the other activity variables excluded, the resultant equation contains just the day length parameter, with no further climatic variables included ($R = -3.93 + 0.44$ D; $r^2 = 0.685$, $F_{(1,21)} = 45.74$, $P < 0.001$). Thus the activity variables are not included in the equations at the expense of ecological parameters. While we still cannot rule out the possibility of the inclusion of the activity variables as statistical artefacts, it is clear that day length is of paramount importance and that inclusion of the activity categories provides greater insight to the biological process involved. Nevertheless, future studies must be mindful of the possibilities of statistical effects in seasonal relationships of activity levels, and that all results are evaluated accordingly.

Day length thus represents an important consideration in seasonal analyses of behaviour, and while analyses using hours per day spent in an activity as the dependent variable may not represent a perfect solution, it appears to be the best option currently available. Given that day length varies annually by over an hour at latitudes of 10° (computed from Griffiths 1976), these findings could have significant implications for most studies of animal behaviour. However, day length variation may only be significant in species that restrict their essential activities to the daylight (or darkness) hours. Many mammals exhibit significant levels of activity during the day and night (Andrews & Birkinshaw 1998; Linnane *et al.* 2001) and thus may not be constrained in the same way by day length. Nevertheless, if observations of these species are confined to daylight, then the methodological implications still need to be carefully considered. However, it might also be the case that such considerations are not necessary when dealing with behaviours that are highly seasonal in nature (such as reproduction in certain species). Clearly future research must be mindful of both the ecological and methodological constraints imposed by day length variation, and additional work is required to fully elucidate its importance in seasonal analyses of animal behaviour.

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