

Behavioral Adaptations to Heat Stress and Water Scarcity in White-Faced Capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica

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ABSTRACT We examined thermoregulatory behaviors in a wild population of white-faced capuchins (*Cebus capucinus*) inhabiting a highly seasonal dry forest in Santa Rosa National Park (SRNP), Costa Rica. The dry season in SRNP lasts ~5 months and is characterized by high ambient temperatures regularly exceeding 37°C, low relative humidity, and the near absence of precipitation. This study demonstrates that capuchins rest more and travel shorter distances during the hottest and driest hours of the day, and suggests that they extend their tongues to lower body temperature via evaporative cooling. Seasonal weather patterns and group movement data reported here are based on 940 h of observations on three social groups of capuchins (wet season: 370 h, dry season: 570 h). In the dry season, the proportion of time spent resting increased at higher temperatures whereas

the proportion of time spent traveling decreased. Distance traveled between location points taken at half-hour intervals decreased significantly as temperature increased, although the correlation was not strong. Capuchins exposed their tongues during hot, dry, windy conditions, and this behavior was much more frequent in the dry season. Temperature was significantly higher and humidity significantly lower for “tongue-out” events than expected for a random event in the dry season. Finally, as surface water became scarce, home-range areas of heavy use became increasingly centered on the remaining permanent water sources. These results suggest that heat stress and water scarcity are significant influences on the behavior of capuchins in hot, dry conditions. *Am J Phys Anthropol* 138:101–111, 2009. © 2008 Wiley-Liss, Inc.

Like all homeothermic animals, primates can maintain an approximately constant body temperature with cardiovascular adjustments only within a particular range of ambient temperatures known as the thermoneutral zone (TNZ). At ambient temperatures above or below the TNZ, primates may regulate their body temperature with both physiological and behavioral adjustments (Elizondo, 1977). Physiological processes used by primates to regulate body temperature outside the TNZ include sweating (e.g., common squirrel monkey: *Saimiri sciureus*: Nadel and Stitt, 1970; Stitt and Hardy, 1971; Japanese macaque, *Macaca fuscata*: Nakayama et al., 1971; rhesus macaque, *Macaca mulatta*: Elizondo, 1977) and panting (thick-tailed greater bush baby, *Otolemur crassicaudatus*, slow loris, *Nycticebus coucang*, potto, *Perodicticus potto*: Hiley, 1976) to lower the body temperature, and shivering (Elizondo, 1977) to raise the body temperature. Behavioral processes used to regulate body temperature vary widely across species and locations, and can include resting in shade (yellow baboon, *Papio hamadryas cyanocephalus*: Stelzner, 1988), adopting certain body postures (yellow baboon: Stelzner and Hausfater, 1986; black-and-gold howler monkey, *Alouatta caraya*: Bicca-Marques and Calegario-Marques, 1998), altering activity schedules (yellow baboon: Stelzner, 1988), adjusting interindividual spacing (long-tailed macaque, *Macaca fascicularis*: Schino and Troisi, 1990; Japanese macaque: Wada et al., 2007), inhabiting caves (chacma baboon, *Papio ursinus*: Barrett et al., 2004), hibernating (fat-tailed dwarf lemur, *Cheirogaleus medius*: Dausmann et al., 2004), sand-bathing (chacma baboon: Brain and Mitchell, 1999; white-front capuchins,

Cebus albifrons: Field, 2008), and orienting the ventrum away from the sun (yellow baboon: Pochron, 2000) or wind (yellow baboon: Stelzner and Hausfater, 1986).

There are two broad methods of dealing with heat stress, which we define as the external forces acting to move an organism away from thermal homeostasis above the TNZ. Following Stelzner and Hausfater (1986), we will refer to these methods as behavioral thermoregulation and heat stress avoidance. There are at least four nonexclusive strategies that an animal may use to moderate its body temperature when ambient temperature exceeds the TNZ: 1) selecting cooler microclimates, 2) avoiding physical exertion, 3) adopting body postures that facilitate convection or radiation of body heat, and 4) deliberately exposing moist body surfaces or respirating heavily to promote evaporative heat loss. Strategies 1 and 2 may be considered as avoidance of heat stress

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whereas strategies 3 and 4 may be considered as behavioral thermoregulation (Stelzner and Hausfater, 1986).

This study investigates strategies 2 and 4 in wild white-faced capuchins (*Cebus capucinus*) inhabiting a seasonally hot and dry forest. Capuchins are known to be highly adaptable monkeys. They are generalists with respect to both diet and habit, and they can thrive in a wide range of environmental conditions (Fragaszy et al., 2004). Yet, like other haplorhine primates (Stitt and Hardy, 1971; Johnson and Elizondo, 1979; Le Maho et al., 1981; Genoud et al., 1997), they likely possess a relatively narrow TNZ compared to many other kinds of mammals (Leary, 2008). Hill et al. (2004) argue that temperature represents an important ecological constraint on primates, and we propose that capuchins living in a hot, dry environment are good subjects for the study of behavioral strategies to regulate body temperature.

We also examine the influence of water scarcity on capuchin behavior and ranging patterns. Water balance is a critical factor to consider for interpreting responses to heat stress in dry environments. At temperatures above the TNZ, the maintenance of thermal balance in simians depends chiefly on the effectiveness of evaporative heat loss (Elizondo, 1977). Thus, increasing heat stress leads to increased water loss via evaporation and ultimately a loss of thermoregulatory ability if the animal becomes too dehydrated. Brain and Mitchell (1999) found that drinking water can reduce body temperature in chacma baboons living in an extremely arid environment by as much as 3°C over the course of an hour. We expect both high temperature conditions and water scarcity to be important influences on the behavior patterns of our study capuchins. In particular, we expect capuchins to respond to heat stress by reducing physical activity and increasing usage of areas that contain permanent water. This study seeks to answer the following specific questions:

1. Does the potential for heat stress vary seasonally?
2. Does the activity budget change with ambient temperature? If so, do the changes appear to minimize energetically costly activities at high temperatures?
3. Do capuchins use specific self-directed behaviors to regulate body temperature?
4. Is home-range usage affected by water scarcity?

METHODS

Study site

This study was carried out in Santa Rosa National Park (SRNP), one of the four nationally protected areas in northwestern Costa Rica that comprise the 147,000 hectare Area de Conservación Guanacaste. SRNP encompasses 49,515 hectares of mosaic habitat dominated by highly seasonal dry deciduous forest (Fedigan et al., 1996; Fedigan and Jack, 2001). The region experiences a dry season from mid-December to mid-May, and a rainy season from late-May to early-December. The dry season in SRNP is characterized by high ambient temperatures regularly exceeding 37°C, low relative humidity, and the near absence of precipitation. Large tracts of regenerating forest become completely devoid of leaves during the late dry season, while small patches of primary and old-secondary forest remain green. Although surface water

remains naturally in some areas of the park throughout the year, the study area is particularly dry and nearly all natural water sources used by the monkeys in this study dry up completely before the end of the dry season. During the driest months, the capuchins may utilize small artificial sources of water, such as cattle troughs and outdoor sinks. These exist as a result of the park's legacy as a former cattle ranch and its current infrastructure to accommodate tourists and researchers.

Study groups and subjects

We observed three social groups (CP, EX, and LV) of well-habituated white-faced capuchins and collected focal data on all sexually mature individuals in all the three groups. The average age at first birth in our study females is 6 years, at which point they appear socially equivalent to older females. However, male white-faced capuchins reach sexual maturity (subadulthood) before they attain the robust body size and high social status associated with complete physical maturity (Fedigan et al., 1996). Thus, our sample was comprised of individuals belonging to three age/sex categories of sexually mature individuals: subadult males (6–10 years), adult males (>10 years), and adult females (>5 years) (Fedigan et al., 1996).

CP group ($N = 18$ –21 members) included three adult males, two subadult males and three adult females during the study. EX group ($N = 6$ –9 members) included one to two adult males, no subadult males and two to three adult females over the course of the study. LV group ($N = 14$ –17 members) included one adult male, three subadult males, and five adult females during the study.

Data collection

Seasonal weather patterns and group movement data reported here are based on 940 total hours of observation from two separate field seasons. The first data collection period encompassed 2.5 early wet season months from mid-May 2006 until the end of July 2006. The second data collection period lasted from the beginning of January 2007 until the end of April 2007 and included the four hottest, driest months of the dry season. Most analyses presented here focus on data collected during the dry season months of January–April. We followed a single group from sunrise to sunset whenever possible (~5:00–18:00 h), although collection days of shorter length occurred frequently. We utilized two major data-collection procedures: half-hourly recording of temperature, humidity, and location; and focal animal samples. These methods are described in detail below.

Temperature, humidity, and location. We recorded ambient temperature and relative humidity with a thermohygrometer (Fisher Scientific) every 30 min on the half-hour. The precision of the device was 0.1°F (0.056°C) for temperature and 0.1% for relative humidity. Microclimate variation in the patchy regenerating forest of SRNP can significantly affect temperature (Chapman, 1988). To more accurately represent the conditions actually experienced by the capuchins, we took temperature and humidity readings only when observers were standing beneath monkeys. We recorded locations concurrently on the half-hour using Garmin GSP 12 and Garmin GPS 76 handheld GPS receivers.

TABLE 1. Data collected per individual

Group	Focal	Age/sex class	No. of instantaneous samples	No. of focal samples	Follow hours
CP	BH	Subadult male	222	6	9.3
	ED	Adult female	276	6	11.7
	LL	Adult male	282	6	11.7
	MO	Subadult male	268	6	11.4
	NN	Adult male	275	6	11.3
	RR	Adult male	283	6	11.8
	SA	Adult female	280	6	11.6
	SI	Adult female	277	6	11.7
	SS	Adult female	290	6	12.0
	TT	Adult female	270	6	11.2
	ZZ	Adult female	272	6	11.4
			2,995	66	125.1
EX	AN	Adult female	330	7	13.8
	AR	Adult male	335	7	14.0
	AT	Adult male	327	7	13.5
	CL	Adult female	337	8	14.0
	EL	Adult female	329	7	13.7
			1,658	36	69.0
LV	BB	Adult female	315	7	13.3
	CH	Adult female	335	9	13.9
	CY	Adult male	310	7	13.0
	DL	Adult female	297	7	12.5
	KL	Adult female	306	7	13.0
	MZ	Subadult male	327	7	13.6
	NU	Subadult male	317	7	13.4
	SL	Adult female	346	9	14.4
	WW	Subadult male	332	7	13.9
			2,885	67	121.0

Focal animal samples. This study uses focal animal samples (Altmann, 1974) from the dry season months only, drawing on 315 total follow hours on 25 individuals (Table 1). F.A.C. collected or oversaw in person the collection of all behavioral data analyzed in this study. We followed each focal animal for 2 h continuously, during which we recorded all self-directed behaviors and social interactions involving the focal animal. We took instantaneous samples of the focal animal's state behavior every 2.5 min throughout the entire focal sample.

Data analysis

Activity budgets. We calculated activity budgets in the dry season from instantaneous samples of state behavior during focal samples and examined proportion of time spent in five mutually exclusive behavior states: Rest, travel, forage, social, and vigilant. Behavior states that did not fit into one of these five categories were relatively rare and were excluded from this analysis. We calculated proportions separately for each focal animal ($N = 24$) then averaged across subjects. One individual (NU) was excluded from this analysis because he had no follow-time in the "low" temperature category (see below). We used the temperature recorded at the half-hour nearest to the instantaneous sample to assign the observation into low, medium, or high temperature category. We did not include observations if the nearest half-hour with a recorded temperature was more than 15 min away. We defined temperature category boundaries as +1 and -1 standard deviation from the mean of all systematically obtained temperature readings in the dry season ($N = 1,073$, Table 2). This resulted in the following category limits: 1) low: $T \leq 26.834^{\circ}\text{C}$, 2) medium: $26.834^{\circ}\text{C} < T < 33.510^{\circ}\text{C}$, 3) high: $T \geq 33.510^{\circ}\text{C}$. The limits for the medium temperature category correspond approximately to the TNZ reported by Stitt and Hardy

(1971) for squirrel monkeys ($25\text{--}35^{\circ}\text{C}$), neotropical monkeys that are closely related to capuchins. Similar data for capuchins were not available. We applied an arcsine transformation on all proportions to stabilize the variance for statistical tests. We analyzed for differences among temperature categories using Friedman's tests, since the variance in proportions for some behaviors still failed to meet equality assumption necessary for parametric tests. We used *posthoc* Wilcoxon tests to examine pairwise category differences where the Friedman's test was significant.

Distance traveled. We calculated distance between location points taken at successive half-hours throughout the day in the dry season months and assigned an average temperature to each 30-min interval by averaging the two temperatures that bound it. Thus, each 30-min interval contributed one distance and one temperature. Locations and temperatures for missed half-hour samples were excluded from the analysis rather than estimated; this occurred when we temporarily lost the focal group or when it was raining (to avoid damaging the instruments). We analyzed the three social groups separately to avoid group-size or home-range quality effects that would confound any data pooling across groups. We applied square-root transformations to distances to satisfy the parametric assumption of equal variances and examined the relationship between temperature and distance traveled using multiple regression analysis carried out in R, version 2.3.1 (R Development Core Team, 2007). Square-root of distance traveled was the response variable and we entered three continuous explanatory variables into the model: temperature, relative humidity, and distance traveled in the previous half-hour. We excluded from the analysis any data points missing any of these three variables and obtained the minimal adequate model for each group following Crawley (2002). We first

TABLE 2. Temperature and humidity trends by month

Month	Mean	Absolute min	Avg daily min	Avg daily max	Absolute max	Mean daily diff
Temperature (°C)						
May 06	29.7	24.7	25.7	32.8	37.1	7.2
Jun 06	27.2	23.4	24.7	29.2	32.3	4.6
Jul 06	27.0	23.1	25.0	28.9	31.7	3.9
Jan 07	29.1	22.6	24.6	32.4	34.7	7.8
Feb 07	30.2	20.7	23.6	34.5	37.8	10.9
Mar 07	30.8	21.6	25.2	34.8	37.8	9.6
Apr 07	31.3	22.6	25.4	34.9	38.9	9.4
Relative humidity (%)						
May 06	69.3	39.5	58.0	85.4	91.9	27.4
Jun 06	82.4	51.0	74.2	91.4	99.7	17.2
Jul 06	84.7	70.1	77.3	92.1	98.9	14.8
Jan 07	62.2	44.4	52.6	74.7	80.6	22.1
Feb 07	53.9	22.6	41.4	75.2	91.9	33.9
Mar 07	55.0	38.2	45.4	70.7	78.8	25.3
Apr 07	60.8	36.1	48.0	78.4	94.3	30.4

fit the maximal model by including all three explanatory variables and their interaction terms, and then removed nonsignificant terms in a backward selection process until only significant terms remained.

Thermoregulation and self-directed behaviors. We examined the relationship between several self-directed behaviors and 1) ambient temperature and 2) relative humidity to determine if these behaviors occurred in weather conditions that were significantly different from the systematically collected (“baseline”) weather data. Baseline for this analysis is based on all temperature and relative humidity measurements that were collected on a half-hour during a focal sample in the dry season ($N_{\text{temperature}} = 583$, $N_{\text{humidity}} = 581$). The self-directed behaviors tested include: self-groom, drink water, rub hand against branch, scratch, sneeze, tongue-out, and yawn. Not all of these behaviors are hypothesized to play a role in thermoregulation, but for thoroughness, we included every self-directed behavior that occurred greater than 50 times. The hypothesized role of urine-washing in thermoregulation is the subject of several other studies (Robinson, 1979; Roeder and Anderson, 1991; Campos et al., 2007; Miller et al., 2007; Campos, 2008) and is not dealt with here. For this analysis, we assigned the temperature or relative humidity recorded at the half-hour nearest to the behavior’s occurrence. Observations were not included if the nearest half-hour with a recorded temperature or relative humidity was more than 15 min away.

The assigning procedure described above means that each temperature associated with a behavior is one of the 583 baseline temperatures. Thus, for a behavior occurring N times, the N assigned temperatures (one for each occurrence of the behavior) are in essence a single “draw” of N baseline temperatures sampled with replacement. We used bootstrapping to examine if the mean of this single-observed draw was unusual by comparing it to the means of 10,000 simulated draws. Each simulated draw consisted of N baseline temperatures selected randomly with replacement from the entire set of baseline temperatures. The values occupying the highest and lowest 0.5% positions after sorting the 10,000 means were taken as the upper and lower bounds for 99% confidence intervals. The result is considered to be significant if the observed mean temperature or relative humidity at which a self-directed behavior occurred falls outside the confidence interval.

Home-range usage. We estimated home ranges using the “adaptive sphere of influence” Local Convex Hull method (α -LoCoH) (Getz and Wilmer, 2004; Getz et al., 2007). α -LoCoH is a recently developed approach to modeling home ranges and utilization distributions that performs better than standard kernel methods, particularly in cases where there are “hard boundaries” and substantial unused areas within the home range (see Getz et al., 2007 for details). These properties make α -LoCoH well-suited for dealing with the patchy distribution of forest at SRNP, which may include large clearings and grasslands that are not used by the monkeys. We calculated home ranges using only points taken systematically at half-hour intervals. We used the LoCoH R script and graphical user interface available at <http://locoh.cnr.berkeley.edu>. The script was executed in R, version 2.3.1 (R Development Core Team, 2007), and the results were exported to ArcGIS 9.2 for analysis. The software implementation of LoCoH for R makes use of the following packages: *adehabitat* (Calenge, 2006), *gpclib* (Peng, 2007), *ade4* (Chessel et al., 2004), and *shapefiles* (Stabler, 2006).

The α -LoCoH method requires a user-specified parameter, α , that influences the shapes of the utilization distribution isopleths (UDIs). We followed Getz et al. (2007) in choosing an initial value of α equal to the maximum distance between any two points in a given set, then adjusting until small lacunae were removed and large unused areas remained outside of the 100% UDI. Although this introduces a degree of arbitrariness, the α -LoCoH method is relatively robust against suboptimal choices of α (Getz et al., 2007). By contrast, the shapes of the probability contours generated by commonly used parametric kernel methods depend heavily on the choice of a smoothing factor (h); there is no universally accepted method for choosing a value of h that is biologically relevant for a given data set of ranging points.

RESULTS

Seasonal trends in temperature and relative humidity

Temperature was more variable over the course of a typical day in the dry season months than in the wet season months (see Fig. 1). Temperature peaked between hours 1300–1330 and was lowest between hours 0600–0630 (see Fig. 1). Mean daily minimum temperatures were approximately equal across the seven study

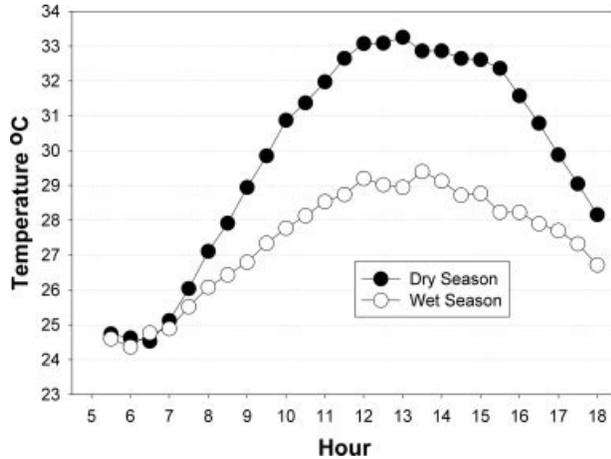


Fig. 1. Mean temperature by hour of the day, calculated from half-hourly measurements of temperature taken whenever observers were with study subjects.

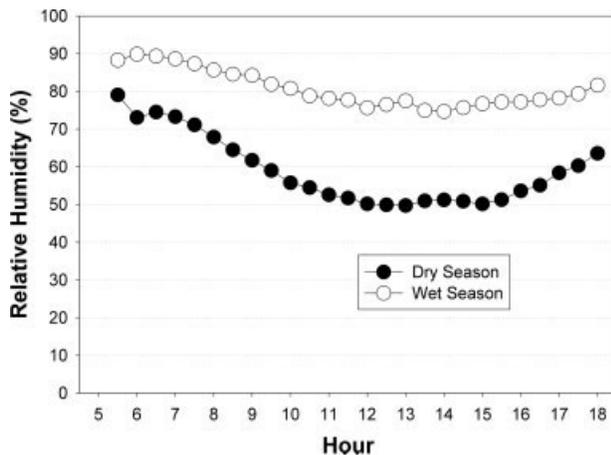


Fig. 2. Mean relative humidity by hour of the day, calculated from half-hourly measurements of humidity taken whenever observers were with study subjects.

months, while mean daily maximum temperatures were generally higher in the dry season months (Table 2). The hottest month, April, occurred at the end of the dry season. Relative humidity was lower on average across all hours of the day in the dry season months than in the wet season months (see Fig. 2). Although relative humidity varied little throughout the day in the wet season months, during the dry season there was a distinct trough in the early afternoon with minimum values occurring between hours 1200 and 1500. February and March were the two driest months (Table 2). Temperature and humidity values in May were intermediate, presumably because the transition between dry and wet seasons occurred in May.

Activity budget at low, medium, and high temperatures during the dry season

Table 3 summarizes the Friedman's tests for within-behavior differences under the three temperature condi-

tions. Proportion of time resting increased consistently with increasing temperature (Table 3). Within the resting category, significant differences were found between medium and low conditions and between high and low conditions; the medium-high difference approached significance. Resting was the most frequently observed behavior state in the high temperature condition. Both the proportion of time traveling and proportion of time foraging decreased consistently with increasing temperature (Table 3). Significant differences were found between all temperature conditions for both traveling and foraging (Table 3). Foraging was the most frequent behavior overall, particularly in the low temperature condition where it accounted for nearly half of the activity budget. No differences were found among temperature conditions for proportion of time engaged in social behavior or vigilance.

Influences on distance traveled

The minimal adequate models of distance traveled are presented in Table 4. Distance traveled in the previous half-hour was retained as a significant explanatory variable for all three groups. Temperature was a significant explanatory variable for EX group and approached significance for LV group. Relative humidity was eliminated from all the three models, as were all interaction terms. Although these variables produced statistically significant models for all the three groups, the adjusted R^2 values were uniformly low (CP: 0.083, EX: 0.156, LV: 0.135). This indicates that the explanatory power of the models was relatively weak.

Other potential thermoregulatory behaviors during the dry season

Tongue-out and Yawn occurred in significantly hotter and drier conditions compared to baseline; that is, they occurred at mean temperatures above the 99% bootstrap confidence interval (BCI) for temperature and below the 99% BCI for humidity (Table 5). Scratch and Rub Hand occurred in significantly cooler and more humid conditions compared to baseline, below the 99% BCI for temperature and above the 99% BCI for humidity (Table 5). All other self-directed behaviors occurred in conditions that did not differ significantly from baseline.

Seasonal variation in ranging patterns

Home-range boundaries and ranging patterns changed considerably between wet and dry season months (Figs. 3–5). Home ranges were larger in all three groups during the dry season months, but this result could simply be an artifact of the greater number of location points that were used for constructing the UDIs in the dry season (location points in dry season: CP = 463, EX = 221, LV = 406; location points in wet season: CP = 272, EX = 72, LV = 222). This caveat applies to all home-range analyses presented here; nevertheless there were a few unambiguous seasonal trends with respect to permanent water sources.

More locations with permanent water fell within at least one group's home range during the dry season. The increased use of these locations was particularly striking. During wet season months, one permanent water source was located in CP group's 75% UDI and two were located in LV group's 100% UDI; none were located in EX group's

TABLE 3. Friedman's tests of activity budget differences at low, medium, and high temperatures

	Temperature category ^a			N	Chi-Square	Df	P	Posthoc Wilcoxon tests P-values		
	Low	Medium	High					Med-Low	High-Med	High-Low
Rest	0.076	0.227	0.335	24	25.2	2	<0.001*	<0.001*	0.074	<0.001*
Travel	0.232	0.176	0.133	24	14.083	2	0.001*	0.021*	0.014*	0.001*
Forage	0.461	0.361	0.282	24	15.25	2	<0.001*	0.002*	0.015*	<0.001*
Social	0.060	0.077	0.080	24	4.442	2	0.115	—	—	—
Vigilant	0.139	0.125	0.127	24	0.083	2	0.989	—	—	—

^a Values indicate proportion of samples in the following temperature categories: low: $T \leq 26.834^{\circ}\text{C}$; medium: $26.834^{\circ}\text{C} < T < 33.510^{\circ}\text{C}$; high: $T \geq 33.510^{\circ}\text{C}$.

* Significant results using $\alpha = 0.05$.

TABLE 4. Multiple regression analysis with square root of distance traveled as the response variable and temperature, relative humidity, and distance traveled in the previous half-hour entered as explanatory variables

Group					
CP	Model	Adj. R^2	df	F	P
			1, 345	32.43	<0.001
		Variables	df	F	P
		Previous distance	1	32.428	<0.001
		Residuals	345		
	Coefficients	Estimate	t	P	
	(Intercept)	5.752	11.862	<0.001	
	Previous distance	0.302	5.695	<0.001	
EX	Model	Adj. R^2	df	F	P
			2, 164	16.33	<0.001
		Variables	df	F	P
		Previous distance	1	24.641	<0.001
		Temperature	1	8.023	0.005
	Residuals	164			
	Coefficients	Estimate	t	P	
	(Intercept)	12.903	4.187	<0.001	
	Previous distance	0.287	3.712	<0.001	
	Temperature	-0.259	-2.832	0.005	
LV	Model	Adj. R^2	df	F	P
			2, 308	25.1	<0.001
		Variables	df	F	P
		Previous distance	1	46.701	<0.001
		Temperature	1	3.491	0.063
	Residuals	308			
	Coefficients	Estimate	t	P	
	(Intercept)	9.273	4.062	<0.001	
	Previous distance	0.335	6.17	<0.001	
	Temperature	-0.132	-1.868	0.063	

The models shown are minimal adequate models that retain only explanatory variables that are significant or that approach significance.

home range. Thus, none of the six permanent water sources was located inside a zone of heavy use (<50% UDI) by any group during the wet season months. By contrast, in the dry season months all three groups had at least one water source in an area of heavy use. CP group's zone of heaviest use (25% UDI) was centered on a permanent water source, one additional water source was located in the 75% UDI, and two more were in the 100% UDI (see Fig. 3). One permanent water source was located in EX group's 25% UDI (see Fig. 4). Finally, LV group had

two permanent water sources in their 25% UDI, one in the 50% UDI, and one in the 100% UDI (see Fig. 5).

DISCUSSION

Energy expenditure decreases at high temperatures

Capuchins at SRNP appear to follow a strategy of heat stress avoidance and behavioral thermoregulation in which energy expenditure is minimized at high temperatures and maximized at low temperatures. We base this assessment on differences in the proportion of time spent in three behavior states: rest, travel, and forage. Resting is clearly the least energetically costly behavior state. Capuchins have a variety of resting postures that tend to be used in specific contexts (Fragaszy et al., 2004); however, only one of these postures occurs commonly during daytime resting in warm, dry conditions. During the day, monkeys typically rest on their ventrum with all four limbs hanging down below the substrate. This posture is identical to the "stretched" posture described by Bicca-Marques and Calegario-Marques (1998) as a heat-dissipating posture in black-and-gold howler monkeys. Proportion of time resting increased consistently with temperature. Resting was the most frequently observed behavior state in the high temperature condition, accounting for 33.5% of the activity budget. This represents a marked increase from the low temperature condition, at which resting accounts for only 7.6% of the activity budget. Traveling and foraging are both high-cost activities. Foraging by capuchins is often extractive and vigorous, with monkeys expending considerable effort to pry away bark, break twigs, and penetrate hard-husked fruits. Foraging monkeys make frequent use of small substrates that require precise body control, bracing, and powerful grip. Likewise, the mode of arboreal locomotion used by capuchins involves frequent running, leaping, and climbing. In the low temperature condition, foraging and traveling together accounted for ~70% of the activity budget. Proportion of time traveling and foraging both decreased consistently with increasing temperature. Overall, there is a clear trade-off pattern in capuchins' activity budget for reduced energy expenditure at high temperatures and increased energy expenditure at low temperatures, and we propose that water conservation is an important underlying principle. At high temperatures, evaporative heat loss becomes the primary mechanism upon which capuchins rely to maintain a stable body temperature (Elizondo, 1977). Because evaporative heat loss requires the loss of moisture, by avoiding overexertion at high ambient temperatures capuchins are also minimizing water loss.

TABLE 5. Mean temperature for self-directed behaviors compared to 99% bootstrap confidence intervals (BCI)

Behavior	N	Temperature			Relative humidity		
		Mean (°C)	99% Lower BCI	99% Upper BCI	Mean (%)	99% Lower BCI	99% Upper BCI
Self-groom	544	30.55	30.35	31.09	57.21	55.48	57.99
Drink water	62	31.11	29.65	31.77	55.88	53.02	60.64
Rub hand	232	29.69 ^a	30.17	31.29	59.08 ^a	54.86	58.70
Scratch self	2003	30.06 ^a	30.54	30.91	59.38 ^a	56.07	57.40
Sneeze	100	30.86	29.87	31.55	55.42	53.85	59.77
Tongue out	253	31.94 ^a	30.20	31.25	50.54 ^a	54.94	58.58
Yawn	204	31.75 ^a	30.14	31.29	53.44 ^a	54.71	58.82

^a Mean outside the 99% BCI.
 Boxed cells indicate which confidence limit was exceeded.

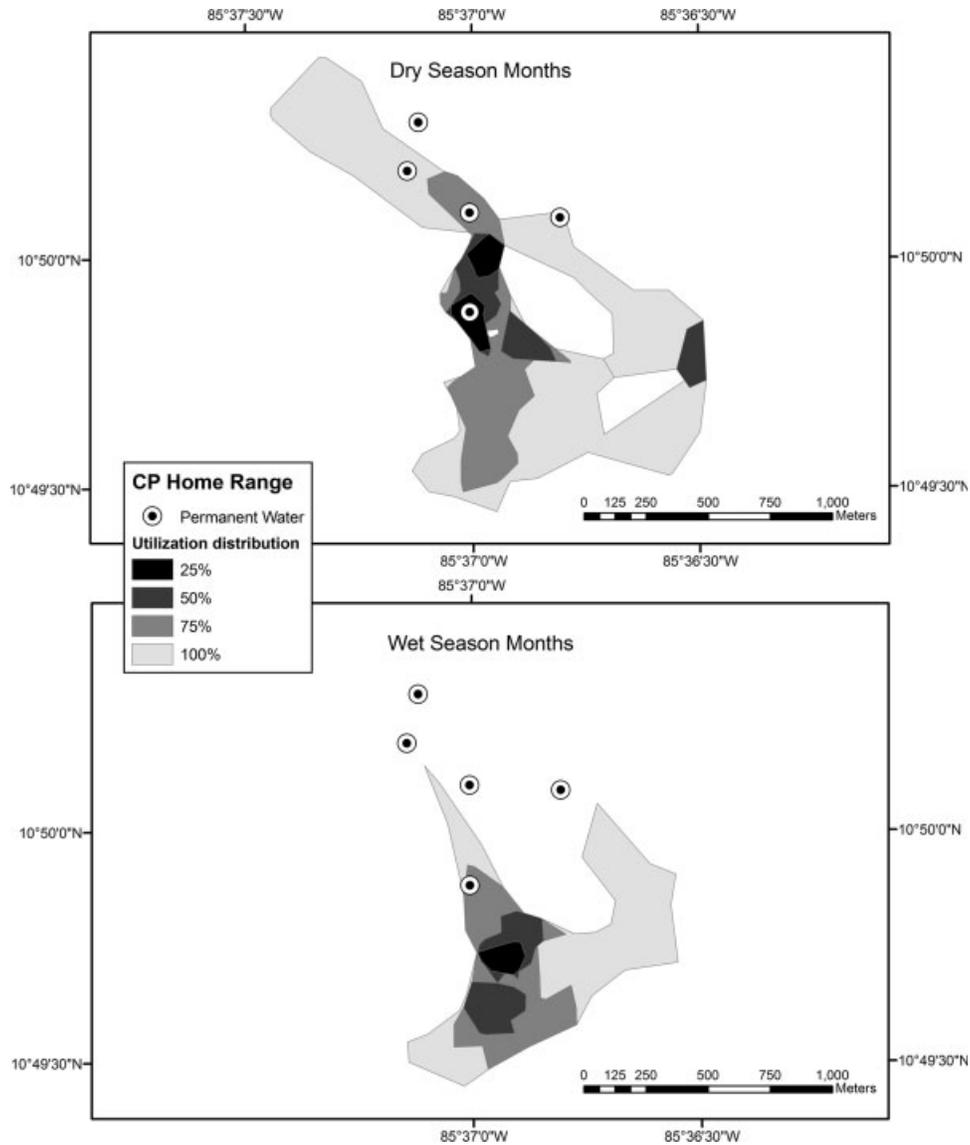


Fig. 3. Adaptive Local Convex Hull (a-LoCoH) home ranges in dry and wet season months for CP group. Home ranges are based on location points taken at half-hour intervals for all focal subjects in CP group. Utilization distribution isopleths (i.e., polygon boundaries) indicate the probability of encountering an animal within that polygon at any given time.

Temperature has a weak effect on distance traveled

We predicted that distance traveled would vary in inverse relation to temperature. Although this prediction

was supported in EX group and approached significance in LV group, the influence of temperature on distance traveled was weak overall. The model's poor fit could be due to any combination of the following issues. First, the two environmental variables included in the model,

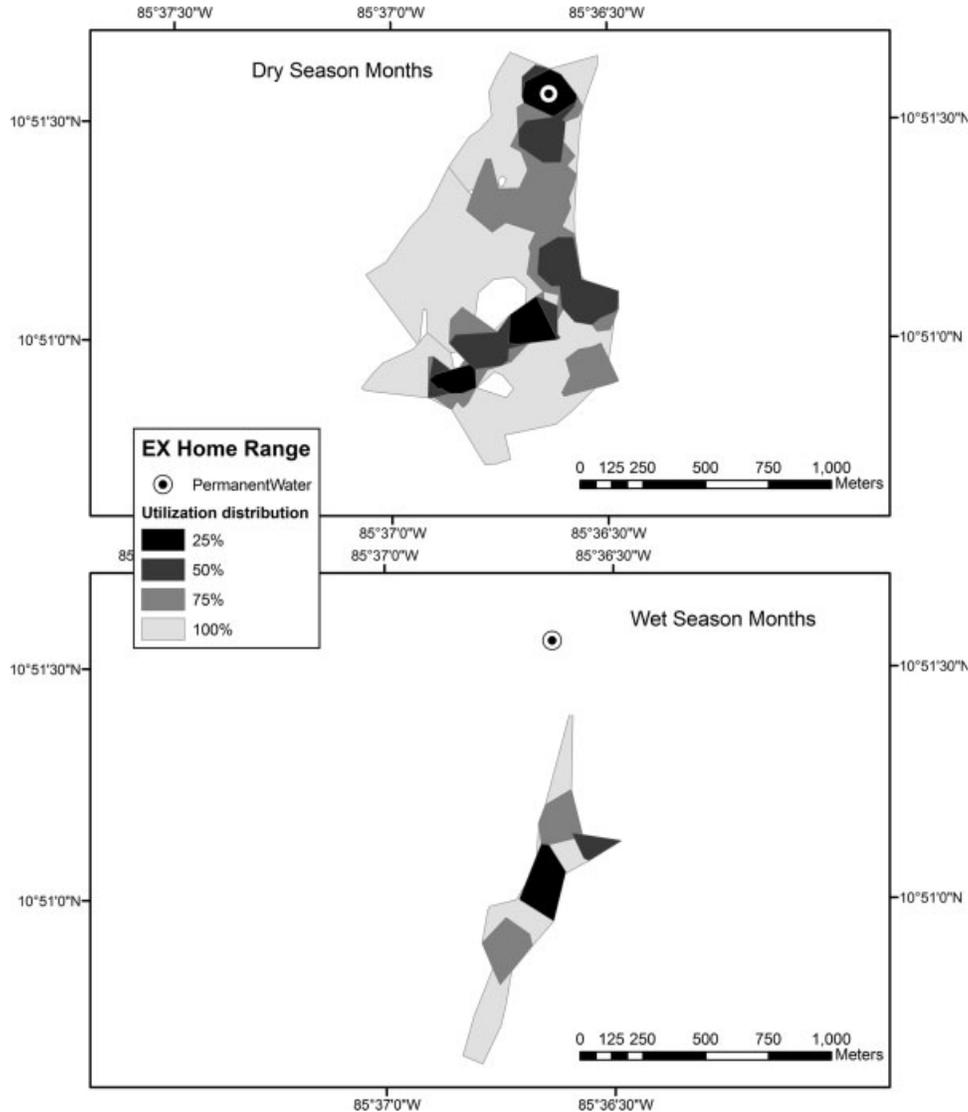


Fig. 4. Adaptive Local Convex Hull (a-LoCoH) home ranges in dry and wet season months for EX group. Home ranges are based on location points taken at half-hour intervals for all focal subjects in EX group. Utilization distribution isopleths (i.e., polygon boundaries) indicate the probability of encountering an animal within that polygon at any given time.

ambient temperature and relative humidity, can produce at best a very rough approximation of the thermal conditions actually perceived by the monkeys. Perceived temperature also depends on wind speed, solar radiation, and nonlinear interactions between all of these variables. Although Hill et al. (2004) proposed an index for perceived environmental temperature that integrated these factors for chacma baboons, such an index cannot be easily applied to different species with different thermal characteristics. For example, the effects of humidity on perceived temperature depend heavily on the degree to which an animal relies on evaporative cooling for thermoregulation; the effects of wind speed depend on insulating characteristics of the fur to resist thermal convection; the effects of solar radiation depend on coat coloration and surface area-to-volume ratios. An accurate biophysical model of capuchins' thermal characteristics with respect to these variables was beyond the scope of this study, and so a greatly simplified model was utilized. A second limitation on the model is that distance

traveled in any given half-hour probably depends on numerous other factors that could not be included in this model. These may include the monkeys' current location relative to food resources or favored resting spots as well as seasonal variation in the desirability of these resources. For example, Pochron (2005) showed that the quality of baobab fruit at a site in Tanzania varied between the dry and lush seasons, causing yellow baboons to change their travel patterns to that resource. In addition, there is probably a large semirandom component to distance traveled that may be affected by events occurring earlier in the day or the location of neighboring social groups and predators. Furthermore, if food availability is lower in the dry season, the capuchins may have been forced to continue traveling long distances during hot periods of the day to meet their nutritional requirements, as in yellow baboons (Pochron, 2001). Finally, it is possible that environmental stress has a genuinely weak effect on distance traveled.

Despite the model's poor fit, a number of conclusions can be drawn. First, distance traveled in the previous

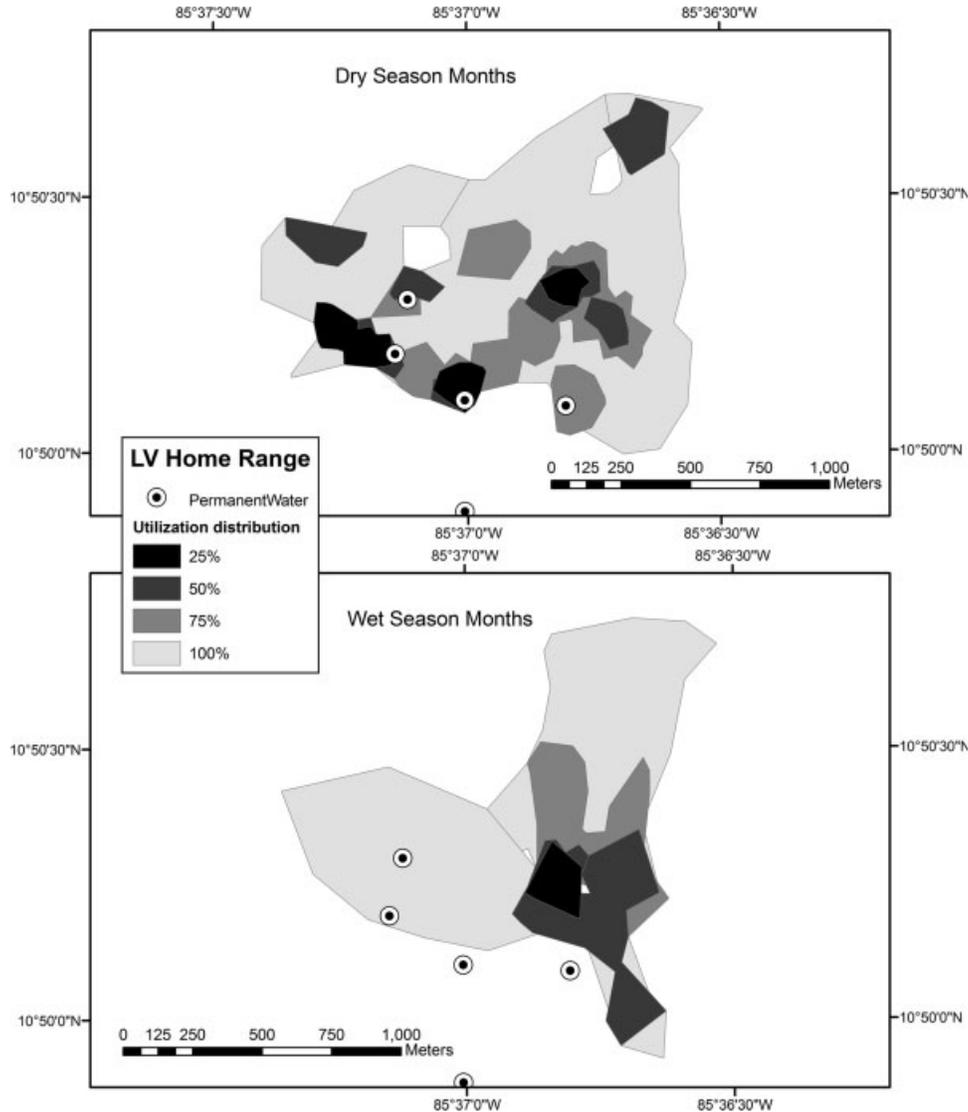


Fig. 5. Adaptive Local Convex Hull (a-LoCoH) home ranges in dry and wet season months for LV group. Home ranges are based on location points taken at half-hour intervals for all focal subjects in LV group. Utilization distribution isopleths (i.e., polygon boundaries) indicate the probability of encountering an animal within that polygon at any given time.

half-hour was retained as a significant predictor of distance traveled in the subsequent half-hour for all three groups. The regression coefficients for distance traveled in the previous half-hour were all positive, ranging from 0.287 to 0.335. This indicates a continuation of the previous state and suggests a pattern of long (relative to 30 min) bouts of traveling and resting rather than frequent short bursts of traveling followed by short recuperation periods. Second, the influence of temperature on distance traveled differed in strength among the three groups. When temperature was retained in the model, the regression coefficients were negative; this partially supports our prediction of an inverse relationship between temperature and distance traveled.

Tongue-out is a thermoregulatory behavior

This study provides strong evidence that capuchins extend their tongues in hot, dry conditions to lower body temperature via evaporative heat loss. “Tongue-out”

occurred at 0.6°C above the 99% BCI for mean temperature and 4.4 percentage points below the 99% BCI for mean relative humidity. Thus, “tongue-out” was nonrandom with respect to both of these environmental indices. Although wind speed data were not recorded, observers noted a strong tendency for “tongue-out” to occur contemporaneously with gusts of wind. Evaporative cooling would be most effective under hot, dry, windy conditions. Yawning also occurred in significantly hotter and drier conditions, but this is likely a byproduct of the association between yawning and resting. Because resting becomes increasingly common at higher temperatures, we cannot conclude that yawning has any thermoregulatory value. By contrast, there is no reason to expect “tongue-out” to occur more frequently in association with resting. Rubbing the hands together and scratching occurred in significantly cooler and more humid conditions compared to baseline. However, it is unlikely that these behaviors are related to thermoregulation. Monkeys appeared to rub their hands most often while forag-

ing for insects, particularly in ant-defended *Acacia* trees. Foraging was significantly more frequent at lower temperatures than at higher temperatures. Scratching is a more puzzling case because it was not obviously associated with any particular behavioral context. However, with mean daily minimum temperatures in the mid twenties Celsius (Table 2) during the dry season at SRNP (approximately equal to the lower boundary of the TNZ), it is doubtful that these capuchins ever experienced significant cold stress. We suggest that scratching is unlikely to have a thermoregulatory function, because the mean temperature at which scratching occurred (30.1°C) is still well above the point at which capuchins would feel need to resort to behavioral mechanisms to raise body temperature.

Home-range usage in the dry season is influenced by permanent water sources

Seasonal ranging differences appeared to be influenced by the locations of permanent water sources in the dry season. All three groups increased their use of areas that contained a permanent water source, including several locations that were never visited during wet season months. Furthermore, the “core” (<50% utilization distribution) of all three group’s home ranges during the dry season included at least one permanent water source. As long as water was available, the capuchins visited at least one source daily to drink. Visits to water holes often had the appearance of goal-directed forays, with long periods of rapid, coordinated travel ending at the water source. These locations appear to dictate the movements of capuchins in SRNP during the dry season, and we suggest that water should be considered a vital resource for capuchins in very dry conditions.

CONCLUSIONS

This study provides evidence that 1) heat stress and water scarcity are significant influences on the behavior of capuchins in hot, dry conditions; 2) the capuchins use a number of behavioral adjustments to avoid overexertion and dehydration; and 3) at least one specific self-directed behavior has a thermoregulatory function. Capuchin monkeys travel shorter distances, rest more, and travel and forage less during the hottest and driest hours of the day. Capuchins expose their tongues during hot, dry, windy conditions to lower body temperature via evaporative heat loss. Finally, as water becomes scarce, home-range areas of heavy use become increasingly centered on the remaining permanent water sources.

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