PRIMATES, 27(4): 449–463, October 1986

Posture, Microclimate, and Thermoregulation in Yellow Baboons

JEFFREY K. STELZNER
Cornell University
and GLENN HAUSFATER
University of Missouri

ABSTRACT. This report describes thermoregulatory behavior of free-ranging yellow baboons (*Papio cynocephalus*) in Amboseli, Kenya. While resting in trees during early morning hours, baboons are directly exposed to thermal effects of wind and sun. We hypothesized that these animals would respond to microclimatic changes by altering their posture and body orientation so as to minimize thermal stress. The results of this study indicate that air temperature, solar radiation, and wind velocity interact in their effect on behavior as predicted by this hypothesis. Specifically, the most salient cue for trunk orientation choice is wind direction, while posture is primarily influenced by air temperature. In sum, our results clearly demonstrate that when baboons are unable to minimize thermal stress by selecting a more favorable microenvironment, they do so by altering their posture.

Key Words: Behavior; Thermoregulation; Biometeorology; Microclimate; Baboon; *Papio*; Amboseli National Park.

INTRODUCTION

This report describes behavioral responses of yellow baboons (*Papio cynocephalus*) to changes in their thermal environment. Baboons, like all animals, exchange heat with their environment through radiation, convection, conduction, and evaporation (GATES, 1980). Net rates of heat exchange depend both on thermal characteristics of the environment, such as air temperature, thermal radiation, and wind velocity, and on thermal properties of the animal, such as metabolic heat production, thermal conductance, body mass, and body shape (PORTER & GATES, 1969; PATTERSON, 1986). Given these constraints, animals may choose either to avoid thermally stressful environments or to thermoregulate within them. Avoidance behavior involves modification of activity schedules and selection of microenvironments; thermoregulation involves both physiological and behavioral mechanisms. This study focuses exclusively on the latter phenomenon, thermoregulation—and in particular examines changes in posture and body orientation as means of avoiding thermal stress.

Behavioral thermoregulation has been studied intensively in reptiles, and lizards especially have been shown to exhibit thermally-dependent microenvironmental preferences (WALDSCHMIDT, 1980; HUEY & PIANKA, 1977; PORTER & JAMES, 1979; PORTER & TRACY, 1980; ROUGHGARDEN et al., 1981) and changes in skin color (NORRIS, 1967). In fact, STEVENSON (1985) recently concluded from heat-transfer models that behavioral adjustments by lizards and other ectotherms, particularly in times of activity, were more important than physiological mechanisms in the control of body temperature. In contrast, most theoretical and empirical work on mammalian thermoregulation (SATINOFF, 1978) has concentrated on physiological mechanisms. Nevertheless, several studies have suggested that behavior may be an important component of mammalian thermoregulation. For example, SATINOFF (1978) investigated neural control of thermoregulation in mammals, and concluded that behavioral responses were used to counter small thermal displacements, while physiological responses (e.g., shivering, sweating) were invoked only when behavioral controls were inadequate. Interestingly, while pertinent data on mammalian behavioral thermoregulation has been derived from studies on primates in laboratories or outdoor compounds, very little data is available on primate responses to thermal stress in their natural environment.

In controlled experiments, primates clearly respond to changes in their thermal environment. Specifically, under laboratory conditions, even small changes in ambient temperature and incident radiation lead to concomitant adjustments in posture and activity (ADAIR & STITT, 1971; GALE et al., 1970; ADAIR, 1977). Similarly, primates in outdoor enclosures (DAHL et al., 1982; DAHL & SMITH, 1985) alter the frequency of basking, huddling, and social activities according to weather conditions. But, of course, the range of microhabitats available to monkeys in a pen are rather more restricted than is the case for, say, free-ranging baboons on the East Africa savannah. Thus, in a sense, the climate-behavior relationships reported in laboratory or compound studies constitute hypotheses that remain to be verified for particular primate species in their natural environment.

This study was intended to determine whether baboon postures and behavior would vary in a consistent manner in relation to climatic conditions. More specifically, we asked whether the posture, body orientation, and extent of interindividual contact shown by baboons changed over the morning hours in relation to the changing thermal conditions they experienced in their sleeping trees.

The choice of sleeping trees as the microhabitat of interest may require explanation. Essentially, we hoped to carry out this study in a manner similar to that used in laboratory studies, but with the baboons free to move about in their natural environment, and experiencing ambient climatic conditions. Amboseli baboons in their sleeping trees constitute a naturally-occurring approximation to a controlled laboratory experiment. Basically, during the months of the study (July–August 1978) air temperatures dropped to about 6°C each night, conditions under which baboons would be expected to radiate large amounts of heat to the clear night skies. Thus, at dawn the baboons are surrounded by a uniform and quite cool environment which gradually warms around them as the sun rises. We hypothesized that at this time we should find baboons in specific postures and body orientations that minimized heat loss. Furthermore, we hypothesized that as solar radiation increased throughout the morning, baboons would shift to postures and orientations that increased their interception of the warming rays of the sun thus constituting a form of basking. Again, such basking behavior has been the focus of a large amount of speculation in the literature on primates, but has rarely, if ever, been documented quantitatively.

However, the thermal situation in which baboons find themselves each morning cannot be dealt with simply by changing from huddling to basking as the day progresses. This is so because the winds can be strong during morning hours. Furthermore, there is great day-to-day variability in wind velocity and cloud cover, both climatic elements that substantially affect the baboons ability to warm themselves via basking. Thus we predicted that there would be an interaction between solar radiation and windspeed as these variables jointly affect baboon postures and orientations.

Obviously, one might ask why baboons do not merely come down from the trees and huddle on the ground protected from wind for a few hours after sunrise each morning. However, it is important to remember that baboons retire to sleeping trees each night for good reason: the trees provide protection from nocturnal terrestrial predators, namely lions and leopards in Amboseli. Furthermore, areas beneath the sleeping trees are typically comprised of a dense shrub understory, and thus provide numerous hiding places for predators even after the peak of nocturnal hunting activity has passed. Effectively, then, baboons are confined to their sleeping trees—that is, in unfavorably cool thermal microenvironment—early in the morning. In sum, baboons in their sleeping trees early in the morning can thermoregulate only through postural adjustments and behavior, and not through microenvironment selection.

SUBJECTS AND METHODS

STUDY SITE AND SUBJECTS

The subjects of this study were a single social group ("Hook's Group") of 40 yellow baboons (*Papio cynocephalus*) in the Amboseli National Park of Kenya. Details of the foraging and ranging ecology of the Amboseli population have been described by ALTMANN and ALTMANN (1970) and POST et al. (1980). The study group was not provisioned or manipulated in any way, but as a result of long-term observations, have become habituated to the presence of observers at close range. Data for this report were collected in July–August 1978.

Each night, yellow baboons spend ten or more hours sleeping on the larger branches of mature yellow-barked acacia (*Acacia xanthophloea*) trees (HAUSFATER & MEADE, 1982). Branches of adjacent trees within a grove usually overlap, and baboons can cross from one tree to another without descending to the ground. The sparse Acacia canopy system, however, does not greatly attenuate wind or radiation. As a result, baboons cannot rely on foliage to reduce heat loss; rather the baboons are exposed to the full effects of convective cooling and radiative emission to the cold night sky.

DATA COLLECTION PROCEDURES

Daily sampling began shortly after dawn, and continued until all individuals had descended from the sleeping trees. During this period, we carried out scan samples (ALTMANN, 1974) on all baboons of the study group that remained in trees. Scan samples were taken at 20-min intervals, and an average of 2.4 hrs per day were devoted to sampling. For all individuals we recorded trunk orientation, posture, body contact, and activity, as described below.

TRUNK ORIENTATION

Various investigators (TREAGER, 1965; CENA & CLARK, 1973; ØRITSLAND & RONALD, 1978; WALSBERG et al., 1978) have analyzed the effects of fur properties on rates of heat exchange; longer fur reduces wind penetration and convective heat loss, but also dissipates incoming solar radiation. Baboons, like many mammals, have thicker fur on their dorsum (back and shoulders) than on their ventrum (chest and abdomen). Thus, for baboons sitting in trees, facing into wind caused the thinly-furred ventrum, as well as unfurred hands, feet and muzzle to be directly exposed to wind penetration. Similarly, changes in body orientation relative to solar azimuth altered the effective surface area available for absorption of solar radiation. Thus, trunk orientation relative to the direction of wind and solar radiation was potentially important for several avenues of heat exchange.

Trunk orientation was defined as the bearing, in degrees magnetic, of the sagittal plane, as viewed from the rear (dorsum or posterior) of the subject baboon. Orientation relative to sun or relative to wind was computed as the angular difference between trunk orientation and the direction from which the sun was shining or the wind was blowing, respectively. Orientation to wind and sun as used in this study was therefore identical to the relative azimuth measure used in previous studies of behavioral thermoregulation, for example in lizards (MUTH, 1977; WALDSCHMIDT, 1980).

POSTURE

Changes in posture alter the effective size of an animal's body (GATES, 1980), and can thereby serve to regulate heat exchange. At the same time, animals may position body elements so as to differentially expose body regions whose surface area, insulation and color cause them to act as "heat windows" of special thermoregulatory significance (BAKKEN, 1981). Limbs are particularly important avenues of heat loss (KERSLAKE, 1972), owing to their small diameter and concomitantly high surface-to-volume ratio. For baboons, as noted above, the thinly-furred ventrum may be of similar importance.

We initially described posture by recording the degree to which limbs were adducted and/or the ventrum covered by the limbs. We later found that baboons used a finite set of limb positions, and postures were grouped for analysis into four categories: *hunch* (limbs adducted, spine flexed, chin resting on ventrum); *closed* (limbs adducted, spine and neck not as in hunch); *intermediate*; and *open* (limbs abducted, ventrum exposed). Hunched and closed postures minimized trunk and limb exposure, while open postures maximized exposure.

BODY CONTACT

Inter-individual body contact (i.e., huddling), like posture, affects both effective body size and differential exposure of body parts. Body contact was recorded as *extensive* if the trunk or head of a baboon contacted the trunk, head, upper arm or thigh of another baboon, *minimal* for other forms of contact (e.g., the tails of two individuals touching), or *none*.

ACTIVITY

Activity states for each individual were initially scored as *resting*, *moving*, *feeding*, or

Table 1. Posture categories used in study.

Analysis category	Observation categories	Ventrum exposure	Extremity exposure
Open	Open sit	2	2
Intermediate	Normal sit, side prone, back prone, quadrupedal stand, flexed forelimb stand, bipedal stand	2	1
Closed	Protected sit, closed sit, flexed sit	0	1
Hunch	Hunch	0	0

Observation categories were combined for analysis into categories, rated by degree of exposure to wind and sun as follows: 0 = exposed; 1 = intermediate; 2 = not exposed.

social behavior, following the definitions of SLATKIN and HAUSFATER (1976). However, for the purpose of the present analysis, all records were recoded as either *passive* (resting state) or *active* (all other states).

MICROCLIMATE MEASUREMENT

Energy exchange between animals and terrestrial environments is a function of air temperature, direct shortwave radiation, diffuse shortwave radiation, down- and upwelling longwave radiation, wind velocity, substrate temperature, and water vapor pressure density (PORTER & GATES, 1969). In this study, we measured only those variables likely to be of greatest microclimatic importance for individuals in trees: air temperature, total downwelling solar radiation, and wind velocity. In addition, we recorded wind and sun azimuths.

Microclimate samples were obtained concurrently with samples of behavior, at 20-min intervals. All measurements were taken 30 cm above ground, in an unshaded area free of vegetation and at least 50 m upwind of the sleeping trees. This procedure was designed both to minimize microclimatic variation due to vegetation or terrain, and to avoid undue interference with normal baboon activities. Since baboons within sleeping trees were in a comparatively open microhabitat, albeit much higher above ground level, it seems safe to assume that the measurements of meterological variables used in this study were very strongly correlated with the conditions actually experienced by baboons. Furthermore, changes in meteorological variables measured on the ground were almost certainly related in a direct and biologically meaningful fashion the changes in these variables experienced by baboons in the trees.

Air temperature (T_{air}) was recorded to the nearest 0.2°C with an Omega 2175A digital thermocouple thermometer equipped with a copper-constantan probe. The probe responded rapidly to changes in temperature, and was protected from effects of environmental radiation by an aluminum shield. *Solar radiation* (SR_{tot}) was measured with a LiCor pyranometer equipped with a cosine-corrected silicon radiation sensor. The sensor was attached to a flat board which was placed on the ground and leveled by means of an attached bubble level. Total downwelling solar radiation, the sum of both direct and diffuse components, was recorded, to the nearest $1.0\ W \cdot m^{-2}$. *Wind velocity* (V_{wind}) was measured with a Thermonetics HWA-103 hot-wire anemometer. The instrument was sensitive to low and variable windspeeds common at low elevations; velocities were recorded to the nearest $0.005\ m \cdot sec^{-1}$. Point values of wind velocity were estimated from the mean of six (6) instantaneous readings taken at 3-sec intervals.

Wind azimuth and solar azimuth were estimated to the nearest whole degree magnetic, using a Bunton compass to determine magnetic north. Wind azimuth was scored as indeterminate when winds were either very low in velocity or highly turbulent. Since solar azimuth differed only slightly across all scan samples in the study, the pooled mean value was used for analysis. Similarly, wind azimuth changed only very slowly over the course of any morning, and in fact showed very little variation across the entire study period. As a result, baboon orientations relative to wind were highly correlated with those to sun. To address the effects of this correlation on bivariate analyses, we computed for each scan sample the angular difference between wind and solar azimuth; the absolute value of this difference we termed relative wind-sun azimuth (AZ_{ws}).

We used the AZ_{ws} values in analyses as follows. If orientation to wind was independent of relative wind-sun azimuth, then baboons responded to wind irrespective of sun position, implying that wind was more important than sun in determining orientation. A significant association between orientation to wind and AZ_{WS}, in contrast, signified that sun direction influenced orientation.

ANALYSIS PROCEDURES

While in trees, baboons were subject to heat loss via convection and heat gain via solar radiation. We therefore examined the relationship of behavioral responses to the intensities of wind, sun, and both factors combined (PORTER & JAMES, 1979). For analysis, orientations to wind were grouped into three categories: *towards wind* (orientations within the 90-degree sector centered on wind azimuth); *away from wind* (the opposite 90-degree sector); and *oblique to wind* (the two remaining sectors). Orientations to sun were similarly categorized. For each scan sample, we computed the proportion of individuals in each response category, and analyzed these measures in relation to microclimatic data from the nearest 20-min interval.

Our previous informal field observations of baboons in their sleeping trees strongly suggested that the animals adopted more open postures, and displayed greater activity, as the morning progressed. To quantify this pattern, we first looked for simple bivariate relationships between behavioral responses on one hand, and microclimatic conditions on the other. For this purpose we generated a correlation matrix, using data from all scan samples, for the set of all microclimatic and behavioral variables combined, after transforming behavioral proportion data via the arcsin-square-root method (SNEDECOR & COCHRAN, 1980).

While this technique allowed us to search for broad trends, we also expected that distinct thermoregulatory responses in posture and behavior might occur only under extreme microclimatic conditions. We therefore computed eight additional matrices, each based on samples drawn from either the upper or lower quartile of one of four meteorological variables: air temperature; solar radiation; wind velocity; and unsigned wind-sun azimuth difference. In other words, we asked whether the baboons showed consistent response to, say, air temperature on mornings that were exceptionally warm (i.e., upper T_{air} quartile), or, alternatively, exceptionally cool (i.e., lower T_{air} quartile). In the discussion that follows we consider only those correlation coefficients (r) which exceeded the two-tailed 0.05 significance level (SNEDECOR & COCHRAN, 1980).

RESULTS

OVERALL PATTERNS

Table 2 summarizes significant correlations between microclimate and behavior (trunk orientation, posture, body contact, and activity) for all samples combined. In general, baboons responded to temperature, solar radiation and wind velocity as one might expect were their primary early morning problem that of conserving heat and/or raising body temperature. Specifically, as air temperature and solar radiation increased, or wind velocity declined, baboons moved from hunched postures and/or extensive body contact (negative correlations with T_{air} and SR_{tot}, positive correlation with V_{wind}), to open postures, minimal body contact, and greater activity (positive correlations with T_{air} and SR_{tot}, negative correlation with V_{wind}). Given these broad trends across all samples, we then focused on thermo-

Table 2. Correlation matrix summary, behavior vs microclimate, using data from all scan samples ($N = 138$).

	Meteorological variables				
Behavioral response	T_{air}	SR_{tot}	V_{wind}	AZ_{ws}	Time
Orientation towards wind		−0.211	−0.227		−0.238
Orientation away from wind					
Orientation towards sun				0.447	
Orientation away from sun				−0.306	
Open posture	+0.397	+0.508	+0.309		+0.383
Hunch posture	−0.634	−0.628	−0.263		−0.667
Minimal body contact		+0.220	+0.195	−0.340	+0.326
Extensive body contact		−0.220	−0.195	+0.340	−0.326
Passive activity	−0.438	−0.334			−0.359
Active activity	+0.438	+6.334			+0.359

Correlation coefficients listed only if significant at the $\alpha = 0.05$ level. Abbreviations for microclimate variables as defined in text. Proportion data arcsin square-root-transformed prior to analysis.

regulatory responses under extreme meteorological conditions, using data from the top and bottom quartiles of the microclimate distribution.

TRUNK ORIENTATION TO WIND

Because baboons are more heavily furred on their backs than on their ventrum and extremities, we predicted that animals would face away from cool winds, reducing effective surface area and thus convective heat loss. A preliminary one-way analysis of variance showed that, across all scans, the numbers of animals facing toward, oblique to, and away from wind

Table 3. Correlation matrix summary, orientation to wind in relation to microclimate during cool/windy intervals (upper portion) vs. warm/calm intervals (lower portion).

Microclimate variable	Level	N	Orientation to wind	T_{air}	SR_{tot}	V_{wind}	AZ_{ws}	Time
			COOL/WINDY					
T_{air}	Low	34	Towards		−0.368			−0.370
			Oblique				−0.404	
			Away					
SR_{tot}	Low	34	Towards					
			Oblique					
			Away					
V_{wind}	High	33	Towards					−0.351
			Oblique		+0.375			
			Away					
			WARM/CALM					
T_{air}	High	32	Towards			−0.447		
			Oblique		+0.626	+0.431		
			Away	−0.379	−0.563			
SR_{tot}	High	34	Towards			−0.378		
			Oblique		+0.587			
			Away	−0.360	−0.589			
V_{wind}	Low	37	Towards					
			Oblique					
			Away					

Data partitioned by upper (High) or lower (Low) quartile of corresponding microclimate variable. Correlation coefficients are listed only if significant at the $\alpha = 0.05$ level. Abbreviations for microclimate variables as defined in text. Proportion data were arcsin square-root-transformed prior to analysis.

differed significantly ($p<0.05$, $N = 138$). Specifically, averaged across the entire morning, baboons were more than twice as likely to have their backs to wind (37.9 %) as to face into wind (17.5 %).

This result was consistent with the notion of heat loss avoidance, but convective heat loss is obviously influenced not just by trunk orientation but also by air temperature (T_{air}) and by wind velocity (V_{wind}). To address the conjoint effects of T_{air} and V_{wind} on orientation to wind, we carried out a series of analyses using datasets obtained for mornings that fell in the upper and lower quartile of the distribution of these two meteorological variables.

At high air temperatures, the proportion of animals facing towards wind (Table 3, row 10) was negatively related to wind velocity. In other words, the proportion of individuals facing toward the wind on a warm morning depended primarily on wind velocity; at higher velocities few individuals opted to face into the wind. No such relationship was seen at low air temperatures (Table 3, row 1). In short, baboons rarely faced towards cold winds, and faced towards warm winds only at low velocities. Similarly, high levels of either air temperature or solar radiation exerted strong influence on choice of other orientations to wind. Specifically, when air temperature and solar intensity were high, animals were more likely to face oblique (sideways) to wind (Table 3, rows 11 and 14, positive correlation with SR_{tot}) rather than directly away from wind (Table 3, rows 12 and 15, negative correlations with T_{air} and SR_{tot}).

Viewed in another way, these correlations indicate that baboons avoided cold or high-velocity winds by facing directly away from them, but were less strict in doing so if they experienced warm air or bright sun. Similarly, when air temperatures were low, the proportion of individuals facing wind was negatively correlated with solar radiation (Table 3, row 1), again suggesting the importance of solar warming to baboons in the early morning. This relationship, however, may have been secondary to a simple time-of-day effect, since (1) solar radiation and time-of-day were positively correlated during the morning, and (2) relative sun position did not influence orientation to wind, as would be expected for a direct solar heating effect. Nevertheless, our results clearly indicated that wind was the most salient cue for orientation during the early morning.

TRUNK ORIENTATION TO SUN

Given the effects of air temperature and solar radiation on orientation to wind, we expected that baboons would respond to increasing solar intensity by facing toward the sun and basking. We tested this hypothesis by using the wind-sun azimuth difference measure. As mentioned previously, if orientation to sun changes independently of wind azimuth, then it should not be influenced by wind-sun azimuth. In fact, at low air temperatures the unsigned difference in azimuth of wind vs. sun was significantly associated with the proportion of individuals facing the sun (Table 4, row 1). In other words, on cool mornings the animals were more likely to select a particular body orientation with respect to sun position when they thereby also placed the wind at their backs.

However, as the air gradually warmed about them each morning, baboons were increasingly likely to ignore wind altogether and orient directly towards the sun. Thus, within the upper quartile of air temperatures few baboons faced directly away from sun, and conversely, the proportion facing directly toward sun increased with increasing air temperature (Table 4, rows 10 and 12). Nevertheless, it is important to emphasize that individuals ignored wind and

Table 4. Correlation matrix summary, trunk orientation to sun in relation to microclimate during cool/windy intervals (upper portion) vs. warm/calm intervals (lower portion).

Microclimate variable	Level	*N*	Orientation to sun	T_{air}	SR_{tot}	V_{wind}	AZ_{ws}	Time
			COOL/WINDY					
T_{air}	Low	34	Towards				+0.353	
			Oblique		−0.374			
			Away					
SR_{tot}	Low	34	Towards				+0.398	
			Oblique			−0.424		
			Away				−0.398	
V_{wind}	High	33	Towards				+0.609	
			Oblique					
			Away					
			WARM/CALM					
T_{air}	High	32	Towards	+0.355			+0.508	
			Oblique		+0.454	+0.360		
			Away	−0.458				−0.476
SR_{tot}	High	34	Towards	+0.350			+0.548	
			Oblique					
			Away					
V_{wind}	Low	37	Towards					
			Oblique		−0.499			
			Away					

Data partitioned by upper (High) or lower (Low) quartile of corresponding microclimate variable. Correlation coefficients are listed only if significant at the $\alpha = 0.05$ level. Abbreviations for microclimate variables as defined in text. Proportion data were arcsin square-root-transformed prior to analysis.

faced toward the sun only at the very highest air temperatures they experienced in their sleeping trees. Conversely, at very low air temperatures, baboons essentially responded to wind alone (Table 4, row 1) while ignoring sun position altogether.

In sum, we view baboon trunk orientations as a two-phase response to wind and sun. In the very early morning, when wind is high and solar radiation low, baboons simply face away from wind. Later in the morning, as air temperatures rise, wind exerts less influence on body orientation, and baboons position themselves so as to face towards the increasingly-bright sun. The extent of this reorientation process is dependent both on solar radiation and on wind velocity.

POSTURE

Postural changes affect body surface area, and hence influence both heat loss (e.g., via convection) and heat gain (e.g., via radiation). From our previous analyses, it seemed likely that heat loss was of major concern for baboons, becoming negligible only during warmer intervals, when basking might occur. Thus, we expected that baboons would remain primarily in highly adducted postures, thus complementing heat loss avoidance obtained through trunk orientation.

Indeed, our field observations showed that baboons assumed a typical sequence of postures over time. Early in the morning, nearly all individuals sat in hunched postures, with the spine curved, chin dropped against the ventrum, and all limbs held close to the body. Typically, these animals later raised their heads, straightened their backs, and extended their limbs slightly. Eventually, as social activity increased, animals adopted a wider range of postures,

Table 5. Correlation matrix summary, posture in relation to microclimate during cool/windy intervals (upper portion) vs. warm/calm intervals (lower portion).

Microclimate variable	Level	*N*	Posture	T_{air}	SR_{tot}	V_{wind}	AZ_{ws}	Time
			COOL/WINDY					
T_{air}	Low	34	Open	+0.394				
			Hunch	−0.465				
SR_{tot}	Low	34	Open					
			Hunch					
V_{wind}	High	33	Open	+0.587	+0.684			+0.466
			Hunch	−0.670	−0.704			−0.692
			WARM/CALM					
T_{air}	High	32	Open		+0.385	+0.364		
			Hunch	−0.378	−0.612			
SR_{tot}	High	34	Open			+0.362		
			Hunch	−0.363	−0.511			
V_{wind}	Low	37	Open					
			Hunch	−0.581	−0.533	−0.355		−0.690

Data partitioned by upper (High) or lower (Low) quartile of corresponding microclimate variable. Correlation coefficients are listed only if significant at the $\alpha = 0.05$ level. Abbreviations for microclimate variables as defined in text. Proportion data were arcsin square-root-transformed prior to analysis.

including sitting with limbs extended, lying prone, and standing. This phase was brief on days when the group descended from trees earlier than usual. These subjective impressions were confirmed quantitatively via correlation analysis (Table 5).

On cool mornings (i.e., lower air temperature quartile) baboons remained almost exclusively in hunched (highly adducted) postures, regardless of solar intensity, sun position, and wind velocity (Table 5, row 2). Basically, Table 5 shows that baboons transited from these hunched postures to more open postures (row 1, positive correlation with T_{air}) in response to slight increases in air temperature, even though the morning might still be relatively cool compared to the overall distribution of morning temperatures. Similarly, body contact between individuals affects body surface area much as postural adjustments do, and indeed, body contact trends paralleled those for posture.

Additionally, because muscular activity generates metabolic heat, it seemed likely that animals would combat heat loss during the early morning by engaging in active locomotory and other behaviors. Just the opposite was the case, however: interestingly, baboons become more active later in the morning, as solar intensity increased (Table 6, rows 5 and 6), when wind velocities were high (upper quartile).

Neither of these relationships are easily explained on thermoregulatory grounds: convective heat loss due to wind should counteract heat gain from the sun, while relative wind-sun azimuth should not be thermally significant for activity level. The positive effect of wind velocity may be secondary, owing to a positive correlation of wind velocity with time-of-day. Similarly, the relative wind-sun azimuth relationship with activity may simply reflect a strong correlation between activity and posture. All in all, activity would not seem to be a key component of the behavioral thermoregulation strategy of baboons.

MULTIVARIATE ANALYSES

The correlation analyses summarized in Tables 2–6 indicated that microclimatic variables interacted in their effect on behavior, and that particular components of microclimate (e.g.,

Table 6. Correlation matrix summary, activity in relation to microclimate during cool/windy intervals (upper portion) vs. warm/calm intervals (lower portion).

Microclimate variable	Level	N	Activity state	T_{air}	SR_{tot}	V_{wind}	AZ_{ws}	Time
			Cool/windy					
T_{air}	Low	34	Passive					
			Active					
SR_{tot}	Low	34	Passive				−0.362	
			Active				+0.362	
V_{wind}	High	33	Passive		−0.357			−0.431
			Active		+0.357			+0.431
			Warm/calm					
T_{air}	High	32	Passive					
			Active					
SR_{tot}	High	34	Passive					
			Active					
V_{wind}	Low	37	Passive					
			Active					

Data partitioned by upper (High) or lower (Low) quartile of corresponding microclimate variable. Correlation coefficients are listed only if significant at the $\alpha = 0.05$ level. Abbreviations for microclimate variables as defined in text. Proportion data were arcsin square-root-tarnsformed prior to analysis.

Table 7. Stepwise multiple regression results, behavior in relation to microclimate.

Behavior response	Microclimate variable	Sign of corr	%variance explained
Orientation towards sun	AZ_{ws}	+	19.95
Open posture	SR_{tot}	+	26.12
Intermediate posture	SR_{tot}	+	24.53
Hunch posture	T_{air}	−	40.20
Active activity	T_{air}	+	19.45

Proportion data were arcsin square root-transformed prior to analysis. Independent (microclimate) variables were entered or removed using $F_{crit} = 1.0$. Only those models are listed in which the first-entered microclimate variable explained at least 15% of the variance in the behavioral response. Abbreviations for microclimate variables defined in text.

wind) were more important than others in influencing certain behavioral responses. To obtain more precise weightings of the role of specific meteorological variables in influencing baboon behavior, we further analyzed our data using stepwise multiple regression. Briefly, microclimatic variables (T_{air}, SR_{tot}, V_{wind}, AZ_{ws}) and time-of-day were used as linear predictors of transformed behavioral proportion data. The order of microclimate variables in each model thus provided an objective measure of their potential thermoregulatory importance. Table 7 summarizes the five strongest regression models, i.e., those which explained at least 15% of the variance in behavior.

Briefly, orientation to wind and body contact were not strongly predicted by any microclimate variables, and are thus absent from tables. This absence, however, does not reflect the absence of influence of microclimate on the variables, but rather the miniscule variance in those behaviors in the first place: essentially, baboons faced away from wind, and stayed in extensive body contact whenever possible during the morning. Orientation to sun did vary throughout the morning and was positively predicted by the relative direction of wind, but not by solar intensity. This is consistent with previous analyses that indicated that trunk orientation was governed mainly by wind rather than sun. In contrast, solar intensity did influence the frequency of relatively open postures (Table 5, row 7; Table 7, row 2): baboons basked at warm air temperatures as the sun grew brighter.

Hunched (highly adducted) postures were related more strongly to changes in air temperature than to solar radiation under cool, windy conditions (Table 5, rows 2 and 4); this again suggests wind avoidance, since convective heat loss is a function of air temperature. Just as for trunk orientation, animals adopted heat conservation measures in response to wind-mediated cooling. Activity increased in conjunction with air temperature, while solar radiation did not enter into the regression model. This suggests that the open postures of activity may incur more heat loss, but that losses are compensated for by increased metabolism. The frequency of open postures did respond to solar intensity; animals probably bask rather than become more active in bright sun.

In sum, multivariate analysis merely confirmed the relationships found through bivariate analyses. The fact that our quartile-partitioned bivariate models fit well, while linear-predictor models were less informative, strongly suggests that microclimate variables interacted in a nonlinear fashion in their effect on behavior. Microclimatic variables also interact nonlinearly in physical processes of heat exchange (GATES, 1980; KERSLAKE, 1972); this functional similarity between behavioral and thermal processes supports the notion that changes in posture and body orientation serve a thermoregulatory function.

DISCUSSION

BEHAVIORAL THERMOREGULATION

Taken together, these results suggest that baboons act to avoid heat loss in the morning. Specifically, baboons face away from wind (especially cool wind), stay in hunched postures most of the time, and only rarely exhibit basking behavior. ANDERSON and MCGREW (1984) report similar responses in Guinea baboons (*Papio papio*). Wind velocity and air temperature are the strongest influences on trunk orientation and posture, implying that convective heat loss (a combined function of air velocity and temperature) is the most important determinant of thermoregulatory behavior.

When air temperature and solar radiation rise, the risk of convective heat loss decreases, and only under these circumstances do baboons face oblique to or directly towards wind. At the very highest air temperatures and solar intensities, some individuals may face directly towards the sun and bask; this response is probably masked most of the time by the baboons assiduous avoidance of convective cooling effects. In fact, when wind and sun come from the same direction, baboons may lose more heat by facing the wind than they gain by facing the sun.

Under warm conditions, yellow baboons in Amboseli decrease interindividual body contact and increase activity. In contrast, ANDERSON and MCGREW (1984) state that huddling in *Papio papio* was not correlated with minimum air temperature. Both sets of results are in fact consistent—baboons apparently conserve heat under a wide range of cool conditions (i.e., regardless of nighttime minimum air temperature), and modify this baseline behavior only under the warm conditions of late morning. In sum, posture and body orientation thus appear to be the primary component of the behavioral thermoregulation strategy of baboons in trees. Body contact supplements postural adjustments, while activity seems to be unimportant as a thermoregulatory mechanism.

NON-THERMAL ECOLOGICAL FACTORS

In our particular study, posture and body orientation were significantly influenced by microclimate. Behavior is not always so tightly linked to thermal environment, particularly during foraging or social activity (INGRAM & LEGGE, 1970; SHARMAN, 1980) and postural adjustments in particular may often be of less thermal significance than microenvironment selection (MOEN, 1973; STEVENSON, 1985). On this basis, we predict that postural thermoregulation in mammals such as baboons will be most clearly expressed by animals engaging in resting, grooming, or other low-activity behaviors. More generally, thermoregulatory behavior is one component in the general problem of optimizing costs and benefits of competing ecological factors, a topic of broad interest among behavioral ecologists.

CONCLUSIONS

1. Resting baboons alter their posture and body orientation in response to changes in their surrounding microclimate during the early morning. Postural adjustments are accompanied by functionally similar changes in body contact. Gross activity level seems unimportant as a thermoregulatory mechanism.
2. Air temperature and wind direction are the most salient cues for baboon posture and body orientation; solar heating is significant only under warm, calm conditions. Convective heat loss was the primary component of thermal stress under the conditions of this study.
3. Microclimate variables such as air temperature, wind velocity, and solar radiation interact nonlinearly in their effects on behavior, much as they interact in physical heat transfer processes.

Acknowledgements. Research support was provided by the Joseph Henry Marsh Fund and the National Science Foundation (U.S.A.). Field work in Kenya was made possible by the Office of the President, Ministry of Tourism and Wildlife, and the Amboseli Park Warden. The authors thank Dr. STUART ALTMANN and TERESA CHIAERLLI for their comments on earlier drafts of this manuscript.

REFERENCES

ADAIR, E. R., 1976. Autonomic thermoregulation in squirrel monkey when behavioral regulation is limited. *J. Appl. Physiol.*, 40: 694–700.

———, 1977. Skin, preoptic, and core temperatures influence behavioral thermoregulation. *J. Appl. Physiol.*, 42: 559–564.

——— & J. T. STITT, 1971. Behavioral temperature regulation in the squirrel monkey: effects of midbrain temperature displacements. *J. Physiol. (Paris)*, 63: 191–194.

——— & B. A. WRIGHT, 1976. Behavioral temperature regulation in the squirrel monkey when response effort is varied. *J. Comp. Physiol. Psychol.*, 90: 179–184.

ALTMANN, J., 1974. Observational study of behavior: sampling methods. *Behaviour*, 49: 227–267.

ALTMANN, S. A. & J. ALTMANN, 1970. *Baboon Ecology: African Field Research.* S. Karger, Basel.

ANDERSON, J. R. & W. C. MCGREW, 1984. Guinea baboons (*Papio papio*) at a sleeping site. *Amer. J. Primatol.*, 6: 1–14.

BAKKEN, G. S., 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.*, 60: 337–384.

———, 1981. A two-dimensional operative-temperature model for thermal energy management by animals. *J. Therm. Biol.*, 6: 23–30.

BERNSTEIN, I., 1972. Daily activity cycles and weather influences on a pigtailed monkey group. *Folia Primatol.*, 18: 390–415.

BRUNS, E. H., 1977. Winter behavior of pronghorns in relation to habitat. *J. Wildl. Manag.*, 41: 560–571.

CENA, K. & J. A. CLARK, 1973. Thermal radiation from animal coats: coat structure and measurements of radiative temperature. *Phys. Med. Biol.*, 18: 432–443.

DAHL, J. F., I. S. BERNSTEIN, & L. WILLIAMS, 1982. Thermoregulation and social structure of a captive group of rhesus macaques. *Int. J. Primatol.*, 3: 273.

——— & E. O. SMITH, 1985. Assessing variation in the social behavior of stumptail macaques using thermal criteria. *Amer. J. Phys. Anthropol.*, 68: 467–477.

GALE, C. C., M. MATTHEWS, & J. YOUNG, 1970. Behavioral thermoregulatory responses to hypothalamic cooling and warming in baboons. *Physiol. Behav.*, 5: 1–6.

GATES, D. M., 1980. *Biophysical Ecology*. Springer-Verlag, New York.

HAUSFATER, G. & B. J. MEADE, 1982. Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates*, 23: 287–297.

HUEY, R. B. & E. R. PIANKA, 1977. Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology*, 58: 1066–1075.

——— & M. SLATKIN, 1976. Cost and benefits of lizard thermoregulation. *Quart. Rev. Biol.*, 51: 363–384.

INGRAM, D. L. & K. F. LEGGE, 1970. The thermoregulatory behavior of young pigs in a natural environment. *Physiol. Behav.*, 5: 981–987.

KERSLAKE, D. M., 1972. *The Stress of Hot Environments*. Cambridge Univ. Press, Cambridge.

LUSTICK, S., B. BATTERSBY, & M. KELTY, 1978. Behavioral thermoregulation: orientation to the sun in herring gulls. *Science*, 200: 81–83.

MOEN, A. N., 1973. *Wildlife Ecology, an Analytical Approach*. W. H. Freeman, San Francisco.

MUTH, A., 1977. Thermoregulatory postures and orientation to the sun: a mechanistic evaluation for the zebra-tailed lizard *Callisaurus draconoides*. *Copeia*, 1977: 710–720.

NORRIS, K. S., 1967. Color adaptation in desert reptiles and its thermal relationships. In: *Lizard Ecology, a Symposium*, W. W. MILSTEAD (ed.), Univ. of Missouri Press, Columbia, MO, pp. 162–229.

ØRITSLAND, N. A. & K. RONALD, 1978. Solar heating of mammals: observations of hair transmittance. *Int. J. Biometeorol.*, 22: 197–201.

PATTERSON, J. D., 1986. Shape as a factor in primate thermoregulation. In: *Proceedings of the IXth Congress of the International Primatological Society. Vol. 1: Current Perspectives in Primate Social Dynamics*, D. M. TAUB & F. A. KING (eds.), Van Nostrand Reinhold, New York, pp. 228–242.

PORTER, W. P. & D. M. GATES, 1969. Thermodynamic equilibria of animals with environment. *Ecol. Monogr.*, 39: 227–244.

——— & F. C. JAMES, 1979. Behavioral implications of mechanistic ecology II: the African rainbow lizard, *Agama agama*. *Copeia*, 1979: 594–619.

——— & C. R. TRACY, 1980. Biophysical analyses of energetics, time-space utilization, and distributional limits of lizards. In: *Lizard Ecology Symposium*, R. HUEY, T. SCHOENER, & E. PIANKA (eds.), Harvard Univ. Press, Cambridge, MA.

POST, D., 1978. Feeding and ranging behavior of the yellow baboon (*Papio cynocephalus*). Unpubl. doctoral dissertation. Yale Univ., New Haven, Connecticut.

———, G. HAUSFATER, & S. A. MCCUSKEY, 1980. Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender, and dominance rank. *Folia Primatol.*, 34: 170–195.

ROUGHGARDEN, J., W. P. PORTER, & D. HECKEL, 1981. Resource partitioning of space and its relationship to body temperature in *Anolis* lizard populations. *Oecologia (Berlin)*, 50: 256–264.

SALE, J. B., 1970. The behavior of the resting rock hyrax in relation to its environment. *Zool. Afr.*, 5: 87–99.

SATINOFF, E., 1978. Neural organization and evolution of thermal regulation in mammals. *Science*, 201: 16–22.

SHARMAN, M., 1980. Feeding, ranging, and social organization of the Guinea baboon (*Papio papio*) in Senegal. Unpubl. doctoral dissertation, Univ. of St. Andrews, Scotland.

SLATKIN, M. & G. HAUSFATER, 1976. A note on the activity of a solitary male baboon. *Primates*, 17: 311–322.

SNEDECOR, G. W. & W. G. COCHRAN, 1980. *Statistical Methods*. Iowa State Univ. Press, Ames, Iowa.

STEVENSON, R. D., 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Amer. Naturalist*, 126: 362–386.

STOLZ, L. P. & G. S. SAYMANN, 1970. Ecology and behavior of baboons in the Northern Transvaal. *Ann. Transvaal Mus.*, 26: 99–143.

TREAGER, R. T., 1965. Hair density, wind speed, and heat loss in mammals. *J. Appl. Physiol.*, 20: 796–801.

VELLEMAN, P. F. & D. C. HOAGLIN, 1981. *Applications, Basics, and Computing of Exploratory Data Analysis*. Duxbury Press, Boston.

WALDSCHMIDT, S., 1980. Orientation to the sun by the iguanid lizards *Uta stansburiana* and *Sceloporus undulatus*: hourly and monthly variations. *Copeia*, 1980: 458–462.
WALSBERG, G. E., G. S. CAMPBELL, & J. R. KING, 1978. Animal coat color and radiative gain: a re-evaluation. *J. Comp. Physiol.*, 126B: 211–222.

—Received *May 8, 1986*; Accepted *August 7, 1986*

Authors' Names and Present Addresses: JEFFREY K. STELZNER, *University of California, San Diego, Physics Department B-019, La Jolla, California 92093, U.S.A.*; GLENN HAUSFATER, *University of Missouri, Division of Biological Sciences, 110 Tucker Hall, Columbia, Missouri 65211, U.S.A.*