

WESTERN CHIMPANZEE (*PAN TROGLODYTES VERUS*) USE OF
MICROCLIMATES IN A SAVANNA-WOODLAND
ENVIRONMENT: BEHAVIORAL
THERMOREGULATION

by

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DEDICATION

This thesis is dedicated to my family, for encouraging me to choose my own path in life. I also dedicate this work to the primates I have had the privilege to observe over the years.

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CHAPTER I: INTRODUCTION

Introduction

Environmental pressures are central to understanding early hominin (i.e., bipedal ape) evolution. Given the open savanna-woodland environmental context associated with early members of the hominin lineage, it has been hypothesized that they faced thermoregulatory selective pressures associated with high temperatures, which led to bipedalism, hair loss, and increased body size (Wheeler, 1984, 1991a, 1991b 1994). However, given the difficulties of ascertaining behavior from the early hominin fossil record, it remains unclear how these selective pressures would have influenced the behaviors of members of our ancestral lineage in thermally stressful environments. Researchers look to nonhuman primates currently living in equatorial savanna habitats, specifically baboons (*Papio* sp.) and chimpanzees (*Pan troglodytes*), as referential models to provide insight into how early hominins may have behaved in this type of environment (DeVore & Hall, 1965; Moore, 1996; Sponheimer et al, 2006; Wheeler, 1984).

Savanna chimpanzees can add to our knowledge of early hominin behavior, as they are a combination of the homologous and analogous models, being our closest living relatives and inhabiting the savanna biome that may have selected for unique human traits (Moore, 1996). The savanna habitat is defined as a landscape with both grass and trees in an arid or semi-arid climate with high temperatures, and precipitation acting as a limiting factor on wood cover (Sankaran et al., 2005). In a study of the habitat and chimpanzees of Mt. Assirik, Senegal, McGrew et al. (1981) concluded that due to the

similarity in environment between this region of Senegal and that of Plio-Pleistocene hominids, the Mt. Assirik chimpanzee community was the best model for investigating adaptation in early hominins. Moore (1996) also supports the use of savanna chimpanzee referential models for early hominins as well as the last common ancestor between humans and chimpanzees.

The Fongoli Western chimpanzee (*Pan troglodytes verus*) community in Senegal is a good referential model for better understanding early hominid adaptations, as they are one of only two habituated communities of chimpanzees that inhabit a savanna woodland landscape (Pruetz & Bertolani, 2009). This group of chimpanzees faces strong ecological pressures, in the form of heat stress and water scarcity, which greatly affects their biology (Wessling et. al., 2018) and their behavior. Fongoli apes exhibit a number of behaviors hypothesized to avoid heat stress, such as cave use (Pruetz, 2007), resting extensively during daily peak temperatures and soaking in water during the transition from dry to wet season (Pruetz & Bertolani, 2009), selective use of gallery forests for shade (Pruetz & Bertolani, 2009), and being active at night during the dry season (Pruetz 2018). The behavioral adjustments of cave use and nighttime activity in response to temperature have not been recorded in any other chimpanzee population (Pruetz, 2007, 2018). It is unclear (1) how much these behaviors and use of habitats and microhabitats reduce heat stress and (2) if this population is at the limit of its ability to thermoregulate. If the current environment the Fongoli chimpanzees inhabit is at the extremes of their ecological niche, then these apes may not be able to adjust to future warming in the coming decades. Given that Senegal is the northernmost extent of chimpanzees' range in Africa, the latter question is especially concerning for conservation biologists.

The purpose of this research was to investigate if Fongoli chimpanzees are at the extent of their behavioral flexibility in response to heat stress by measuring key environmental variables as well as the apes' behavior under various conditions. A thermal imaging camera was used in combination with environmental data collected by data loggers to determine heat load experienced by the chimpanzees in the different microclimates, or the small-scale environmental conditions, used by the community (Bramer et al., 2018). Using a biophysical model (Niche Mapper™), I then verified whether this population will be able to adjust to climate change conditions in the future. Niche Mapper was used in collaboration with its creator, Dr. Warren Porter from the University of Wisconsin-Madison. Data obtained from several sources were combined to create a biophysical model of a Western chimpanzee in the Fongoli, Senegal environment including: environmental data collected at the Fongoli site, physical measurements obtained from captive chimpanzees at the National Center for Chimpanzee Care of the M.E. Keeling Center and Schoonaert et al. (2007), and predictions regarding future environmental conditions from the Inter-governmental Panel on Climate Change (IPCC). My research aids in determining which areas within the habitat of Critically Endangered Western chimpanzees will be exceptionally challenging for these apes and could be extrapolated to inform our understanding of limits for other chimpanzee subspecies as well (Humble et al., 2016).

Specifically, I hypothesized that data collected on temperature, relative humidity, and wind speed would illuminate the importance of various microhabitats for Fongoli chimpanzees. Thermal images of the chimpanzees were expected to show a higher heat signature in the open grassland and woodland areas in comparison to the caves and closed

canopy gallery forests, based on temperature differences in these areas (Pruetz, 2007). I predicted that, using a biophysical model of the chimpanzees (Niche MapperTM), at some point Fongoli chimpanzees will not be able to thermoregulate efficiently, as measured by metabolic rate and evaporative water loss, in the increasingly warmer conditions predicted by the IPCC, especially if the cave and gallery forest microhabitats are lost. These latter areas are the target of artisanal mining in southeastern Senegal (Boyer-Ontl, 2017).

Primate Models for Hominin Evolution

Paleontological and archaeological records are forms of direct evidence that can be used to make inferences regarding early hominins (bipedal primates belonging to humans' own taxonomic Tribe Hominini). However, certain characteristics, such as most behaviors, cannot be inferred from fossil or archeological evidence. Because direct evidence is rare in the fossil record, referential models are necessary to reconstruct early hominin behavior (Tooby & DeVore, 1987).

Researchers look to primates as referential models for better understanding early hominins and the last common ancestor between the human lineage and chimpanzees (DeVore & Hall, 1965; Moore, 1996; Sponheimer et al, 2006; Wheeler, 1984). Other species that have been used as referential models for hominin behavior include baboons (*Papio anubis*: DeVore & Washburn, 1963; Strum & Mitchell, 1987), chimpanzees (*Pan troglodytes*: McGrew, 1981) and bonobos (*P. paniscus*: Zihlman et al., 1987). There are two types of referential models commonly used, analogous and homologous. Analogous models look to species that are similar to the referent because they are thought to share a common adaptation, for example an adaptation to a specific environment. Homologous

models are species that are closely related evolutionarily to the referent and therefore, are thought of as more likely to adapt in an evolutionarily similar manner to the same selective pressures (Moore, 1996).

Baboons are often chosen as analogous referential models for early hominins because they characteristically live in a savanna environment (Strum & Mitchell, 1987). Hominins are thought to have developed bipedalism, hairlessness, and increased body size due to adaptation to an open savanna habitat or a transition from a closed canopy to an open woodland habitat (Bobe & Behrensmeyer, 2004; Wheeler, 1984, 1992, 1994). Therefore, non-human primates who have adapted to live in this type of environment, like baboons, may exhibit convergent behavior with early hominins. Chimpanzees and bonobos are common homologous referential models due to their close evolutionary relation with modern humans (Britten, 2002). Today, chimpanzees are the most commonly used referential models for early hominin behavior (Sayers & Lovejoy, 2008). However, anthropologists disagree on the validity of this model, depending on the questions asked.

In their 1987 paper, Tooby and DeVore start a discussion refuting the validity of using chimpanzees as referential models for hominin behavior, which has lasted decades and is ongoing. The main argument articulated by those against chimpanzee referential models is that anthropologists should not use chimpanzees as a literal (i.e., direct analogy) model for early hominins. Instead, they state that data obtained from chimpanzees should be combined with other non-human primate findings as well as fossil evidence to create conceptual models for early hominins and the last common ancestor (Tooby & DeVore, 1987, Sayers & Lovejoy, 2008). However, it is important to note that

none of the proponents of chimpanzee referential models argue that only chimpanzees should be used as representations of early hominins or the last common ancestor. Instead, proponents state that chimpanzee behavior is valuable in aiding anthropologists' understanding of how hominins may have behaved and what makes them unique in comparison to non-human primates (Moore, 1996; Stanford, 2012)

Chimpanzees have been used to explore hominin behavior for several decades. One of the first cases for the referential chimpanzee was made by Tanner (1981), who presented these apes as a model for the female role in human evolution. Before, savanna baboons were the favored models due to their aforementioned adaptation to a savanna environment and the male dominance hierarchies that were thought to be important in human evolution (DeVore & Washburn, 1963). The baboon model lost traction after Strum and Mitchell's (1987) research showed the importance of female reproductive strategies in baboon society (Moore, 1996). This resulted in the frequent use of chimpanzees as a referential model for early hominins, especially once chimpanzees were discovered to inhabit a similar savanna environment.

Climate modeling has allowed researchers to determine the type of environment early hominins likely inhabited. Kappelman et al. (1997) and Reed (1997) used fossil mammals to determine the habitat structure of regions where early hominins like Australopithecines lived. These studies concluded that hominins were living in regions that were a mixture of open grassland and woodland, with small patches of closed forest (Cerling et al., 2011; Kappelman et al 1997; Reed 1997). This type of environment is similar to that of some savanna landscape chimpanzees, in particular the Fongoli community in Senegal (Pruetz & Bertolani 2007). Studying these populations can inform

anthropologists' understanding of how hominin traits evolved during the transition from a closed forest to an open woodland habitat.

Behavioral Adjustments in Primates: A Method of Thermoregulation

Primates are homeotherms that regulate their body temperature using various behavioral adjustments, which include shade use, body posture, alteration of activity schedules, cave use, and adjustment of inter-individual spacing (Campos & Fedigan, 2009). Homeotherms are animals that keep their body temperature at a constant level (Elizondo, 1977). When a homeotherm's body temperature raises or lowers within a specific range, the thermo-neutral zone, it is able to regulate body temperature through its cardiovascular system. However, some homeothermic animals live in environments that cause body temperature to be outside of the thermo-neutral zone; when this occurs an animal may adjust through behavioral or physiological processes (Elizondo, 1977). Adjustments used by primates in a savanna habitat are of particular interest because they do not have the physiological cooling mechanisms that other savanna mammals employ to maintain body temperature, for example the carotid rete for brain cooling (Mitchell et al., 1987; Brain & Mitchell, 1999). Physiological adjustments used by primates include panting, and sweating (Campos & Fedigan, 2009).

In wild chimpanzee populations, it is extremely difficult to measure physiological adjustments without using invasive methods. Therefore, researchers often focus on behavioral adjustments utilized by wild chimpanzee communities. The Fongoli chimpanzees appear to behaviorally thermoregulate through use of different habitats (Pruetz & Bertolani, 2009). Fongoli is a semi-arid savanna-woodland environment consisting of gallery forest, woodland, bamboo woodland, and open grassland habitats,

with forests accounting for less than 3% of the apes' home range (Pruetz, 2018). It has been suggested that Fongoli chimpanzees use caves and gallery forests to avoid heat stress (Pruetz 2007, Pruetz & Bertolani 2009). Open grassland and woodland are the hottest habitats that the chimpanzees use (Pruetz, 2018). Although the temperatures of the habitats as well as the apes' use of them have been quantified, it is unclear how much the use of these habitats affects the body temperature of the individuals within this community of chimpanzees.

Measuring Wild Primate Thermal Stress

Collecting body temperature measurements from wild primates is difficult, especially when researchers need multiple temperature measurements across an extended period. Three main methods have been used to collect this type of measurement: fecal temperature decline (Jensen et al., 2009), subcutaneous implants (Brain & Mitchell, 1999) and thermal imaging cameras (Thompson et al., 2016, 2017). Fecal temperature decline involves collecting fecal samples from individuals and measuring the temperature every 2-20 seconds. Jensen et al. (2009) state the importance of starting the fecal temperature measurements as soon as possible after defecation occurs and continuing measurements until the temperature finishes declining in order to ensure accurate body temperature estimation. The fecal temperature decline method is not practical for research that requires frequent body temperature measurements in different locations; however, it can be used as validation to determine if other non-invasive methodologies are capturing an accurate representation of core body temperature.

Brain and Mitchell (1999) were the first to study the variation of wild nonhuman-primate body temperature by surgically implanting temperature telemeters. They placed

the telemeters in the peritoneal cavities of two adult male free-ranging baboons (*Papio hamadryas ursinus*) in Namibia and found that their body temperature fluctuated 5.3°C and could even exceed 41°C (Brain & Mitchell, 1999). Implanted telemeters require isolating individuals, darting them, and administering anesthetic, each of these steps can be dangerous for a wild chimpanzee's health. Since this species is endangered, such invasive methods should be avoided.

Thompson et al. (2017) used subcutaneous implants and a thermal imaging camera (FLIR E60bx) to measure surface body temperature of mantled howler monkeys (*Alouatta palliata*). They found that a thermal imaging camera was a reliable measurement of surface body temperature for primates who cannot undergo more invasive methods and identified the surface of the dorsum as the area of the body best approximating subcutaneous temperature (Thompson et al., 2017). Thermal imaging temperature measurements can be skewed by factors including the angle of the body surface when the image is taken, distance between the camera and animal, solar radiation, and wet fur (Faye et al., 2016; McCafferty, 2007). It is important to note that surface body temperature is not a proxy for core body temperature. Peripheral regions of the body are impacted by ambient conditions and often act as thermosensors for the body's thermoregulatory response (Roberts, 1988). However, surface body temperature can be used as a measure of the thermal stress an individual is experiencing.

Temperature varies across an individual's body surface. In particular, regions with high vascularization lacking insulation (i.e. hair and fur) act as thermal windows and are more affected by ambient conditions in comparison to body temperature. These thermal windows allow animals to transfer heat to their surrounding environment when heat

stressed (Tattersall & Cadena, 2010). Insulated skin covered in hair better represents the temperature of the superficial layer of the body rather than the ambient conditions (Romanovsky, 2014). When comparing thermal images of the face and dorsum of howler monkeys, Thompson et al. (2017) found that the surface temperature of the face was more variable than the dorsum and reflective of ambient conditions, whereas the temperature of the dorsum was more reflective of subcutaneous temperature. Therefore, insulated skin temperature is a better measurement of the temperature of the underlying tissues and can be used to look at the body's thermoregulatory response to its environment.

Measuring Microclimates

Behavioral responses demonstrate the importance of microclimates in an animal's habitat. For example, animals seek shaded regions like caves or a forested canopy during high temperatures to prevent overheating (Pruetz & Herzog, 2017; Duncan & Pillay, 2013) Microclimates are the actual climatic conditions that animals experience, a combination of the broader climate of the region and the organisms' specific habitats within the environment (Bramer et al, 2018). Climatic conditions have an extremely important impact on a primate's body temperature, thus affecting their thermoregulation processes. The microclimates previously mentioned, caves and gallery forest, appear to help the Fongoli chimpanzees avoid heat stress, protecting individuals from hyperthermia (Pruetz 2007; Pruetz & Bertolani, 2009). Additionally, Thompson et al. (2017) stated that collecting the microclimate conditions at the same time as the thermal image is captured increased the reliability of the body temperature model in their study (Thompson et al., 2017).

It is also important to examine the daily fluctuations of the different microclimates used by primates to better understand the responses behind their activity budgets and travel patterns. There are a large variety of methods used to collect microclimate data in primate habitats. These include data loggers, local weather stations, and remote weather satellites (Hill, 2006; Thompson et al., 2016; Gestich et al., 2014). Data loggers are the best method for measuring the temperature of multiple microhabitats, as weather stations and remote satellites measure the climate across a large area and therefore are not conducive to recording the small-scale weather variation that primates directly experience (Bramer et al., 2018). Researchers recommend including wind speed and relative humidity in microclimate studies as these have been shown to influence the perceived temperatures of an animal (Bramer et al., 2018).

Climate Change Impacts on Non-Human Primates and Niche Mapper

Nonhuman primates are likely to face 10% greater warming in comparison to the global mean due to climate change (Graham, 2016). Graham (2016) used data from the World Climate Research Programme's Coupled Model Intercomparison Project to calculate annual increases in temperature and precipitation (Solomon et al., 2011). However, this data is extremely broad scale and does not show how the specific areas that the primates live in will be affected. This is why new technologies, which include microclimate modules, are extremely useful for animal researchers to determine how a particular species will be directly impacted by climate change (Bramer et al., 2018). One of these smaller scale modules is called Niche MapperTM, a microclimate and endothermic biophysical model, which is used to determine if an animal will be able to thermoregulate in future climatic conditions.

The microclimate model in Niche Mapper uses local weather station data to calculate the climatic conditions of an animal's habitat, which can be set in today's climate or in a future predicted climate. Output from the microclimate model calculates the hourly environmental conditions in the sunniest and shadiest locations available to the animal. These calculations include the environment above and below ground, including the microclimatic conditions at the animal's height (Porter, 2016)

The endothermic model of Niche Mapper uses physical measurements and heat transfer laws to calculate heat balance and allowable metabolic rates of an animal, such as a mammal or bird (Fort et al., 2009). This endothermic model places the animal within the environmental conditions specified by the microclimate model and calculates the animal's energetic expenditure. It assumes that the animal will attempt to minimize energetic spending; therefore, if the animal's metabolic rate reaches +/- 5% the target minimum value, then the animal will use behavioral or physiological adjustments to stay within the range (Porter, 2016).

A combination of the endothermic and microclimate modules has been used to determine the potential climate change impact on a variety of species, including elk (*Cervus elaphus*), pika (*Ochotona princeps*), seabirds (*Phalacrocorax auritus*), and vervet monkeys (*Chlorocebus pygerythrus*) (Long et al., 2014; Mathewson et al., 2017; Fort, Porter, and Gremillet, 2009; Mathewson et al., 2018). Mathewson et al. (2017) discovered that pikas with a smaller body size and less dense hair will have a higher chance of survival in a warmer predicted climate. Additionally, Mathewson et al. (2018) tested the model's ability to predict the body temperature in free-ranging vervet monkeys. The model accurately predicted the body temperature of the vervet monkeys within +/-

0.5°C 91% of the time during a five-year study period. Such research has shown that Niche Mapper can be a useful tool for measuring heat stress in animals, especially for predicting climate change impacts on a population.

Project Summary

In light of continued and future climate change, it is important to determine the actual microclimatic conditions animals experience and combine this information with the different technologies that can be used to measure microclimate variability and wild animals' body temperature. In this study, I analyze the climatic conditions of the microhabitats used by the Fongoli chimpanzees via data logger technology, how they adjust their behavior to these conditions based on their activity patterns, and how these behavioral adjustments impact chimpanzees' ability to thermoregulate based on thermal imaging technology. I then use a biophysical model (Niche Mapper) to predict whether this population would survive the hypothesized environmental conditions in the future. Given that Niche Mapper and thermal imaging are novel technologies, using these in my research can demonstrate the potential of these technologies for the future study of thermoregulation in animals.

CHAPTER II. WESTERN CHIMPANZEE USE OF MICROCLIMATES, A FORM OF BEHAVIORAL THERMOREGULATION

Introduction

A transition from a closed forest environment to an open woodland savanna is hypothesized to have played a significant role in human evolution (Cerling et al., 2011). Thermoregulatory pressure is thought to have led to bipedalism, hairlessness, and increased body size in the hominin lineage (Wheeler 1984, 1991a, 1991b 1994). However, it is unclear how high thermal stress would have influenced the behavior of early hominins. Chimpanzees inhabiting savanna biomes are considered good homologous and analogous referential models for early hominins, as they are *Homo sapiens*' closest living relatives and live in an environment thought to have selected for unique *Homo* traits (McGrew et al., 1981; Moore, 1996). The Fongoli chimpanzee community in Senegal is a useful model as they are only one of two fully habituated groups of chimpanzees that inhabit an open savanna-woodland environment. The Fongoli community lives in the hottest and driest environment where habituated chimpanzees are studied today (Pruetz & Bertolani, 2009).

The Fongoli chimpanzee community faces significant biological stress in the form of high temperatures and water scarcity, confirmed by their physiological responses (e.g., c-peptide, creatinine and cortisol levels: Wessling et al., 2018). This group of chimpanzees shows unique responses to these conditions. In response to high temperatures, the Fongoli apes use specific habitats like caves and gallery forest (Pruetz, 2007; Pruetz & Bertolani, 2009), are active at night (Pruetz, 2018), and soak in pools of

water (Pruetz & Bertolani, 2009). These behaviors and use of habitats are hypothesized to play a significant role in the chimpanzees' thermoregulation (Pruetz & Bertolani, 2009); however, it is unclear how much these behaviors reduce heat stress.

Thermoregulation is an important behavioral and physiological process used by animals to adjust to their environment. These processes become vital when an animal faces environmental conditions that place it outside of its thermo-neutral zone (Elizondo, 1977). Primates are homeotherms, which are animals that maintain a constant body temperature (Elizondo, 1977). When their body temperature is outside of their thermo-neutral zone, non-human primates must adjust behaviorally and physiologically. Behavioral adaptations used by non-human primates include shade use, body posture, alteration of activity schedules, cave use, and adjustment of inter-individual spacing (Campos & Fedigan, 2009).

Understanding the behavioral and physiological processes wild animal populations use to maintain body temperature can be difficult, as commonly used methods in the past have required invasive body implants (Brain & Mitchell, 1999). However, new non-invasive technologies have increased the ability of researchers to understand the behavioral and physiological adaptations animals use to live in a particular environment. These technologies are particularly useful for studying threatened species. By allowing researchers to better understand the stressors affecting a particular population, we can be better informed in our conservation decisions

Thermal imaging is a relatively new technology, which can be used to non-invasively measure the surface body temperature of non-human primates. Thompson et al. (2017) found that thermal imaging can be used to estimate the subcutaneous body

temperature of howler monkeys (*Alouatta palliata*); this was the first use of thermal imaging to measure surface body temperature of wild non-human primates. The aim of my study was to quantify the thermoregulatory benefit the Fongoli chimpanzees receive through behavioral thermoregulation. I use thermal imaging to explore how the Fongoli chimpanzees adjust to heat stress by using different habitats, shade cover, and behavioral adjustments.

I hypothesized that data collected on temperature and relative humidity would illuminate the importance of various microhabitats for Fongoli chimpanzees and thus apes living in environments that are more open. It has been shown that Fongoli chimpanzees use caves and gallery forests to avoid heat stress (Pruetz, 2007, Pruetz & Bertolani 2009). Open plateau/short-grass grassland and woodland are the hottest habitats that the chimpanzees use (Pruetz, 2007). Therefore, thermal images of the chimpanzees were expected to show a higher heat signature in the open habitats (grassland and woodland areas) in comparison to closed habitat types such as caves and gallery forests, based on temperature differences in these areas (Pruetz, 2007). Additionally, thermal images were expected to show a higher heat signature in low levels of shade cover, due to increased solar radiation and during active behaviors, like traveling and feeding, which may expose individuals to hotter microclimates.

Methods

Study Site

The Fongoli chimpanzee community lives in the Kedougou region in southeastern Senegal. Fongoli is a semi-arid savanna environment consisting of gallery forest (2%), woodland (46%), grassland (16%), open plateau/short grass-grassland (20%), bamboo

(12%) habitats, and horticultural fields (4%), with forests (closed canopy habitat types) accounting for less than 3% of the apes' home range (Pruetz, 2018; Table 2.1). There are two distinct seasons: a long dry season, October to May, and a short wet season, June to September. Fongoli averages 945mm of rain annually with an average temperature of 28.3°C, but the temperature can reach as high as 45.9°C in the dry season (Wessling et.al., 2018). The chimpanzee community averages 32 individuals (2006-2018) and currently numbers 34 (Fongoli Savanna Chimpanzee Project, unpublished data). They fission into smaller parties during the dry season, with an average of 15 individuals in a party (Pruetz & Bertolani, 2009).

Table 2.1: Definitions of Fongoli Habitats: modified from (Bogart & Pruetz, 2011)

Definitions of Fongoli Habitats	
Gallery forest	Tropical semideciduous lowland closed canopy forest
Woodland	Drought-deciduous lowland woodland with a canopy cover [40%. Grasses dominate understory. Certain areas may be considered closed canopy seasonally (rainy season) when canopy cover is >80%
Bamboo woodland	Contains isolated palms and deciduous trees. Understory composed of <i>Oxytenanthera abyssinica</i> (bamboo), which reaches >2 m height in rainy season
Tall-grass grassland	Savanna with isolated deciduous trees with a height of at least 2 m. <i>Gardenia</i> spp. common. 40% canopy cover. Predominated by elephant grass (<i>Pennisetum purpureum</i>), reaching 2–4 m tall
Short-grass grassland (plateau)	Savanna with isolated deciduous shrubs less than 3 m. tall. <i>Combretum</i> spp. common. Short grasses include species of <i>Cynodon</i> and <i>Chrysopogon aucheri</i> . Soils composed of laterite rock
Cave	Rock shelter

Data Collection

I conducted research at the Fongoli field site (12°39' N, 12°13' W) from June-August 2019. During this period, I collected data on the environmental condition

(temperature, relative humidity, and wind speed) of microhabitats used by the Fongoli chimpanzees, including caves and all habitat types (e.g., gallery forests, long-grass grassland, woodland, bamboo woodland, and open plateau/short-grass grassland). Hobo™ (Pro V2 Internal Temp/TH) data loggers were placed at a 1-meter height in the gallery forest, woodland, and bamboo woodland and at a 10-centimeter height in the open plateau/short-grass grassland and cave. A 1-meter height was chosen to best represent the environmental conditions at shoulder height of the chimpanzees. The shorter height of the data loggers in the open plateau and cave was due to the lack of vegetation able to hold the data logger securely. These data loggers measured the temperature and relative humidity at 10-minute intervals.

In order to validate the environmental data, I also collected data on the actual environmental conditions experienced by the chimpanzees. I followed adult males (n=12, Table 2.2) of the group per Fongoli Savanna Chimpanzee Project (FSCP) protocol. Data collection on females is restricted to prevent over habituation to humans, as infant chimpanzees are at risk of poaching for the pet trade (Pruetz & Kante, 2010). Using a Kestrel Environmental Meter, I measured temperature, relative humidity, and wind speed. Every 10 minutes that the individual was visible, I collected data on focal subject activity (resting, traveling, social, feeding, or soaking: Appendix 1), habitat type, and the microclimate conditions, including percent of a subject's body that was shaded (0, 25, 50, 75, or 100%). Focal follows consisted of an all-day follow (typically sunrise to sunset) of one adult male. If a focal was lost and not found within 20 minutes, I followed the next male on the list. Subject male order followed the previous month's order, with modification, as males were not always located on a given day given the fission-fusion

nature of chimpanzee social grouping. I followed my focal subject with one of the FSCP research assistants, Michel Sadiakho, who has worked for the FSCP since 2008 and Jacques Keita, who has worked for the FSCP since 2015.

Table 2.2: Adult Male Study Subjects: Each study subject’s code, dominance rank, and age.

Subject Code	Dominance Rank	Age
JM	1	~21 years
LT	2	~20 years
BO	3	~22 years
MI	4	~20 years
DW	5	~17 years
LP	6	~25 years
KL	7	>30 years
DF	8	>30 years
LX	9	15.5 years
BI	10	>30-35 years
BN	11	>30-35 years
SI	12	>35 years

At the Fongoli site, I used a thermal imaging camera (FLIR® E75) to measure the temperature of chimpanzee surface body in each of the microhabitats, levels of shade, and during different activities. Additionally, I looked at the difference in surface body temperature between individuals to see if there was any variation within the group. I used the Thompson et al. (2017) protocol, which was modified following a year-long study using thermography at Fongoli (Pruetz, unpublished data; Wackerly, 2018). This data was collected in a semi-systematic method. Images of adult male subjects in different habitats and microhabitats were taken opportunistically within 10-minute

intervals (example of an image in Figure 2.1). The dorsum was chosen as the priority body part for temperature measurement, as Thompson et al. (2017) found that it was best for measuring subcutaneous body temperature. However, images of other body parts were taken to determine if they did not differ significantly from the dorsum temperature and could be included in analysis. Research shows that thermal imaging measurements can be skewed by factors including the angle of the body when the image is taken, distance between the camera and animal, solar radiation, and wet fur (Faye et. al., 2016; McCafferty, 2007). Therefore, thermal images for this project were taken when the following conditions were met: 1) Subject was within 15 meters. 2) The subject's body surface of interest was directly facing or oblique to the camera. 3) Subject was not in direct sunlight. 4) The subject's dorsum was at least partially dry.

Thermal images were analyzed using FLIR Tools (version 6.4.18039.1003). Emissivity was set at 0.98, the accepted value for mammalian skin and fur (Steketee, 1973). The temperature, relative humidity, and distance were adjusted in FLIR Tools to match the environmental conditions collected when the thermal photo was taken. Temperatures of the back, front, side, head, and limbs were collected from the photo if they were easily identified from the image without any obstruction; this prevented any unreliable temperature readings.

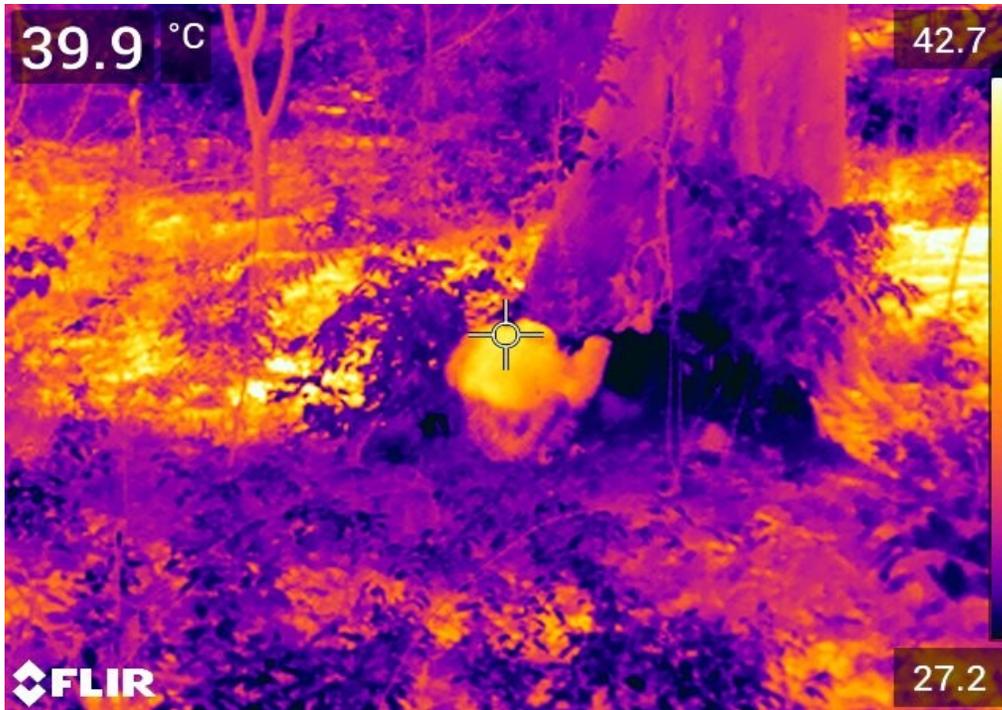


Figure 2.1: Example of a thermal image taken at Fongoli (Surface of the chimpanzee dorsum hair within the denoted point had an average temperature of 39.9°C. Darker dorsum hair (lower back) is wet from soaking.)

Data Analysis

In order to determine which body parts could be used to measure surface body temperature and if there was a difference in temperature between individual males, I used one-way ANOVAs in SPSS (25.0.0.1). To examine the difference in surface body temperature between habitats, percent of body shaded, and subjects' activity I used a one-way ANOVA. I addressed the question of how the use of different microclimates affects the surface body temperature of Fongoli chimpanzees, and thus their ability to thermoregulate by using a multiple linear regression to determine the impact of activity, habitat, shade cover, environmental temperature, relative humidity, and wind speed on surface body temperature of individuals.

A MANOVA was used to measure the difference in environmental conditions, temperature and relative humidity between habitats at 3-hour intervals. This comparison demonstrates the importance of collecting microclimatic data to better understand the environmental conditions to which primate species are directly responding. For all significant ANOVAs, a Bonferroni post-hoc test was performed. This post-hoc test was selected because it is a conservative test and useful for determining significance when there are multiple comparisons (Lee & Lee, 2018).

Results

Data collection included 239.67 focal subject male observation hours with 892 data points comprising thermal images meeting the requirements to obtain temperature measurements. During observation, chimpanzees used specific habitats at different frequencies: bamboo woodland (8.2%), gallery forest (29.7%), open plateau/short grassland (4.6%), woodland (57.1%), grassland (0.2%), and caves (0.2%) (Figure 2.2). Additionally, they heavily used full shade cover, 0% (0.09%), 25% (1%), 50% (3.5%), 75% (5.4%), and 100% (89.2%) (Figure 2.3). Behaviorally, the chimpanzees spent the majority of their time resting (52.6%), followed by feeding (20.7%), socializing (10.4%), traveling (14%), and soaking in pools of water (2.2%) (Figure 2.4).

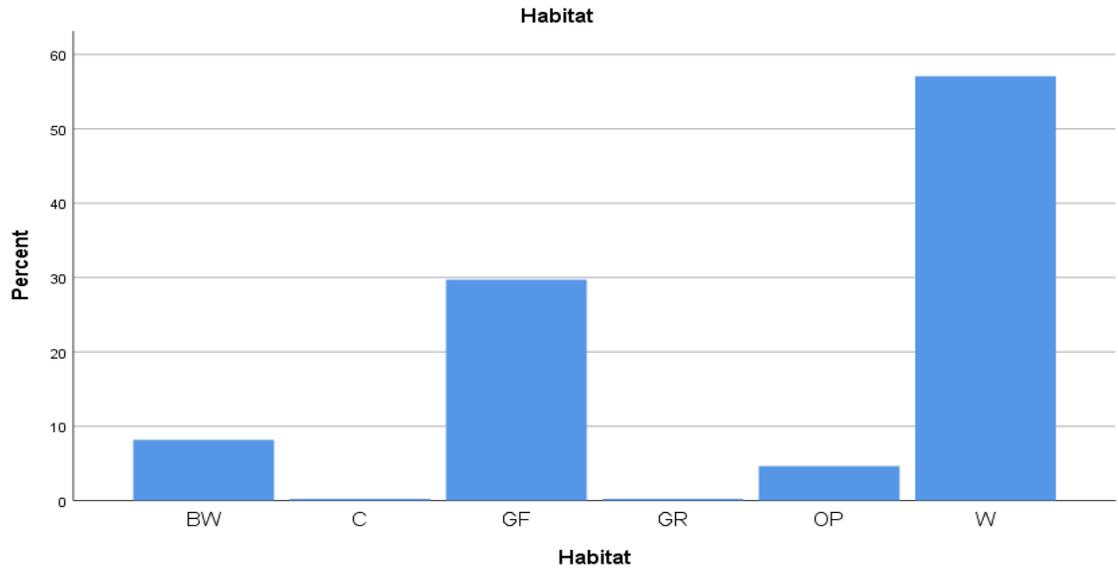


Figure 2.2: Fongoli Chimpanzee Habitat Use (Percentage of time spent in each habitat type: bamboo woodland (BW), cave (C), gallery forest (GF), tall-grass grassland (GR), open plateau/short-grass grassland (OP), and woodland (W).)

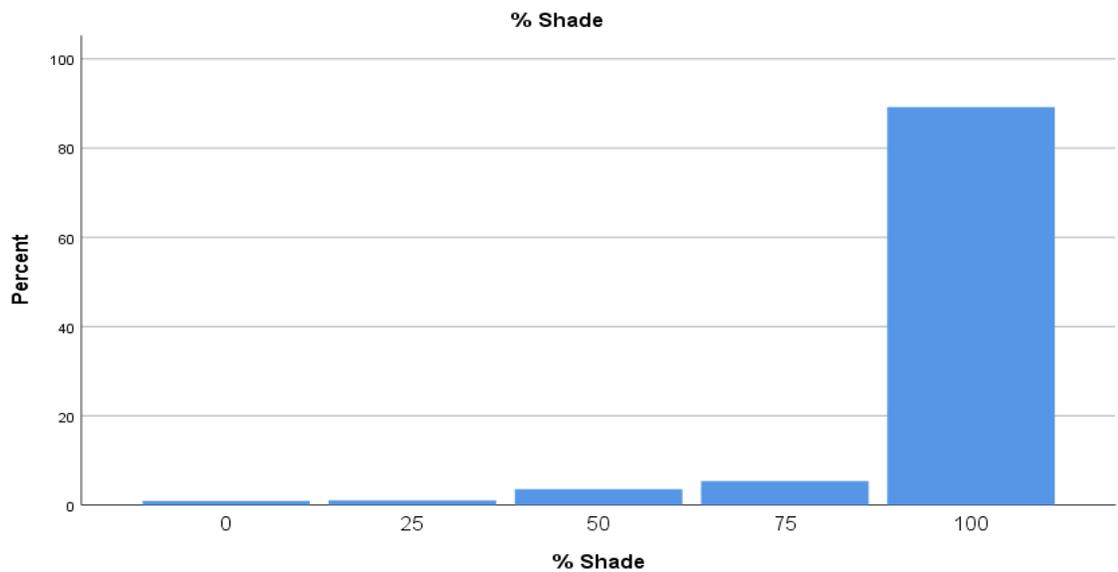


Figure 2.3: Fongoli Chimpanzee Shade Cover Use (Percentage of time spent in each level of shade cover: 0%, 25%, 50%, 75%, and 100%.)

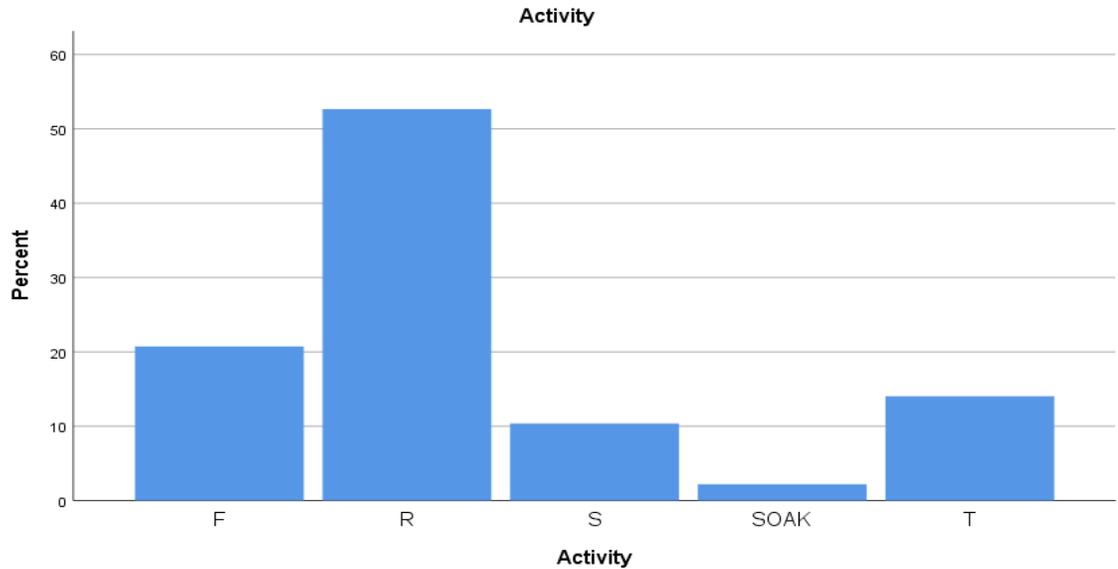


Figure 2.4: Fongoli Chimpanzee Activity Budget (Percentage of time used for each activity: feeding (F), resting (R), social (S), soaking (SOAK), and traveling (T).)

Environmental Conditions

A MANOVA revealed that there was a significant difference in temperature ($n = 1434$, $df = 5$, $F = 15.106$, $p=0.000$) and relative humidity ($n = 1434$, $df = 5$, $F = 66.259$, $p= 0.000$) between habitats used by the Fongoli chimpanzees (Figure 2.5 and Figure 2.6). Bonferroni post-hoc analysis revealed that there was a significant difference in temperature and relative humidity between some of the habitats (Appendix 2). In particular, the temperature in the gallery forest and cave was significantly lower compared to the open plateau/short-grass grassland, long-grass grassland, and bamboo woodland ($p < 0.05$), but not significantly different from the woodland habitat. The humidity in the cave and gallery forest was significantly higher than other habitats ($p < 0.05$).

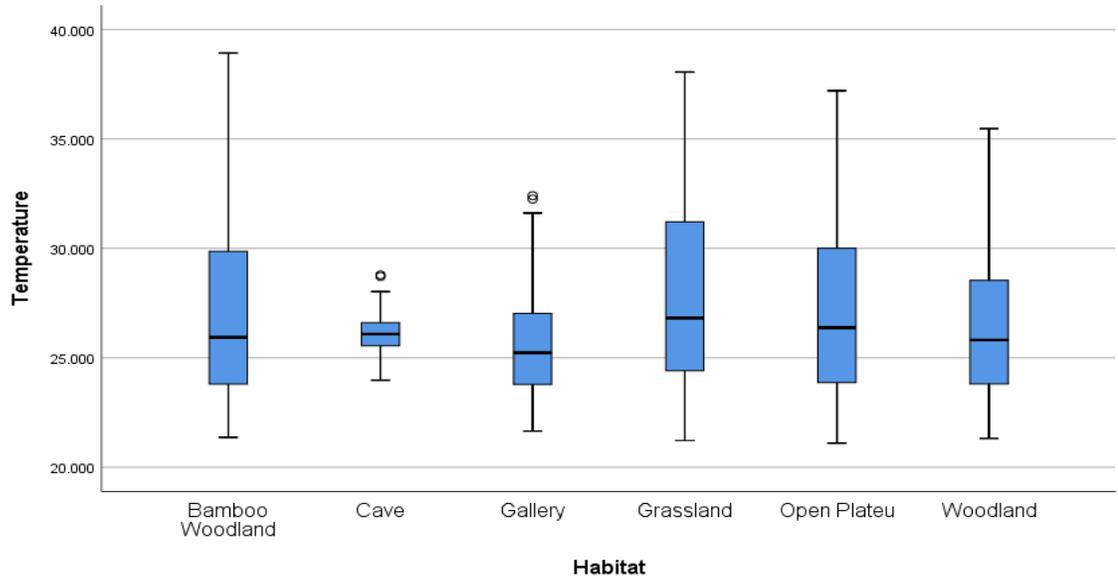


Figure 2.5: Difference in Ambient Temperature Between Habitats

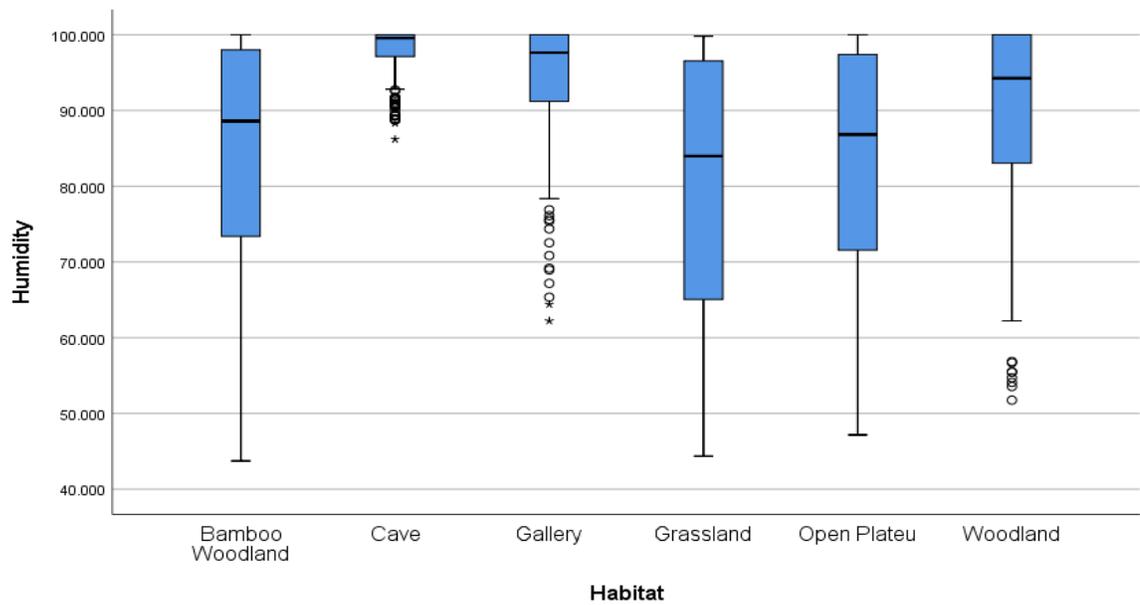


Figure 2.6: Difference in Relative Humidity Between Habitats

Surface Body Temperature

A one-way ANOVA showed that there was a significant difference in the average surface temperature between the different body parts of the chimpanzee subjects (Figure 2.7; $n=1,667$, $df=4$, $F=20.878$, $p = .000$). Bonferroni post-hoc revealed that the

temperature of the dorsum differed from the limbs and side (Table 2.3; $p < .05$).

Therefore, data points that included temperatures from the limbs and side were excluded from further analysis.

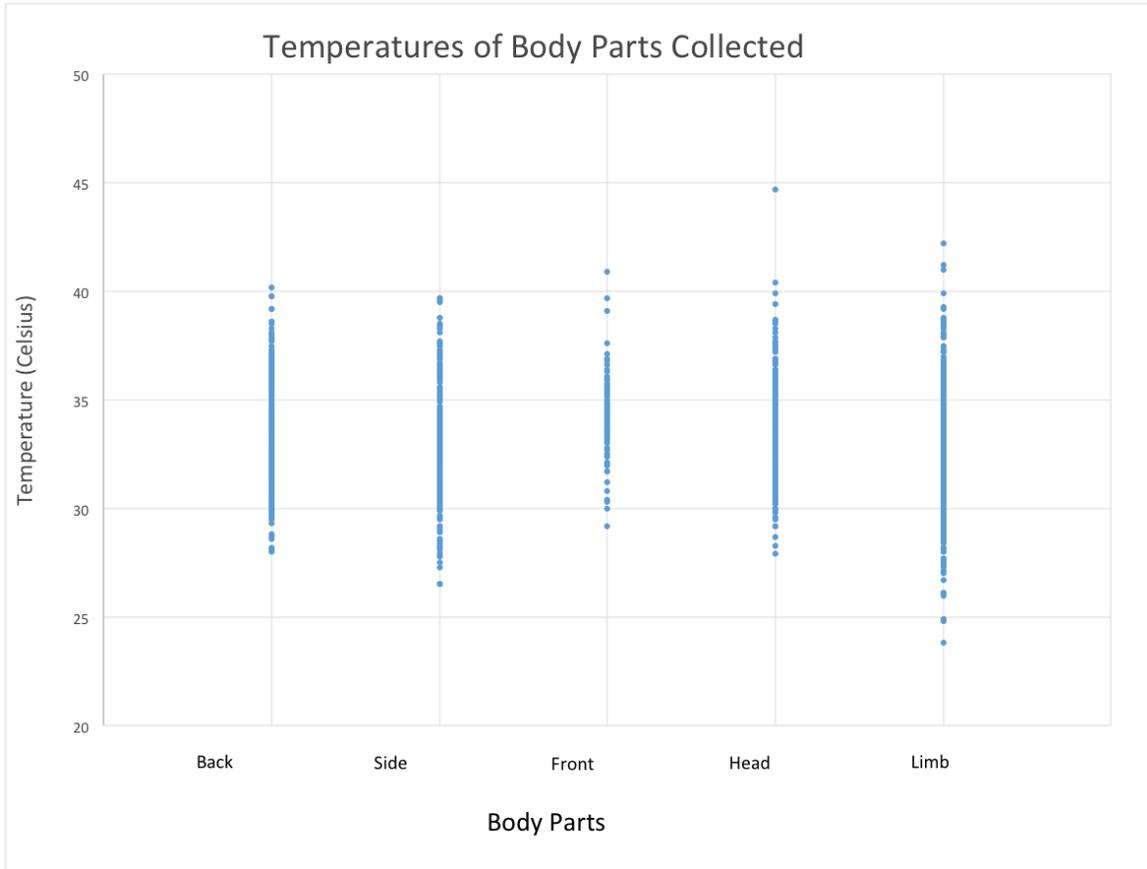


Figure 2.7: Body Part Temperatures (The temperature measurements taken from the different body parts of the Fongoli chimpanzees using thermal images.)

Table 2.3: Bonferroni Post Hoc Analysis of Difference in Surface Body Temperature Between Body Parts.

(I) Body Part		Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Back	Front	-0.541	0.306	0.774	-1.401	0.319
	Head	-0.016	0.184	1.000	-0.534	0.502
	Limbs	1.104*	0.155	0.000	0.668	1.541

Table 2.3 Continued						
	Side	.742*	0.195	0.001	0.196	1.289
Front	Back	0.541	0.306	0.774	-0.319	1.401
	Head	0.524	0.315	0.965	-0.362	1.411
	Limbs	1.645*	0.299	0.000	0.803	2.487
	Side	1.283*	0.322	0.001	0.379	2.187
Head	Back	0.016	0.184	1.000	-0.502	0.534
	Front	-0.525	0.315	0.965	-1.411	0.362
	Limbs	1.120*	0.173	0.000	0.634	1.607
	Side	.759*	0.209	0.003	0.171	1.346
Limbs	Back	-1.104*	0.155	0.000	-1.541	-0.668
	Front	-1.645*	0.299	0.000	-2.487	-0.803
	Head	-1.120*	0.173	0.000	-1.607	-0.634
	Side	-0.362	0.184	0.495	-0.879	0.156
Side	Back	-.742*	0.195	0.001	-1.289	-0.196
	Front	-1.283*	0.322	0.001	-2.187	-0.379
	Head	-.759*	0.209	0.003	-1.346	-0.171
	Limbs	0.362	0.184	0.495	-0.156	0.879
Based on observed means.						
* The mean difference is significant at the 0.05 level.						

There was a significant difference in the mean surface body temperature between individuals shown by a one-way ANOVA, using environmental temperature as a covariate (Figure 2.8; $n=747$, $df=12$, $F=48.193$, $p=.000$). Bonferroni post-hoc tests revealed that three individuals, BN, SI and JM differed significantly ($p < 0.05$) from the other individuals, BN and SI were the oldest and lowest ranking males in the study, while JM was alpha male.

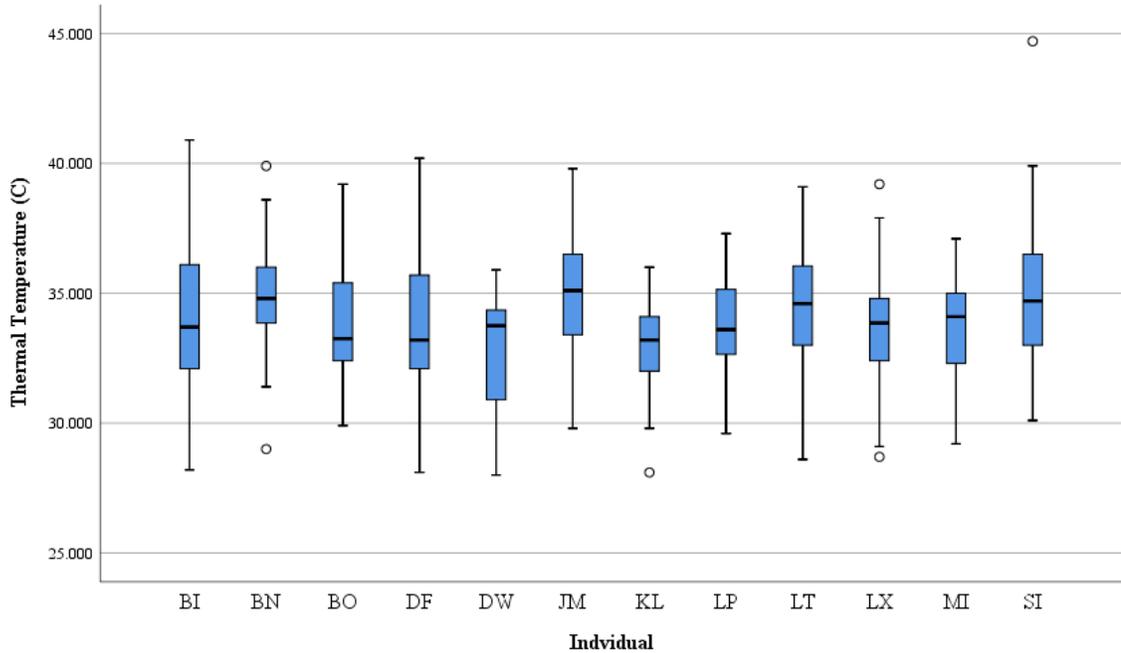


Figure 2.8: Surface Body Temperature of Adult Male Fongoli Chimpanzees

A one-way ANOVA showed that there was a significant difference in surface body temperature between habitat types (Figure 2.9; $n=743$, $df=3$, $F=14.158$, $p=0.000$). A Bonferroni post-hoc showed that the chimpanzees had a significantly higher surface body temperature in the open plateau/short-grass grassland habitat in comparison to the bamboo woodland, gallery forest, and woodland habitats (Table 2.4; $p<0.05$). The cave and long-grass grassland habitats were removed from analysis, due to a low sample size. There was also a difference in surface body temperature between the varying levels of shade cover (Figure 2.10, $n=743$, $df=4$, $F=15.362$, $p=0.000$). In particular, a Bonferroni post-hoc test revealed that the chimpanzees had a significantly lower surface body temperature when completely covered by shade in comparison to 0%, 50%, and 75% shade cover (Table 2.5; $p<0.05$). Additionally, chimpanzees exhibited a significant difference in surface body temperature according to behavior (Figure 2.11; $n=743$, $df=4$,

F=8.811, p=0.000). A Bonferroni post-hoc revealed that the chimpanzees had a lower surface body temperature while resting in comparison to feeding and socializing (Table 2.6; p<0.05).

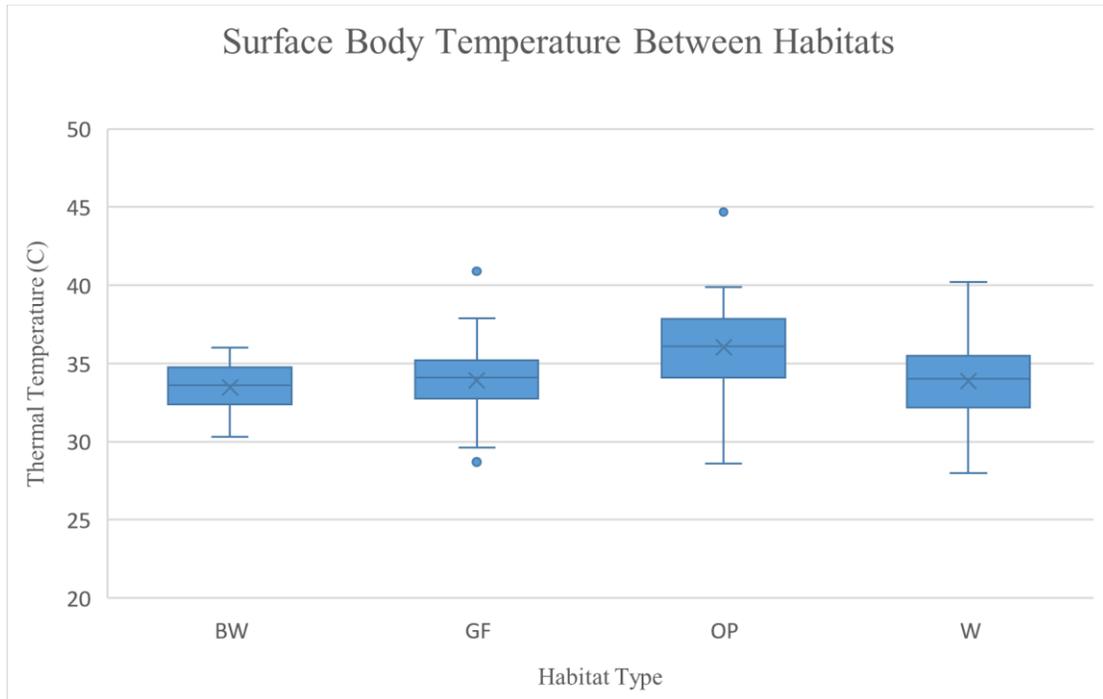


Figure 2.9: Difference in Surface Body Temperature of Adult Male Fongoli Chimpanzees Between Habitats (Average surface body temperature between the bamboo woodland (BW), gallery forest (GF), open plateau/short-grass grassland (OP), and woodland (W).)

Table 2.4: Bonferroni Post Hoc Analysis of Differences in Surface Body Temperature Between Habitats

(I) Habitat		Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
BW	GF	-0.43801	0.365117	1.000	-1.40388	0.52787
	OP	-2.56444*	0.465209	0.000	-3.79510	-1.33379
	W	-0.41272	0.344701	1.000	-1.32459	0.49914
GF	BW	0.43801	0.365117	1.000	-0.52787	1.40388
	OP	-2.12644*	0.365117	0.000	-3.09231	-1.16057
	W	0.02528	0.188968	1.000	-0.47461	0.52518

OP	BW	2.56444*	0.465209	0.000	1.33379	3.79510
	GF	2.12644*	0.365117	0.000	1.16057	3.09231
	W	2.15172*	0.344701	0.000	1.23986	3.06359
W	BW	0.41272	0.344701	1.000	-0.49914	1.32459
	GF	-0.02528	0.188968	1.000	-0.52518	0.47461
	OP	-2.15172*	0.344701	0.000	-3.06359	-1.23986

Based on observed means.
 * The mean difference is significant at the 0.05 level.

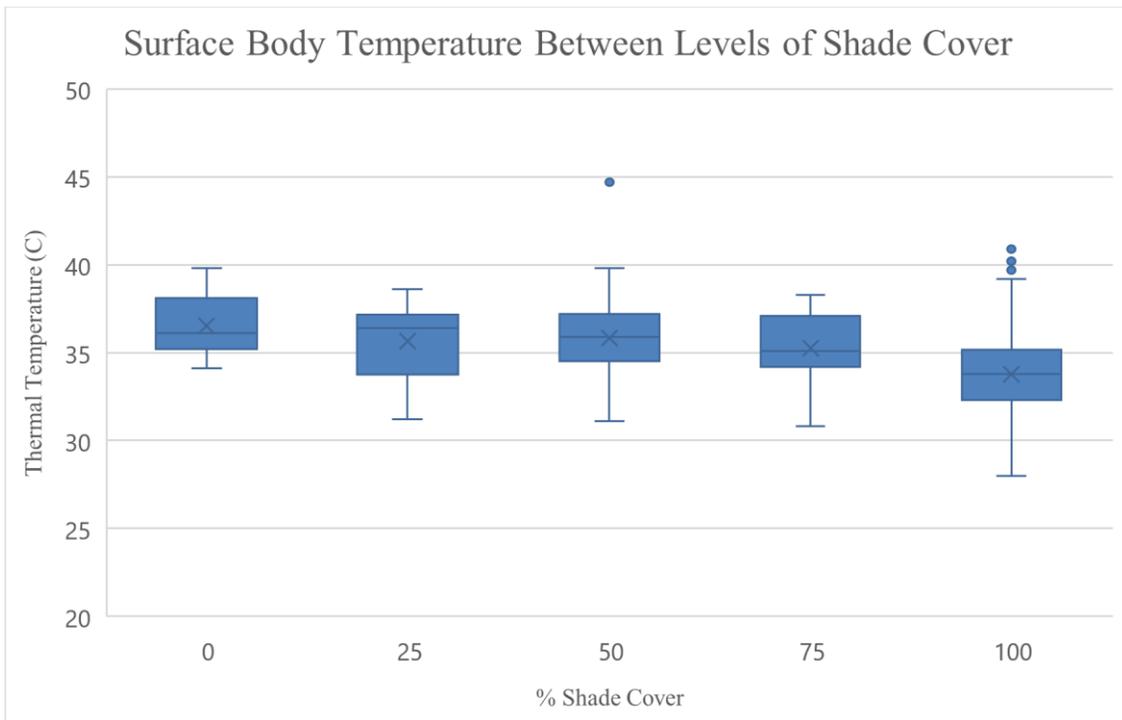


Figure 2.10: Difference in Surface Body Temperature Between Levels of Shade Cover (Average surface body temperature between 0%, 25%, 50%, 75%, and 100% shade cover.)

Table 2.5: Bonferroni Post Hoc Analysis of Differences in Surface Body Temperature Between Levels of Shade Cover

(I) % Shade		Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
0	25	0.87857	1.213804	1.000	-2.53889	4.29604
	50	0.67373	0.912985	1.000	-1.89678	3.24424
	75	1.27039	0.875522	1.000	-1.19464	3.73542
	100	2.77050*	0.829087	0.009	0.43620	5.10479

25	0	-0.87857	1.213804	1.000	-4.29604	2.53889
	50	-0.20484	0.973074	1.000	-2.94453	2.53485
	75	0.39182	0.938014	1.000	-2.24916	3.03280
	100	1.89193	0.894828	0.348	-0.62746	4.41131
50	0	-0.67373	0.912985	1.000	-3.24424	1.89678
	25	0.20484	0.973074	1.000	-2.53485	2.94453
	75	0.59666	0.489991	1.000	-0.78291	1.97623
	100	2.09676*	0.401171	0.000	0.96727	3.22626
75	0	-1.27039	0.875522	1.000	-3.73542	1.19464
	25	-0.39182	0.938014	1.000	-3.03280	2.24916
	50	-0.59666	0.489991	1.000	-1.97623	0.78291
	100	1.50011*	0.306490	0.000	0.63719	2.36303
100	0	-2.77050*	0.829087	0.009	-5.10479	-0.43620
	25	-1.89193	0.894828	0.348	-4.41131	0.62746
	50	-2.09676*	0.401171	0.000	-3.22626	-0.96727
	75	-1.50011*	0.306490	0.000	-2.36303	-0.63719

Based on observed means.
 *. The mean difference is significant at the 0.05 level.

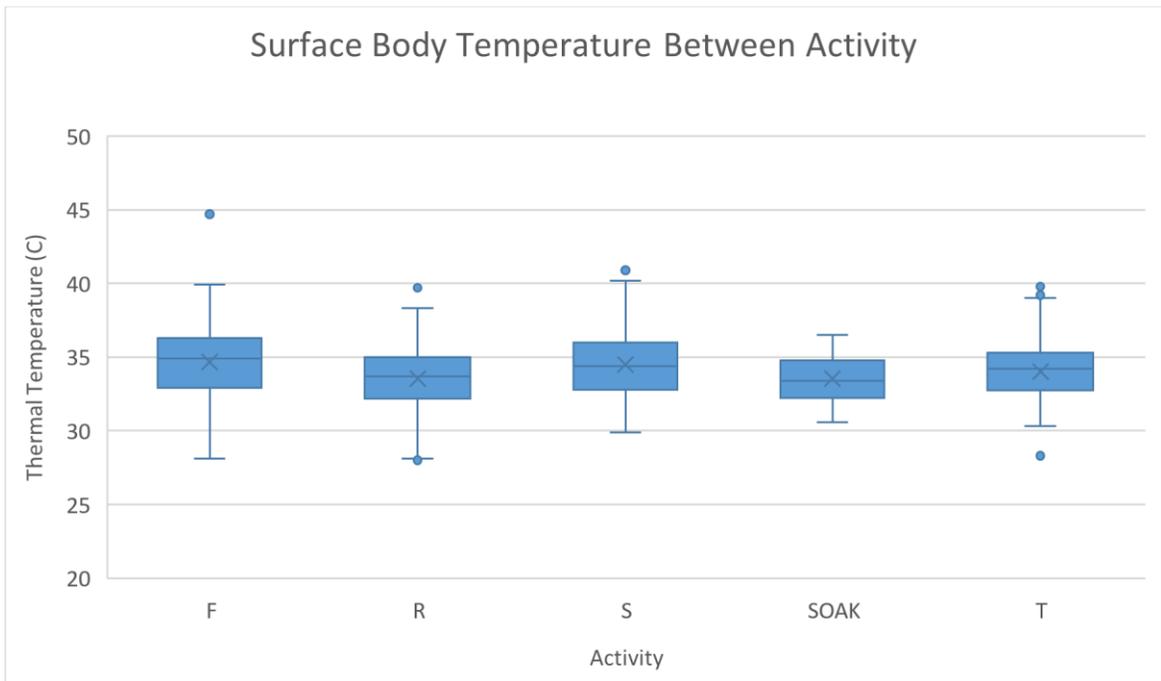


Figure 2.11: Difference in Surface Body Temperature Between Behaviors (Average surface body temperature between the chimpanzees feeding, resting, socializing, soaking, and traveling.)

Table 2.6: Bonferroni Post Hoc Analysis of Differences in Surface Body Temperature Between Behaviors

(I) Activity		Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
F	R	1.13837*	0.206967	0.000	0.55565	1.72108
	S	0.20425	0.301507	1.000	-0.64465	1.05314
	SOAK	1.16636	0.616548	0.589	-0.56953	2.90225
	T	0.65294	0.256699	0.112	-0.06979	1.37568
R	F	-1.13837*	0.206967	0.000	-1.72108	-0.55565
	S	-.93412*	0.276619	0.008	-1.71294	-0.15530
	SOAK	0.02799	0.604767	1.000	-1.67473	1.73072
	T	-0.48543	0.226949	0.328	-1.12440	0.15355
S	F	-0.20425	0.301507	1.000	-1.05314	0.64465
	R	.93412*	0.276619	0.008	0.15530	1.71294
	SOAK	0.96212	0.643284	1.000	-0.84905	2.77328
	T	0.44870	0.315558	1.000	-0.43976	1.33715
SOAK	F	-1.16636	0.616548	0.589	-2.90225	0.56953
	R	-0.02799	0.604767	1.000	-1.73072	1.67473
	S	-0.96212	0.643284	1.000	-2.77328	0.84905
	T	-0.51342	0.623540	1.000	-2.26900	1.24216
T	F	-0.65294	0.256699	0.112	-1.37568	0.06979
	R	0.48543	0.226949	0.328	-0.15355	1.12440
	S	-0.44870	0.315558	1.000	-1.33715	0.43976
	SOAK	0.51342	0.623540	1.000	-1.24216	2.26900

Based on observed means.
 *. The mean difference is significant at the 0.05 level.

Habitat, shade cover, activity, environmental temperature, relative humidity, and wind speed were included in a multiple linear regression. The model was a significant predictor of 49.1% of the variation in surface body temperature, $F(6, 736) = 118.51, p = 0.000$. Activity ($B = .149, p < 0.05$), habitat ($B = .274, p < 0.05$), shade cover ($B = -.017, p < 0.05$), environmental temperature ($B = .392, p < 0.05$), and wind speed ($B = .262, p <$

0.05) contributed significantly to the model. Relative humidity ($B=-0.013$, $p=0.215$) did not contribute significantly to the model.

Multiple linear regression equation:

$$\text{Body Temperature} = 28.099 + (.149*\text{activity}) + (.247*\text{habitat}) + (-.017*\text{shade cover}) + (.392*\text{environmental temperature}) + (.262*\text{wind speed}) + (-0.013*\text{relative humidity})$$

Discussion

This study used thermal imaging to examine Fongoli chimpanzee use of habitat types and microclimates as a form of behavioral thermoregulation in a savanna landscape. The results of this study can be used to investigate chimpanzee behavioral thermoregulation, which has important implications for how early hominins may have adapted to a savanna-woodland habitat. Additionally, Western chimpanzees are critically endangered and predicted to experience increasingly hot and dry conditions in the near future (Humble et al., 2016; IPCC, 2014). By better understanding the Fongoli chimpanzees' use of specific habitats and how this affects their surface body temperature, we can predict how they will be impacted by deforestation and the warming climate.

Surface Body Temperature

A major aim of this study was to determine how the use of specific habitats influenced the surface body temperature of the male Fongoli chimpanzee subjects. I predicted that the chimpanzees would exhibit a higher surface body temperature in the open (woodland, grassland and bamboo woodland) habitats in comparison to closed canopy (cave and gallery forest) habitat types. Due to the low frequency of cave and long-grass grassland habitat use during data collection, these habitats was excluded from

analysis. Before the analysis of habitat influence on surface body temperature, I first examined whether male subjects differed in surface body temperature to explore the variation in surface body temperature in the Fongoli males.

Results showed that the surface body temperatures of the individual male chimpanzees differed significantly. In particular, Siberut (SI), Bandit (BN), and Jumkin (JM), had a higher surface body temperature than the other individuals. SI and BN are estimated to be some of the oldest individuals in the Fongoli chimpanzee group, and they are the two lowest ranking adult males as well. Since they were adults at the time the Fongoli study began, their exact age is unknown, but a higher surface body temperature could be a sign of age or potential health issues. Low rank may also figure into this difference. In contrast, JM is the highest ranking male (i.e., alpha male) in the Fongoli group, and is a young adult, so a higher surface body temperature could be a result of stress or other symptoms that arise due to a high rank, for example metabolic costs (Muller & Wrangham, 2003). More research is needed to inform the relationship between surface body temperature and health at Fongoli in particular and in chimpanzees in general. All male subjects were included in further analysis, as it is unclear if the differences in surface body temperature between individuals is biologically significant.

There was a significant difference in the Fongoli chimpanzees' surface body temperature between habitats. The results supported my hypothesis that the chimpanzees would have a significantly higher average surface body temperature in the open plateau/short-grass grassland (36.04°C) in comparison to the closed gallery forest (33.9°C). This means that the Fongoli chimpanzees are able to reduce thermal stress by selecting for specific habitats, and that the open plateau/short-grass grassland exposes

them to an increased heat load. However, the results did not support my hypothesis that the chimpanzees would have a higher average surface body temperature in the bamboo woodland in comparison to the closed habitats. Instead, chimpanzees experienced their lowest average surface body temperature in the bamboo woodland (33.47°C), which was significantly lower than the open plateau habitat. The low surface body temperature in the bamboo woodland may be explained by the study period. Data collection took place during the dry-wet season transition, when the environmental differences between habitats are not as extreme as the peak of the dry season. As studies have shown, the Fongoli chimpanzees do not face as much heat and water stress during this period (Wessling et al., 2018), as surface water availability increases dramatically.

The results support my hypothesis that there would be a significant difference in surface body temperature between the varying levels of shade cover. The Fongoli chimpanzees had a significantly lower average surface body temperature in 100% shade (33.76°C) in comparison to 75% shade (35.26°C), 50% shade (35.85°C), and 0% shade (36.53°C). A lack of significance between 100% and 25% shade could be explained by the low sample size of 25% shade (n=6). This means that the apes here can behaviorally thermoregulate by selecting for areas with higher shade in order to reduce surface body temperature. A reduction in surface body temperature does not necessarily mean that the chimpanzees are reducing their core body temperature. However, surface body temperature can be used as a proxy for the thermal load that the chimpanzees are experiencing, because the peripheral regions of the animal act as a thermosensor for the body's thermoregulatory response (Roberts, 1988). Therefore, these results demonstrate

that the chimpanzees are able to reduce thermal load and thus heat stress through shade use.

Additionally, adult male chimpanzees at Fongoli exhibited significantly different surface body temperatures between behaviors. Specifically, they had a significantly lower temperature while resting (33.55°C) in comparison to feeding (34.69°C) and socializing (34.48°C). This finding could be attributed to the habitats and environmental attributes of where the Fongoli chimpanzees choose to rest, in the gallery forest or woodland and in full shade (Pruetz & Bertolani, 2009). The multiple linear regression did show that the environmental conditions (environmental temperature and wind speed) and habitat had a larger role in determining surface body temperature, in comparison to behavior. Specific food resources may force the chimpanzees to select warmer microclimates with higher solar radiation. For example, while collecting data, I observed that many of the termite mounds used by the chimpanzees were on the edge of wooded habitats next to the hotter, grassland habitat. Bogart and Pruetz (2008) found that time spent on termite consumption increased with temperature. Termite fishing is a low energy activity, which could outweigh the physiological stress caused by the high temperatures (Bogart & Pruetz, 2008).

Interestingly, the average surface body temperature of the chimpanzees while soaking in water (33.52°C) was similar to the temperature while resting. Yet, there was not a significant difference in temperature while soaking compared to any other behaviors, like feeding and socializing. The low sample size (n=14) could explain the lack of significance, as thermal images could not be used if all of the fur in the image was wet. This is an extremely interesting behavior, because no other groups of wild

chimpanzees have been found to soak in water in response to high temperature (Pruetz & Bertolani, 2007). Further research could explore the thermoregulatory benefit the chimpanzees receive by this behavior.

The combined effects of activity, habitat, shade cover, environmental temperature, and wind speed all contributed significantly to a linear regression model. The regression accounted for 49.1% of the variation in surface body temperature. In regards to abiotic factors, higher environmental temperature, increased wind speed, and lower shade cover predicted a higher surface body temperature. The results of this study imply that the Fongoli chimpanzee group is able to significantly reduce surface body temperature, and thus thermal stress, through behavioral thermoregulation. In particular, habitat selection, specific behaviors, and shade use resulted in a lower surface body temperature.

Microclimates

Temperature and relative humidity differed significantly between habitats. During the month of July, the gallery forest and cave had an average temperature cooler than the open plateau/short-grass grassland, bamboo woodland and grassland habitats. Additionally, both the cave and gallery forest had a significantly higher average relative humidity than all other habitats. The largest difference in environmental temperature and relative humidity was between the grassland and cave (a 2.25°C, 17% difference). These results support my prediction that the open grassland habitats and bamboo woodland would have a higher temperature and lower relative humidity in comparison to the closed gallery forest and cave, following other studies that were conducted at different times at Fongoli (Pruetz 2007; Pruetz & Bertolani 2009). It is important to note that this data was

taken at the beginning of the wet season in Fongoli, and therefore does not represent the extreme differences between habitats that has been reported at the site and is a conservative view of environmental differences here.

The results of this study demonstrate the importance of gathering microclimatic data in the different habitats used by non-human primates. Many studies use local weather stations to record the variation in environmental conditions a population experiences (Bramer et al., 2018), which ignores the variation in temperature and relative humidity throughout an animal's home range. Microclimate data collection is necessary in order to identify the specific environmental conditions individuals in a population experience.

Habitat Use

During the study period, the Fongoli chimpanzee group used the forested habitats more frequently in comparison to open habitats. Specifically, the chimpanzees used gallery forest 29.7% of the time, even though it only accounts for 2% of the Fongoli chimpanzee home range (Pruetz, 2018). This can be attributed to the high quality resources provided by this habitat, including shade, water, and important foods including *Saba* fruit (Pruetz and Bertolani, 2009). Cave use, a means used by the Fongoli chimpanzees to avoid heat stress was low, accounting for 0.2% of habitat use. This is likely due to data collection beginning in the transition from the dry to wet season, while the chimpanzees utilize caves mainly at the peak of the dry season (Pruetz, 2007).

There was a strong selection for shade by Fongoli chimpanzees, with individuals in full shade cover 89.2% of the time. However, the study period consisted of frequent periods of overcast skies; this means that some of the shade use may have been

overestimated. Behaviorally, the chimpanzees spent a large portion of their activity budget resting (49.7%). Additionally, males soaked in small pools of water, accounting for 2.4% of their activity budget, which appears to be a response to heat stress that this group utilizes in the beginning of the wet season when the rains begin but before temperatures drop (Pruetz and Bertolani, 2009). The soaking behavior during this study period could account for the lack of cave use, as a preferred behavioral adjustment to heat stress when water is available. Caves appear to be avoided once relative humidity increases and their interiors become damp (Pruetz, personal communication.).

Western chimpanzees are critically endangered, with populations in some areas declining over 80% in the past 30 years (Kühl et al., 2017). The Fongoli chimpanzee group is threatened by activities associated with small and large-scale gold mining and a warming climate. Conservation efforts are focused on preserving important habitat for Western chimpanzees in Senegal. This study aids conservation efforts, by demonstrating the chimpanzees' reliance on these forested habitats to avoid heat stress, even outside the dry season, and these habitat types are targets of artisanal mining in southeastern Senegal (Boyer-Ontl, 2017).

Implications for Early Hominins

An open savanna-woodland habitat is hypothesized to have played a large role in human evolution (Cerling et al., 2011; Kappelman et al 1997; Reed 1997). Studying non-human primates, particularly chimpanzees that live in this type of environment can aid our understanding of how early hominins may have behaviorally adapted. This study helps quantify the thermoregulatory benefit hominins may have received by using specific habitats, prioritizing shade use when experiencing heat stress, and how specific

behaviors may have made them more susceptible to overheating. As this study did not encapsulate the most stressful period for the Fongoli chimpanzee group, I recommend further data collection, which could aid our understanding of how hominins may have adapted to extreme thermal stress. However, this study does give insight into behavioral thermoregulation during the transition from a dry to wet season.

CHAPTER III: USE OF A BIOPHYSICAL MODEL TO MEASURE WESTERN CHIMPANZEE ABILITY TO THERMOREGULATE TODAY AND IN FUTURE PREDICTED CLIMATES.

Introduction

Over 31,000 plant and animal species are currently threatened with extinction (IUCN Red List, 2020). This number is expected to grow with the looming threat of climate change (Thomas et al., 2004). It is imperative to understand how species respond to environmental conditions in order to interpret how they will be affected by a changing climate. Environmental conditions, in particular, temperatures, play a significant role in determining the species range of non-human primates as well as their behavior, physiology and demographic characteristics (Korstjens et al., 2010; Mitchell et al., 2009; Campos et al., 2017). It is estimated that over 60% of primate species are already threatened with extinction, and non-human primates are expected to face 10% greater warming in comparison to the global mean given their largely tropical distribution (Estrada et al., 2017; Graham et al., 2016).

However, it is difficult to determine how specific species and populations will be affected by a changing climate. This makes it problematic to establish the best methods for conservation, as it is unclear if it will protect areas that species will be able to tolerate in the near future. Modeling is a useful tool for predicting how the future climate will affect specific populations. In fact, there have been several studies that use statistical models to explore climate change impacts on non-human primates including parasite distribution impact on several lemur species health (Barrett et al., 2013), reproductive parameters of the Milne Edward's sifaka (*Propithecus edwardsi*) (Dunham et al., 2011),

and suitable habitat distributions for geladas (*Theropithecus gelada*) (Dunbar, 1998), gorillas (*Gorilla beringei* and *Gorilla gorilla*) and chimpanzees (*Pan troglodytes* and *Pan paniscus*) (Lehmann et al., 2010), titi monkeys (*Callicebus personatus*) (Gouveia et al., 2016), and Borneo orangutans (*Pongo pygmaeus*)(Struebig et al., 2015). The majority of these are correlative models, which look at how the distribution of suitable habitat for the species will change in the coming years. However, this may not be the best way to determine how species will be affected by climate change. The aforementioned studies use current distributions with specific environmental predictors to determine suitable habitats in a future predicted climate. Yet, climate change is likely to bring novel environments that species have not been exposed to or observed to inhabit by researchers (Pacifi et al., 2015). It is unclear if a species' current realized niche is representative of its fundamental niche (Guisan & Thuiller, 2005). This means that species may have the capacity to live in environments introduced by the changing climate.

Mechanistic models use species-specific parameters including functional traits, physiological tolerances, and equations for energy and mass exchange to calculate an animal's fundamental niche, and thus their ability to survive in a predicted climate (Pacifi et al., 2015). This type of model is better able to estimate whether a species will be able to survive in conditions that they are not currently exposed to (Kearney & Porter, 2009). One of these mechanistic models is called Niche MapperTM, a microclimate and endothermic biophysical model, which uses heat transfer laws to calculate heat balance and allowable metabolic rates of an animal (Fort et al., 2011). Niche Mapper is a useful tool to quantify the thermal stress experienced by a population, especially for species

facing reduced metabolic rates, increased evaporative water loss, and a reduction in activity in response to heat stress (Mathewson et al., 2018).

The Fongoli group of Western chimpanzees (*Pan troglodytes verus*) in Senegal already experiences significant heat stress in the form of high environmental temperature and water scarcity in their savanna landscape (Pruetz 2007, Pruetz & Bertolani 2009, Wessling et al., 2018). Primates are homeotherms, which means that they maintain a constant core body temperature (Elizondo, 1977). When endotherms are in an environment that causes the animal to have a core body temperature outside of a specific range, the thermo-neutral zone, the animal must employ behavioral or physiological processes to maintain homeothermy. Behaviors used by the Fongoli chimpanzees in response to high temperatures include use of specific habitats and extensive resting behavior during the dry season (Pruetz, 2007; Pruetz & Bertolani, 2009), night activity (Pruetz, 2018), and soaking in water (Pruetz & Bertolani, 2009). The affect of this habitat and behavior use for thermoregulation was explored in Chapter II. However, it is unclear how the Fongoli chimpanzees' physiological processes, specifically metabolic rate and evaporative water loss, respond to their environment and what this means for the future of this population.

This study uses Niche Mapper to quantify the thermal stress experienced by the Fongoli chimpanzee group in Senegal in today's climate, as well as what this thermal stress may look like in the future predicted climates of 2020-2039, 2040-2059, and 2080-2099. Thermal stress is measured as the allowable metabolic rate and evaporative water loss predicted by the model. Additionally, I use the model to determine how this thermal stress will affect the available hours for activity. I predicted that this model would show

that the Fongoli chimpanzees, as well as the chimpanzee population in the savannas of Senegal as a whole, will face increasing thermal stress, in the form of reduced metabolic rate and increased evaporative water loss, in each successive period.

Methods

Microclimate Model

Environmental data for Fongoli, Senegal was obtained from Adagio, an application with a global climate database (New et al., 2002) used by the creators of Niche Mapper to determine average monthly local microclimate conditions. The application gives monthly minimum and maximum temperature, wind speed, cloud cover, and minimum and maximum relative humidity for a location. These environmental conditions were added to the model along with substrate properties, vegetative cover, geographic location, and time (Table 3.1). Substrate properties of the ground were measured from soil collected from Fongoli, Senegal and vegetative cover was estimated based on images of the Fongoli habitat across seasons. The microclimate model produces an hourly profile of the microclimate conditions from a 2-meter height to ground level, and separate profiles are created for full shade and full sun environments. A full description of the microclimate sub-model can be found in Fuentes and Porter (2013).

Table 3.1: Microclimate Model Inputs

Model Input	Value Used
Substrate thermal conductivity (W/m°C) ¹	0.35
Substrate density (kg/m ³) ¹	2650
Substrate reflectivity (%) ²	0.11
Substrate specific heat (J/kg-K) ¹	837

Table 3.1 Continued	
Timing of daily minimum/maximum air ¹	Sunrise/1 hour after solar noon
Timing of daily minimum and maximum ¹ relative humidity ¹	1 hour after solar noon/sunrise
Cloud cover (%) ⁴	0-99.6
Shade (%) ⁵	0-100
Wind Speed Range (m/s) ⁵	0.1-3.0
Daily Relative Humidity (%) ⁴	19-100
Free water surface (%) ⁵	0 (November-June) ⁵ (July-October)
Animal height (cm)	86

¹ Estimated, ² Measured the reflectivity of soil sample retrieved from Fongoli, ³ Estimated, ⁴ Adagio (New et al., 2002), ⁵ Observed values measured at Fongoli

For future predicted climates, data was obtained from World Bank Group's Climate Change Knowledge Portal (<https://climateknowledgeportal.worldbank.org/country/senegal/climate-data-projections>). The projected climate data in this portal comes from the Coupled Model Intercomparison Project in the Intergovernmental Panel on Climate Change's (IPCC) Fifth Assessment Report (AR5). I used the RCP 6.0 medium-high emission climate scenario because it is more conservative than the RCP 8.5 scenario but still represents the threat wildlife faces if carbon emissions are not significantly reduced. The projected change (median of all climate models of RCP 6.0) in monthly maximum and minimum temperature for each time-period was added to today's minimum and maximum temperature in the microclimate model. The calculated minimum and maximum temperatures for each month across time-periods is provided in Table 3.2, and a visual of the predicted change in maximum monthly temperature in Figure 3.1. Changes in precipitation across time-periods were not added, as models showed a wide range (-46% to + 48%) of change; however, it is important to note that most models show a decrease in precipitation (Harris et al., 2014). Therefore, the model used in this study may be conservative in this regard.

Table 3.2: Environmental Temperature Inputs for Microclimate Model

Month	Max/Min Temperature (C°)			
	Today	2020-2039	2040-2059	2080-2099
January	34.4/17.1	35.3/18.2	35.9/18.6	37.1/20
February	37.2/20	38.2/21.1	38.8/21.5	40.3/23.1
March	39.4/23	40.5/24.1	40.9/24.5	42.3/25.8
April	40.8/25.5	41.7/26.6	42.1/26.8	43.6/28.4
May	40/26.2	41.2/27.3	41.3/27.5	42.8/29.1
June	35.8/24	36.9/24.9	37.2/25.3	38.8/26.6
July	32.4/22.9	33.6/23.8	33.8/24.1	35.2/25.2
August	34.7/28	35.6/28.8	36.0/29.	37.6/30.2
September	33.2/22	34.1/22.8	34.4/23.1	35.8/24.1
October	35.7/22	36.6/22.8	37.0/23.3	38.2/24.5
November	35.7/19.4	36.9/20.4	37.2/20.8	38.6/22.3
December	33.5/16.3	34.5/17.3	35.1/17.7	36.5/19.2

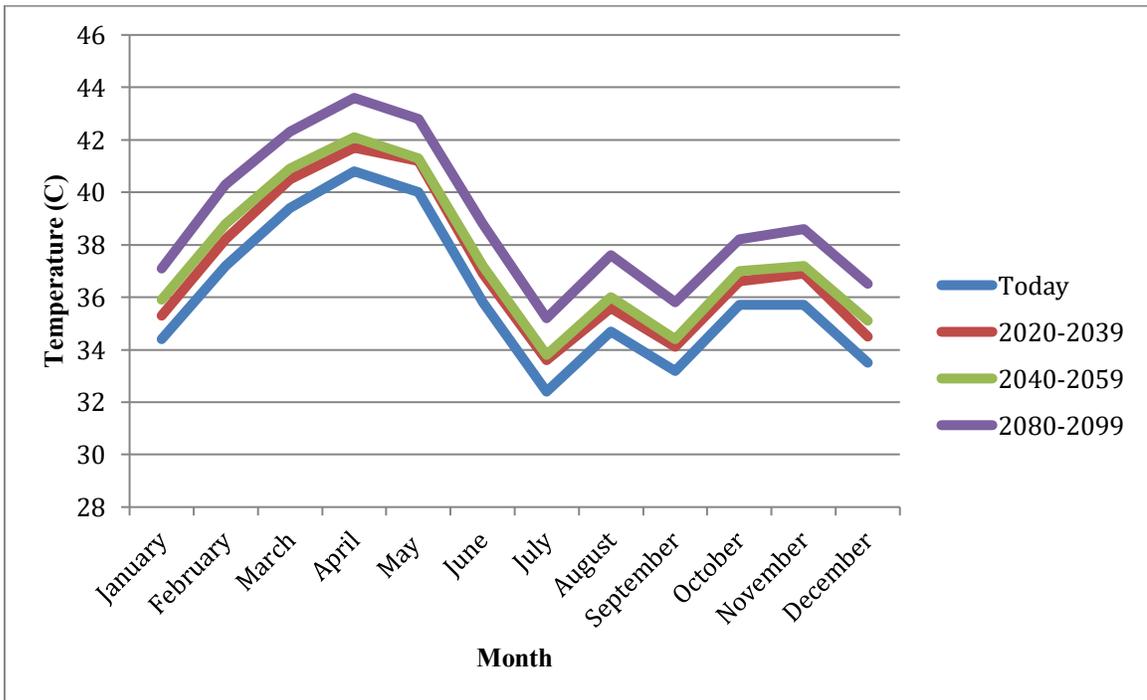


Figure 3.1 Predicted Change in Maximum Monthly Temperature

Endothermic Model

For the endothermic model, I obtained physical body measurements from Schoonaert et al. (2007) and hair measurements from a male chimpanzee at the National Center for Chimpanzee Care of the M.E Keeling Center. Other physical parameters were obtained from the literature and listed in Table 3.3. The endothermic model creates shapes of the animal in interest based on physical parameters and uses the hourly environmental conditions to solve the heat balance equation for the animal. A full explanation of the heat balance equations involved in the endothermic model can be found in Mathewson and Porter (2013). Based on the physical parameters, the model first calculates the metabolic heat production necessary for the animal to maintain core body temperature in the microclimate conditions with no shade. If the metabolic rate is above or below the target metabolic rate, then the animal will either adjust behaviorally or physiologically. For inactive hours, the target metabolic rate is equal to the resting metabolic rate. For active hours, the target metabolic rate is equal to a set multiple of the resting metabolic rate to represent the increased energy required to be active.

For the interests of this study, I examined behavioral and physiological processes implemented to avoid heat stress. If the chimpanzees' metabolic rate dropped below the target, the ape would first adjust behaviorally by seeking shade cover. The model allows animals to use caves in order to thermoregulate; however, this option was removed after the model predicted that the chimpanzee would use the caves at extremely high frequencies, which is not realistic for the Fongoli chimpanzee group. If the shade-seeking behavior was not sufficient in bringing the metabolic rate back to target then physiological processes were implemented. Physiological processes included increasing

thermal conductivity, which simulates vasodilation, increasing core body temperature (with a set maximum core temperature), and increasing sweating (Mathewson et al., 2018).

In this study, I measure heat stress as a reduced metabolic rate and increased evaporative water loss. The model chimpanzee was placed in the predicted environmental condition for each time-period as specified above. I compared the daily metabolic rate, evaporative water loss, and available hours of activity across time-periods for the average day of each month. A flow chart of the model is provided in Figure 3.2.

Table 3.3: Endothermic Model Inputs

Model Input	Value Used
Body mass (kg) ¹	56 kg
Head length/diameter (cm) ¹	25.3/7.5
Trunk length/ diameter (cm) ¹	56.8/17.5
Arm length/diameter (cm) ¹	86.3/5.94
Leg length/diameter (cm) ¹	57.9/6.25
Neck length/diameter (cm) ²	3.75/7.5
Head fur depth/length (mm)	10/20
Neck fur depth/length (mm)	10/20
Trunk fur depth/length (mm)	12/31 (dorsal) 21/53 (ventral)
Arm fur depth/length (mm)	12.5/47
Leg fur depth/length (mm)	15/47
Hair diameter (um) ³	109.7
Hair reflectivity (%) ⁴	20
Hair Density (1/cm ²) ⁵	43
Core Body Temperature ⁶	Default: 37.2 Min: 34.6 Max: 39.5
% Skin Wet (Sweat) ⁷	5-88
Flesh Thermal Conductivity (W/mC) ⁸	0.412-2.8

Table 3.3 Continued	
Resting Metabolic Rate ⁹	$3.39 \cdot \text{mass}^{0.75}$
O ₂ Extraction Efficiency ¹⁰	20
Activity Multiplier for Metabolic Rate ¹¹	2.5 (March-May) 3.0 (June-February)

¹ (Schoonaert et al., 2007), ² Estimated based off chimpanzee images, ³ (Chernova, 2014), ⁴ (Wheeler, 1991a), ⁵ (Sandel, 2013), ⁶ (Jensen et al., 2009), ⁷ (Hiley, 1976), ⁸ (Cho, 1969), ⁹ (Gordon et al., 1972), ¹⁰ (Lacombe, 2002), ¹¹ Estimated from Fongoli Chimpanzee Activity Budget.

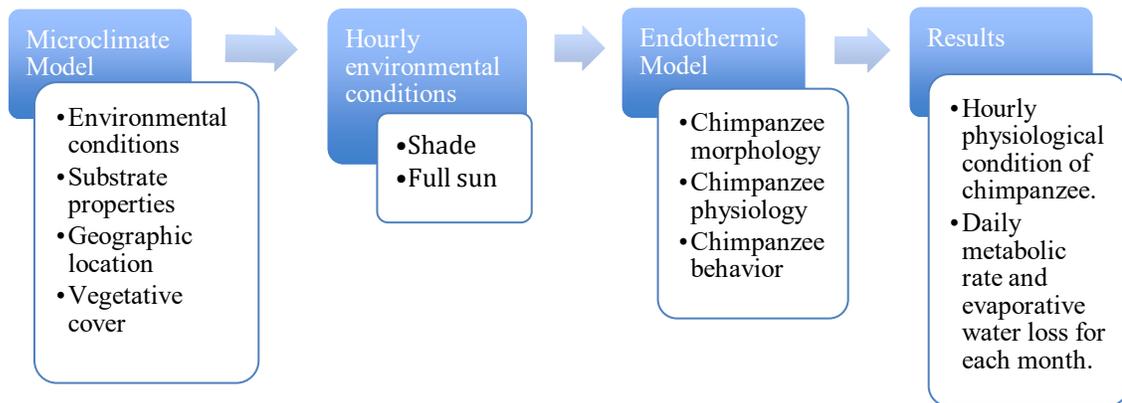


Figure 3.2: Flow chart of the Niche Mapper™ Model

Results

The model output demonstrates several trends in the heat stress response of chimpanzees in Fongoli, Senegal. Across the climates tested, the 56 kg model chimpanzee has a lower metabolic rate in the dry season (October-May) in comparison to the wet season (June-September), with the exception of August (17.1 MJ/D) (MJ/D= megajoules per day) (Figure 3.3). Additionally, the metabolic rate is particularly high in January (17.3 MJ/D) in comparison to other dry season months. Evaporative water loss was highest during the peak of the dry season, April and May, whereas, the lowest evaporative water loss is calculated to be during the wet season and the beginning of the dry season (Figure 3.4). The model did not show a general trend in available hours for

activity between seasons. Instead, the highest available activity hours generally occur in April, July, and September (Figure 3.5).

Comparisons between today's climate and the predicted climates of 2020-2039, 2040-2059, and 2080-2099 show noticeable differences in the physiological processes calculated. In general, the metabolic rate is predicted to stay the same or reduce over time, evaporative water loss is predicted to increase over time, and the number of hours available for activity is expected to stay the same or decrease over time. The most prominent difference in the metabolic rate between climate periods occurs during the wet season and the end of the dry season (May). For example, during the month of August, the metabolic rate drops from 17.1 MJ/D in today's climate to 15.15 MJ/D in the predicted climate of 2080-2099. In contrast, the difference in evaporative water loss between climate periods is greatest during the dry season in comparison to the wet season. For the month of April, the evaporative loss increases from 2.2 kg/D (kg/D= kilograms per day) in today's climate to 3.12 kg/D in the predicted climate of 2080-2099. The largest increase occurs for the month of January, an evaporative water loss of 1.05 kg/D in today's climate in comparison to a loss of 2.47 kg/D in the 2080-2099 climate.

The change in activity hours is similar to the difference in metabolic rate between periods. There is a larger decrease in available hours for activity during the wet season in comparison to the dry season. The available activity hours for the chimpanzees reduces the most across periods during the months of June, July, and September. In June, the activity hours decrease from 10 hours in today's climate to 6 hours in the climate predicted for 2080-2099. July and September decrease from 13 available activity hours in

today's climate to 9 in 2080-2099. There are no differences in available activity hours predicted by the model between periods for December through April.

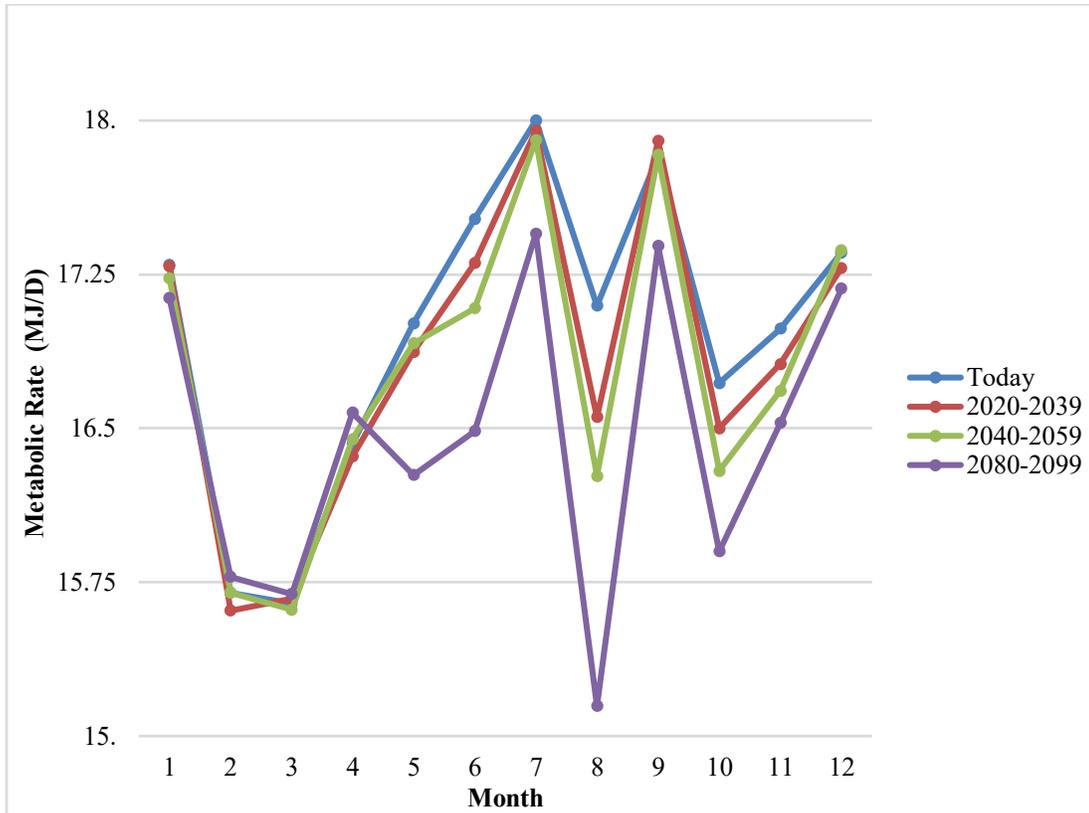


Figure 3.3: Metabolic Rate (MJ/D) Between Periods

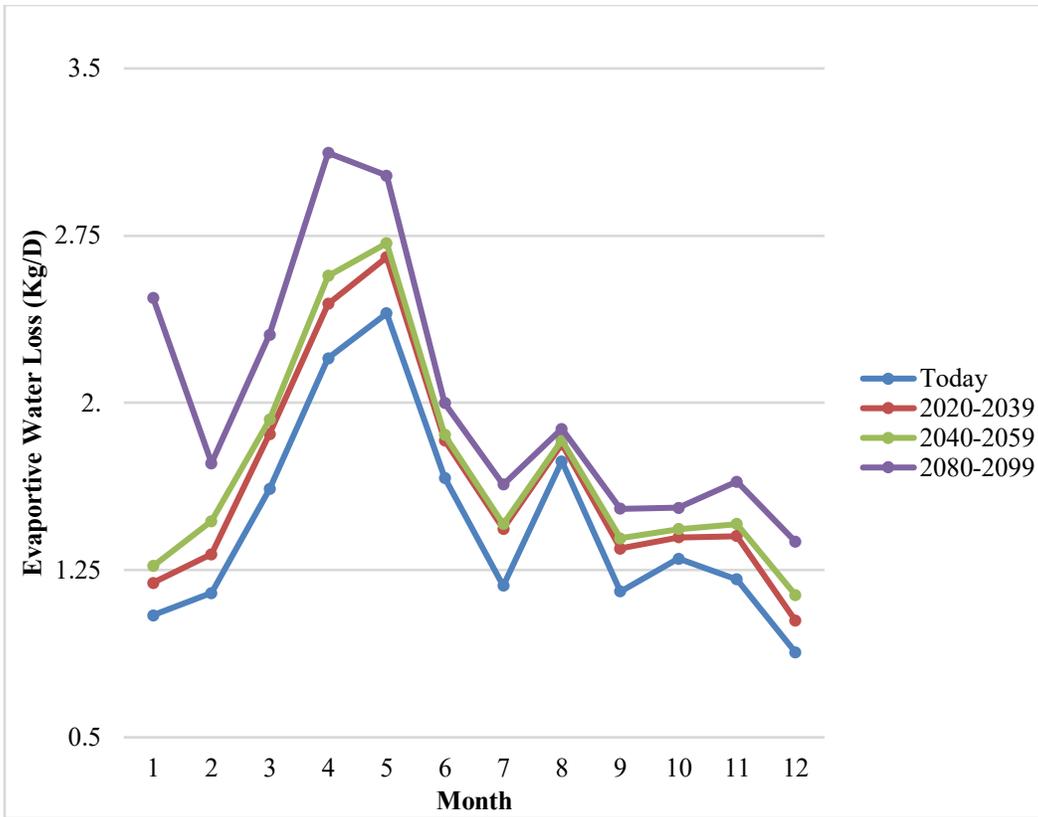


Figure 3.4: Evaporative Water Loss (Kg/D) Between Periods

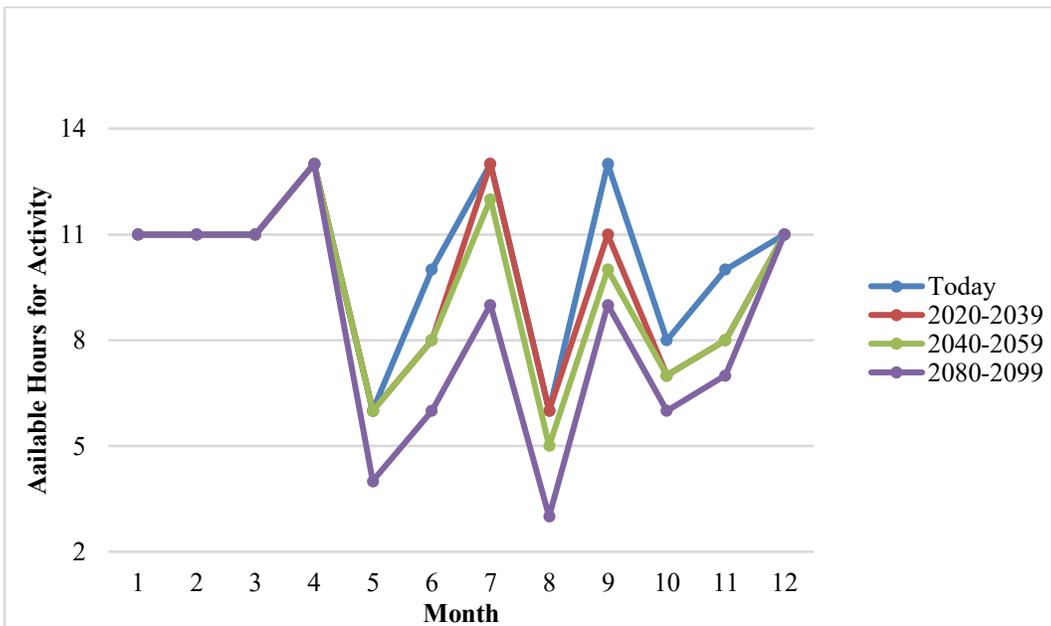


Figure 3.5: Available Activity Hours Between Periods

Discussion

The aim of this study was to explore how climate change will influence the Fongoli chimpanzee group's physiological processes used for thermoregulation. The results show that the predicted changing climate will affect the chimpanzees' metabolic rate, evaporative water loss, and available hours for activity. This has important implications for the survival of the Fongoli chimpanzee group and others in Senegal as the region becomes warmer and drier. The results of this study can be used to aid conservation decisions, as it quantifies the thermal stress the chimpanzees may soon experience.

Trends in Today's Climate

In today's climate, the model shows the chimpanzees' lowest metabolic rates occurring in the dry season, specifically during the months February-April. This period, the late dry season, is characterized as having the highest environmental temperatures and lowest precipitation. Therefore, the model attempts to reduce metabolic heat production to reduce hyperthermia. This finding matches previous research on the Fongoli chimpanzees, which has shown that they have a higher level of stress hormones in the dry season due to high temperatures and low water availability (Wessling et al., 2018). Additionally, the dry season is calculated to have the highest levels of evaporative water loss, which is to be expected due to the high temperatures during this period. Evaporative water loss is an important physiological process utilized by primates to reduce core body temperature and prevent hyperthermia (Mitchell et al., 2009).

Surprisingly, the number of available hours for activity did not follow a seasonal trend. In today's climate, the model estimates that the chimpanzees will have the lowest

available hours for activity in May and August. More analysis is needed on the sensitivity of the chimpanzee model to specific environmental conditions. However, May is a transitional month from the dry to wet season and is characterized by the highest heat index of all months. The combination of the high temperatures and increasing relative humidity reduce the chimpanzee's ability to lose heat. It has been found that increasing humidity at high environmental temperatures reduces an animal's evaporative water loss (Walters et al., 2014). Humidity is hypothesized to increase the physicochemical gradient of the skin (Walters et al., 2004), which would result in a decreased ability to lose water, reduced energy for activity, and an increase in core body temperature. Additionally, August is the month at Fongoli with the highest precipitation and has a relatively higher average temperature in comparison to other rainy months, which could also result in decreased evaporative water loss and less hours available for activity.

Effect of Climate Change on Chimpanzee Thermoregulation

As predicted, the model shows a decrease in chimpanzees' metabolic rate between climate periods. However, this decrease does not occur for all months. Some of the dry season months, December-April, have either no reduction or very minor changes ($\pm 0.2\text{MJ/D}$) in the chimpanzee's metabolic rate. In the wet season, there is a noticeable reduction in metabolic rate, with the largest change in August. The reduction in metabolic rate is due to the increased predicted maximum and minimum environmental temperatures. These temperatures place the model chimpanzee outside of its thermo-neutral zone, causing the core body temperature to rise. In response, evaporative water loss increases. If evaporative water loss is not sufficient in maintaining body temperature, the metabolic rate is reduced (Mathewson et al., 2018). As mentioned previously, high

levels of humidity reduce an animal's ability to lose heat through evaporative water loss. The larger reduction in metabolic rate in the wet season in comparison to the dry season can be explained by the reduced ability to lose heat through evaporative water loss due to the high humidity.

The model calculates that the evaporative water loss will increase with time for all months. There is a larger increase in the dry season months in comparison to the wet season. With the largest increase in evaporative water loss occurring in April, a period of high temperatures and low water availability, this month can be expected to remain the most stressful period for the Fongoli chimpanzees. It is important to note that the model does not consider water availability when calculating evaporative water loss. During the dry season, the Fongoli chimpanzees experience extreme water scarcity. Although the chimpanzees normally drink once per day during dry season months, there have been uncommon observations of the chimpanzees going without water for a day (Pruetz, personal communication). This means that the water loss predicted in this model to maintain body temperature may not be possible. More research is needed on the amount of water available to the chimpanzees in foods, for example, to determine if they will be able to use this level of evaporative water loss for thermoregulation. If not, it is likely that the chimpanzees will become more susceptible to hyperthermia in the warming climate.

Due to the seasonally low water availability at Fongoli, it is unclear if the available hours for activity are accurate estimates. However, the model's calculation can still be used to determine the affect climate change will have on the activity budget of the Fongoli chimpanzees, as it is likely a more conservative estimate than real life. The hours available for activity do not follow a seasonal trend, during the months of May-November

the available hours for activity are estimated to decrease. This means that the model chimpanzee will not have a high enough metabolic rate for activities like traveling and feeding. A domino effect may occur, as less time spent foraging would lead to less energy available to the chimpanzees for important behavioral and physiological processes. The Fongoli chimpanzees already move and feed at night during the dry season to avoid high daytime temperature (Pruetz, 2018). It is possible that this behavior will increase as temperatures continue to rise; however, nocturnal activity exposes the group to predators. A decrease in activity hours during May and August is concerning, as the model already predicts that the chimpanzees will have low activity during these months in today's climate. The month of August is a period of low fruit availability for the chimpanzees, which may result in low nutrient intake (Pruetz, 2006). August is predicted to become increasingly stressful for the chimpanzees' physiologically, they may not be able to adapt to this environmental stress as efficiently as they would during months of high fruit availability, for example, during the month of May.

Implications

Modeling is a useful tool for measuring the physiology of wild animal populations, especially when more invasive methodologies need to be avoided. Niche Mapper's model of a 56 kg male chimpanzee demonstrates that the Fongoli chimpanzee group will experience increased heat stress in the predicted warming climate. This research quantifies the thermoregulatory cost across months and between periods, which can be used in conservation decisions. The model shows that evaporative water loss will be extremely important for the chimpanzees to maintain body temperature and a target metabolic rate for activities necessary for survival. It is important to note that even when

overheating is not fatal, hyperthermia can have negative physiological affects that can lead to reduced survival and reproductive fitness (Speakman & Krol, 2010).

As demonstrated by Wessling et al. (2018), water scarcity is significantly stressful for the Fongoli chimpanzees. My research shows that water will be continue to be a limiting resource for the apes. Additionally, behaviors used by the chimpanzees to avoid heat stress including cave use, water soaking, nocturnal behavior and shade seeking will become increasingly important in reducing thermoregulatory costs. Conservation efforts should be focused on protecting areas with water and shade resources, in particular gallery forests, which make up only 3% of the Fongoli habitat (Pruetz, 2018).

CHAPTER IV: CONCLUSIONS

The findings presented in this thesis demonstrate the use of novel technologies, thermal imaging and biophysical modeling to explore chimpanzees' use of behavioral and physiological processes to thermoregulate in a semiarid biome. I aimed to determine the thermoregulatory benefit the Fongoli chimpanzee group receives through behavioral thermoregulation. Additionally, I sought to demonstrate the significance of microclimates for animal species and show why researchers should collect data on these environments. I used biophysical modeling to explore how the Fongoli chimpanzee group will be affected by climate change and if they will be able to survive in future conditions.

In Chapter II, I use thermal imaging technology to explore how behavioral thermoregulation affects the surface body temperature of the Fongoli chimpanzees. The results showed that habitats use, access to shade resources, and specific behaviors have an affect on surface body temperature, and thus thermal stress experienced by the chimpanzees. This finding demonstrates that habitats, like gallery forests, are crucial for the survival of the Fongoli chimpanzee group. Additionally, access to gallery forests, where the relatively few permanent water sources available to apes in the late dry season are found, is likely to become increasingly important in the changing climate.

Climate change is a growing threat to many species, including Western chimpanzees and especially those living in savanna environments. It is unclear how species will be specifically impacted and if they will be able to survive in new environmental conditions. Western chimpanzees are Critically Endangered, with over an 80% population decline in some regions within the past 30 years (Kühl et al., 2017). This species is currently threatened by habitat loss and fragmentation (Boyer-Ontl 2017).

Research has shown that some chimpanzee subspecies (*P.t. troglodytes* and *P.t. ellioti*) may lose important habitat in the changing climate (Sesink Clee et al., 2015); however, there has been no research on how Western chimpanzees will be affected by climate change.

In Chapter III, I use the biophysical model (Niche Mapper™) to explore whether the Fongoli chimpanzees will be able to thermoregulate in the changing climate. Results of this study found that the predicted climate will place the chimpanzees in an environment with increasing thermal stress over the next ~80 years. Water availability is predicted to remain a limiting factor for the Fongoli chimpanzees. It is unclear if the chimpanzees will have access to enough water in order to utilize the physiological process of evaporative water loss and prevent overheating under extreme temperatures. Although the Fongoli chimpanzees have access to at least two permanent dry season water sources, such limited water availability essentially restricts their ranging behavior related to feeding and foraging. Additionally, the continued upsurge in artisanal gold mining in the area has produced conflict between chimpanzees and humans who target areas with permanent water for mining and where the use of mercury to obtain the gold has polluted certain water sources (Boyer-Ontl. in prep., Fongoli Savanna Chimpanzee Project, unpublished data). The model demonstrates the importance of conserving habitats that allow the chimpanzees to reduce heat stress, for example caves and gallery forests.

The results presented here can also be used to understand the thermoregulatory pressures faced by early hominins in open savanna-woodland environments. This study can be used to quantify the benefits hominins would have received by having access to

important shade resources and how specific behaviors may have exposed them to greater thermal stress. As this study demonstrates, water is a vital resource to survival in extreme environments, like Fongoli. Hominins would have needed access to stable water resources in order to thermoregulate in the high temperatures occurring in savanna-woodland environments.

APPENDIX SECTION

Appendix 1:

Definitions of Behaviors	
Feeding	The actual ingestion and foraging of a food resource.
Socializing	Both aggressive and affiliative behaviors, including vocalizations, grooming, playing and dominance displays.
Resting	Inactive sitting or laying down.
Traveling	Directional movement including bipedal and quadrupedal walking and running, as well as climbing.
Soaking	Immersion of body into a pool of water.

Appendix 2: Bonferroni Post Hoc Analysis of Differences in Ambient Temperature and Relative Humidity Between Habitats

Dependent Variable	(I) Habitat	(J) Habitat	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Temp.	Bamboo Woodland	Cave	.966*	0.294	0.016	0.101	1.831
		Gallery Forest	1.507*	0.294	0	0.642	2.372
		Grassland	-0.744	0.294	0.173	-1.610	0.121
		Open Plateau	0.003	0.294	1	-0.862	0.868
		Woodland	0.712	0.294	0.236	-0.154	1.577
	Cave	Bamboo Woodland	-.966*	0.294	0.016	-1.831	-0.101

		Gallery Forest	0.541	0.294	0.995	-0.324	1.406
		Grassland	-1.710*	0.294	0	-2.576	-0.845
		Open Plateau	-0.963*	0.294	0.016	-1.828	-0.098
		Woodland	-0.254	0.294	1	-1.120	0.611
	Gallery Forest	Bamboo Woodland	-1.507*	0.294	0	-2.372	-0.642
		Cave	-0.541	0.294	0.995	-1.406	0.324
		Grassland	-2.251*	0.294	0	-3.116	-1.386
		Open Plateau	-1.504*	0.294	0	-2.369	-0.639
		Woodland	-0.795	0.294	0.104	-1.660	0.070
	Grassland	Bamboo Woodland	0.744	0.294	0.173	-0.121	1.610
		Cave	1.710*	0.294	0	0.845	2.576
		Gallery Forest	2.251*	0.294	0	1.386	3.116
		Open Plateau	0.747	0.294	0.168	-0.118	1.612
		Woodland	1.456*	0.294	0	0.591	2.321
	Open Plateau	Bamboo Woodland	-0.003	0.294	1	-0.868	0.862
		Cave	.963*	0.294	0.016	0.098	1.828
		Gallery Forest	1.504*	0.294	0	0.639	2.369
		Grassland	-0.747	0.294	0.168	-1.612	0.118
		Woodland	0.709	0.294	0.242	-0.156	1.574

	Woodland	Bamboo Woodland	-0.712	0.294	0.236	-1.577	0.154
		Cave	0.254	0.294	1	-0.611	1.120
		Gallery Forest	0.795	0.294	0.104	-0.070	1.660
		Grassland	-1.456*	0.294	0	-2.321	-0.591
		Open Plateau	-0.709	0.294	0.242	-1.574	0.156
Humidity	Bamboo Woodland	Cave	-13.953*	1.162	0	-17.368	-10.538
		Gallery Forest	-10.160*	1.162	0	-13.575	-6.745
		Grassland	3.117	1.162	0.111	-0.298	6.532
		Open Plateau	0.234	1.162	1	-3.181	3.649
		Woodland	-5.712*	1.162	0	-9.128	-2.297
	Cave	Bamboo Woodland	13.953*	1.162	0	10.538	17.368
		Gallery Forest	3.793*	1.162	0.017	0.378	7.208
		Grassland	17.070*	1.162	0	13.655	20.485
		Open Plateau	14.183*	1.162	0	10.772	17.602
		Woodland	8.241*	1.162	0	4.826	11.656
	Gallery Forest	Bamboo Woodland	10.160*	1.162	0	6.745	13.575
		Cave	-3.793*	1.162	0.017	-7.208	-0.378
		Grassland	13.277*	1.162	0	9.862	16.692
		Open Plateau	10.394*	1.162	0	6.979	13.809

		Woodland	4.448*	1.162	0.002	1.033	7.863
	Grassland	Bamboo Woodland	-3.117	1.162	0.111	-6.532	0.298
		Cave	-17.070*	1.162	0	-20.485	-13.655
		Gallery Forest	-13.277*	1.162	0	-16.692	-9.862
		Open Plateau	-2.883	1.162	0.198	-6.298	0.532
		Woodland	-8.829*	1.162	0	-12.244	-5.414
	Open Plateau	Bamboo Woodland	-0.234	1.162	1	-3.649	3.181
		Cave	-14.187*	1.162	0	-17.602	-10.772
		Gallery Forest	-10.394*	1.162	0	-13.809	-6.979
		Grassland	2.883	1.162	0.198	-0.532	6.298
		Woodland	-5.946*	1.162	0	-9.362	-2.531
	Woodland	Bamboo Woodland	5.712*	1.162	0	2.297	9.128
		Cave	-8.241*	1.162	0	-11.656	-4.826
		Gallery Forest	-4.448*	1.162	0.002	-7.863	-1.033
		Grassland	8.829*	1.162	0	5.414	12.244
		Open Plateau	5.946*	1.162	0	2.531	9.362

Based on observed means.

*** The mean difference is significant at the .05 level.**

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