Assessing Variation in the Social Behavior of Stumptail Macaques Using Thermal Criteria

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ABSTRACT   This paper reports a method for comparing the environments of nonhuman primates based on biophysical, thermal criteria. The method is applied to an analysis of behaviors exhibited by group-living stumptail macaques (*Macaca arctoides*), documented by a group-scan observation technique, to test the hypothesis that the expression of social behavior is dependent on thermal conditions. Thermal conditions are identified by considering sky cover and the relative cooling power of the environment. The results show that the rates of occurrence of affiliative, play, and solitary behaviors are altered significantly at a relative cooling power at or above 550 kcal/m^2/hr under cloudy conditions and at or above 600 kcal/m^2/hr under sunny conditions. In addition, the rates of occurrence of play, sexual, aggressive, and submissive behavioral states are also significantly different under cloudy, rather than sunny, conditions over particular ranges of cooling. It is possible to conclude that thermal criteria affect the expression of social behaviors by stumptail macaques. This is consistent with studies of huddling behavior exhibited by stumptail macaques and rhesus macaques (*M. mulatta*), and suggests that 1) certain changes in the expression of social behaviors may be thermoregulatory in at least some nonhuman primate species and 2) thermal criteria are likely to be useful tools when conducting comparative analyses of behavioral data collected on animals in outdoor environments.

The behavior of animals may be constrained by a number of variables, including the thermal properties of their environments. Thermal conditions may determine and restrict the geographic range of nonhuman primates, but these conditions can fluctuate widely during 24-hr periods, from season to season, at different latitudes, and with change of location within one habitat (Dahl, 1980, 1981). Little information is available on how temporal fluctuations in thermal conditions impact on primates. This paper decribes a method for comparing the thermal properties of certain temporally fluctuating environments and their effect on the expression of social behaviors exhibited by a captive group of stumptail macaques (*Macaca arctoides*). This is achieved by describing some basic biophysical theory, deriving a practical measure of environmental, thermal conditions, and applying this measure to assess variability in the expression of group behaviors in stumptail macaques.

The influence of weather conditions on the social behavior of cercopithecoid monkeys (Bernstein, 1972, 1975, 1976, 1980) indicates the presence of significant differences in behavior when comparisons are made among data collected under broad and qualitatively distinctive ranges of conditions, e.g., "cold environments when temperatures were below 0°C and skies were fair" versus "fair weather when the temperature varied between 10 and 26.7°C" (Bernstein, 1972:392–393). The critical measure of thermal condi-

tions used was ambient temperature, a measure that has been reported frequently in ecological studies. However, energy flow between an animal's body surface and its environment results from a more complex set of identifiable environmental variables than ambient temperature alone, including windspeed, solar radiation, and humidity (Campbell, 1977; Porter and Gates, 1969; Tracy, 1972). An attempt has recently been made to assess these environmental variables and to derive a simple, practical measure of thermal conditions in order to examine how variations in primate behavior (or morphology) may associate with fluctuations in environmental conditions (Dahl, 1980, 1981; Dahl and Smith, 1982; Dahl et al., in press). Central to the success or failure of this attempt has been detailed consideration of the variables that effect energy flow to and from an animal's body surface.

ENERGY FLOW

When energy losses at an animal's surface exceed energy gains, the resultant is negative energy flow from the surface and the animal will cool down. The converse is also true; when energy gains exceed losses, the animal will heat up. In living animals, a balance between gains and losses is usually achieved so that heat gains are equal to heat losses and the animal is said to be thermoneutral with its environment. Campbell (1977) has identified ten variables that contribute to heat loss or gain at an animal's surface. Shortwave radiation (S_i), longwave radiation (L_i), shortwave absorptivity (a_S), longwave absorptivity (a_L), and metabolic heat per unit area (M) all contribute to heat gain. Heat lost from the surface can be determined by considering longwave emittance (Lo_e), latent heat lost through evaporation (λE), heat lost by conduction (G), heat lost by convection (H), and rate of heat storage in the animal (q).

Five of the above variables (a_S, a_L, Lo_e, M and q) are properties of the animal rather than of the environment. These and other physical properties of the animal are excluded from the definition of a measure of environmental conditions, although they may be significant in applying the measure and in interpreting results. For example, Walsberg et al. (1978) has demonstrated how dark- and light-colored coats of animals are affected differently under different conditions of simulated solar radiation and windspeed, suggesting that animals with dark-colored coats may acquire lower heat loads under ecologically realistic conditions than those forms with light-colored coats. It follows that a group of predominantly black-coated monkeys might respond differently to certain fluctuations in thermal conditions than would a predominantly white-coated group. When a study group is polytypic with respect to coat color, as are stumptail macaques, details of this polytypy must be provided if experiments are to be empirical; data derived from groups with radically different coat color compositions may not be directly comparable. Similarly, differences in size and shape (Patterson, in press) also require attention.

Among the remaining environmental variables, S_i (shortwave radiation) and L_i (longwave radiation) are directly related to the energy from the sun that impinges on the animal's surface. Solar radiation at the earth's surface varies with time of day, time of year, and elevation, and it is affected during daytime by cloud cover. These variables must be incorporated when environments are compared. Finally, G (heat lost by conduction), H (heat lost by convection), and λE (heat lost through evaporation) vary with ambient temperature, windspeed, and humidity. These variables could be measured in an ideal experimental situation, but such measurements are difficult to make while also examining social behavior. Practical simplification can be achieved, however, by applying the concept of environmental cooling (Siple and Passel, 1945).

Environmental cooling, which was devised in the Antarctic as a method for predicting the probability of frostbite in humans, is a direct measure of heat loss based on the following formulation:

$$v \times 100 + (10.45 - v)(33 - T_a) = K_0$$

where v is the wind velocity (m/sec), T_a is the temperature of the air (°C), and K_0 is the cooling power of the atmosphere (kcal/m²/hr). This can be taken as the resultant of heat lost by conduction (H) and convection (G), but it does not take into consideration latent heat lost through evaporation (λE). Humidity was assumed to be uniformly zero at the Antarctic because of the low temperatures in that region and, hence, λE was considered to be a constant. If humidity can be taken into account, however, K_0 becomes a useful quantitative measure of the thermal environment since it can be applied over a wide range of

conditions; windspeed (v) and ambient temperature (T_a) are readily measurable with an anemometer and a thermometer (and see below). Humidity fluctuates with time of day and with the passage of moist or dry air masses over a study site. As an initial approximation, humidity is inferred to be low when there is no cloud cover and high when there is cloud cover, for any particular time of day. The validity of this approximation can be tested against empirical data.

APPLICATION OF A SIMPLE METHOD FOR COMPARING ENVIRONMENTS

When considering a general energy flow model, it would appear that the immediate environmental impact of thermal variables on a primate species can be compared by the following methods.

1. Measuring windspeed and ambient temperature at the study site and computing K_0 as an estimate of variations in H and G.
2. Categorizing data into subsets by the presence or absence of clouds in order to account for variations in λE, S_i, and L_i.
3. Categorizing behavioral data into subsets by time of day and time of year in order to account for additional variations in λE, S_i, and L_i with changes in the inclination and declination of the sun and changes in circadian fluctuations in the level of humidity.
4. Considering differences in elevation if behavioral data are to be compared among groups of individuals at different sites.

In other words, for each subset of data, λE, S_i, and L_i can be limited to a similar, small range, leaving K_0 as the only variable that is actually measured.

Within any subset of data, an estimate of heat loss due to environmental cooling is a *relative* measure, since the actual cooling at an animal's surface may be different for at least one reason. The presence and distribution of hair on an animal's surface tends to retard cooling, so for any measure of K_0 the actual heat lost will be less owing to the insulative properties of the pelage. The measure of cooling that is applied, therefore, is an inferred, relative estimate, designated $r\hat{K}_0$, and the cooling that is actually experienced by the animals will be less than $r\hat{K}_0$.

Moreover, the windspeed and temperature in each animal's immediate environment are difficult to measure. Based on Yoshino (1974), the immediate environment of an animal is termed *microclimate* and the environment of

an entire group is termed *macroclimate*. The macroclimate of the space occupied by an entire group is easier to measure, and it is reasonable to assume that all microclimates within an area will fluctuate with the measured macroclimate. Certain microclimates may exhibit lower or higher cooling powers than indicated by the macroclimatic measure of $r\hat{K}_0$. It has been inferred (Dahl, 1981; Dahl et al., 1982, in press; Dahl and Smith, 1982) that captive individuals of two macaque species change location in order to occupy spaces offering conditions that are closest to thermoneutrality. Hence, the actual cooling in spaces occupied by group members will probably be less than macroclimatic $r\hat{K}_0$ when weather is relatively cool and greater than macroclimatic $r\hat{K}_0$ when relatively hot.

To interpret results, it must be remembered that changes in the frequency of social behaviors that accompany changes in thermal conditions should not be observable when animals are thermoneutral with respect to their environment, since this condition typically encompasses an appreciable range. Furthermore, any changes in social behavior that are observed will probably be different under conditions of cooling (potential negative energy flow from the animal) positive energy flow to the animal). Because of the relative nature of $r\hat{K}_0$, conditions of cooling can be expected when the measured value of $r\hat{K}_0$ is much greater than zero, and conditions of thermoneutrality can be expected when the value of $r\hat{K}_0$ is a little greater than zero. Given an estimate of an environment's thermal conditions from the energy flow model of Campbell (1977) and application of the concept of environmental cooling (Siple and Passel, 1945), the hypothesis that social behavior varies with fluctuations in thermal conditions (as measured by $r\hat{K}_0$ with consideration of cloud cover) remains to be tested. Based on earlier work with stumptail macaques (Cahl and Smith, 1982) that demonstrated how huddling behavior differs under different conditions of $r\hat{K}_0$, some significant differences in rates of occurrence of solitary and affiliative behaviors should be detectable.

MATERIALS AND METHODS
Study animals

The subjects under study were 36 group-living stumptail macaques (*Macaca arctoides*). The composition of the group on the

TABLE 1. Physical characteristics of the study subjects[1,2]

Subjects	No.	Age range[3] (months)	Body weight (kg) $\overline{X}^3$ (± SD)	Body weight (kg) $\overline{X}^4$ (± SD)	Pelage color[5]
Adult					
Males	4	61–119[6]	15.2 (2.7)	14.8 (3.2)	2 YB, 1 BB, 1 DB
Females	14	63–228	9.3 (1.6)	9.3 (1.3)	9 YB, 2 RB, 3 DB
Subadult					
Males	1	52	9.9 (—)	11.8 (—)	YB
Females	4	53–58	6.9 (0.7)	7.0 (0.5)	1 YB, 2 RB, 1 BB
Juvenile					
Males	5	16–37	4.4 (1.0)	4.8 (0.8)	2 YB, 3 DB
Females	7	16–41	4.3 (1.5)	4.7 (1.4)	1 YB, 2 RB, 4 DB

[1]If environmental, thermal criteria are to be applied empirically, the subjects must be comparable (see text for additional explanation).
[2]See also Smith and Byrd (1983) and Smith and Peffer-Smith (1984).
[3]At start of study.
[4]At end of study.
[5]YB = yellow brown; BB = black, brown; RB = russet brown; DB = dark brown.
[6]Minimum age; animal obtained from the wild.

first day of the study (December 17, 1979) and individual physical characteristics relevant to thermal criteria (see above) are shown in Table 1. Body weight is an important factor when considering metabolic rate, surface area, and rates of heat storage. Pelage coloration is associated with absorptivity and emittance (see above). A group of stumptail macaques whose composition, age, size, and coloration are different from those of the present group might exhibit different responses under similar thermal conditions. The group was provided a surplus amount of food at all times in order to minimize constraints on metabolic energy requirements.

Study site

Research was conducted at the Yerkes Regional Primate Research Center Field Facility, 25 km northeast of Atlanta, Georgia (approximately 34°N latitude, 84°W longitude) at an elevation of about 350 meters above sea level. The outdoor enclosure (30 m × 30 m) and two adjacent buildings are located on the slope of a hill facing southwest and are described elsewhere (Smith and Peffer-Smith, 1984).

Behavioral data collection

Data were collected from December 1979, to March 1980, by three observers using a microprocessor-based data collection system

(Smith and Begeman, 1980). This work was the first part of a larger psychopharmacological study (Smith and Byrd, 1983) during which a control data base was generated; no experimental procedures with drugs were conducted during this initial period. A scan-sample technique (Altmann, 1974) was used in which the behavioral state of each group member was sampled at 1-min intervals for 60-min periods. This technique is appropriate for the social situation in the present study, since the behavioral states of the macaques were "lumped into a few easily distinguishable categories" (Altmann, 1974:259). These have been identified in detail (Smith and Byrd, 1983:Table II and p. 15) as aggressive, submissive, affiliative, general social, play, sexual, and self-directed or solitary behavioral states. The scan-sample technique is a type of instantaneous sampling in which group members are sampled within a short time period so that the record approaches a simultaneous sample on all individuals. Following Altmann (1974), an attempt was made to keep the time spent sampling each animal as brief as possible; this was always less than 1.7 sec; i.e., all 36 animals were sampled within the 60-sec sampling period. In most scan samples, however, the time was approximately 1.1 or 1.2 sec. If an ad hoc assumption is made that "no more than one transition [between behavioral states] can

TABLE 2. Environmental conditions for each data subset

	No.	Relative cooling power[1] of the environment (kcal/m²/hr)			Relative humidity (%)[2]		Sky cover[2]	
		Range	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD
Sunny[1]								
Morning	14	400–770	596.8	119.0	24.7	31.2	3.43	3.51
Midday	18	325–775	506.7	138.3	41.1	13.9	2.39	2.62
Afternoon	13	250–600	413.5	126.1	38.4	12.7	2.85	2.76
Cloudy[1]								
Morning	22	400–825	541.6	115.5	75.6	17.8	9.84	0.32
Midday	18	325–700	533.0	107.9	58.6	22.9	9.69	0.55
Afternoon	15	275–700	482.3	118.4	59.0	21.9	9.63	0.58

[1]Determined at the study site.
[2]Determined from National Oceanographic and Atmospheric Administration publications.

occur between consecutive samples" (Altmann, 1974:260), the resulting data can be considered essentially equivalent to those of focal-animal sampling for estimates of rate and relative frequency of occurrence. Results are taken here as the rate per unit time that group members were in a particular behavioral state, expressed as $\overline{X}$/hr. Although this is not the method of choice for examining rates, it was used here so that group-scan data could be compared with focal-animal sampling rates, which were central to the ongoing psychopharmacological research. Given the absence of this constraint, it may have been more productive to calculate the percentage of time an animal was in each behavioral state (Altmann, 1974), although calculations of percentage of time based on scan-sampling data also present limitations.

Identification of environmental conditions

Testing began either at 1000 hr (morning time slot), at 1200 hr (midday time slot), or at 1400 hr (afternoon time slot). Ambient temperatures (T_a), windspeeds (v), and the presence or absence of clouds were recorded prior to each group-scan observation session. The greatest windspeed during a 1-min period was recorded and measured by a Dwyer anemometer positioned 6 m above the surface of the enclosure. The objective was to measure macroclimates (Yoshino, 1974), since microclimates are variable within the compound. Cloudy conditions were identified when no shadows were cast by the sun. From windspeeds and ambient temperatures measured at the study site, relative estimates of maximum environmental cooling ($\pm$ 20 kcal/m²/hr) were obtained based on Terjung (1966). Using Terjung's nomogram, it was found, for example, that at 21°C with a windspeed of 5

mph, $r\hat{K}_0$ is approximately 275 kcal/m²/hr, but at 21°C with a windspeed of 15 mph, $r\hat{K}_0$ is 350 kcal/m²/hr; moreover, at 10°C with the same windspeeds, $r\hat{K}_0$ is 530 kcal/m²/hr and 690 kcal/m²/hr, respectively. Clearly, ambient temperature is not an appropriate measure of thermal conditions in windy environments. Reports from the National Oceanographic and Atmospheric Administration for 1980 were consulted in order to obtain independent macroclimatic measures of relative humidity and sky cover. Median records from Athens and Atlanta, Georgia, were used to determine the validity of the assumption that humidity is high during cloudy conditions and low during sunny conditions.

RESULTS

Data on 100 group-scan tests were obtained between December 18, 1979, and March 28, 1980, and environmental details for the morning, midday, and afternoon time periods under sunny and cloudy conditions are shown in Table 2. As measured by $r\hat{K}_0$, the environment became warmer as the day progressed under either cloudy or sunny conditions. The assumed correspondence between cloud cover and humidity is supported for the morning scans, but it is not as applicable for scans conducted later in the day; humidity can only be considered adequately for one-third of the data (see Table 2).

If relative environmental cooling is the best indicator of thermal conditions during either sunny or cloudy days, random fluctuations in behavioral rates with an increase in $r\hat{K}_0$ would support the null hypothesis. To test this hypothesis, the data were divided into subsets based on two criteria: 1) the presence or absence of cloud cover; and 2) the smallest,
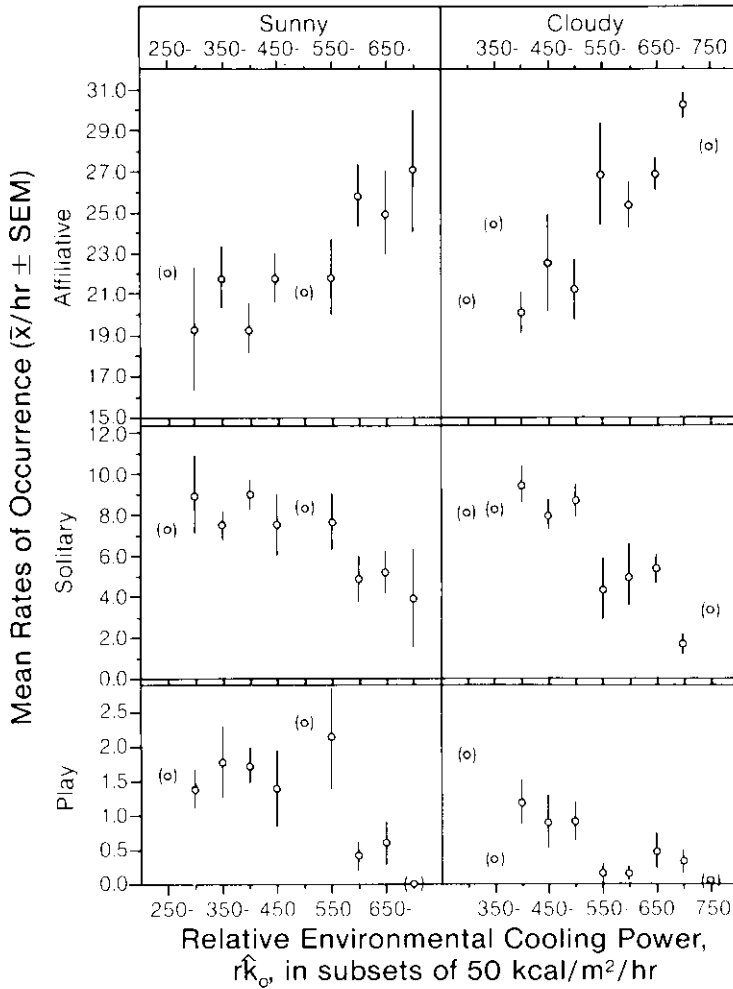
Fig. 1. Mean rates of occurrence (± SEM) for affiliative, solitary or self-directed, and play behavioral states calculated for limited ranges of relative environmental cooling of 50 kcal/m²/hr when the stumptail macaque group was experiencing either sunny (left) or cloudy (right) conditions; circles in parentheses represent the median of only two observations. Note the marked difference in all three rates for cooling powers above 600 kcal/m²/hr (sunny) and above 550 kcal/m²/hr (cloudy) from rates for lower cooling powers.

most meaningful ranges of rK_0, given an error of 20 kcal/m²/hr (see above)—i.e., 50 kcal/m²/hr (250–299, 300–349, 350–499 kcal/m²/hr, etc.). The mean and the standard error of the mean for each behavioral rate were computed for each subset and plotted against $r\hat{K}_0$. If the null hypothesis is supported, these measures will oscillate randomly around a single rate. However, a difference in the mean rate of occurrence is apparent for affiliative, solitary, and play behaviors when $r\hat{K}_0$

was higher than 600 kcal/m²/hr under sunny conditions and when $r\hat{K}_0$ was higher than 550 kcal/m²/hr under cloudy conditions (Fig. 1). The rate of occurrence of affiliative behavioral states increased as $r\hat{K}_0$ increased; rates of play and solitary behaviors decreased as $r\hat{K}_0$ increased (Table 3). Moreover, the rate of occurrence of solitary behavior decreased again at 700 kcal/m²/hr under cloudy conditions. Using the Mann-Whitney U test, the distinctions at 550 kcal/m²/hr (cloudy) and at

TABLE 3. Rates of occurrence of three behavioral states under different conditions of cloud cover and relative environmental cooling power

Behavioral state	Sunny conditions (kcal/m²/hr)		Cloudy conditions (kcal/m²/h)	
	≤ 599[1] (n = 28)	≥ 600[1] (n = 17)	≤ 549[1] (n = 35)	≥ 550[1] (n = 20)
Affiliative				
X̄/hr	20.71	25.20	21.13	26.87
SD	3.90	4.72	4.11	3.69
Solitary				
X̄/hr	8.20	5.56	8.56	4.81[2] 2.49[3]
SD	2.52	3.40	2.57	2.97[2] 1.14[3]
Play				
X̄/hr	1.71	0.52	1.04	0.20
SD	1.07	0.64	0.95	0.28

[1]Relative environmental cooling power; (n) = number of group scans in sample.
[2]$r\hat{K}_0$ = 550–699 kcal/m²/hr.
[3]$r\hat{K}_0$ = ≥ 700 kcal/m²/hr.

600 kcal/m²/hr (sunny) were statistically significant ($P \leq 0.05$) (Table 4).

Data collected during sunny and cloudy conditions were compared visually by means of graphs (Simpson and Roe, 1939) and by application of the Mann-Whitney U test (Siegel, 1956). No differences were apparent for rates of affiliative and solitary behaviors, except at a range of 550–600 kcal/m²/hr. The statistical significance of this distinction cannot be tested, however, because of the small size of one sample. Nevertheless, differences are testable for other behaviors, and significant distinctions were found in play, sex, aggression, and submission under particular ranges of cooling (see Table 5).

DISCUSSION

The results demonstrate that rates of occurrence of some types of behavior undergo significant alterations with increased environmental cooling and/or in the presence of cloud cover regardless of time of day and of some changes in humidity. Since both cooling and cloud cover affect thermal conditions, the results support the hypothesis that the thermal conditions of the environment affect the expression of social behavior of stumptail macaques. This is consistent with an earlier report (Dahl and Smith, 1982) that the huddling behavior of this species may be thermoregulatory. Therefore, since these animals may huddle together in order to maintain an equilibrium between positive and negative energy flows rather than a negative

energy flow, it would appear that increases in cooling 1) increase the rate of occurrence of affiliative behavioral states and decrease the rate of self-directed or solitary behavioral states and 2) decrease the rate of occurrence of play behaviors. As an alternative to huddling, however, individuals can move into sunny areas when there is no cloud cover, and they do this in relation to $r\hat{K}_0$ (Dahl and Smith, 1982). It follows that subtle distinctions in play, sexual, aggressive, and submissive behavioral states among the group under sunny and cloudy conditions may be consistent with the changes observed in the rate of huddling. For example, rates of submission and aggression may be higher under cloudy conditions within the cooling power range of 450–600 kcal/m²/hr when spacing mechanisms are constrained, but sexual and play behaviors may occur at a lower rate under cloudy conditions when more members of the group are huddled together (see Table 5).

The data on stumptail macaques regarding use of the sun and huddling are consistent with data on rhesus macaques (*Macaca mulatta*) studied at the same location (Dahl et al., in press). The study on rhesus macaques also included details of the social structure of huddling and how this structure changes with increasing $r\hat{K}_0$; huddles are formed by different individuals under different conditions of environmental cooling. It was possible to conclude that the social preference or affiliative thresholds that prevent social contacts a) among individuals from different matrilines and b) between adult males and

TABLE 4. *Comparisons among mean rates of occurrence of solitary, affiliative, and play behavioral states at low and high ranges of relative environmental cooling power for sunny and cloudy conditions*

| | Behavioral state | | | | | |
| | Solitary | | Affiliative | | Play | |
	Sunny	Cloudy	Sunny	Cloudy	Sunny	Cloudy
Sky cover Cooling range (kcal/m²/hr)						
Low	400–599	450–549	400–599	450–549	400–599	450–549
High	≥ 600	≥ 500	≥ 600	≥ 550	≥ 600	≥ 550
$\bar{X}$ rate (SD)						
Low	7.97 (2.38)	8.28 (2.76)	20.82 (3.93)	21.80 (4.53)	1.80 (1.25)	0.94 (0.94)
High	5.56 (3.40)	4.26 (2.83)	25.20 (4.72)	26.85 (3.71)	0.52 (0.66)	0.20 (0.28)
n_1	17	20	17	20	17	20
n_2	17	21	17	21	17	21
R_1	235.5	276.5	372.5	549.5	399.5	329
R_2	359.5	588.5	222.5	311.5	195.5	532
U	82.5	66.5	70.5	101.5	42.5	119
Ucrit	87.0	—	77.0	—	57.0	—
Z	—	3.74	—	2.83	—	2.37
P	≤ 0.05	≤ 0.00022	≤ 0.02	≤ 0.0046	< 0.002	≤ 0.0178

Mann-Whitney U test (two-tailed) is used to test the null hypothesis that behavioral states have the same distribution, regardless of $r\dot{K}_o$, for a prediction of differences that does not state direction (Siegel, 1956). All differences are significant at the .05 level.

TABLE 5. *Comparisons of rates of occurrence of aggression, submission, sex, and play behaviors under sunny and cloudy conditions for high and low ranges of relative environmental cooling power*[1]

| | Behavior | | | | | | | |
	Aggression		Submission		Sex		Play	
Range of $r\dot{K}_o$ (kcal/m²/hr)[3]	350–549	≥ 600	450–649	≥ 650	300–499	≥ 550	250–499	≥ 550[2]; ≥ 600[3]
$\bar{X}$ rates (SD)[3]	0.52 (0.38)	0.41 (0.20)	0.29 (0.09)	0.43 (0.24)	0.51 (0.29)	0.38 (0.30)	1.60 (0.81)	0.20 (0.28)
$\bar{X}$ rates (SD)[2]	0.54 (0.25)	0.59 (0.19)	0.45 (0.19)	0.49 (0.29)	0.32 (0.27)	0.44 (0.85)	1.07 (0.96)	0.75 (0.91)
n_1	19	15	16	8	19	20	22	20
n_2	30	17	33	11	21	21	23	21
R_1	426.5	308.9	279.5	84.0	307.5	459.0	412.0	346.0
R_2	783.5	219.0	944.5	106.0	512.5	402.0	623.0	515.0
U	333.5	66.1	144.5	48.0	117.5	171.0	159.0	136.0
Ucrit	75	—	19	—	—	—	—	—
Z	1.10	—	2.55	—	2.30	1.02	2.13	1.93
p	> 0.05	≤ 0.05**	≤ 0.0108**	> 0.05	≤ 0.0214**	> 0.05	≤ 0.0332**	≤ 0.0268*

[1] Descriptive statistics are shown for each data subset, and except where indicated by an asterisk the Mann-Whitney U test is used as in Table 4.
[2] For cloudy conditions.
[3] For sunny conditions.
* Significant if directionality is assumed from the result in the previous column and, hence, if a one-tailed test is applied.
** Significant difference at $\alpha = 0.05$ (two-tailed test).

matrilineal aggregations are lowered at a cooling level of about 500 kcal/m^2/hr. If stumptail macaques exhibit similar changes in affiliative thresholds, then significant qualitative as well as quantitative changes in behavioral states may occur as a result of thermal conditions. Therefore, study groups that experience varying thermal conditions may exhibit subtle variations in behavioral states that many observers regard as entirely comparable.

Can the conditions of thermoneutrality for a macaque species be inferred from assessments of social behavior using $r\hat{K}_0$? The energy flow model indicates that the rate of heat loss from an animal's surface, represented by $r\hat{K}_0$, will be balanced, to some extent, by heat gain from the sun when no cloud cover is present. Terjung (1966) states that solar radiation retards cooling by approximately 200 kcal/m^2/hr over unshaded surfaces, although this will vary with time of day, season, latitude, and elevation. Depending on the type of cloud cover (e.g., cumulonimbus vs. altostratus translucidus), the potential heat gain from the sun is significantly reduced during cloudy conditions (Campbell, 1977). It can be argued from this that $r\hat{K}_0$ will provide a more accurate indication of actual heat loss during cloudy conditions than on sunny occasions. On the other hand, there is less humidity during sunny conditions (see Table 2); thus, evaporation from the surface of the respiratory tract (λE) will be a greater contributor to heat lost during sunny conditions than during cloudy conditions. Results obtained for changes in the rates of occurrence of affiliative, play, and solitary behavioral states indicate that the distinction in actual overall cooling between sunny and cloudy conditions corresponds to only 50 kcal/m^2/hr; rates of occurrence of the behaviors increase or decrease at 550 kcal/m^2/hr during cloudy conditions and at 600 kcal/m^2/hr during sunny conditions.

These estimates of the cooling power of the environment apply to the maximally exposed animal and to the group's macroclimate, so that the cooling experienced will be less for most, if not all, of the spatially dispersed group members. If an arbitrary reduction of 100 kcal/m^2/hr of cooling is assumed to be achieved by nonsocial behaviors such as changes in posture (Patterson, in press), independent of sun and shade, then the lower limit of thermoneutral conditions for stumptail macaques can be inferred to be between 500 and 550 kcal/m^2/hr. This is equivalent to temperatures of approximately 11°C at a windspeed of 5 mph, 15°C at a windspeed of 10 mph, 16°C at a windspeed of 15 mph, and 17°C at a windspeed of 20 mph. At windspeeds less than 3 mph, $r\hat{K}_0$ is an unreliable measure of conditions, but thermoneutrality may well be maintained at temperatures as low as 3–5°C when there is no wind (see Terjung, 1966:151). The upper limit of the stumptail macaque's thermoneutral range cannot be estimated on the basis of the data presented here, since the lowest $r\hat{K}_0$ sampled was 250 kcal/m^2/hr. Analysis of data derived from lower levels of $r\hat{K}_0$ (Dahl, 1981) and of data derived from rhesus macaques suggests that this limit is close to 300 kcal/m^2/hr under sunny conditions, which is equivalent to a temperature of 20°C at a windspeed of 5 mph, or up to 23°C at windspeed of 20 mph. These inferences can, of course, be examined experimentally under controlled conditions by established techniques (e.g., Adair, 1976, 1977).

The significance of the results from the present study of stumptail macaques can be viewed within at least two contexts. First, members of a cohesive social group may gain a thermal advantage, under certain environmental conditions, if the social relationships among group members can be adjusted so that individuals can huddle together; *groups can occupy certain habitats that would otherwise be too cool for an individual.* What is the nature of this thermal advantage? Patterson (in press), following the work of Meeh (1879), Gould (1977), and Swan (1974), has pinpointed the importance of an animal's shape in thermoregulation; theoretically, an animal can change its shape by changing its posture and, thus, may alter the relationship between surface area and body mass. In the present context, huddling can, in effect, be regarded as a change in the shape of a group so that the exposed surface area is decreased and, therefore, the area over which heat can be lost is decreased. The relative advantage of huddling can be assessed by considering surface area alone for two extreme situations: the group as isolated individuals; and the group when all individuals are crowded together in one huddle. By oversimplification, in order to obtain an indication of the relative differences in animal surface area, the shape of an isolated individual can be assumed to be the same as that of the huddle. This assumption permits us to estimate the

relative surface area from the surface law (Kleiber, 1961:181). Assuming that the density of an isolated animal and the density of the huddle are the same, their surface areas are in proportion to the two-thirds power of their weights (i.e., $W^{0.7}$). The relative surface area of the group was calculated from individual weights, and this was 134.9 when all individuals were isolated, but it was 41.4 when the animals were huddled together; the surface area was reduced to less than one-third of the total for all individuals when the group was in one huddle. As stated above, this does not consider change in shape; if an isolated animal is regarded as a spheroid and a huddle as a heteromorph, the actual reduction in surface area of the huddle will be less (Patterson, in press). Since the study of variable surface geometery is still in its infancy, and since a revision of the mathematics of surface area (Swan, 1974) is long overdue, an attempt to determine the exact thermal benefits of huddling, based on theory alone, is problematic. Experimental manipulation of interindividual access under controlled, laboratory conditions is still possible, however. Nevertheless, it is clear that one thermal benefit of huddling results from a significant decrease in exposed surface area. If the exposed surface area of an isolated individual is taken, for heuristic purposes, as 3 m^2, then a group of 36 isolated individuals at a cooling power of 600 $kcal/m^2/hr$ will potentially lose $3 \times 36 \times 300$ kcal, or a total of 64,800 kcal, from its surface area. If huddling reduces this average exposure by one-half, the group may save approximately 33,000 kcal every hour while it remains in a huddle.

The second significant context concerns the possible improvement of laboratory investigations (where animals are studied outdoors) and of some field studies. Based on the present study, it is clear that behavioral variations that are attributable to thermal conditions could confound experimental results. For example, rates of play behavior could be measured for control and experimental conditions, with most control observations conducted under cloudy conditions having an $r\hat{K}_0$ higher than 550 $kcal/m^2/hr$ and with most experimental observations conducted under sunny conditions having an $r\hat{K}_0$ less than 599 kcal/m/hr. If thermal conditions are ignored, a spurious result could be obtained; that is, under control conditions, the measure of play behavior would be approximately 0.20 compared to 1.72 under ex-

perimental conditions (see Table 3), when this variation has no relation to the actual experimental conditions.

Another example provides additional support for the argument that environmental standardization is an important methodological tool. Consider a laboratory investigation of the influence of reproductive hormones on the social behavior of outdoor-living rhesus macaques. Although rhesus macaques breed seasonally, not all rhesus females exhibit estrus synchronously. For example, females without infants breed earlier than females with infants; i.e., some females breed in August and others breed later in the year. Clearly, behavioral data collected on females that breed in early August will be different from data collected on females that breed in late September if the weather is appreciably different at these two times. Similarly, if a series of experiments to determine the effects of abused drugs on social behavior were conducted throughout periods with dissimilar environmental conditions, spurious data might result unless weather conditions were adequately taken into account.

Applications of this standardization approach should be as varied as the types of investigations and study sites involved. One simple application to field studies would be to divide the data base only according to sky cover. On the other hand, humidity might be more appropriate in studies of primates that inhabit the floors or canopies of the forest, and $r\hat{K}_0$ would probably be more productive in studies of terrestrial primates that inhabit open environments. Measures of $r\hat{K}_0$ in an open, terrestrial environment are not overly complicated. Adequate hand-held anemometers and simple armored thermometers can readily be deployed at 30-min or at hourly intervals in order to provide data on $r\hat{K}_0$. These types of applications could serve as additional tools for evaluating ecological data on foraging strategy, habitat preference, and/ or biomass. For example, the energy value of foods consumed on cool, cloudy, moist days might be higher than the energy value of foods eaten on warm, sunny, dry days, which may be chosen for their higher water content. In this context, it is emphasized that both the biophysical variables contributing to an environment and the physical features of animals are complex. Reduction of weather conditions to one or two variables, such as cloud cover and cooling power, is a radical simplification. However, this type of ap-

proach may be one of the few productive methods available for assessing the influence of environmental conditions on the behavior of nonhuman primates.

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