ABSTRACT

As opportunistic generalists occupying a range of ecological niches, chacma baboons (*Papio ursinus*) are considered a highly flexible species of relatively low conservation priority. Underlying their ecological flexibility is a repertoire of behavioral strategies observed in response to ecological stressors. Although these strategies are relatively well-documented, we know very little about how they impact upon an individual's thermal and energetic physiology, which can influence population-level reproductive potential in the face of climatic warming. Here, we used Niche Mapper^{TM} to construct a biophysical model that integrates morphometric, autonomic, and behavioral inputs to predict the core body temperature of chacma baboons in response to varied microclimate conditions. The predictive integrity of the model was confirmed by comparing model outputs with the core body temperature of a free-living chacma baboon equipped with an intra-abdominal temperature-sensitive data logger. When behavioral thermoregulation was incorporated, our model predicted body temperature within 1.5°C of the observed temperature for 94% of hours. Of the tested behavioral thermoregulatory responses, shade-seeking provided the greatest thermal benefit, reducing predicted core body temperature by an average of 0.9°C during daytime hours. Evaporative heat-dissipation strategies (sweating or swimming) were also highly effective in circumventing hyperthermia in our modeled individual, with an average body temperature reduction of 0.6°C. Our findings underscore the critical importance of behavioral thermoregulatory strategies coupled with access to essential microhabitat features, water and shade, to achieve homeothermy in a warming climate.

KEY WORDS

Behavior; body temperature; Niche Mapper; thermoregulation

T_b = core body temperature
NM = Niche Mapper
UCT = upper critical temperature of the thermoneutral zone
LCT = lower critical temperature of the thermoneutral zone

INTRODUCTION

Chacma baboons (*Papio ursinus*) are habitat generalists and are widely distributed in southern Africa across a range of habitat types (Sithaldeen, 2019). Despite their ecological flexibility (Henzi and Barrett, 2005; Fischer et al., 2019) and low conservation priority (Sithaldeen, 2019), chacma baboons are expected to face substantial climate-induced reductions (~32-75%) in suitable habitat area before 2070 (Hill and Winder, 2019). Suitable habitat area has been identified through correlative species distribution modeling based on environmental characteristics of the species' realized niche over the last 20 years (Hill and Winder, 2019. In addition, chacma baboons confront an increasing threat of anthropogenic disturbance, which already excludes them from central areas of their potential niche due to human population density and anthropogenic land use (Stone et al., 2015). Although baboons often persist in anthropogenically disturbed habitats, ranging in these areas has been associated with elevated glucocorticoid and aggression levels (Chowdhury et al., 2020). With restricted opportunity for genetic adaptation due their slow life-histories (Johnson et al., 2003), and a limited capacity for dispersal (Bowman et al., 2002), the survival of chacma baboons in this changing landscape is likely to depend entirely on physiological and behavioral plasticity (Berg et al., 2010; Fuller et al., 2010). While a handful of studies have examined how environmental pressures impact the broad physiological stress responses of chacma baboons (Weingrill et al., 2004; Chowdhury et al., 2020), and others have recorded the behavioral adjustments made by chacma baboons in response to environmental pressures (Barrett et al., 2004; Hill, 2006), we know very little about how these pressures affect the animal's thermal physiology, nor the direct role that behavioral adjustments have on thermal performance.

Understanding the extent to which chacma baboons can rely on behavior to complement autonomic thermoregulation, as well as defining the limitations of available thermoregulatory responses, is key if we are to make predictive estimates about the survival and distribution of chacma baboons, and other species, in the face of climate change. Observational studies have provided useful accounts of the range of behaviors used by baboons in response to challenging climatic conditions (Stelzner and Hausfater, 1986; Stelzner, 1988; Brain and Mitchell, 1999; Hill, 2006). The direct utility of these behaviors in assisting the animal's thermal performance, however, has received less attention. Similarly, while other studies provide valuable insights into the core body temperature patterns of captive baboons (Funkhouser et al., 1967; Hiley, 1976; Brain and Mitchell, 1999), we know of only one study that has simultaneously recorded the core body temperature of free-living baboons while collecting contemporaneous records of the animal's behavior (Brain and Mitchell, 1999). This baboon study identified high heat load as an important thermal stressor to chacma baboons, highlighting their dependence on drinking water to avoid hyperthermia (Brain and Mitchell, 1999).

An animal's thermoneutral zone (TNZ) is the range of ambient temperatures in which the animal can maintain its core body temperature without adjusting its metabolic rate or increasing evaporative water loss (Porter and Kearney, 2009). Homeothermy—the ability to maintain a core body temperature within a narrow range when subjected to a wide range of environmental temperatures—is achieved through a combination of autonomic and behavioral processes. These processes affect the rate and directionality of the movement of heat energy between an animal and its proximate environment via conductive, convective, radiative, and evaporative heat transfer (Porter and Gates, 1969). When ambient temperatures exceed the critical temperature boundaries of an animal's TNZ, they will engage in autonomic heat dissipation strategies, which may include evaporative heat loss via sweating (Hiley, 1976; Elizondo, 1988; Best and Kamilar, 2018), panting (Funkhouser et al., 1967; Hiley, 1976; Campos and Fedigan, 2009), and vasodilation (Wyss and Rowell, 1976; Kearney and Porter, 2009). Drinking water is essential to replenish water loss through sweating and panting. Indeed, although baboons appear to 'switch-off' sweating – becoming increasingly hyperthermic – to prioritize water conservation when water-deprived, an absence of available drinking water over prolonged periods is likely to be a major threat to baboon homeothermy and survival (Brain and Mitchell, 1999; Mitchell et al., 2009). Alternatively, when ambient temperatures fall below an animal's TNZ, they will engage in autonomic heat retention strategies, which may include vasoconstriction (Funkhouser et al., 1967) and piloerection (Chaplin et al., 2013). Autonomic processes, however, can be costly in terms of energy expenditure and water loss. Behavioral strategies, which tend to be less costly in terms of internal resources spent, are therefore likely to be favored to assist in body temperature regulation (Fuller et al., 2014). However, behavioral thermoregulation can also be costly if it comes at the expense of feeding or drinking opportunities.

In hot conditions, baboons have been observed to select cooler, shaded microclimates including caves (McGrew et al., 2003; Barrett et al., 2004; Hill 2006), sandbathe (Brain and Mitchell, 1999), engage in abducted postures, relocate to elevated microclimates (e.g., trees and cliffs) that promote heat dissipation and decrease incident incoming solar radiation (Stelzner and Hausfater, 1986; Hill, 2006), and spend more time resting (Hill, 2006). In cold conditions, baboons spend more time in warmer microclimates (Hill 2006), sun-bask (Stelzner and Hausfater, 1986), engage in curled or hunched postures that reduce heat dissipation (Stelzner and Hausfater, 1986), and spend more time traveling and feeding (Hill, 2006). Baboons also increase inter-individual body contact (hereafter, huddling) in an apparent attempt to reduce heat loss and maximize heat gain (Stelzner and Hausfater, 1986). Despite the recognition that behavior is an important component of primate thermoregulation among the arsenal of responses an animal uses to protect themselves from climatic stressors, very few studies have directly examined how behavior affects core body temperature patterns in a free-ranging primate (chacma baboons: Brain and Mitchell, 2009; lemurs: Schmid, 2000; Schmid et al. 2000; Dausmann, 2005; vervet monkeys: Lubbe et al., 2014; McFarland et al., 2015, 2019, 2020a,b, 2021, 2022; Henzi et al., 2017).

In addition to the complementary autonomic and behavioral strategies that underpin body temperature regulation, the costs required to maintain a stable core body temperature also vary according to an animal's fundamental morphometric characteristics (Chaplin et al., 2014). Energetically, larger-bodied animals benefit in cooler conditions from their low surface-area to volume ratio, which limits convective heat loss at their body surface (Chaplin et al., 2013) and facilitates heat storage in cold temperatures (Brain and Mitchell, 1999). Further, large-bodied animals can support greater reserves of fat and longer coats (Chaplin et al., 2013). Meanwhile, mammals with small bodies that geometrically facilitate heat dissipation may be advantaged in warm conditions (Brain and Mitchell, 1999; Fuller et al., 2016). As such, body geometry measurements, for example, torso and limb lengths and diameters, are critical to evaluating an animal's body surface available for the movement of heat energy. Pelt characteristics such as follicle density, hair diameter, and pelt depth also affect the insulative properties of the fur layer by enabling a layer of motionless trapped air, which makes up 90% of the pelt's volume (Porter et al., 1994; Gebremedhin and Wu, 2001). Overall pelt reflectivity can affect the incoming solar heat load, and therefore energy requirements for thermoregulation, while coat pigmentation is also thought to provide various adaptive functions including photoprotection, structural support, and microbial resistance (Walsberg, 1983; Hubbard et al., 2010).

Biophysical models such as NicheMapper^{TM} (Porter and Mitchell, 2006; hereafter, 'NM') can be used to predict an animal's thermal performance as a function of environmental conditions, animal morphology, and behavior. NM is a bioenergetic modeling program that simulates the transfer of heat energy and mass between an animal and its microclimate on the premise of understood principles of thermodynamics (Porter and Mitchell, 2006). When accurately parameterized, NM has a broad range of applications, allowing the user to make predictions about an animal's core and surface body temperatures, metabolic rate, evaporative water loss, and oxygen requirements (Kearney et al., 2021). NM has been used to simulate a wide range of extant endotherms, including the American pika (Moyer-Horner et al., 2015), giant panda (Zhang et al., 2018), elk (Long et al., 2014), polar bear (Mathewson and Porter, 2013), grizzly bear (Rogers et al., 2021), koala (Briscoe et al., 2016), and vervet monkey (Mathewson et al., 2020).

This study is in-part modeled after Mathewson et al. 2020, which aimed to validate NM's ability to predict the core body temperature of free-ranging vervet monkeys using field-collected body temperature data for the first time. Here, we build on this previous work and, using a baboon model, evaluate the relative energetic benefits afforded by a range of autonomic and behavioural thermoregulatory options used in response to climatic stress. To do so, we employ NM to examine the relative contribution of autonomic, behavioral, and morphological properties to the thermal performance of chacma baboons in a range of simulated conditions. We adopt a four-stage process to substantiate a meaningful baboon thermal model. First, we simulate the baboon model in controlled environmental conditions (i.e., a simulated metabolic chamber) to delineate the species' thermoneutral zone (TNZ) and identify the upper (UCT) and lower (LCT) critical limits of this zone when thermoregulatory responses or metabolic rate adjustments are needed to maintain a constant core body temperature. Second, we run a series of sensitivity analyses in controlled microclimate conditions to identify which morphological and autonomic parameters have the largest impact in extending the UCT and LCT of the thermoneutral zone. Third, we run an 'optimized' model by simulating the animal sub-model within a microclimate that represents the environmental conditions experienced by our wild baboon population. This facilitates a direct comparison between NM's optimized model predictions of body temperature with core body collected from a wild baboon in those same conditions, which allows us to evaluate the predictive strength of the model. Finally, we run an optimized model that incorporates behavioral options (i.e., huddling, tree-climbing and tree-sleeping, swimming, and shade-seeking) to examine how each behavior—individually and collectively—improves NM's predictions of body temperature. Thus, we can determine the relative importance of each behavioral thermoregulatory strategy in mediating core body temperature. Collectively, our findings will provide new information on the thermal and energetic benefits associated with a range of morphological, physiological, and behavioral traits observed in chacma baboons and other endotherms.

MATERIAL AND METHODS

Data collection

Study site and wild subject data

Data were collected from a troop of wild chacma baboons living on the Samara Private Game Reserve in the Eastern Cape, South Africa (32°22'S, 24°52'E). Baboons were fully habituated to the presence of researchers and were individually recognizable. The troop consisted of 10 adult and 6 subadult males, 17 adult and 4 subadult females, and 22 juveniles and infants. The study troop's habitat is described as a semi-arid shrubland that experiences seasonal climates characterized by hot, wet summers and cold, dry winters (McFarland et al., 2014). This area falls within the geographic range of "suitable habitat area" described by Hill and Winder, 2019. Annual rainfall does not tend to exceed 400mm, and air temperatures tend to fluctuate between -5°C and 40°C (McFarland et al., 2014). On average, daily temperatures reach a maximum of 38.97°C and a minimum of 13.13°C in summer (Dec-Feb), and a maximum of 25.5°C and minimum of 4.02°C in winter (June-Aug) at this site. Additional site climate data for this site can be found in Supplementary Materials, Table A.7.

Core body temperature measurements

Four wild chacma baboons (one adult male, two sub-adult males, and one juvenile female) were immobilized and surgically equipped with intra-abdominal temperature-sensitive data loggers (for full surgical procedures see McFarland et al., 2015). Loggers recorded core body temperature (T_b) at five-minute intervals for a continuous duration of six months (November 2017 to May 2018), after which data loggers were removed. Baboon body masses (kg) were recorded using a scale prior to each surgery. A tape measure was also used to measure the dimension of each baboon body part (head, neck, torso, legs, arms, tail: Supplementary materials, Table A.1). Following both surgeries, recovering animals were monitored by researchers and veterinarians and released back into the group within two hours of immobilization. No long-term sequelae were observed because of surgical intervention, and normal behavior resumed within one or two days. All capture and surgical procedures were approved by the University of the Witwatersrand Animal Ethics Research Committee (Protocols 2017/10/67C) and conformed with the legal requirements of South Africa.

Morphometrics

Additional morphometric data were collected from an unmounted pelt of a subadult chacma baboon procured from a local taxidermist in Graaff-Reinet, Eastern Cape, South Africa. The pelt was shipped to UW-Madison, USA (CITES Export Permit #242429). Dry pelt reflectivity was measured using an ASD portable spectrophotometer across wavelengths from 350 to 2500 nm dorsally and ventrally on the head/neck, torso, forelimbs, and hindlimbs (Supplementary materials, Table A.2). Pelt depth (Table A.1) was determined by measuring the distance from the skin to the pelt surface with a ruler. Hair density was measured by counting the number of hairs within a 1x1cm^2 stencil in three locations on each body area (Supplementary materials, Table A.3). Hair length (cm) was measured by randomly sampling 10 hairs from each body area using a ruler (Supplementary materials, Table A.4). Dorsal and ventral hair diameters (μm) for each body part were measured using a microscope under 400x total magnification with a 0.01mm calibration slide (Supplementary materials, Table A.5). The mean pelt depth, hair length, density, and diameter were calculated for each body region.

Data Analyses

Niche Mapper

Niche Mapper (NM) is a biophysical model that consists of two interacting sub-models (Porter and Mitchell, 2006). The microclimate model defines the local hourly microenvironments available, which are the constraints for solving the hourly heat and mass balance of an animal in the animal model. Implemented cooperatively, these models integrate morphological, autonomic, and behavioral inputs to generate a species-specific energy balance equation, which can be solved to predict the animal's metabolic rate and core body temperature within a specified microclimate (Fig.1).

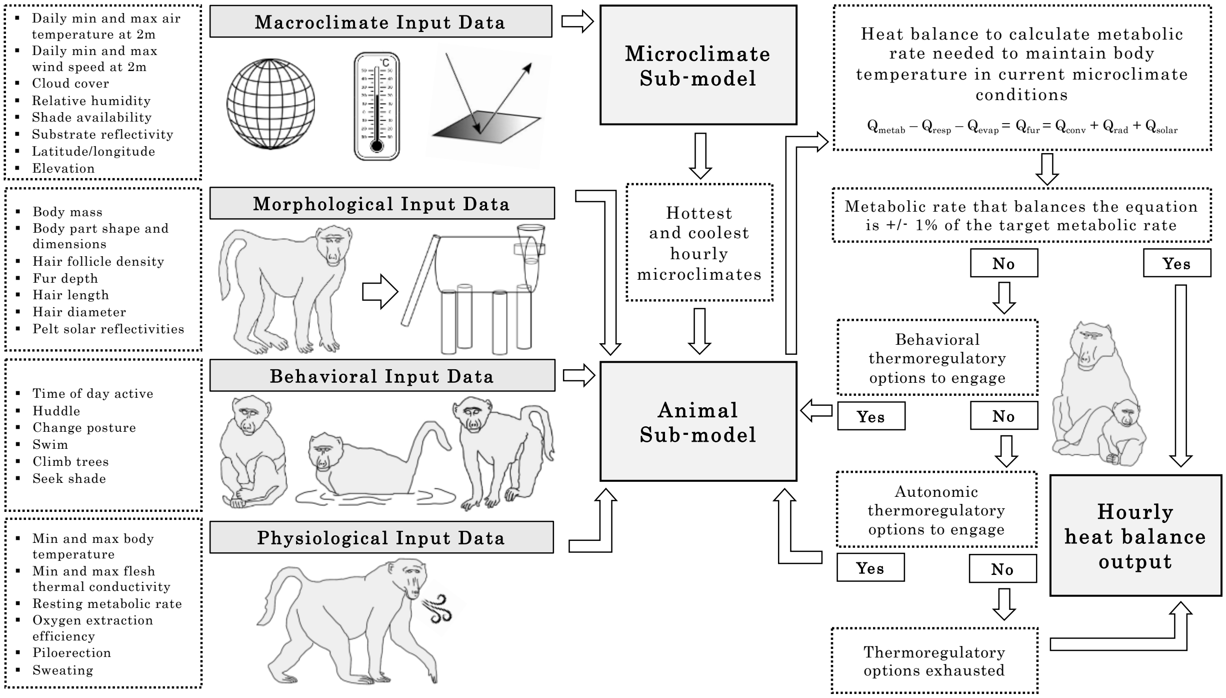

Fig.1. Niche Mapper animal sub-model and microclimate sub-model processing sequence. Adapted from Mathewson et al., 2020.

Microclimate submodel

For a detailed description (i.e., computational subroutines and R scripts) of the NM microclimate submodel see Kearney and Porter (2017). Briefly, the microclimate submodel uses user-supplied inputs of macroclimate data (e.g., daily maximum/minimum air temperature, wind speed, relative humidity at 2m height, and cloud cover), availability of overhead shade, substrate properties, and geographic location to a calculate hourly microclimate conditions from 2m below ground to 2m above ground, including conditions at animal height. When shade is available, microclimate conditions in maximum and minimum shade are calculated to bound the available microclimate conditions.

Animal submodel

In NM, the baboon model's heat loss to, or gain from, the environment is a function of the animal's physiological and morphological characteristics interacting with the microclimate conditions (Kearney and Porter, 2009; Porter and Gates, 1969). For a detailed description (i.e., energy balance equation specifics and computational subroutines) of the NM animal submodel see Kearney et al., 2021. The baboon animal model is a summation of representative 3D shapes for which thermodynamic properties are known and body surface conditions can be computed. For each body part—the head, torso, arms, legs, and tail—a shape option is selected from one of the following simple geometries: cylinder, sphere, ellipsoidal cylinder, ellipsoid, or truncated cone (Fig.2). Morphometric inputs for each body part then include vertical and horizontal diameters and lengths. Pelt reflectivity, pelt depth, hair follicle density, hair diameter, and hair length are specified for each body part on both the dorsal and ventral surfaces. The animal's body mass and density are also supplied by the user. A subadult male was selected as the representative chacma baboon, given they possess a body size that is intermediate for adult males and females. Though comparable in size to an adult female, the subadult male demographic eliminates the variability in energetic demands associated with reproductive status for adult females.

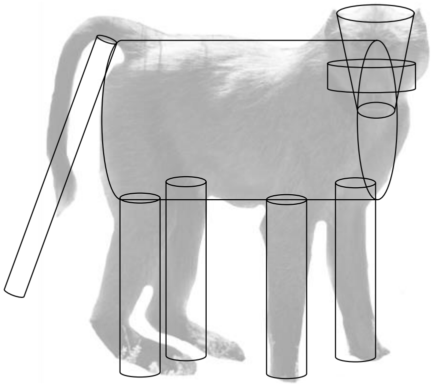

Fig.2. Morphometric inputs illustrated as the 3-dimensional shapes selected in the model.

The surface temperature for any given body part is calculated as a gradient from the core to the skin surface based on the assumed core temperature, evenly distributed heat generation in the tissue, the geometry, and the distance from core to skin. Realistically, certain body tissues (heart, liver, brain, and skeletal muscle) produce disproportionally more heat. However, in our model, the assumption of uniform heat generation is necessary to calculate the temperature gradient from the core to the skin for each body section (head, neck, torso, forelimbs, hindlimbs, tail). The model also allows a - 5°C deviation from core body temperature in tail and leg appendages. This deviation helps minimize metabolic heat production in cold conditions. For a given metabolic rate for a limb in a given set of environmental conditions, the core-to-surface temperature gradient will remain the same when assuming distributed heat generation in the limb's flesh. However, by dropping the regulated core temperature, the gradient shifts down, lowering the surface temperature closer to air temperature. Thus, heat loss to the environment is reduced while assuming the same metabolic rate and uniform heat generation in the limb.

Heat exchange with the environment is determined at the body surface, which is either skin or fur. A fur layer is incorporated into the model as a porous layer of air and keratin, the boundary of which serves as the transmission point for heat fluxes. The fur's thermal conductivity is calculated from hair diameter, length, density and pelt depth. Since the absorption of incoming solar radiation is affected by surface reflectivity, reflectivity, surface area, and silhouette area are needed for solar energy absorption calculations to account for the effect of incoming solar energy (Gates, 2012; Porter et al., 1994; Kowalski and Mitchell, 1979).

The animal's energy balance equation (Kearney and Porter, 2009; Mathewson and Porter 2013) integrates sources and sinks of energy affecting heat movement between the animal submodel and the proximate microclimate conditions generated by the microclimate sub-model. Using this energy balance equation, NM calculates the target metabolic rate (W) needed to maintain a user-supplied core body temperature (°C) range while the simulated animal achieves a heat balance for each hour of the day. When the animal is inactive, the target metabolic rate is set to the resting metabolic rate. In this balance, for the animal to maintain its core body temperature, metabolic heat generation in the flesh (Q_{met}), less heat lost through the respiratory tract (Q_{resp}) must be able to flow through any pelage (Q_{fur}) and equal net heat flux between the animal surface to the environment: convective (Q_{conv}), radiative (Q_{rad}) and solar input (Q_{sol}) (Fig. 1).

For each hour of the day, NM calculates this heat balance. A calculated metabolic rate above the animal's target metabolic rate (i.e., resting metabolic rate hours when inactive; an active metabolic rate for hours when active) for that hour, indicates cold stress since additional metabolic heat production will be needed to maintain the body temperature. A calculated metabolic rate below the target metabolic rate indicates heat stress since additional heat dissipation will be needed to maintain the body temperature at the target metabolic rate. When active, a user-specified activity multiplier (Supplementary materials, Table A.6) is applied to the resting metabolic rate to generate an active target metabolic rate. Activity level is thus specified for diurnal, nocturnal, and crepuscular hours.

If the calculated metabolic rate deviates from the target metabolic rate by more than 1%, thermoregulatory options are engaged to attempt to reach a heat balance at the target metabolic rate. Behavioral thermoregulatory options (e.g., seeking shade, swimming) can be engaged to ease thermal stress. Once these behavioral options are exhausted, autonomic thermoregulatory strategies are initiated, including vasodilation/vasoconstriction, body temperature adjustment, piloerection, and evaporative water loss via panting or sweating. Specific to body temperature adjustments, NM's calculations begin each hour attempting to maintain the user-supplied average body temperature but will adjust the body temperature up or down by 0.1°C increments within user-specified maximum and minimum values until the animal reaches heat-balance with its environment. The calculated body temperature for a given hour is the body temperature that satisfies the heat balance equation at the target metabolic rate. If all thermoregulatory options are exhausted before a heat balance can be achieved at the target metabolic rate, the closest metabolic rate is output as the hourly metabolic rate. Final metabolic rates below the target rate indicate heat stress (i.e., activity limitations or hyperthermia) in those environmental conditions; final metabolic rates above the target rate indicate cold stress and a need for additional metabolic heat production to avoid hypothermia.

Thermoneutral zone determination

The thermoneutral zone (TNZ) identifies the range of ambient air and radiant temperatures in which an animal can maintain its core body temperature without adjusting its metabolic rate or increasing evaporative heat loss. Thermoregulatory strategies engage above or below the TNZ, therefore it is necessary to identify the upper (UCT) and lower (LCT) critical limits of this zone to understand when these parameters should be engaged in further modeling. Additionally, the thermoneutral zone serves as a baseline for comparison to contextualize the impact of autonomic and behavioral thermoregulatory responses engaged in subsequent simulations. To evaluate the limits of the TNZ, body temperature in the modeled animal was held constant at 37.5°C, the mean observed core body temperature of the biologged individual during the observation period (Supplementary materials, Fig.A.1), while allowing up to a -5°C deviation from core body temperature in tail and leg appendages.

Upper critical temperature was defined as the maximum air temperature at which the modeled chacma baboon is no longer able to maintain its resting metabolic rate without sweating or panting, while the lower critical temperature was that at which the metabolic rate would need to increase in order maintain its core body temperature (Curtis, 1983; Mitchell et al., 2018; Mathewson et al., 2020). Thus, a change in the predicted metabolic rate could be used to identify the temperature at which thermoregulation would need to be activated to ensure survival prospects. The subadult male chacma baboon was simulated in a metabolic chamber with a starting air temperature of -10°C that increased incrementally by 1°C until it reached 45°C. Air, ground, and sky temperatures were set equal. Solar radiation was omitted, with relative humidity set to 5% and wind speed to 0.1m/s (Mathewson et al., 2020). The TNZ was compared across basal metabolic rate (BMR) options before a BMR of 25.84 was selected based on a mass-based regression equation for mammals (Gordon et al., 1972) for the modeled 15kg baboon. This BMR was slightly higher than previously reported for non-pregnant, non-lactating adult female baboons of comparable mass (Wene et al., 1982; Bielert and Busse, 1983) because a growing subadult individual would likely have an elevated BMR (Rosenfeld et al., 2015). Additional physiological inputs, including the BMR activity multiplier, are available in Supplementary Materials, Table A.6.

Sensitivity analyses

Our second objective was to perform a sensitivity analysis of the baboon model to examine which morphological and autonomic inputs have the greatest effect on the NM's predictions of metabolic heat production and body temperature. NM morphological (hair density, hair diameter, pelt depth) and autonomic (vasoconstriction, vasodilation, piloerection, panting, sweating) inputs were adjusted from those values used in the standardized TNZ simulation (Table A.1, Table A.3,

Table A.5) to cover a range of values observed in the literature or collected data (Table 1). All other parameters remained disengaged or constant while one was adjusted. Analyses were conducted in a simulated metabolic chamber (as above) in which the simulated baboon was modeled as inactive and in a standing posture with all limbs extended and in contact with the ground (20% surface area) for diurnal, crepuscular, and nocturnal hours, with no heat storage allowed to simulate the proximate response to the immediate environmental conditions. Since all microclimate conditions aside from temperature were consistent within the metabolic chamber throughout the sensitivity analysis, NM behavioral adjustments that incorporate microclimate manipulation (e.g., tree-climbing and shade-seeking) were omitted from the metabolic chamber sensitivity analysis. We controlled for the effect of posture by modeling the baboon in a limb-abducted posture for all parameter adjustments but included a simulation in a curled posture for comparison. The model outputs for all iterations of the sensitivity analyses were metabolic rate (W) and core body temperature (°C).

Table 1. Variable adjustments for morphological and autonomic parameters included in the sensitivity analysis.

Parameter	*Adjustment*	*Default Value(s)*	*Values trialed*
Body mass	kg	15	15
Resting metabolic rate[1]	W	3.39 x mass (kg)$^{0.75}$ = 25.84	3.39 x mass (kg)$^{0.75}$ = 25.84
Core body temperature	°C	Starting: 37; Min: 35; Max: 40	Starting: 37; Min: 35; Max: 40
Flesh thermal conductivity[2]	(Wm^{-1}°C^{-1})	Starting: 1.0; Min: 0.4; Max: 2.8	Starting: 1.0; Min: 0.4; Max: 2.8
Hair density	no./cm^2	Hair densities in Table A.3	50, 200, 400, 600, 800, 1000
Hair diameter	µm	Hair diameters in Table A.5	50, 70, 90, 110, 130
Piloerection	Pelt depth as % of hair depth	Pelt depths in Table A.1	0, 25, 50, 75
Sweating	% body surface wet	Not allowed (0%)	0, 5, 10, 15, 20, 25, 30
Panting[3]	Maximum: minimum O_2 extraction efficiency (%)	Not allowed (20%:20%)	(20:20), (20:15), (20:10), (20:5)

Vasoconstriction/ Vasodilation[2]	Starting, minimum, and maximum flesh thermal conductivity (W/(m·K))	Starting: 1.0; Min: 0.4; Max: 2.8	(0.6, 0.4, 0.8), (1.0, 0.8, 1.2), (1.4, 1.2, 1.6), (1.6, 1.6, 2.0), (2.2, 2.0, 2.4), (2.6, 2.4, 2.8)

[1] Gordon et al., 1972. Mass regression equation for mammals.
[2] Cho, 1969. Flesh thermal conductivity values for both cold and warm living flesh.
[3] Larcombe, 2002. Standard oxygen extraction efficiency for mammals.

Optimized microclimate model

Our third objective was to examine and validate NM’s ability to predict core body temperature with the animal model within an appropriate microclimate sub-model. That is, whereas the previous sensitivity analyses were performed in a metabolic chamber allowing the direct and incremental control of environmental temperatures, optimized models were simulated within microclimate conditions generated to encompass daily variation in local environmental conditions experienced by our baboon troop across multiple seasons (Supplementary materials, Table A.7). Specifically, we modeled the microclimate at the present site between December 1 and April 30 to coincide with the data logger data collection period.

The microclimate model was based on 2m shaded air temperature, wind speed, and relative humidity data collected at an onsite weather station (Hobo U12, Onset Computer Corporation, Pocasset, USA) (Lubbe et al., 2014) situated within the home range of the study animals. Cloud cover approximations for the location were extracted from Wilson and Jetz (2016), in which monthly cloud frequencies were derived using Moderate Resolution Imaging Spectroradiometer satellite images twice per day over 15 years over 1km units. Precipitation data were extracted from the Niche Mapper Global Climate Extractor for the site coordinates at 850m elevation (New et al., 2002).

The microclimate model used the mean of daily maximum and minimum values of air temperature, wind speed, and relative humidity, as well as percent cloud cover and shade availability, substrate reflectivity and thermal properties, and local slope, aspect, elevation, latitude and longitude, and hourly variance in solar radiation (Mathewson et al., 2020; Table

A.7). The microclimate model compiles these conditions to simulate the animal's microclimate at an hourly resolution for each day at the height of the animal to encompass the full range of environmental conditions to which an animal would be exposed. The heat and mass balance equations are solved for the animal's metabolic requirements (heat energy and associated water, air, and food) to maintain a specified body temperature in the given conditions for that hour in both shade and full sun.

Once the allowed autonomic strategies (i.e., piloerection, sweating, panting, vasodilation/vasoconstriction: Table 1) are attempted, the model calculates the core body temperature resulting from the energetic demands imposed by the environment, as well as the adjusted metabolic rate required to satisfy the animal's energy balance to maintain a consistent core body temperature. NM will adjust the body temperature starting with the input average core body temperature and shifting by 0.1°C increments until the animal reaches a heat-balance with its environment while maintaining a body temperature between the specified maximum and minimum values. To parameterize a thermal maximum and minimum for the subadult male baboon model, core body temperature data were extracted from a bio-logger explanted from a subadult male. The observed body temperature mean (37.5°C), minimum (35.3°C), and maximum (39.5°C) were input into the model (Supplementary Materials, Figure A.1). We then assessed whether the NM optimized model reliably predicts core body temperature by comparing model output to the observed body temperature.

Behavioral parameters

Our final objective was to examine whether behavioral parameters improve NM's predictions of body temperature. We followed the same process as described above for the optimized model, but in addition to consistent morphological and autonomic inputs (Table A.1, Table A.3), also incorporated huddling, tree-climbing, shade-seeking, and swimming behavioral options (Table 2). Huddling behavior engaged only at night, and was modeled by simulating multiple individuals in contact, reducing the body surface available for heat exchange with the environment (Mathewson et al., 2020). To simulate tree-climbing, our baboon was modeled in an elevated microclimate two meters off the ground. This microclimate promotes heat dissipation by moving the animal away from the warm ground surface and providing greater wind exposure. Shade-seeking in our model prevents energetic gains via direct incoming solar radiation, as well as providing a cooler contact substrate for the animal on a ground surface that is not absorbing solar radiation. Swimming/wading behavior was modeled by increasing surface wetness up to a maximum of 30% to facilitate evaporative heat loss.

When an adjustment in metabolic rate was required to maintain the animal's core body temperature in the given environmental conditions for that hour, or if the metabolic rate exceeded 1% of the target rate, behavioral thermoregulatory options were engaged to ease energetic demands. Once these behavioral options were exhausted, autonomic strategies were engaged. We assessed whether the NM optimized (including behavior) model reliably predicts core body temperature by calculating the percentage of hours for which the model was able to predict T_b within 1.5°C and 1°C, as well as the average difference between predicted and observed T_b across all hours. Finally, we calculated the average effect of engaging each individual behavioral strategy on predicted T_b over the entire study period during daytime, nighttime, and all hours to evaluate the overall utility of each response.

Table 2. Biophysical model adjustments for trials of the optimized model in which behavioral thermoregulatory options were engaged (left column) and disabled (right column).

	Thermoregulatory behaviors engaged	**Thermoregulatory behaviors disabled**
Start, Max, Min T_b	37; 40; 35	37; 40; 35
Seeking ground shade	Yes	No
Maximum available shade	100%	25%
Seek wind protection	Yes	No
Night shade/cold protection	Yes	No
Active in shade in day; posture	No; lie	No; lie
Tree sleep	Yes	No
Huddle at night (50% ventral & 50% dorsal coverage)	Yes	No
Concurrent Tc increase	Yes	Yes
T_c increase increment (°C)	0.1	0.1
T_c Trigger water loss (°C)	38.0	38.0
O_2 extraction efficiency increment (%)	1.0	1.0
Skin wetness increment (%)	1.0	1.0
Concurrent T_c decrease	Yes	Yes
T_c decrease increment (°C)	0.1	0.1
Piloerection increment (%)	1.0	1.0
Piloerect (% of hair length)	50	50
Sweating (15% max wet surface)	Yes	Yes
Swimming (30% max wet surface)	Yes	No

RESULTS

Thermoneutral zone

When all body parts were modeled in contact with the ground (a “limb-abducted” posture) and limb and tail appendages could fluctuate to temperatures up to 5°C below the specified (mean observed) core body temperature of 37.5°C, the predicted thermoneutral zone for chacma baboons ranged from a lower critical temperature (LCT) of 21°C to an upper critical temperature (UCT) of 26°C (Fig.3).

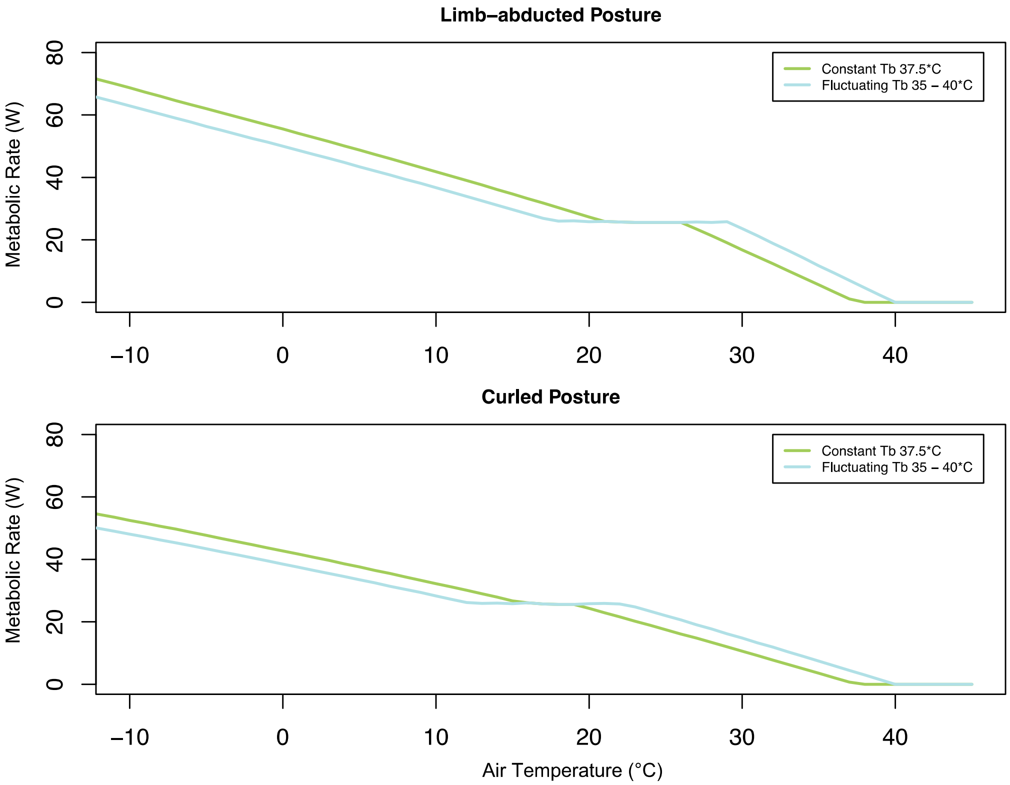

Fig.3. Results of a Thermoneutral Zone (TNZ) determination run for a modeled subadult male chacma baboon. The individual was modeled as inactive in both a limb-abducted posture (upper) and a curled posture (lower). For each posture, one simulation allowed body temperature to fluctuate between 35 and 40°C, while a static body temperature of 37.5°C was specified for a second simulation. When the core body temperature was set to 37.5°C and modeled in a limb-abducted posture, the TNZ was 21-26°C. The LCT and UCT extended to 18 and 29°C respectively when the core body temperature was allowed to fluctuate in the limb-abducted posture. In a curled posture, the TNZ was 13-22°C when T_b could fluctuate, and 16-19°C when set to a constant T_b of 37.5°C.

Sensitivity analysis

When the modeled baboon's core body temperature was held constant at 37.5°C in the metabolic chamber, adjustments to surface wetness (simulating sweating or swimming) had the greatest impact on the UCT of the thermoneutral zone (Fig.4), increasing the UCT of the thermoneutral zone from 26°C to 29°C with 5% surface wetness. A 10%, 15%, and 20% wet fur surface extended the upper threshold of the thermoneutral zone from its dry upper limit by 6°C, 8°C, and 9°C, respectively. Surface wetness of 30% increased the UCT to 44°C. High frequency panting, with a minimum allowed oxygen extraction efficiency of 5%, increased the UCT from 26°C (no panting) to 32°C. Minimum oxygen extraction efficiencies of 15% and 10% extended the UCT to 27°C and 28°C, respectively.

Piloerection extended the LCT of the thermoneutral zone; when the simulated baboon could increase the pelt depth to 75% of the hair length, the LCT dropped to 16°C from 21°C, while a pelt depth equal to 50% of hair length lowered the LCT to 18°C. Adjustments to anatomical characteristics were also examined for their effect on TNZ boundaries. Uniformly reducing hair density across the body surface to 50 hairs/cm^2 increased the UCT to 32°C, compared to an UCT of 21°C when a hair density was set to 800+ hairs/cm^2. Changes to hair diameter were less impactful to TNZ thresholds: the UCT increased from 24°C to 28°C when hair diameter was decreased from the observed maximum (130μm) to the observed minimum (50μm). Flesh thermal conductivity adjustments (vasoconstriction and vasodilation) had the least impact of the examined adjustments on the thresholds of the thermoneutral zone. Modeled across a range from 0.4-2.8 Wm^{-1}k^{-1}in incremental ranges of 0.4 Wm^{-1}k^{-1}, flesh thermal conductivity adjustments increased the UCT to 26°C, and lowered the lower TNZ threshold to 19°C.

Postural adjustments were highly effective in lowering the LCT of the thermoneutral zone. When transitioning from the default posture in which limbs are abducted from the torso and in contact with environmental surfaces into a curled posture with limbs tucked into the body core and the head modeled upright, the LCT decreased from 21°C to 16°C.

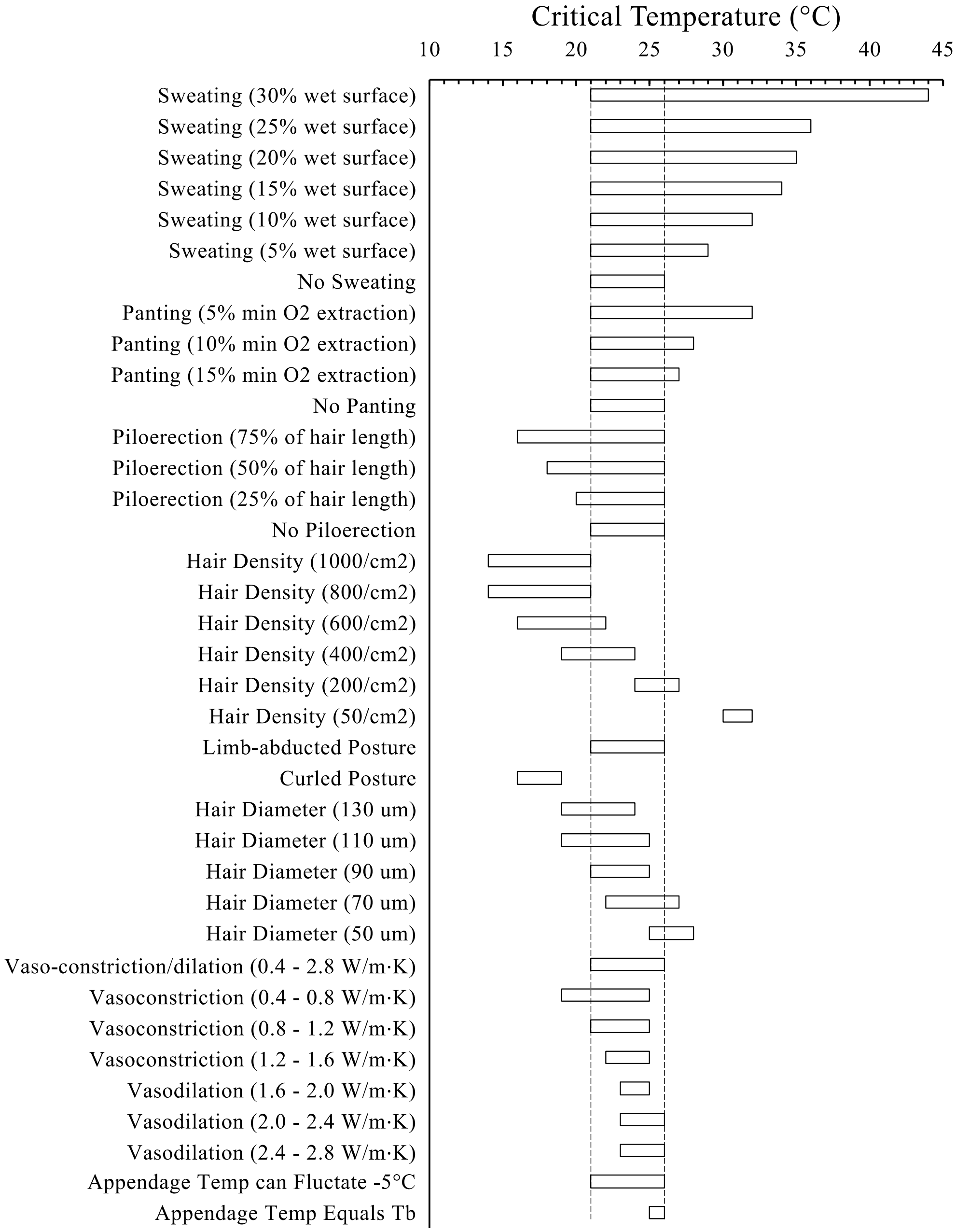

Fig.4. Results of a metabolic chamber sensitivity analysis demonstrating the effects of parameter adjustments on the upper and lower critical temperature limits of the thermoneutral zone. Dashed lines indicate upper and lower critical temperature of the thermoneutral zone in default conditions. Core body temperature was set to remain at the average observed temperature: 37.5°C. Specific model adjustments are described in Table 1.

Optimized model (excluding behavior)

An ‘optimized model’ incorporating autonomic heat dissipation and heat retention thermoregulatory responses was used to predict hourly core body temperatures for all hours of every day, December through May. Behavioral thermoregulatory options (swimming, tree-climbing, shade-seeking, and huddling) were disabled apart from posture, which changed depending on whether the baboon was sleeping (curled posture) or active (limb-abducted posture). Without thermoregulatory behaviors engaged, NM predicted T_b within 1.5°C of the observed T_b for 70.14% of hours, and predicted T_b within 1°C for 54.06% of hours within the 151-day study period. On average, across all hours, the model’s core body temperature predictions fell within 1.01°C of the observed T_b.

Optimized model (including behavior)

The optimized model was then modified to include behavioral thermoregulatory options: swimming, tree-climbing, shade-seeking, and huddling. Once these behavioral options were enabled, NM’s ability to predict T_b within 1.5°C of the observed T_b improved from 70.14% of hours to 94.01% of hours. Furthermore, the model’s ability to predict T_b within 1°C of the observed improved from 54.06% to 78.3% of hours throughout the 151-day period (Fig.5). Once behavioral thermoregulation was incorporated, the model predicted T_b within 0.58°C of the observed T_b on average across all hours. During daytime hours (6:00-17:00), the average difference between predicted T_b and observed T_b was 0.465 °C. Model performance by hour is available in supplementary materials, Fig. A.3.

Of the incorporated behavioral options, shade-seeking behavior had the greatest individual impact on T_b (Table 3). In the model, a shaded microclimate inhibits energetic gains via direct incoming solar radiation, as well as provides a cooler contact substrate for the animal, on a ground surface that is not absorbing solar radiation. During daytime hours, shade was particularly effective in decreasing predicted T_b for this reason, reducing predicted T_b by an average of 0.44 °C across all hours of the day (Fig.6.) During daytime hours (6:00-17:00), shade-seeking reduced T_b by an average of 0.86°C. Swimming/wading, which increases surface wetness to facilitate evaporative heat loss, reduced T_b by an average 0.64°C across daytime hours. Tree-climbing, which positions modeled baboon in an elevated microclimate 2 meters off the ground, promotes heat dissipation by moving the animal away from the warm ground surface and providing greater wind exposure and lowered predicted T_b by an average of 0.28°C across daytime hours. Huddling was set only to activate at night, and increased nighttime T_b by an average of 0.18°C. The observed core body temperature most frequently reached temperatures between 38.1-38.2°C (Supplementary Materials, Fig.A.2). Our data align with previous measurements of wild baboon core body temperature, which ranged from 36.0 to 42.7 °C (Brain and Mitchell, 1999).

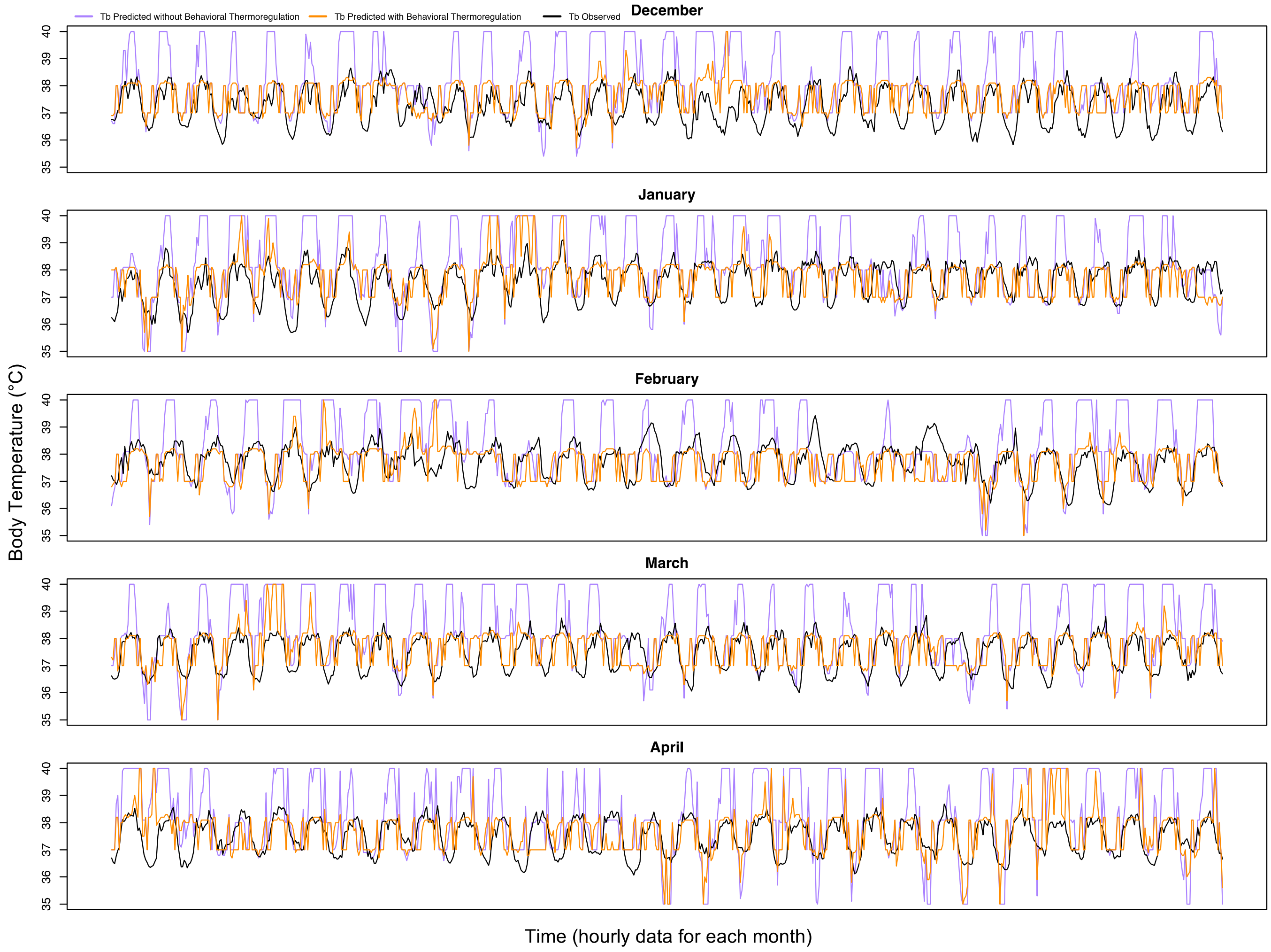

Fig.5. Optimized model's predictions of core body temperature, excluding and including behavioral thermoregulatory options, compared to body temperature (°C) observed for all hours from Dec 1 – April 30. Lines represent T_b predicted by NM when behavioral thermoregulatory options are disabled (purple) or enabled (orange) relative to T_b observed (black).

Table 3. Effect of engaging individual behavioral options on predicted T_b in the optimized model between December 1 and April 30.

	% of hours T_b Predicted was within 1.5°C of T_b Observed	% of hours T_b Predicted was within 1°C of T_b Observed	Mean predicted effect on T_b (°C) (all hours)	Nighttime mean predicted effect on T_b (°C) (18:00-5:00)	Daytime mean predicted effect on T_b (°C) (6:00-17:00)
Behavioral options disabled	70.14	54.06			
Huddling at night only	70.25	52.98	+0.09	+0.18	0
Tree-climbing only	72.93	56.29	-0.19	-0.09	-0.28
Shade-seeking only	85.40	67.49	-0.44	-0.02	-0.86
Swimming only	88.11	73.87	-0.35	-0.07	-0.64
All four behavioral options enabled	94.01	78.30			

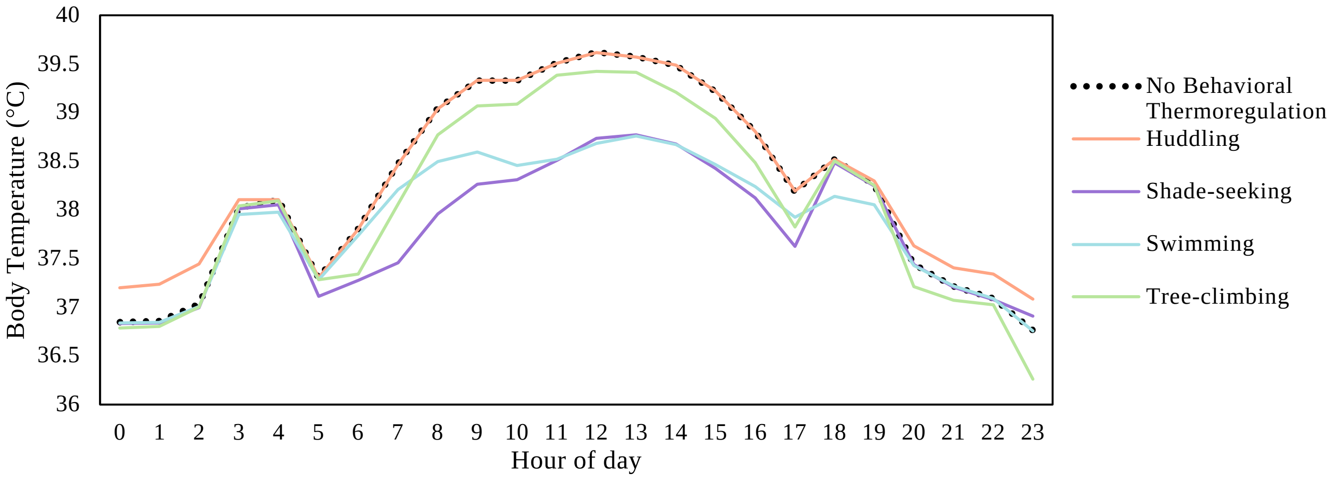

Fig.6. Predicted effect of individual behavioral thermoregulatory responses on average hourly predicted T_b relative to all thermoregulatory behaviors being disabled.

DISCUSSION

Our biophysical model supports the view that behavioral thermoregulation plays an important role in maintaining homeothermy in chacma baboons. Our model specifically highlights the importance of behavioral responses to combat heat stress,and presents the thermal contribution of individual behavioral options in maintaining a relatively consistent T_b (Fig. 6; Table 3). Heatstroke in baboons is characterized by core body temperatures exceeding 40°C (Bouchama, 2005). In laboratory baboons, water deprivation coupled with extended exposure to heat resulted in body temperatures near 41°C (Brain and Mitchell, 1999), at which temperature consequences of acidosis and hypoxia were observed in the fetuses of pregnant females (Morishima et al., 1975). In another study, adverse neurological effects were observed in laboratory baboons subjected to “moderate” heatstroke (core body temperatures exceeding 42.5°C), while “severe” heatstroke (core body temperature exceeding 43°C) was fatal to all individuals (Bouchama, 2005). The regularity of body temperature predictions that attain the user-specified maximum T_b of 40°C when behavioral thermoregulation is disabled (Fig. 5) support the assertion that behavioral thermoregulation is crucial to averting the adverse thermal consequence of heatstroke.

Within the geographic range of chacma baboons, southern Africa currently experiences an average of approximately 3 heat-wave days (days in which maximum temperatures exceed the average maximum of the hottest month by 5°C for 3 or more days) annually (Engelbrecht et al., 2015). Under projected climate forcings, however, 20-80 more heat wave days are expected annually over subtropical southern Africa (Engelbrecht et al., 2015). Considering the hazardous impacts of hyperthermia on chacma baboon survival, and the increasing threat of anomalous heat-wave days, effective heat-dissipation responses may become vital to the persistence of this species in affected areas. Temperatures at this site fluctuate substantially between diurnal and nocturnal hours in all seasons. The difference between the average daily minimum and average daily maximum temperature was 20.3°C in June (mid-Winter), and 27.14°C in December (mid-Summer) (Supplementary Materials, Table A.7). Thus, the daily environmental variation experienced by our study animals necessitate both heat-dissipation (e.g., sweating, shade-seeking) and heat-retention (e.g., vasoconstriction, huddling) thermoregulatory responses across seasons.

Shade-seeking behavior was demonstrated to have the greatest average effect across all modeled hours in reducing the predicted core body temperature. The thermal utility of shade aligns with the findings of previous observational studies, which determined that high perceived temperatures (relative to baboon’s thermoneutral zone) increased the proportion of time baboons spend in the shade (Hill, 2006). Shade availability, however, is impacted by factors including the hourly zenith angle and the presence of shade-generating microhabitat features: caves, cliffsides, trees, or shrubs. Therefore, shade may not be accessible during all daytime hours.

Even if present, shade-use may be comprised by other ecological and social constraints. Baboons have dynamic social structures underpinned by well-established and maintained dominance hierarchies (Hausfater et al., 1982; Bergman et al., 2003). When a resource is rare or valuable and competition costs are low (Johnson et al., 1989) baboons are known to supplant lower-ranking individuals to claim access to that high-quality resource (Patterson et al., 2021; Hamilton and Busse, 1982). Considering the thermoregulatory value of shade, higher-ranking individuals may also monopolize limited shade access by excluding lower-ranking individuals. Additionally, foraging requirements may preclude shade use as a thermoregulatory strategy. That is, seasonal fluctuations in the abundance or quality of food resources may force adjustments in foraging effort, home range use, and use of microhabitat features such as trees (Lewis et al., 2017; Johnson et al., 2015; Hill, 2006) reducing daytime access to shaded habitat features. In particular, increased reliance on anthropogenic food sources in either urban or agricultural landscapes (Walton et al., 2021; Hoffmann and O’Riain, 2012) may impact shade accessibility, for example in crop fields that provide limited refuge (Walton et al).

Barring anthropogenic and social limitations, the future availability of tree shade within chacma baboon suitable habitat is also uncertain. Under projected 1.5°C and 2°C global temperature increases, total leaf area index, or the total one-sided leaf area per unit of ground surface (Watson, 1947; Bréda, 2003; Lawal et al., 2019), is expected to decrease throughout portions of Mozambique, Botswana, Namibia, and western South Africa where chacma baboons are currently distributed (Lawal et al., 2019). However, the density of woody plants within South African grassland and savanna habitats has been observed to increase over the past century, which is thought to be tied to increasing atmospheric CO_2 concentrations (Buitenwerf et al., 2011). Therefore, available shade cover across portions of chacma baboons' range may change unpredictably in coming decades.

Swimming (wading) was also highly effective in decreasing predicted core body temperature by facilitating heat dissipation via evaporative heat loss across the baboon's body surface. Despite the effectiveness of increased surface wetness in reducing core body temperature, there are potential limitations to relying on this strategy. First, this thermoregulatory option relies on access to a substantial volume of standing water, access to which may be unavailable during the dry season (Table A.7). The portion of southern Africa encompassing the current range of chacma baboons is expected to experience reductions in annual precipitation by 2059 ranging from 2.4-5.4% in the west and 2.4-2.7% in the east (Almazroui et al., 2020), accompanied by warming-induced increases in evapotranspiration rates during the dry season (Dai, 2013). Thus, the availability of standing water is expected to diminish across their range.

Despite the obvious utility of standing for drinking and swimming-related benefits, there are several factors that may deter baboons from using water resources. Water-use increases the risk of water-borne diseases (Rideout et al., 1997; Setchell et al., 2007) as well as susceptibility to aquatic predators, such as crocodiles, but also terrestrial predators, such as leopards, which similarly rely on standing water sources for drinking (McFarland et al., 2020a; Kempf, 2009;

Cowlishaw, 1994; Busse, 1980; Altmann and Altmann, 1970). Thus, there may be a trade-off between thermoregulatory water-use and predator and pathogen avoidance, particularly in areas where water is scarce. Behavioral thermoregulation in the water may also detract from the time needed to meet foraging requirements; except for baboon populations that forage directly from aquatic sources (e.g., rivers: Hamilton and Tilson, 1985, coasts: Lewis and O'Riain, 2019). Furthermore, swimming or wading is likely to only afford relatively transient cooling benefits, given core body temperatures typically return to pre-swim temperatures within 0.5-2.5 hours in wild vervet monkeys (McFarland et al., 2020a). Together, this evidece suggests that wading/swimming may not be an effective thermoregulatory option for baboons, especially for those populations inhabiting drier landscapes.

Though to a lesser extent than shade access or swimming, tree-climbing behavior was also effective in decreasing predicted core body temperature. An animal positioned in a tree experiences greater wind speeds compared to a position on the ground (Campbell, 1977; Samson and Hunt, 2012), increasing the rate of convective heat loss. However, like shade-use and swimming behaviors, tree-climbing is limited by the availability of microhabitat features, and daytime access to trees will depend on daily ranging and foraging patterns (Barton, et al., 1992; Stelzner, 1988). Thus, a baboon may not have consistent access to trees during all hours. When exploitable microhabitat features such as trees are unavailable, individuals may instead rely on bodily manipulations to mediate the exchange of heat energy with their environment, for example, shifting posture.

Posture was a particularly important thermoregulatory parameter in our sensitivity analysis. In previous laboratory studies, baboons exposed to simulated desert conditions (including incoming solar radiation) were observed to adopt limb-abducted postures, rather than curled postures that would reduce exposure to radiation (Mitchell et al., 2009). Our findings indicated that a limb-abducted posture, compared to a curled posture, provided a substantially higher upper critical temperature threshold. Thus, postural adjustments provide an energetically-inexpensive and effective behavioral strategy for thermoregulation, and can reduce thermal stress if microclimatic refugia such as trees, shade, or standing water are scarce under predicted climate changes.

Our sensitivity analysis identified a strong effect of hair density on the LCT of the thermoneutral zone, supporting the view that an animal's pelt can help buffer them against environmental temperature (Cooper et al., 2003, Walsberg 1991). Hair characteristics were observed to be variable across sampled body sections, with lowest observed hair densities and diameters on the ventrum. In support of previous assumptions (Stelzner and Hausfater, 1986), exposing this sparsely-furred surface was predicted by our model to be advantageous for heat dissipation in hot conditions, but also threatened excessive heat loss in cold conditions.

In colder conditions, including nighttime hours, huddling behavior can be an effective strategy to decrease the exposed body surface available for convective heat loss to the surrounding air. In our study, huddling positioning that conferred 50% ventral and 50% dorsal coverage had a meaningful effect on core body temperature, particularly between the hours 20:00-3:00. This supports previous findings that have highlighted the important thermal benefits of night-time huddling, particularly to those species that endure cold nighttime temperatures (McFarland and Majolo 2013; McFarland et al., 2015). Another cold-weather thermoregulatory response examined in our sensitivity analysis that had a notable effect was piloerection. Piloerection was modeled as an increase in pelt depth equivalent to a fraction of the average total hair length in that location, and effectively extended the lower critical temperature of the thermoneutral zone to 16°C. This is comparable to the lower critical temperature achieved by assuming a curled posture, according to our model. Although piloerection is an autonomic response resulting from contracted arrector pili muscles attached to the hair follicle base, increased pelt depth can also be achieved through a common primate social behavior: grooming (McFarland et al., 2016). Jointly, it appears that the behavioral strategies of huddling and grooming provide the most substantial thermal benefits when attempting to reduce heat loss in cold microclimate conditions. It is important to note that although our optimized model (including behavioral options) was able to predict T_b within 0.58°C of the observed T_b on average across all hours, it was least effective in predicting T_b during the early morning hours, 3:00 and 4:00. The model appears to over-estimate core body temperature in these cold nighttime conditions (Supplementary materials, Fig A.3.), which may indicate that the maximum pelt depth (conferred through piloerection) and/or body surface coverage (afforded by huddling) may realistically be less than we permitted in the model.

Flesh thermal conductivity was set to a range of observed values (0.4-2.8 W/(m·K)) in our default parameters. When flesh thermal conductivity was constrained to a subset of that range, we could see the effect of vasodilation and vasoconstriction in extending the upper and lower limits of the thermoneutral zone (Fig. 4). Previous laboratory studies observed substantial temperature decreases at appendages and attributed the difference in skin temperatures in the trunk versus skin regions vasoconstriction (Funkhouser et al., 1967). Our model was set to allow appendage (including tail) temperatures to deviate up to 5°C below the baboon’s core body temperature, while vasoconstriction and vasodilation were simulated as adjustments to flesh thermal conductivity. The baboons studied by Funkhouser et al. (1967) did not have tails; thus, the effect of that additional appendage surface on overall temperature was not incorporated.

Though vasoconstriction and vasodilation have been recognized for their thermoregulatory utility (Wyss and Rowell, 1976) our study parameterizes the effects of vasoconstriction and vasodilation responses on body temperature separate from appendage temperature fluctuations.

It is also important to consider that the value of behavioral strategies in mediating baboon homeothermy implicates opportunity costs within their activity budget. Behaviors such as assuming strategic postures, increasing the frequency of visits to scarce water resources, or increasing resting time to minimize added metabolic expenditure have implications not only for this animal's daily energy budget, but also its activity budget. Time that was previously dedicated to movement, foraging, reproduction, or socialization may need to be reprioritized toward meeting the animal's thermal limits, for example, resting in shady cliffside microhabitats (Hill, 2006). To accommodate these requirements in the context of increasing environmental temperatures, we may see changes in daily active hours, for example, by substituting mid-day foraging activity for resting or grooming (Hill, 2006) and increasing activity around dawn and dusk (Levy et al., 2018). However, adopting cathemeral or crepuscular activity patterns may incur risks, including reduced visibility and increased potential to encounter nocturnal predators, including leopards (Busse, 1980). It is also important to consider that sex-age differences in priorities (e.g., reproduction), energy requirements, dominance rank, and thermal limitations are likely to produce differences in behavior, including thermoregulatory behaviors. Inter-individual differences may impact the thermal utility of the discussed behaviors across sex-age classes, warranting further investigation. Adjustments to morphometric and physiological properties would be necessary to generate meaningful predictions about sex-age differences.

This study highlights the relative importance of various thermoregulatory options, supporting previous assumptions that chacma baboon behavioral flexibility is key to body temperature regulation, while also underscoring relevant critical habitat features providing microclimate refugia. Without exploitable microhabitat features, such as trees and water sources, baboons may struggle to maintain their core body temperature effectively. Studies have considered predicted changes in climate to forecast future suitable habitat for chacma baboons and predict reductions in suitable habitat of 36-49.8% by 2050 under a conservative 2.6 RCP climate change scenario (Hill and Winder, 2019). Our findings provide insight into the possible thermal responses of baboons to anticipated changes in landcover or climate. We believe the marked behavioral flexibility observed in chacma baboons will continue to underpin their persistence in the face of changing climate.

When accurately and robustly parameterized, biophysical models facilitate meaningful predictions about the constraints of an animal's physiology and can be used generate predictions about species in both modern and future environmental conditions. Biophysical models have been used to predict the current and future distributions of the American pika (Mathewson et al., 2017), identify suitable habitat for activity in giant pandas (Zhang et al., 2017), and assess the spatial limitations of grizzly bears under both current and future climate conditions (Rogers et al., 2021). We believe our comprehensive examination of an animal's autonomic, morphological, and behavioral repertoire provides a powerful basis for improving the predictive reliability of present and future species distribution models (Hill and Winder, 2019; Mathewson et al., 2017; Kearney and Porter, 2009). Additionally, our findings emphasize the importance of behavioral thermoregulation, which is likely critical for other social endotherms that similarly rely on behavioral adjustments to mitigate thermal and energetic stress (Hetem et al., 2014).

GLOSSARY

Thermoneutral zone: the range of ambient temperatures in which an animal can maintain its core body temperature without adjusting its metabolic rate or increasing evaporative water loss

Homeothermy: the ability to maintain a core body temperature within a narrow range when subjected to a wide range of environmental temperatures

Upper Critical Temperature of the thermoneutral zone: the ambient air temperature threshold at which the animal is no longer able to maintain its resting metabolic rate without engaging evaporative heat dissipation responses

Lower Critical Temperature of the thermoneutral zone: the ambient air temperature threshold at which the animal must increase its metabolic rate in order maintain its core body temperature

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