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Indices of environmental temperatures for primates in open habitats

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Abstract Studies of thermoregulation in primates are under-represented in the literature, although there is sufficient evidence to suggest that temperature represents an important ecological constraint. One of the problems in examining thermoregulation in primates, however, is the difficulty in quantifying the thermal environment, since shade temperatures, solar radiation, humidity and wind speed all serve to alter an animal's 'perceived' temperature. Since animals respond to their perceived temperature, we need methods to account for each of these factors, both individually and collectively, if we are to understand the integrated impact of the thermal environment on primates. Here, we present a review of some thermal indices currently available. Black bulb temperatures can account for the effect of solar radiation, with wind chill equivalent temperatures and the heat index providing quantifiable estimates of the relative impact of wind speed and humidity, respectively. We present three potential indices of the 'perceived environmental temperature' (PET) that account for the combined impact of solar radiation, humidity and wind speed on temperature, and perform a preliminary test of all of the climatic indices against behavioural data from a field study of chacma baboons (*Papio cynocephalus ursinus*) at De Hoop Nature Reserve, South Africa. One measure of the perceived environmental temperature, PET2, is an effective thermal index, since it enters the models for feeding and resting behaviour, and also accounts for levels of allogrooming. Solar radiation intensity is an important factor underlying these relationships, although the wind chill equivalent temperature and humidity enter the models for other behaviours. Future studies should thus be mindful of the impact of each of these elements of the thermal environment. A detailed understanding of primate thermoregulation will only come with the development of biophysical models of the thermal characteristics of the species and its environment. Until such developments, however, the indices presented here should permit a more detailed examination of the thermal environment, allowing thermoregulation to be given greater precedence in future studies of primate behaviour.

Keywords Baboon · Behaviour · Humidity · Solar radiation · Thermoregulation

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Introduction

The importance of temperature and thermoregulation in primate behavioural ecology has received relatively little attention in comparison to other ecological factors (Stelzner, 1988). Nevertheless, a number of studies have reported that primates alter their activity levels in response to thermoregulatory needs (ruffed lemurs *Vericia variegata variegata,* Morland 1993; redfronted lemurs *Eulemur fulvus rufus*, Ostner 2002; black-and-gold howler monkey *Alouatta caraya,* Bicca-Marques and Calegaro-Marques 1998; western black-and-white colobus *Colobus polykomos*, Dasilva 1993; pigtail macaques *Macaca nemestrina*, Bernstein 1972; sooty mangabeys *Cercocebus atys*, Bernstein 1976; gelada *Theropithecus gelada*, Iwamoto and Dunbar 1983). This suggests that the constraints of thermoregulation may represent an important ecological force. In many cases, though, these studies have invoked post-hoc thermoregulatory interpretations rather than specifically addressing the importance of temperature on primate behavioural ecology.

Some of the most detailed studies of thermoregulation in wild primates have been conducted on baboons (*Papio* spp., Stelzner and Hausfater 1986; Stelzner 1988; Brain and Mitchell 1999; Pochron 2000; Hill 1999, 2003). Stelzner (1988) found that the baboons at Amboseli National Park, Kenya, responded to high heat stresses at midday by resting in shade whenever they encountered it. The baboons in this population did not actively seek shade, but rather exploited it opportunistically, such that thermal constraints on habitat choice were only apparent at the microhabitat level. Similar behavioural patterns were observed at De Hoop Nature Reserve, South Africa (Hill 1999), where levels of both resting and grooming in shade increased in response to thermal stress, and thermoregulatory effects on ranging patterns were evident at the habitat level. Pochron (2000) found evidence of sun avoidance by the baboons of Ruaha National Park, Tanzania. However, contrary to predictions based on thermoregulatory constraints, baboons avoided the sun during all activities in the cool, lush season, but only avoided the sun while resting in the hot, dry season. Pochron (2000) attributed this apparent anomaly to the fact that the baboons could not avoid the sun and meet their nutritional requirements in the hot, dry season.

Shade temperatures alone cannot fully account for the above observations. Solar radiation is clearly important in the thermoregulatory behaviour of baboons, since the animals seek shade in response to thermoregulatory stress (Stelzner 1988; Hill 1999, 2003). Pochron (2002) found humidity to be responsible for the patterns of sun avoidance during the lush season at Ruaha, although temperature was most important during the dry season. However, wind speed is also important in certain contexts. Stelzner and Hausfater (1986) found wind speed, along with air temperature and solar radiation, to be the key determinants of body posture while baboons were attempting to conserve heat and raise body temperature in the early morning. Thus, it appears that temperature, solar radiation, humidity and wind speed are all important elements of the thermal environment experienced by baboons. Since primates will respond to their 'perceived' temperature, as opposed to the 'actual' air temperature, it is important to account for each of these factors, both individually and collectively, if we are to fully understand the importance of temperature in primate behavioural ecology.

No accurate indices of perceived environmental temperatures specific to non-human primates exist, since understandably the majority of research has focussed on assessing the impact of the various components of the thermal environment in relation to man (Yaglou 1927; Gagge 1940; Siple and Passel 1945; Steadman 1971; Mount 1979) or upon livestock (Joyce et al. 1966; Webster 1971; Mount 1979). Although some studies have utilised direct body telemetry to examine body temperature fluctuations in baboons (Brain and Mitchell 1999), none have extended this to construct precise biophysical models of the thermal characteristics of baboons and their environment (Stelzner 1988). Therefore, until such developments occur, basic composite measures of the thermal environment are needed to quantify the combined impact of each of the factors influencing perceived temperatures. Here, we present a discussion of the temperature indices currently available, before generating basic composite indices that aim to account for the combined effects of solar radiation, wind speed and humidity on the perceived air temperature. We perform a preliminary test of these indices using behavioural data from two troops of chacma baboons (*Papio cynocephalus ursinus*) at De Hoop Nature Reserve, South Africa, in order to identify the most useful indices of environmental temperatures for future research.

Methods

Study site

De Hoop Nature Reserve (20°24′E, 34°27′S) is a coastal reserve in Western Cape Province, South Africa. De Hoop has a mean annual rainfall of 428 mm and mean annual temperatures of 17.0°C. Due to its southerly latitude, the reserve experiences considerable seasonal variation in both rainfall and temperature, as well as extensive day length variation (range 9.8–14.2 h). A more detailed description of the ecology of the reserve and the data collection methods is given in Hill (1999).

Behavioural data

The data presented here were collected over a 10-month period (March to December 1997) from two troops of chacma baboons : VT, which ranged in size from 40 to 44 individuals over the course of the study, and ST, which numbered 17 to 21 animals over the same period. Data were collected by means of instantaneous scan samples (Altmann 1974) at 30-min intervals for a minimum of five full days each month, with information recorded on the identity and activity state (feeding, moving, allogrooming, resting or autogrooming) of all visible individuals.

Climatic data

The climatic data were primarily recorded at De Hoop Nature Reserve using a Davis Weather Monitor II weather station. This weather station measured the shade temperature, black bulb temperatures and relative humidity. Black bulb temperatures were recorded by a probe placed in a black copper ball (see also Stelzner 1988) that was exposed to direct sunlight throughout the day. All measurements were automatically logged at half hourly intervals, and downloaded to computer every 20–30 days. This information was supplemented with data on wind speed and direction from a weather station at Waenhuiskrans, approximately 25 km from De Hoop, where the weather parameters were recorded on an hourly basis. These data were taken to be a reliable estimate of the wind conditions at De Hoop, and this is supported by the strong relationship between the shade temperatures recorded by the two weather stations during the study period ($r^2 = 0.620$, $F_{1,11,786} = 19{,}226.0$, $P < 0.0001$).

Data analysis

Logistic regression analysis was used to determine the factors that best account for whether an animal is engaged in a specific activity. Although previous studies have shown more sedentary activities to be the primary response to thermal stress (Stelzner and Hausfater 1986; Stelzner 1988; Pochron 2000; Hill 1999), we analyse the thermal environment with respect to feeding, moving, allogrooming, resting and autogrooming, since our primary interest here is in assessing the relative merits of the various climatic indices. It is important to note though, that we would not necessarily expect the thermal environment to be a significant determinant of all of these activities.

A number of variables are incorporated into the models in addition to the temperature and climatic indices. Variation in the timing of behavioural activities throughout the day is a typical feature of primates (Clutton-Brock and Harvey 1977), with a peak in feeding at the beginning of the day, a rise in resting and possibly grooming over the midday period, and a smaller peak in feeding in the afternoon the characteristic pattern (baboons, Altmann and Altmann 1970; rhesus macaques *Macaca mulatta*, Southwick et al. 1965; spider monkeys *Ateles geoffroyi*, Chapman and Chapman 1991). These diurnal effects need to be controlled for, since they may be independent of variation in temperature. Similarly, monthly variation in activities at De Hoop has been shown to correlate with day length (Hill et al. 2003), and these seasonal effects need to be partialled out. Demographic factors are also likely to be important, and differences in activity levels between troops and sexes have been reported at De Hoop (Hill 1999) and at other sites (Gaynor 1994; Bronikowski and Altmann 1996). As a consequence, the effects of sex and troop identity also need to be accounted for in the models. However, individual differences are not accounted for in the analyses since individual identity is not statistically independent of troop identity and sex. Nevertheless, if the analyses are rerun with individual identity as an independent variable, as opposed to troop and sex, the results remain almost identical.

Forward stepwise likelihood-ratio (LR) regression is used to determine the predictor variables to be incorporated into the model, since this method provides the best criterion for determining which variables should be added and removed. A two-step procedure is used that initially examined the non-climatic variables as a first block of the model, before the temperature indices were considered in a second block, with all significant variables selected on the basis of the forward stepwise LR method. In all cases, the models were run only until no independent thermal indices could be included. In reality this often meant that the model was terminated at the first iteration with inclusion of a single temperature index, since none of the remaining measures were statistically or computationally independent of the included variable. All temperature indices were natural log transformed to ensure normality for parametric analysis.

Temperature indices

Single temperature measures used to describe the thermal environment must not only account for the various mechanisms of heat transfer, but also the animal to which they relate (Mount 1979). Much of the previous research on thermal indices has concentrated on humans (Yaglou 1927; Gagge 1940; Siple and Passel 1945; Steadman 1971; Mount 1979). Due to their well-developed layer of fur, most primates are more highly insulated than humans, and as a consequence their convective heat exchange will be less affected by variations in air temperature and wind speed (see also Walsberg and Wolf 1995), and their conductive losses to the ground may also be less marked (Stelzner 1988). The indices currently available are thus not directly applicable to non-human primates. However, while they may not precisely reflect a primate's thermal environment, they may provide a useful assessment of the relative thermal impact for a given set of climatic conditions. Thus, although the indices generate specific temperatures, the values essentially reflect relative measures of thermal loading for given combinations of temperature, solar radiation, wind speed and humidity.

It is possible to measure directly the total downwelling solar radiation. However, its impact on environmental temperatures is most easily assessed through black bulb temperatures (Chappell and Bartholomew 1981; Stelzner 1988), where the temperature recorded by a probe placed in a 'black bulb' exposed to direct sunlight throughout the day serves to measure the influence of direct sunlight. The accuracy of this method can be assessed by comparing data on black bulb temperatures to shade temperatures at De Hoop Nature Reserve for four general categorisations of sunlight conditions: clear sky (sun), clear sky with intermittent cloud (sun/cloud), cloudy with intermittent direct sunlight (cloud/sun) and overcast with no direct sunlight (cloud). Fig. 1 displays the mean difference between black bulb and shade temperatures across these four categories, with temperatures during rainfall included as a baseline measure. The differences between the four sunshine categories are significant (ANOVA: $F_{3,1,275} = 94.50$, $P < 0.0001$), with only the sun versus sun/cloud categories not differing significantly from one another. Black bulb temperatures thus represent an accurate assessment of the influence of solar radiation on perceived temperatures.

To account for the importance of wind speed and humidity, more complex conversions are required. The simplest method to control for the combined influence of air temperature and wind speed is through calculation of the wind chill index (Mount 1979). Initially developed by Siple and Passel (1945) to describe the cooling power of the atmosphere on exposed human flesh, this formula has subsequently been developed to account for the fact that the majority of the skin's surface is adequately clothed (Steadman 1971). Furthermore, rather than determining wind chill in terms of energy loss per unit area for a particular set of atmospheric conditions, the wind chill equivalent temperature is now usually determined instead. The wind chill equivalent temperature is the temperature under standardised conditions that is equal in cooling power to a given combination of actual temperature and wind speed (Mather 1974). Recent modifications to the index have incorporated factors such modern heat transfer theory and reduced the height at which wind speed is calculated, such that wind chill equivalent temperatures are now calculated using the formula:

$$\mathrm{T(wc)} = 13.12 + 0.6215(\mathrm{T}) - 11.37(\mathrm{V}^{0.16}) + 0.3965(\mathrm{T}) \cdot (\mathrm{V}^{0.16})$$

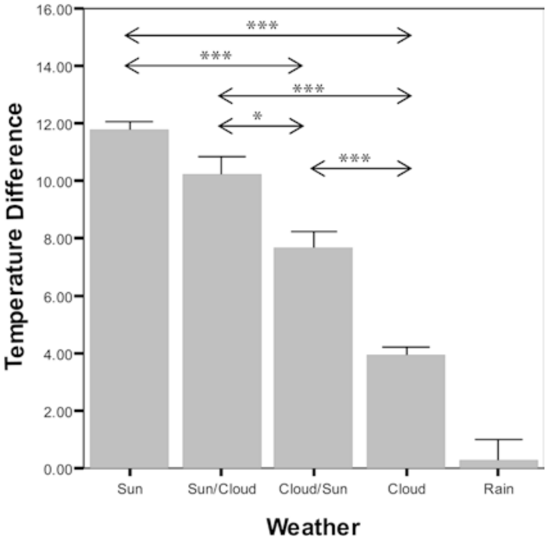

Fig. 1 Mean difference in °C between black bulb temperatures and shade temperatures across general categorisations of weather conditions. *Horizontal lines* indicate significant post hoc differences (Schéffé, * $P < 0.025$, *** $P < 0.001$)

where T(*wc*) is the wind chill equivalent temperature in °C, V is the wind speed in km/h and T is the temperature in °C. Since the wind chill index is only valid for wind speeds of a least 4.83 km/h, wind chill equivalent temperatures should be recorded as the shade temperature at wind speeds below this value.

The temperature-humidity index or heat index was developed as a method for describing the degree of heat stress at various combinations of temperature and humidity (Mather 1974). The heat index generates a predicted temperature under standard conditions equal to that for a given combination of temperature and humidity, and is calculated from the following formula:

$$\begin{aligned}\mathrm{T}(hi) = {} & -8.784694756 + 1.61139411(\mathrm{T}) + 2.338548839(\mathrm{RH}) \\ & - 0.14611605(\mathrm{T}).(\mathrm{RH}) - 0.012308093(\mathrm{T})^2 \\ & -0.016424827(\mathrm{RH})^2 + 0.002211731667(\mathrm{T})^2.(\mathrm{RH}) \\ & + 0.00072546(\mathrm{T}).(\mathrm{RH})^2 - 0.000003582(\mathrm{T})^2.(\mathrm{RH})^2\end{aligned}$$

where T(*hi*) is the heat index in °C and RH is the relative humidity expressed as a percentage. The heat index is particularly designed to assess the impact of humidity on temperature when air temperatures are already high, and the validity of the formula breaks down at temperatures below about 23.89°C (75 F). As a consequence, the heat index should only be computed for temperatures above 24°C, with values for temperatures below this point recorded as the original shade temperature.

Finally, we require a method to account for the combined effects of radiation, wind speed and humidity on the perceived air temperature. Previous attempts to calculate 'perceived' temperatures are not applicable to most primates since they relate specifically to precise biophysical models of humans or livestock (Joyce et al. 1966; Webster 1971; Mount 1979), they fail to account for all of the climatic effects (Yaglou 1927), or they require specific detailed data for computation (Gagge 1940). In the absence of detailed information on scaling these formulae to account for a given primate's anatomy and physiology, it is unlikely that any would produce reliable measures of perceived temperature. However, the primary function of these indices is to produce estimates of thermal load, rather than absolute perceived temperatures. As an alternative, therefore, basic composite measures of the above indices should produce workable estimates of the perceived thermoregulatory loads experienced by animals in natural habitats.

We propose three methods to estimate the 'perceived environmental temperature' (PET). Initially, we compute the indices discussed above sequentially, based on the following formula:

$$\mathrm{PET1} = \mathrm{HI}(\mathrm{WC}(sr))$$

where WC(*sr*) is the wind chill equivalent temperature based upon the black bulb solar radiation temperature in °C, and HI is the heat index based upon the WC(*sr*) value. The initial air temperature is the black bulb temperature, thus accounting for solar radiation, with the wind chill equivalent temperatures then computed on the basis of this value to account for wind speed, before the effect of relative humidity is determined through inputting the computed value into the heat index formula. However, it may not be legitimate to perform such a cumulative sequence of calculations, since there is no way of assessing which factor should be computed first. For example, if the heat index is calculated after the wind chill equivalent temperature then humidity may no longer exert an influence if the calculated temperature is below 24°C. Thus, a more conservative estimate, which separates the 'heating' and 'cooling' elements of the thermal environment, may be calculated based upon the following formula:

$$\mathrm{PET2} = \frac{\mathrm{HI}(sr) + \mathrm{T}(wc)}{2}$$

where HI(*sr*) is the heat index based upon the black bulb solar radiation temperature in °C. While this formula does not completely circumvent the problems with sequential calculations, it should serve to minimise any potential errors. As a third measure, sequential procedures were entirely removed from the calculation, with PET3 computed based on the following formula:

$$\mathrm{PET3} = \frac{\mathrm{T}(sr) + \mathrm{T}(wc) + \mathrm{T}(hi)}{3}$$

where T(*sr*) is the black bulb solar radiation temperature in °C. While this formula alleviates any potential confounds due to sequential calculation, it does not account for any interactions between the variables resulting in cumulative thermal effects. It may thus underestimate the actual 'perceived' temperature. Nevertheless, all three indices are likely to represent an improvement over simple shade temperatures in quantifying the thermal environment, and the relative value of each index can only be established through empirical testing with field data. The remainder of this paper presents a preliminary assessment of the suitability of these indices for future detailed studies of primate thermoregulation through an analysis of activity levels in baboons.

Results

Table 1 displays the final logistic regression models determining the best predictor variables for whether an animal is engaged in feeding, moving, allogrooming, resting or autogrooming behaviour. Time of day forms a significant component of the models for all five activities, suggesting that much of the typical variation observed in the timing of behavioural activities throughout the day is independent of the thermal environment. Seasonal effects are also an important component of all of the models except that for moving activity, confirming that monthly variation in day length results in seasonal variation in activity levels (Hill et al. 2003). Troop effects are evident for feeding and moving behaviour, a result that would be expected given the different foraging patterns of the two troops (Hill 1999). Finally, sex differences are apparent for both resting and allogrooming behaviour, reflecting the higher levels of social grooming by females and the concomitant higher levels of resting in males (Hill 1999).

In terms of climatic variables, only moving time shows no relationships with the temperature indices. Feeding time is a negative coefficient of one of the measures of perceived environmental temperature (PET2), with the probability of feeding declining as perceived temperatures increase. Conversely, resting time is a positive function of PET2, supporting the findings of previous studies where high environmental temperatures force baboons into more sedentary activities, such that feeding levels decline over the midday period.

Autogrooming is a negative function of the wind chill equivalent temperature, indicating that all elements of the thermal environment are not important in the scheduling of certain activities. This is confirmed by the fact that allogrooming is not a function of any of the combined thermal indices, but instead is a negative function of humidity and shade temperatures. Autogrooming increases as wind chill temperatures decline, with the frequency of allogrooming increasing as shade temperatures and humidity decrease. Interestingly, if the

Table 1 Logistic regression analysis to determine the best set of predictor variables for feeding, moving, allogrooming, resting and autogrooming, where PET is the perceived environmental temperature, RH is the relative humidity and T(wc) is the wind chill equivalent temperature

Behaviour	Model and variables	r^2	–2 Log L	χ^2	*df*	Significance	B	Wald	df	Significance
Feed	Model	0.141	16,430.98	1,446.86	24	< 0.0001				
	Hour						–	468.97	14	< 0.0001
	Troop						–0.809	388.28	1	< 0.0001
	Month						–	27.03	1	0.001
	lnPET2						–0.220	14.94	1	< 0.0001
	Constant						0.635	2.97	1	< 0.10
Move	Model	0.064	14,938.05	597.69	15	< 0.0001				
	Troop						1.056	465.07	1	< 0.0001
	Hour						–	75.03	14	< 0.0001
	Constant						–2.491	39.736	1	< 0.0001
Allogroom	Model	0.087	9,642.30	630.65	25	< 0.0001				
	Hour						–	357.87	14	< 0.0001
	Sex						–0.726	94.79	1	< 0.0001
	LnRH						–0.618	16.95	1	< 0.0001
	Month						–	16.67	8	< 0.05
	LnT						–0.497	6.78	1	< 0.01
	Constant						2.968	7.12	1	< 0.01
Rest	Model	0.103	9,862.62	770.63	24	< 0.0001				
	Hour						–	296.75	14	< 0.0001
	Sex						0.547	90.95	1	< 0.0001
	Month						–	62.33	8	< 0.0001
	LnPET2						0.383	22.91	1	< 0.0001
	Constant						2.185	28.02	1	< 0.0001
Autogroom	Model	0.063	1,892.29	117.96	23	< 0.0001				
	Hour						–	39.18	14	< 0.0001
	Month						–	29.97	8	< 0.0001
	LnT(*wc*)						–0.902	6.23	1	< 0.001
	Constant						–5.419	0.35	1	> 0.50

analysis is rerun to include only the heat index, it does not form a significant component of the model, although a significant model is produced with PET2 ($r^2 = 0.085$, $-2LL = 9652.85$, $\chi^2 = 620.11$, $df = 24$, $P < 0.0001$). Interestingly, the relationship with PET2 is positive (PET2 term: B = -0.225, Wald = 7.12, df = 1, p = 0.008) suggesting that overall the relationship between temperature and allogrooming is not linear. This is confirmed by the fact a quadratic model for PET2 produces the best fit ($r^2 = 0.090$, -2LL = 9619.60, $\chi^2 = 653.20$, $df = 25$, $P < 0.0001$; PET2 term: B = -2.776, Wald = 28.60, df = 1, p < 0.0001; $(PET2)^2$ term: B = 0.459, Wald = 34.585, df = 1, p < 0.0001). Overall, this suggests that the combined thermal indices provide an effective measure of the thermal environment, in relation to allogrooming, although the situation is more complex than for some of the other behaviours.

Discussion

Temperature, solar radiation intensity, humidity and wind speed have all been identified as important factors accounting for thermoregulatory responses in baboons (Stelzner and Hausfater 1986; Stelzner 1988, Brain and Mitchell 1999; Pochron 2000). However, previous studies have tended to focus on each of these factors in isolation, without attempting to examine their combined impact on the thermal environment. The analyses presented here illustrate that simple temperature indices, which have often been developed in relation to human thermal physiology, represent useful proxies of the thermal characteristics of a baboon's 'perceived' environment. As a consequence they represent a useful tool in studies of primate thermal ecology.

Of the three measures of the perceived environmental temperature, PET2, computed as the mean of the heating and cooling thermal elements, is the only one to be incorporated into any of the models with the behavioural variables. This suggests that conservative combined temperature measure, PET3, fails to adequately reflect the interactions between the thermal elements, while the potential errors resulting from the order of the sequential calculations for PET1 undermines its sensitivity in accurately quantifying the thermal environment. However, PET2 provides a biologically relevant thermal index and this is reflected by its incorporation into the models for feeding and resting, with significant relationships also produced for allogrooming. The coefficient for PET2 is negative for feeding, with positive relationships for resting and grooming (in the linear equation), indicating that baboons stop feeding and engage in more sedentary activities as environmental heat loads increase (once diurnal, seasonal and demographic effects have been accounted for). These are exactly the behaviours we would predict to correlate with temperature indices, and the relationships are entirely consistent with thermal constraints accounting for the midday peak in resting observed in many studies (Bernstein 1972, 1976).

Solar radiation intensity appears to be the most important parameter underlying the relationships with

PET2. If the logistic regression analyses are allowed to run for additional iterations, such that more than one temperature index is included, the 'black bulb' solar radiation temperature is the next variable added to the model in every case. However, humidity and wind speed clearly modify the degree to which solar radiation impacts upon the baboons, since it is PET2, as opposed to solar radiation intensity, which is incorporated into the models. Nevertheless, the importance solar radiation underlies the significance of exploiting shade as a means of controlling body temperature (Stelzner 1988; Bicca-Marques and Calegaro-Marques 1998; Hill 1999, 2003; see also Stevenson 1985). Furthermore, it suggests that in the absence of detailed climatic records from a weather station, black bulb temperatures represent an easily recorded proxy of the thermal environment that could be collected in most field situations. Alternatively, simple categorical measures of the degree of solar radiation intensity (e.g. Fig. 1) are likely to represent a worthwhile improvement over analyses based on shade temperatures alone.

The importance of solar radiation intensity to perceived temperatures is likely to be greatest for primates inhabiting open habitats. For arboreal or forest-dwelling species, substantial vegetation cover is likely to reduce the importance of solar radiation, although it has been shown to be important in determining the location of resting places in howler monkeys (Bicca-Marques and Calegaro-Marques 1998). Humidity is likely to be of greater significance to high thermal loads in these environments. Humidity was a significant constraint on allogrooming activity for the De Hoop baboons and was also responsible for patterns of sun avoidance by the baboons in the cool, lush season at Ruaha (Pochron 2000). The fact that humidity and shade temperature, as opposed to the heat index, were incorporated into the model for allogrooming may suggest that it is the interaction between humidity and solar radiation that is the key in open habitats. The significant relationship between allogrooming and PET2 may provide a degree of support for this. However, in forest environments, where solar radiation intensity is reduced, humidity and the heat index are likely to be of greater significance, and future studies need to be mindful of this possibility.

Low temperatures and cold stress are also important in activity scheduling, since the wind chill equivalent temperature is the climatic index incorporated into the model for autogrooming behaviour. This highlights the importance of quantifying all elements of the thermal environment, since heat stress is just one aspect of the climatic factors determining behavioural scheduling in primates. This is further supported by the fact that most previous studies of postural thermoregulation in primates have given greater precedence to the importance of cold morning temperatures (Stelzner and Hausfater 1986; Bicca-Marques and Calegaro-Marques 1998).

A complete understanding of primate thermoregulation will only come with the development of biophysical models of the thermal characteristics of the species in question and their environment (Stelzner 1988). However, such models are unlikely to be practical in all situations. Thus, while it will always be necessary to exercise a degree of caution in the output of the indices presented here, they should nevertheless allow us to approach questions on the constraints imposed by the thermal environment in a far more informed fashion than has been possible to date.

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