

Thermal Constraints on Activity Scheduling and Habitat Choice in Baboons

Russell A. Hill*

Evolutionary Anthropology Research Group, Department of Anthropology, University of Durham, Durham DH1 3HN, UK

KEY WORDS De Hoop; primates; shade; temperature; thermoregulation; feeding; grooming; resting

ABSTRACT The importance of thermoregulation as a constraint on behavior has received comparatively little attention in relation to other ecological factors. Despite this, a number of studies suggested that high temperature may represent an important ecological constraint. This paper examines the impact of temperature on activity scheduling in a troop of chacma baboons (*Papio hamadryas ursinus*) at De Hoop Nature Reserve, South Africa. Once the daily, seasonal, and individual effects were controlled for, the “perceived environmental temperature” (PET), which accounts for the relative contributions of solar radiation, wind speed, and humidity on shade temperature, was a significant constraint on behavior. With high PET, feeding declines, and there is an increase in grooming and particularly resting behavior. Baboons thus engage in more sedentary behaviors as temperature

increases, with significantly higher levels of resting and grooming when temperature exceeds the approximate thermal neutral zone for baboons. Seeking shade is an important behavioral response to thermal stress, and PET was a significant determinant of whether an animal was in shade while engaged in either resting or grooming behavior. Furthermore, the proportion of time spent in shade increased across air temperatures that were below, within, and above the thermal neutral zone for baboons. Finally, since resting and grooming are conducted preferentially in certain habitat types, thermoregulatory considerations also impact on patterns of habitat choice and day-journey routes. This suggests that the thermal environment is an ecological variable that should be given greater consideration in future studies of primate behavior. *Am J Phys Anthropol* 129:242–249, 2006. © 2005 Wiley-Liss, Inc.

The theoretical significance of high environmental temperature and thermoregulation has been long debated in studies of human evolution (Wheeler, 1991, 1992a,b, 1993, 1994; Porter, 1993; Chaplin et al., 1994; do Amaral, 1996). The high temperatures and intense solar radiation, associated open savannah environments were implicated as important selective forces in the evolution of hominin bipedalism (Wheeler, 1991), loss of functional body hair (Wheeler, 1992a), body size (Wheeler, 1992b), physique (Wheeler, 1993), and shade-seeking behavior (Wheeler, 1994). It is surprising, therefore, that the thermal environment has received relatively little attention in primate behavioral ecology (Stelzner, 1988). Nevertheless, several lines of evidence suggest that the constraints of thermoregulation represent an important ecological force. A number of studies found primates to alter their activity in response to thermoregulatory needs, with a midday peak in resting thought to be a response to high ambient temperature (Stoltz and Saaymann, 1970; Bernstein, 1972, 1975, 1976). Conversely, other studies found low temperature to be associated with increased feeding activity (Iwamoto and Dunbar, 1983), huddling (Ostner, 2002), postural changes (Stelzner and Hausfater, 1986; Dasilva, 1993), and mother-infant contact (Brent et al., 2003). Recent studies also suggested that temperature plays a role in the terrestrial behavior of chimpanzees (Takemoto, 2004) and habitual cave use by chacma baboons (Barrett et al., 2003). Furthermore, temperature was shown to be a significant factor accounting for population differences in baboon behavioral ecology (Dunbar, 1992; Hill et al., 2000; Hill and Dunbar, 2002), and temperature seasonality is important in explaining patterns of mammal species rich-

ness in sub-Saharan Africa (Andrews and O'Brien, 2000). The thermal environment is thus likely to be a significant ecological constraint on primate behavior.

Baboons are an ideal species for examining the importance of high temperatures on activity patterns (Hill, in press), and were the focus of a number of studies of behavioral thermoregulation in wild primates (Stelzner, 1988; Brain and Mitchell, 1999; Pochron, 2000; Hill, in press). Unlike most mammals of similar body mass and activity patterns inhabiting arid environments, baboons lack known mechanisms for effective brain cooling (Mitchell et al., 1987; Brain and Mitchell, 1999). As a consequence, they require ready access to water for evaporative cooling (Mitchell and Laburn, 1985), and are thus highly susceptible to the costs of thermoregulation at high temperature.

Stelzner (1988) found that at Amboseli National Park, Kenya, baboons responded to high temperatures at midday by resting in shade whenever they encountered it. This suggests that as heat stress increases, animals are forced into more sedentary (and thus less energetic) activ-

*Correspondence to: Dr. R.A. Hill, Evolutionary Anthropology Research Group, Department of Anthropology, University of Durham, 43 Old Elvet, Durham DH1 3HN, UK.
E-mail: r.a.hill@durham.ac.uk

Received 23 July 2004; accepted 5 January 2005.

DOI 10.1002/ajpa.20264
Published online 1 December 2005 in Wiley InterScience (www.interscience.wiley.com).

TABLE 1. Home range composition, vegetation food availability, shade availability, and predation risk of major habitat types at De Hoop

Habitat type	Proportion of range (%)	Bush cover (%)	Tree cover (%)	Food availability	Shade availability	Predation risk
Acacia woodland	15.8	55.8	34.4	High	Very high	High
Burnt acacia woodland	1.2	3.2	0.4	Low	Low	Intermediate
Burnt fynbos	27.6	3.6	0.0	Low	Low	Intermediate
Climax fynbos	25.7	54.0	3.4	Low	High	High
Grassland	11.0	1.6	1.2	Intermediate	Low	Low
Vlei	18.7	0.0	0.0	High	Very low	Low
Cliffs	0.0	—	—	Very low	Low	Very low

ities. Furthermore, since the baboons exploited shade opportunistically as they encountered it, thermal constraints on habitat choice were apparent at the microhabitat level (Stelzner, 1988). Pochron (2000) reported evidence of sun avoidance by baboons at Ruaha National Park, Tanzania. Interestingly, however, the thermoregulatory response was less marked when the heat was most intense; baboons avoided the sun during the lush season, while sun avoidance only occurred while resting in the hot, dry season. While temperature appeared to be driving sun avoidance in the dry season, with humidity responsible in the lush season, it seems that the foraging constraints arising from seasonally restricted food availability during the dry season prevent such a strong thermoregulatory response. Nevertheless, these findings confirm that it is important to account for different elements of the thermal environment (including solar radiation and humidity) if we are fully to understand the integrated impact of the thermal environment on behavior (Hill et al., 2004a).

This paper examines whether the thermal environment operates as a constraint upon baboon activity-scheduling decisions for a population inhabiting a temperate environment. Since resting and grooming increase under higher environmental temperatures, the use of shade as a means of thermoregulation while conducting these activities is assessed. Finally, Cowlshaw (1997) reported baboons to preferentially use certain habitats for different activities; resting and grooming were primarily conducted in low predation risk habitats. Because shade is unlikely to be distributed equally between habitat types, the potential for the thermal environment to act as a constraint on patterns of habitat choice is examined.

METHODS

Study site

De Hoop Nature Reserve (20°24' East, 34°27' South) is a coastal reserve within the Overberg region, Western Cape Province, South Africa. The baboons ranged in an area surrounding the De Hoop Vlei, a large landlocked body of brackish water lined by cliffs along its eastern edge and fed by several freshwater springs. Vegetation is dominated by coastal fynbos, a unique and diverse vegetation type comprising Proteaceae, Ericaceae, Restionaceae, and geophyte species. Seven distinct habitat types were classified on the basis of vegetation structure within the home range of the baboons (Table 1; for detailed descriptions and further information on the ecology of the reserve, see Hill, 1999).

De Hoop has a mean annual rainfall of 428 mm, with a mean annual temperature of 17.0°C. Both rainfall and

temperature show considerable seasonal variation, and shade temperature in the summer months regularly exceeds 25°C. Due to its southerly latitude, De Hoop experiences significant day-length variation (range, 9.8–14.2 hr), with important implications for the behavioral ecology of this population (Hill et al., 2003).

Behavioral data

Data were collected over a 10-month period (March–December 1997) from a single troop of chacma baboons (*Papio hamadryas ursinus*) that ranged in size from 40–44 individuals over the course of the study. Data were collected by means of instantaneous scan samples (Altmann, 1974) at 30-min intervals, with 2–4 adult males and 12–13 adult females sampled for a minimum of 5 full days each month. At each sample point, information was recorded on the identity, habitat type, and activity state (feeding, moving, grooming, or resting) of all visible individuals, as well as whether these activities were conducted in the open or in shade (if grooming or resting). Each scan lasted a maximum of 5 min. The data presented here are from 1,535 scans, resulting in 10,269 point samples over the course of the study, with a mean of 427 samples per male (range, 40–988) and 557 samples per female (range, 58–695). There was no bias in data collection toward either sex, with small sample sizes for certain individuals the result of their disappearance during the study (samples sizes for individuals present for the entire study all exceed 400 point samples). A more detailed description of the data collection methods is given in Hill (1999).

Climatic data and temperature indices

Climatic data were primarily recorded at De Hoop Nature Reserve using a Davis Weather Monitor II weather station, which measured the shade temperature, the temperature recorded by a probe placed in a “black bulb” (which was exposed to direct sunlight throughout the day), and the relative humidity. All measurements were automatically logged at half-hourly intervals such that they were directly comparable to the behavioral scan data. This information was supplemented with data on wind speed and direction from a nearby weather station at Waenhuiskrans, where the weather parameters were recorded on an hourly basis. These data were a reliable estimate of climatic conditions at De Hoop (Hill et al., 2004b).

Temperature is not a perfect element for describing the integrated impact of the atmospheric environment upon mammals (Griffiths, 1976), and factors such as solar radiation, humidity, and wind speed all need to be accounted for, since they may alter the “apparent” air temperature

experienced by the animals. Since baboons are likely to respond to their perceived temperature, as opposed to the “actual” air temperature, it is important that each of these factors be accounted for, both individually and collectively (Hill et al., 2004b). No accurate indices of perceived temperature specific to baboons exist, and a detailed understanding of the integrated impact of the thermal environment and baboon thermoregulation will only come with the development of biophysical models of the thermal characteristics of baboons and their environment (Stelzner, 1988). While some studies utilized direct body telemetry to examine body temperature fluctuations in baboons (Brain and Mitchell, 1999), none extended this to produce detailed indices of the baboon’s thermal environment. However, simple temperature indices, many of which were developed specific to human thermal physiology, represent useful proxies of the thermal characteristics of baboons’ “perceived” environment (Hill et al., 2004b). Following Hill et al. (2004b), therefore, the wind chill equivalent temperature, heat index, and perceived environmental temperature (PET) were computed to assess the integrated impact of key elements of the thermal environment. Perceived environmental temperature was calculated on the basis of the following formula:

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

where HI(sr) is the heat index based on the black bulb solar radiation temperature, and T(wc) is the wind chill equivalent temperature, both in degrees centigrade. This temperature index, which separates the “heating” and “cooling” elements of the thermal environment to produce a composite measure of the temperature experienced, was shown to be the most effective thermal index of a range of measures tested (Hill et al., 2004b).

Data analysis

Logistic regression analysis was used to determine the relationships between activity states and the thermal environment. Each activity state was considered in turn, with the dependent variable coded as to whether or not the particular activity was conducted at each sample point (e.g., feeding/not feeding). In analyses of shade use, the data were restricted to either resting or grooming activity, with the dependent variable coded as to whether or not the animal was in shade. Forward stepwise likelihood-ratio (LR) regression was used to determine the predictor variables to be incorporated into the models, since this method provides the best criterion for determining which variables should be added and removed.

A two-stage logistic regression procedure was employed, with variable selection in both cases on the basis of the forward LR method. In the initial stage, variables that could potentially confound the relationships under investigation were included as the first block of independent variables. Previous studies reported that primate activity follows typical daily (Clutton-Brock and Harvey, 1977) and seasonal (Hill et al., 2003, 2004a) patterns, as well as differing between individuals and sexes (Hill, 1999). Since these relationships are independent of the thermal environment, their effects need to be partialled out. Temperature indices were then entered in the second stage of the model, with shade temperature, solar radiation tempera-

ture, humidity, wind speed, wind chill equivalent temperature, heat index, and perceived environmental temperature included as potential independent variables. In all cases, the models were run only until no more independent thermal indices could be included. For example, if the heat index was selected as the first predictor variable in the second stage of the model, then the constituent elements of this thermal index (shade temperature and humidity) were removed from the list of independent variables. In reality, this often meant that the model was terminated with the inclusion of just a single temperature index, since none of the remaining measures were statistically or computationally independent of the included variable.

For subsequent analyses, air temperature, indexed by the perceived environmental temperature, was classified into three categories: below ($T_{PET} < 25^{\circ}\text{C}$), within ($25^{\circ}\text{C} < T_{PET} < 30^{\circ}\text{C}$), and above ($T_{PET} > 30^{\circ}\text{C}$) the approximate thermal neutral zone (TNZ) for baboons (following Elizondo, 1977). The thermal neutral zone is defined as the temperature range where slight changes in ambient temperatures activate few, if any, physiological thermoregulatory effector responses (Elizondo, 1977). Although the range of the thermal neutral zone utilized here derives from experiments on rhesus macaques (*Macaca mulatta*), it is broadly consistent with those for other species (Elizondo, 1977), and Stelzner (1988) successfully applied these classifications in understanding patterns of baboon microhabitat choice and travel rates for the baboons at Amboseli.

In order to maintain adequate sample sizes in all analyses, a criterion was set of a minimum of five instantaneous scans per individual per category (Cowlshaw, 1998; Isbell and Young, 1993; Hill and Cowlshaw, 2002). If an individual was poorly sampled, such that fewer than five instantaneous scans were recorded in each category, these individuals were excluded from that analysis. Although we do not include sex as an independent variable in logistic regression analyses, the results are identical if sex rather than individual is employed as the independent variable. Similarly, although sample sizes are too small to conduct analyses for males alone, it is important to note that the results remain the same if the analyses are restricted to females. Thus while we might anticipate subtle differences in thermoregulatory response between males and females due to differences in body size, these are not a significant confound to the relationships reported here. Since the data are normally distributed, parametric statistics are employed throughout, with $\alpha = 0.05$ in all cases.

RESULTS

Temperature constraints on activity

For each activity state, Table 2 displays the significant relationships between daily, seasonal, demographic, and climatic variables on whether or not an activity is conducted. Time of day, month, and individual identity are significant determinants for all four activities, confirming their potential importance as confounding variables. Once controlled for, however, all activities show significant relationships with climatic parameters. The probability of an individual feeding declines as PET increases, while resting increases with PET. Both moving and grooming decrease with increasing humidity, with animals also less likely to engage in grooming as wind speed increases. Since high humidity and high wind speed increase and reduce perceived temperatures, respectively, this suggests

TABLE 2. Logistic regression analysis to determine set of predictor variables that best account for whether an animal is engaged in either feeding, moving, grooming or resting at any time¹

	r ²	-2 log L	χ ²	df	P
Feeding Model	0.103	10,776.04	682.73	40	<0.0001
		B	Wald	df	P
Variables					
Hour (C)			276.16	14	<0.0001
Month (C)			17.23	8	<0.03
Identity (C)			86.60	17	<0.0001
In (PET)	-0.260		14.50	1	<0.0001
	r ²	-2 log L	χ ²	df	P
Moving Model	0.027	11,026.92	172.19	40	<0.0001
		B	Wald	df	P
Variables					
Hour (C)			43.13	14	<0.0001
Month (C)			15.36	8	0.052
Identity (C)			74.65	17	<0.0001
In (humidity)	-0.315		6.07	1	<0.02
	r ²	-2 log L	χ ²	df	P
Grooming Model	0.104	6,265.74	505.05	41	<0.0001
		B	Wald	df	P
Variables					
Hour (C)			224.06	14	<0.0001
Month (C)			17.70	8	<0.025
Identity (C)			173.53	17	<0.0001
In (humidity)	-0.502		6.63	1	0.01
In (wind speed)	-0.209		6.04	1	<0.02
	r ²	-2 log L	χ ²	df	P
Resting Model	0.143	6,600.97	737.59	40	<0.0001
		B	Wald	df	P
Variables					
Hour (C)			228.41	14	<0.0001
Month (C)			46.60	8	<0.0001
Identity (C)			161.77	17	<0.0001
In (PET)	0.478		24.06	1	<0.0001

¹ PET, perceived environmental temperature; C, categorical variable.

that the relationship between temperature and grooming may not be a linear one, with grooming mainly occurring at high and low temperatures. This is confirmed by the fact that a quadratic model with PET actually forms the best fit for grooming (r² = 0.106, -2LL = 6259.78.60, χ² = 511.01, df = 41, P < 0.0001; PET term: B = -2.21, Wald = 11.41, df = 1, P = 0.001; PET² term: B = 0.459, Wald = 34.585, df = 1, P < 0.0001). Overall, these results suggest that once the daily, seasonal, and demographic effects are accounted for, high temperature generally leads to a decrease in foraging activities (primarily feeding), with a concomitant increase in nonforaging activity (both resting and grooming).

Thermal neutral zone and behavior

Figure 1 shows the proportion of time spent feeding, moving, grooming, and resting for perceived temperatures above, within, and below the TNZ for baboons. In order to control for possible time-of-day effects (since, for example,

high levels of resting and grooming at dawn and dusk can result in an apparent association of these activities with low temperature), the analyses are restricted to the mid-day period (10:30–15:30 hr). There is a trend of increased grooming and in particular resting as temperature increases, with a concomitant decline in feeding and moving, although not all relationships are significant. Significant differences exist between temperature categories for feeding, grooming, and resting (ANOVA: feeding, F_(2,45) = 4.92, P < 0.02; grooming, F_(2,45) = 3.25, P < 0.05; resting, F_(2,45) = 10.56, P < 0.0001). The relationship for moving is not significant (F_(2,45) = 0.57, P > 0.50). Post hoc analysis indicates that for feeding, the “above” category differs significantly from “below,” while for resting, the “above” category differs significantly from both “within” and “below.” For grooming, the difference between the “within” and “below” categories approaches significance. These results provide compelling support for high thermal loads constraining baboon behavioral options, such that the animals cease foraging and engage in more sedentary activities as environmental temperature increases.

Shade as a response to thermal stress

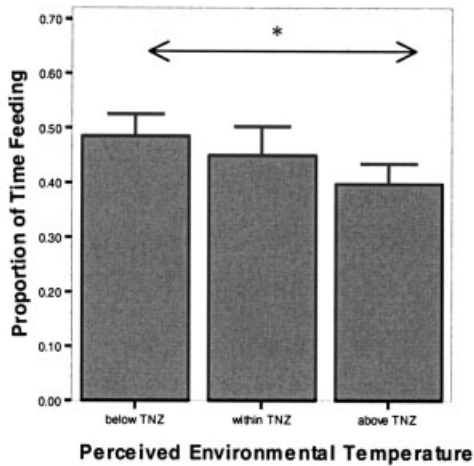
Logistic regression analysis was used to determine the factors that best account for whether an individual conducted an activity in either the open or the shade, given that it was engaged in resting or grooming (behaviors that increase in frequency as temperature increases). The best-fit models are shown in Table 3. For both behaviors, PET is the first climatic measure to be incorporated into the model, and the B value is positive, indicating that the proportion of time spent in the shade increases as environmental temperature increases. Although seasonal and daily effects are incorporated into the final models, there are no significant differences between individuals.

Given that the perceived environmental temperature is a significant determinant of whether a resting or grooming individual is in shade, differences in the proportion of time spent in shade might be anticipated in relation to the thermal neutral zone of baboons. The proportion of time spent in shade increases with temperature for both resting and grooming, and these differences are significant (Fig. 2; ANOVA: resting, F_(2,44) = 28.68, P < 0.0001; grooming, F_(2,41) = 11.23, P < 0.0001). Post hoc comparisons reveal that for resting, the “above” category differs significantly from the other two, while for grooming, it is the “above” and “below” categories that differ significantly. These differences exist even in the absence of controls for potentially confounding time-of-day and seasonal effects. High “perceived environmental temperature” thus places significant thermoregulatory constraints upon baboons that force them to seek shade in order to maintain a thermal balance with their environment.

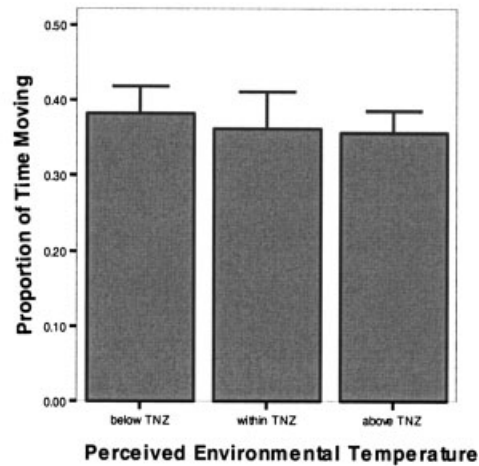
Thermal constraints on habitat choice

If temperature is a constraint on habitat choice, patterns of habitat use while resting or grooming when PET exceeds the thermal neutral zone over the midday period should differ from a baseline of habitat choice for temperatures below and within the TNZ of baboons. It is clear that there is a significant preference for the cliff habitat when temperature exceeds the thermal neutral zone (Fig. 3; one-sample t-test: t = 5.43, df = 11, P < 0.0001), while baboons avoid the acacia woodland (t = -2.47, df = 11,

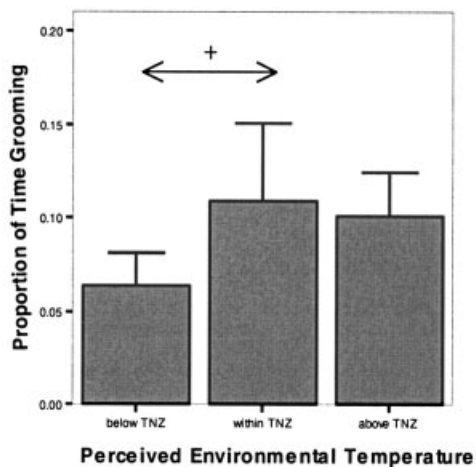
a) Feeding



b) Moving



c) Grooming



d) Resting

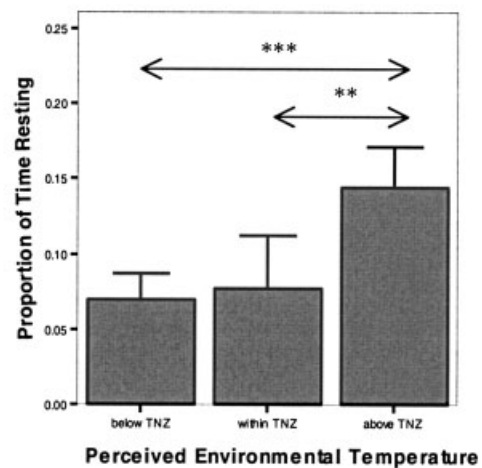


Fig. 1. Mean proportion of time spent in (a) feeding, (b) moving, (c) grooming, and (d) resting activity over midday period (10:30–15:30 hr) for perceived environmental temperatures below, within, and above thermal neutral zone (TNZ) for baboons. Horizontal lines indicate significant post hoc comparisons (Scheffé test, $^+P < 0.075$, $*P < 0.02$, $**P < 0.005$, $***P < 0.001$).

$P < 0.05$). No other habitats differ significantly from baseline value when PET is high ($P > 0.25$ in all cases).

DISCUSSION

The thermal environment acts as a significant constraint on baboon behavioral decision-making processes. As temperature increases, baboons engage in more sedentary activities, and these behaviors are conducted preferentially in shade. Since shade is not equally distributed across the baboon's home range, this impacts on patterns of habitat choice, with the animals spending more time in the cliff habitat and avoiding the acacia woodland when temperatures are high. Environmental temperature is

thus an important ecological constraint on baboon behavior, even for populations inhabiting temperate latitudes.

Both resting and grooming increased in response to high temperature for the baboons at De Hoop. While a number of other studies documented an increase in resting when temperature is high (Stolz and Saayman, 1970; Bernstein, 1972, 1975; Clutton-Brock and Harvey, 1977), records for grooming are few. For example, Stelzner (1988) found no evidence at Amboseli for grooming to increase in response to thermal loads, with inactivity the only behavioral state to correlate with air temperature when the animals were in shade. There are two possible explanations for this.

Firstly, the baboons at Amboseli utilized shade opportunistically as they encountered it, and did not rest for

TABLE 3. Logistic regression analysis to determine best set of predictor variables to explain whether an animal is in shade, given that individual is engaged in resting or grooming activity

	r^2	$-2 \log L$	χ^2	df	P
Grooming is shade					
Model	0.221	913.10	165.69	22	<0.0001
		B	Wald	df	P
Variables	Hour		89.33	14	<0.0001
	Month		41.85	7	<0.0001
	In (PET)	1.862	41.32	1	<0.0001
	r^2	$-2 \log L$	χ^2	df	P
Resting in shade					
Model	0.200	1,113.22	174.90	22	<0.0001
		B	Wald	df	P
Variables	Hour		67.71	14	<0.0001
	Month		25.72	7	0.001
	In (PET)	1.511	20.22	1	<0.0001

long periods (Stelzner, 1988). It seems likely, therefore, that for this population the demands of foraging often outweigh the costs of thermal loading, particularly in such a marginal habitat where time budgets are constrained and where the energetic costs of moving to new habitats may outweigh the thermoregulatory benefits. As a consequence, the likelihood that a baboon will be in a patch of shade with a suitable grooming partner is probably low. At De Hoop, however, long day lengths in the summer months relax the intensity of the foraging constraint over the midday period (Hill et al., 2003). Indeed, variation in day length appears to be the primary factor accounting for differences in thermoregulatory response between baboon populations (Hill, in press). At De Hoop, therefore, baboons are able to take a designated "time-out" in specific habitats in response to high heat loads. Such behavior would result in a much higher proximity of grooming partners, allowing the baboons to manage their social relationships while spending time in shade.

A second and not exclusive explanation may also relate to De Hoop's southerly latitude, since shade temperatures may not be high enough to represent a significant thermal constraint. While the preceding analyses provide support for the importance of thermal constraints when baboons are exposed to direct sunlight, the shade temperature rarely exceeded the thermal neutral zone (Hill, 1999). Mean annual temperature at De Hoop is low relative to other baboon study sites (for comparable data, see Dunbar, 1992), and this situation is thus less likely in more equatorial populations. Shade temperature at Amboseli regularly exceeded 30°C (Stelzner, 1988), and temperatures in excess of 40°C were recorded in the shade at Tsao-bis in Namibia (Cowlshaw, 1993). Thus, once in shade, the baboons at De Hoop may have no further thermal, physiological, or energetic constraints upon activity. Since grooming is potentially an energetic activity (Coelho, 1974), it is unlikely that this activity would be performed where heat loads are high because it would serve to exacerbate the problem. The fact that elevated grooming activities are observed for this population at high temperatures may thus reflect the favorable thermal conditions in shade at this latitude. Nevertheless, the relationships between behavioral states and the thermal environment are generally weaker for grooming than for resting, suggesting the

need for complete inactivity on those occasions where shade temperatures themselves impose significant thermal constraints.

The changes in patterns of habitat choice observed under conditions of thermal stress are also more pronounced for the De Hoop baboons than reported in previous studies. Stelzner (1988) only found evidence for selection at the microhabitat level in the Amboseli population, although the prediction that baboons should have preferred more enclosed habitats in this study may be confounded by predation risk. Nevertheless, temperature constraints on patterns of habitat choice were reported for other mammal species (Piute ground squirrels: Sharpe and Van Horne, 1999). The explanation for population differences in habitat choice is again linked to the increased behavioral flexibility afforded to the De Hoop baboons by longer summer day lengths. The De Hoop baboons are able to select habitat types purely on the basis of thermoregulatory advantages, since sufficient time exists outside of the midday period to satisfy their foraging requirements (Hill, in press).

When temperature exceeded their thermal neutral zone the baboons were more likely to utilize cliffs over the midday period. De Hoop is a relatively treeless environment (a characteristic of fynbos vegetation: Campbell et al., 1979), and even the trees in the acacia woodland are small and shrublike. Cliffs thus represent the only available refuge from predators, and thus the safest habitat for protracted periods of inactivity. The avoided habitat, acacia woodland, is the highest predation risk habitat at De Hoop, although it also offers the greatest levels of food availability and vegetation cover. The fact that acacia woodland offers the greatest access to shade suggests that habitats for grooming and resting under high temperatures are primarily selected in response to predation risk. Thus while seeking shade is the primary motivation for the baboons changing habitats, it is not shade availability but predation risk that determines which habitats are preferred. It is important to remember, though, that cliffs will serve an adequate thermoregulatory function, with overhanging vegetation affording sufficient access to shade and potentially greater access to cooling breezes, since wind speeds are known to increase above ground level (Griffiths, 1976).

The apparent importance of predation risk at De Hoop is an interesting result, since while confirming the general conclusions of Cowlshaw (1997) that resting and grooming are conducted preferentially in low-risk habitats, such marked responses may not be anticipated in a population of relatively low predator density. It is clear, however, that the De Hoop population exhibits a number of behavioral patterns consistent with minimizing predation (Hill, 1999; Hill and Cowlshaw, 2002), indicating that predation risk is not a simple function of the frequency of predator-prey interactions, and that evolved responses may persist in populations following local reduction or extinction of primary predators (Bouskila and Blumstein, 1992).

The preference for cliffs under high temperatures will have significant implications for patterns of habitat choice and ranging pathways, and will also impact diet composition. Cliffs are primarily situated along the De Hoop Vlei in the center of the home range, and provide access to just two of the major habitat types (vlei and climax fynbos: see Hill, 1999). Baboons must respond to temperature cues in the early morning to estimate likely thermoregulatory demands over the midday period, and alter their ranging

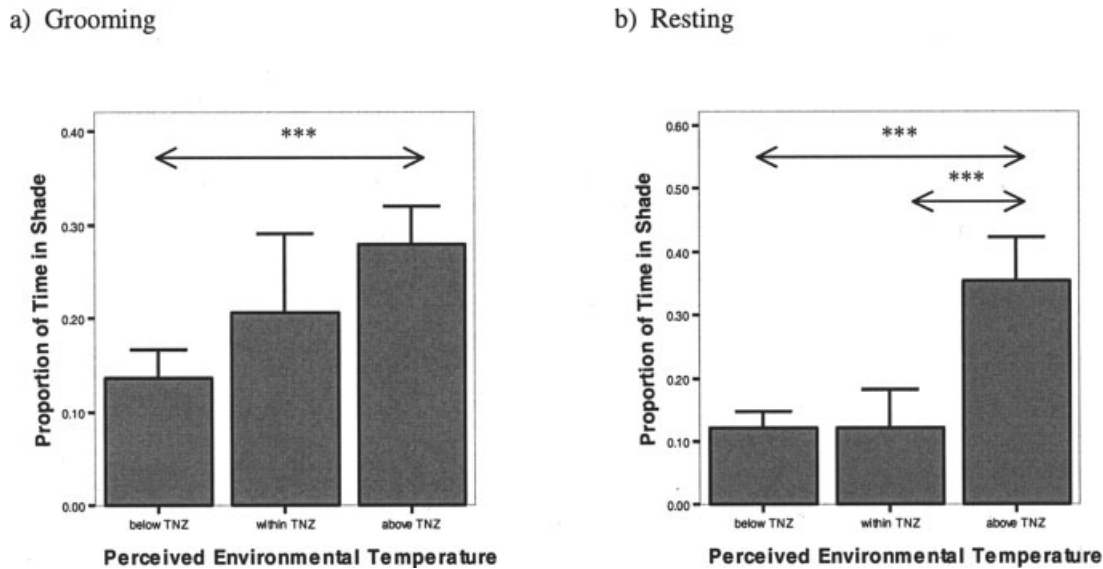


Fig. 2. Proportion of time spent in shade for (a) grooming and (b) resting activity for perceived environmental temperatures below, within, and above thermal neutral zone (TNZ) for baboons. Horizontal lines indicate significant post hoc comparisons (Scheffé test, $***P < 0.0001$).

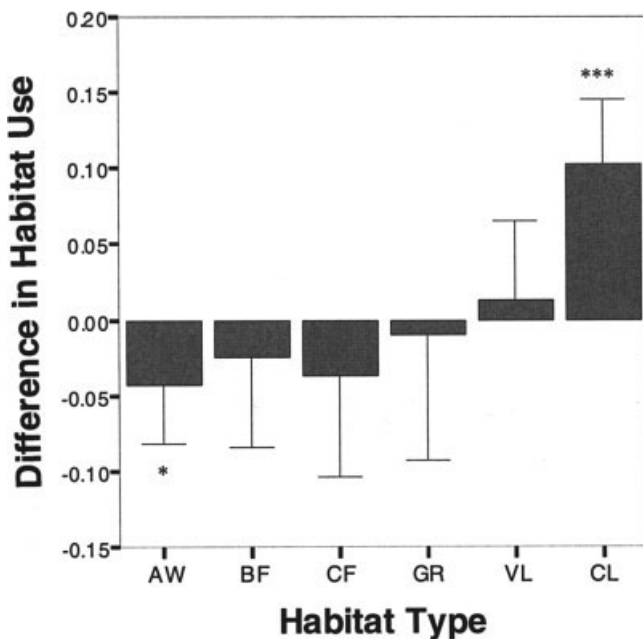


Fig. 3. Mean difference in proportion of time spent in each habitat type while resting or grooming over midday period (10:30–15:30 hr) under conditions of thermal stress ($PET > 30^{\circ}\text{C}$) relative to baseline proportion of time spent in these habitats when temperatures were below or within thermal neutral zone for baboons. AW, acacia woodland; BF, burnt fynbos; CF, climax fynbos; GR, grassland; VL, vlei; CL, cliffs. Asterisks indicate significant deviations from baseline condition (one-sample *t*-test, $*P < 0.05$, $***P < 0.0001$).

patterns to incorporate cliff access when they perceive temperatures are likely to exceed the thermal neutral zone. This clearly has significant implications for analyses of primate foraging strategies, since factors other than food and water availability and predation risk are determining habitat choice and daily ranging patterns.

CONCLUSIONS

The importance of temperature and thermoregulation as a constraint on behavior has received relatively little attention in the primate literature. It is clear, however, that high temperatures and thermal stress are significant constraints on primate activity patterns. The baboons at De Hoop respond to high perceived environmental temperature through engaging in more sedentary behaviors (mostly resting and grooming) and seeking shade in which to perform these activities. Furthermore, since long summer day lengths at De Hoop allow baboons to move to shade for long periods of inactivity when temperatures are high, thermoregulatory constraints also influence patterns of habitat choice in this population. Interestingly, however, thermoregulation alone is insufficient to explain the patterns of habitat choice for these protracted rest periods, since it is predation risk and not shade availability that explains the preference for the cliff habitat. Thus while the thermal environment is an important determinant of the scheduling of resting and grooming activity, as well as a significant constraint on foraging activity through its influence on habitat selection and day-journey routes, other factors undoubtedly remain important. Future studies must thus consider temperature alongside traditional variables such as food availability and predation risk in their analyses of primate behavior.

ACKNOWLEDGMENTS

I am grateful to Louise Barrett, Peter Henzi, and Cape Nature Conservation for logistical support and permission to work at the De Hoop Nature Reserve, and Tony Weingrill for assistance in the field. I thank two anonymous reviewers for their detailed and constructive comments on an earlier version of the manuscript.

LITERATURE CITED

Altmann J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227–267.

- Andrews P, O'Brien EM. 2000. Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *J Zool Lond* 251:205–231.
- Barrett L, Gaynor D, Rendall D, Mitchell D, Henzi SP. 2003. Habitual cave use and thermoregulation in chacma baboons (*Papio hamadryas ursinus*). *J Hum Evol* 46:215–222.
- Bernstein IS. 1972. Daily activity cycles and weather influences on a pigtail monkey group. *Folia Primatol (Basel)* 18:390–415.
- Bernstein IS. 1975. Activity patterns in a gelada monkey group. *Folia Primatol (Basel)* 23:50–71.
- Bernstein IS. 1976. Activity patterns in a sooty mangabey group. *Folia Primatol (Basel)* 26:185–200.
- Bouskila A, Blumstein DT. 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model assessment. *Am Nat* 139:161–176.
- Brain C, Mitchell D. 1999. Body temperature changes in free-ranging baboons (*Papio hamadryas ursinus*) in the Namib Desert, Namibia. *Int J Primatol* 20:585–598.
- Brent L, Koban T, Evans S. 2003. The influence of temperature on the behaviour of captive mother-infant baboons. *Behaviour* 140:209–224.
- Campbell BM, McKenzie B, Moll EJ. 1979. Should there be more tree vegetation in the Mediterranean climate region of South Africa? *J S Afr Bot* 45:453–457.
- Chaplin G, Jablonski NG, Cable NT. 1994. Physiology, thermoregulation and bipedalism. *J Hum Evol* 27:497–510.
- Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organisation. *J Zool Lond* 183:1–39.
- Coelho AM Jr. 1974. Socio-bioenergetics and sexual dimorphism in primates. *Primates* 15:263–269.
- Cowlshaw GC. 1993. Trade-offs between feeding competition and predation risk in baboons. Ph.D. thesis, University College London.
- Cowlshaw GC. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim Behav* 53:667–686.
- Cowlshaw GC. 1998. The role of vigilance in the survival and reproductive strategies of desert baboons. *Behaviour* 135:431–452.
- Dasilva GL. 1993. Postural changes and behavioural thermoregulation in *Colobus polykomos*: the effect of climate and diet. *Afr J Ecol* 31:226–241.
- do Amaral LQ. 1996. Loss of body hair, bipedality and thermoregulation. Comments on recent papers in the *Journal of Human Evolution*. *J Hum Evol* 30:357–366.
- Dunbar RIM. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behav Ecol Sociobiol* 31:35–49.
- Elizondo R. 1977. Temperature regulation in primates. In: Robertshaw D, editor. *International review of physiology: environmental physiology II*, volume 15. Baltimore: University Park Press. p 71–118.
- Griffiths JF. 1976. *Climate and the environment: the atmospheric impact on man*. London: Elek Books Ltd.
- Hill RA. 1999. Ecological and demographic determinants of time budgets in baboons: implications for cross-population models of baboon socioecology. Ph.D. thesis, University of Liverpool.
- Hill RA. In press. Day length seasonality and the thermal environment. In: Brockman DK, van Schaik CP, editors. *Primate seasonality: implications for human evolution*. Cambridge: Cambridge University Press.
- Hill RA, Cowlshaw G. 2002. Foraging female baboons exhibit similar patterns of antipredator vigilance across two populations. In: Miller LE, editor. *Eat or be eaten: predator sensitive foraging among primates*. Cambridge: Cambridge University Press. p 187–204.
- Hill RA, Dunbar RIM. 2002. Climatic determinants of diet and foraging behaviour in baboons. *Evol Ecol* 16:579–593.
- Hill RA, Lycett JE, Dunbar RIM. 2000. Ecological and social determinants of birth intervals in baboons. *Behav Ecol* 11:560–564.
- Hill RA, Barrett L, Gaynor D, Weingrill T, Dixon P, Payne H, Henzi SP. 2003. Day length, latitude and behavioural (in)flexibility in baboons. *Behav Ecol Sociobiol* 53:278–286.
- Hill RA, Barrett L, Gaynor D, Weingrill T, Dixon P, Payne H, Henzi SP. 2004a. Day length variation and seasonal analyses of behaviour. *S Afr J Wildl Res* 34:39–44.
- Hill RA, Weingrill T, Barrett L, Henzi SP. 2004b. Indices of environmental temperatures for primates in open habitats. *Primates* 45:7–13.
- Isbell LA, Young CP. 1993. Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behav Ecol Sociobiol* 32:377–385.
- Iwamoto T, Dunbar RIM. 1983. Thermoregulation, habitat quality and the behavioural ecology in gelada baboons. *J Anim Ecol* 53:357–366.
- Mitchell D, Laburn HP. 1985. The pathophysiology of temperature regulation. *Physiologist* 28:507–517.
- Mitchell D, Laburn HP, Nijland MJM, Zurovsky Y, Mitchell G. 1987. Selective brain cooling and survival. *S Afr J Sci* 83:598–604.
- Ostner J. 2002. Social thermoregulation in redfronted lemurs (*Eulemur fulvus fulvus*). *Folia Primatol (Basel)* 73:175–180.
- Pochron ST. 2000. Sun avoidance in the yellow baboons (*Papio cynocephalus cynocephalus*) of Ruaha National Park, Tanzania. Variations with season, behaviour and weather. *Int J Biometeorol* 44:141–147.
- Porter AMW. 1993. Sweat and thermoregulation in hominids. Comments prompted by the publications of P.E. Wheeler 1984–1993. *J Hum Evol* 25:417–423.
- Sharpe PB, Van Horne B. 1999. Relationships between the thermal environment and activity of Piute ground squirrels (*Spermophilus mollis*). *J Therm Biol* 24:265–278.
- Stelzner JK. 1988. Thermal effects on movement patterns of yellow baboons. *Primates* 29:91–105.
- Stelzner JK, Hausfater G. 1986. Posture, microclimate, and thermoregulation in yellow baboons. *Primates* 27:449–463.
- Stoltz L, Saayman GS. 1970. Ecology and behaviour of baboons in the Transvaal. *Ann Transvaal Mus* 26:99–143.
- Takemoto H. 2004. Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *Am J Phys Anthropol* 124:81–92.
- Wheeler PE. 1991. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling. *J Hum Evol* 21:107–115.
- Wheeler PE. 1992a. The influence of the loss of functional body hair on the energy and water budgets of the early hominids. *J Hum Evol* 23:379–388.
- Wheeler PE. 1992b. The thermoregulatory advantages of large body size for hominids foraging in savannah environments. *J Hum Evol* 23:351–362.
- Wheeler PE. 1993. The influence of stature and body form on hominid energy and water budgets: a comparison of *Australopithecus* and early *Homo* physiques. *J Hum Evol* 24:13–28.
- Wheeler PE. 1994. The thermoregulatory advantages of heat storage and shade-seeking behaviour to hominids foraging in equatorial savannah environments. *J Hum Evol* 26:339–350.