Thermo-imaging bipedalism on the savanna: Chimpanzee locomotion at Fongoli, Senegal and implications for the evolution of hominin bipedalism

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Thermo-imaging bipedalism on the savanna: Chimpanzee locomotion at Fongoli, Senegal and implications for the evolution of hominin bipedalism

by

Nicole Wackerly

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

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Program of Study Committee:
Jill D. Pruetz, Co-major Professor
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The student author, whose presentation of the scholarship herein was approved by the program of study committee, is solely responsible for the content of this thesis. The Graduate College will ensure this thesis is globally accessible and will not permit alterations after a degree is conferred.

Iowa State University
Ames, Iowa
2019

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ABSTRACT

Pressures associated with savanna habitats, such as heat stress, are often cited to explain adaptive traits in hominins, like the evolution of bipedalism. Wheeler’s (1984) physiological model, for instance, predicts that bipedal posture reduces contact with UV radiation by lessening the total body area exposed to direct sunlight. Chimpanzees occupying a savanna mosaic environment provide a unique opportunity to assess aspects of these hypotheses, such as how thermal stresses impact furred apes in a hot, arid and open environment. This study followed chimpanzees at the Fongoli site in Senegal, as they are thus far the only habituated savanna woodland community. Chimpanzees here display more bipedal behavior than is observed at other sites and are known to soak in pools and use caves to cope with heat stress. Apes here are, therefore, good living primate models to use in assessing selective pressures associated with hot, arid savanna environments. This research tested the hypothesis that body temperature differs between the array of positional behaviors used by West African chimpanzees throughout their home range; more specifically, bipedalism was predicted to correlate with a lower chimpanzee body temperature when compared to quadrupedal positions. Using a thermo-imaging camera to record individual body temperatures, I evaluated the heat load related to various postural and locomotor behaviors, specifically that of bipedalism. Results reveal lower body temperatures associated with bipedalism when compared to positions like sit and quadrupedal stand. These data offer support to models of hominin evolution that suggest bipedalism confers a thermoregulatory advantage.
Questions regarding what makes humans unique have perplexed scientists for some time. One such question relates to the origins of hominin bipedality, something that anthropologists continue to debate. Selective pressures associated with savanna habitats are frequently invoked to explain adaptive traits, such as the ability to walk upright on two feet. One of the major hypotheses to explain the evolution of bipedalism in the hominin lineage looks to heat stress as the ultimate selective pressure. With less total body area exposed, bipedal posture is predicted to reduce UV radiation exposure (Wheeler, 1984). Throughout this thesis, this assumption will be addressed by examining chimpanzees occupying a savanna mosaic habitat.

Chimpanzees are commonly used as referential models in exploring hypotheses concerning hominin evolution due to their close evolutionary relationship to humans (i.e., homology), but the parallels in habitat with early hominins (Cerling et al., 2010; Domínguez-Rodrigo, 2014) make savanna chimpanzees an even better model for this research. Studying chimpanzees occupying a savanna mosaic environment provided a unique opportunity to assess questions regarding the thermoregulatory advantages of bipedalism and how thermal stresses impact furred apes in a hot, dry and open environment. Chimpanzees at the Fongoli site in Senegal are the focus of this research, as they are the only community occupying a savanna woodland habitat that are fully habituated to observers to date. Moreover, chimpanzees at this site exhibit significantly more bipedal behavior than is observed at other sites (Tourkakis, 2009). To obtain chimpanzee body temperatures, a thermo-imaging camera (FLIR E75bx IR) was employed, as Thompson et al. (2017) demonstrated the reliability of this methodology as a non-
invasive means to examine primate body temperature. Addressed throughout this study are the array of positional behaviors used by West African chimpanzees in relation to body temperature. These findings will test our interpretation of early models of bipedal evolution in hominins, as well as further our understanding of chimpanzee thermoregulation.

**Evolution of bipedalism in hominins**

There are several, litigious hypotheses regarding the selective pressures influencing the evolution of habitual bipedalism in hominins. Several researchers advocate for the idea that bipedalism freed the hands of hominins, as they were no longer used as support during locomotion, allowing hominins to carry necessary items (Bartholomew & Birdsell, 1953; Gebo, 1996; Videan & McGrew, 2002). Efficiency in load carrying has, therefore, been an argued selective pressure, as living in an environment where resources are dispersed would make carrying an important ecological adaptation, whether carrying food or transporting items (Bartholomew & Birdsell, 1953; Gebo, 1996; Videan & McGrew, 2002), such as defensive tools (Washburn, 1968).

Bipedal behavior is also often observed in display and defense contexts, like stone throwing (Fifer, 1987), which has been argued as a precursor to bipedal locomotion. Bipedal threat displays can be incessant and lengthy, and have therefore been argued as an important piece in the origins of habitual bipedalism due to their likely contribution to the success of hominids during intraspecific competition (Jablonski & Chaplin, 1993). As bipedal posture can make hominids appear larger, this behavior may have begun as a means of predator defense (Walter, 2004), alerting the predator of the prey’s vigilance and deterring attack. Walter (2004) suggests this bipedal posture was later co-opted for locomotion. Similarly, bipedal hopping in
species like the kangaroo rat (*Dipodomys deserti*) has been put forth as an evolutionary means to enhance predator avoidance and escape (Djawdan and Garland, 1988; McGowan & Collins, 2018), and later exapted to facilitate success in a desert environment.

With the substantial amount of time occupied by feeding and foraging in primate activity budgets, explanations for the evolution of bipedalism often consider this activity central to their hypotheses (Leuttenegger, 1987). Hunt (1994, 1996) proposes that bipedal posture was likely a precursor to bipedal locomotion, suggesting the posture evolved alongside arm-hanging as a specialized feeding adaptation for small fruits. Stanford (2006) and Tuttle (1975) also suggest bipedalism originated in an arboreal, feeding context, whether as a feeding posture (Tuttle, 1975; Stanford, 2006) or for movement on large branches (Tuttle, 1975). Other researchers argue that both postural and locomotor bipedalism would have been favored by natural selection (Wrangham, 1980; Rose, 1976; Jolly, 1970). They suggest the importance of postural bipedalism in gathering food and locomotor bipedalism in moving between food patches, focusing more on a terrestrial context. While the hypotheses put forth to explain bipedal evolution diverge and are widespread, it is more likely that many selective forces worked in shaping the evolution of bipedalism and that these hypotheses are not mutually exclusive.

**Bipedal evolution and thermoregulation**

While there is hardly consensus regarding the selective forces that shaped bipedal evolution in the hominin lineage, this study focuses on one of the major hypotheses that looks to heat stress as the ultimate selective pressure. The origin of habitual bipedalism in hominins is often associated with a shift in habitat from one of closed canopy rainforest to a more open woody-savanna (Wheeler, 1991b; Cerling et al., 2010; Domínguez-Rodrigo, 2014). The change
to a savanna habitat introduces new hardships, such as increased levels of direct solar radiation which can induce hyperthermia (Wheeler, 1984, 1991b). Wheeler (1984) suggests that to overcome the challenges of existing in a hot, dry and open environment, bipedalism would have been a favored mode of locomotion. He explains this as a need for protection of the brain from thermal stress with reference to the lack of an efficient selective brain cooling mechanism in primates. Primates lacking a carotid rete, a physiological means of protecting the brain (Hayward & Baker, 1969; Wheeler, 1991b), must instead make use of other means, such as behavioral shifts, to limit extreme rises in body temperature (Wheeler, 1984, 1991a, 1991b). Wheeler posits that adaptations lessening heat stress or enhancing heat dissipation would have faced strong selective pressures. Bipedalism not only reduces surface area exposed to direct sunlight, but also increases exposure to airflow by raising body surfaces above the ground (Wheeler, 1984, 1985, 1991a, 1991b, 1992).

Ruxton and Wilkinson (2011) offered a critique to Wheeler’s models by suggesting the endogenous heat load incurred by bipedal locomotion in an open environment would negate any gained thermoregulatory advantages. They argue that hair loss must have occurred prior to habitual bipedalism, as bipedalism would not otherwise be beneficial in thermoregulation. Dávid-Barrett and Dunbar (2015), however, took issue with the model produced by Ruxton and Wilkinson (2011), as they did not take into account activity scheduling and altitude of early hominins. The Ruxton and Wilkinson (2011) model includes bipedal locomotion rather than simply a stationary bipedal posture; however, their model does not account for activity budget and suggests that hominins were consistently moving throughout the day. While Dávid-Barrett and Dunbar (2015) agree that constant locomotion will negate any benefits of bipedalism, australopithecine time budget models imply only 16% of the day was devoted to travel
(Bettridge, 2010). Moreover, the altitude at which australopithecines existed far-exceeds what is known for modern chimpanzees (Dávid-Barrett & Dunbar, 2015). With altitude and activity budget included in their updated model, Dávid-Barrett and Dunbar (2015) conclude that there is a substantial thermal advantage to being bipedal in an open habitat, even for a furred ape; however, such benefit does not come through in a shaded environment.

**Chimpanzees as referential models**

Research suggests that throughout the Plio-Pleistocene, early hominins were existing in a more open savanna habitat that was characteristically a mosaic due to patches of closed, wooded habitats in addition to more open grassland (Kappelman, et al. 1997; Reed, 1997; Cerling et al., 2010; Domínguez-Rodrigo, 2014). Chimpanzees at Fongoli, Senegal inhabit a similar environment (Pruetz & Bertolani, 2009). Fongoli chimpanzees home range consists of woodland, grassland, bamboo and gallery forest habitats (Pruetz, 2006; Pruetz et al., 2008). An informative method in behavioral reconstruction of early hominins is the use of referential models, involving the behavior, ecology and social systems of nonhuman primate species (Stanford, 1991; Stanford, 2006). Which nonhuman primate species to choose is based on homology (similarity attributable to common descent) or analogy (similarity attributable to common adaptation) to the referent (Moore, 1996).

Savanna chimpanzees offer use of a referential model based on both homology and analogy, owing to their close evolutionary relationship to humans and similarities in habitat to early hominins that are expected to result in common adaptations. This type of model is of particular value to paleoanthropologists, as it can inform the feasibility of evolutionary hypotheses as well as generate revised interpretations or ideas (Moore, 1996). This project set
forth to test the aforementioned hypotheses of hominin bipedal evolution by examining the heat load faced by chimpanzees in a savanna mosaic environment. A thermo-imaging camera was used to record savanna chimpanzee posture and locomotion throughout their home range and across seasons. By use of savanna chimpanzees as a referential model, this study can enhance our models of hominin evolution and thus our understanding of the evolution of bipedalism.

**Behavioral thermoregulation**

Both behavior (e.g. microhabitat selection) and physiology (e.g. evaporative cooling) are important means of thermoregulation (Campos & Fedigan, 2009; Kosheleff1 & Anderson, 2009; Chaplin et al., 2014; Duncan & Pillay, 2013; Lopes & Bicca-Marques, 2017). When an animal is beyond its thermoneutral zone, however, behavioral strategies to combat thermal stresses may reduce the energetic demand of physiological thermoregulation (Hey, 1975; Brain & Mitchell, 1999; Hill, 2006; Terrien et al., 2011; Lopes & Bicca-Marques, 2017). Studies of behavioral adjustments to a high thermal environment tend to examine changes in positional behavior as well as microhabitat choice.

Research on titi monkey (*Callicebus bernhardi*) thermoregulation conclude that these primates rely on both microhabitat selection and their postural behaviors to combat thermal stresses (Lopes & Bicca-Marques, 2017). When temperatures exceeded the thermoneutral zone, titi monkeys amplified use of heat-dissipating postures and avoided areas of high sun exposure. Changing positional behavior alters the rate of heat dissipation, as the body’s surface-to-volume ratio exposed to the environment is modified accordingly. Additionally, Stelzher and Hausfater’s (1986) study on yellow baboons (*Papio cynocephalus*) in Amboseli National Park concluded that the baboons alter their postures and body orientation with changes in their
microclimate. For instance, to avoid heat loss in the morning, the baboons maintained hunched postures and oriented their trunks away from the wind. Behavioral changes were particularly apparent during low-activity behaviors like grooming or resting.

Stelzher’s (1988) later study on yellow baboons furthered this idea of behavioral thermoregulation through their increased use of resting behavior, particularly in shaded regions. Hill (2006) looked at chacma baboon (*Papio hamadryas ursinus*) activity scheduling in relation to thermal constraints and noted an increase in sedentary behaviors (i.e. grooming and resting) with higher temperatures, as well as a higher proportion of time spent in shaded environments. Strategies to avoid heat stress were also apparent in white-faced capuchins (*Cebus capucinus*) at Santa Rosa National Park, who were recorded traveling less and resting more during the hottest and driest times of the day throughout the dry season (Campos & Fedigan, 2009). Interestingly, these primates also employed a “tongue-out” behavioral strategy to cope with hotter, drier, and windy conditions, more frequently in the dry season (Campos & Fedigan, 2009).

**Thermo-imaging chimpanzees**

Behavioral responses to thermal environments by other primate species enhance the likelihood that early hominins also exercised such behavioral shifts. Using a thermo-imaging camera, I evaluated the relationship between positional behavior and body temperature in chimpanzees occupying a savanna environment. Not only do they share similarities in habitat to early hominins, but Fongoli chimpanzees also exhibit significantly more bipedal behavior than has been observed at other sites (Tourkakis, 2009). They are frequently bipedal during male displays, vigilance and feeding (Tourkakis, 2009). By thermo-imaging bipedal chimpanzees
with a FLIR E75bx IR camera, one can assess the associated heat load through use of point temperature measurements on individual dorsum.

Chimpanzees at Fongoli make use of its mosaic landscape to avoid intense sunlight during the hottest times of day and of year (Pruetz & Bertolani, 2009). Fongoli chimpanzees exhibit behavioral adjustments linked to heat stress (Pruetz & Bertolani, 2009; Pruetz, 2018; Wessling et al., 2018), such as cave use, water use, extensive resting and nocturnal behavior. Chimpanzees occupying this extreme savanna environment were recently found to show seasonal variation in stress and dehydration levels, with levels peaking when water was scarce and when temperatures were highest in the late dry season (Wessling et al., 2018). Duncan & Pillay (2013) suggest the importance of shade use in thermoregulation, as the captive chimpanzees in their study displayed a sun-avoidance strategy, particularly during the hottest hours of the day. Additionally, wild chimpanzees in the Budongo Forest of Uganda are observed to adjust activity levels in accordance with ambient temperature and sun exposure (Kosheleffl, & Anderson, 2009). Temperatures in the late dry season at Fongoli, when most trees lose their leaves, are characteristically higher, regularly exceeding 40° Celsius (Pruetz, 2007). This was anticipated to significantly proliferate stresses associated with UV radiation, as these high temperatures are beyond the thermal neutral zone for chimpanzees (17-29° C: Bruhn & Benedict, 1936) and exceed their mean core body temperature of 37.2° C (Jensen et al., 2009; Morrison, 1962). Therefore, thermal stresses associated with open (i.e. grasslands and open woodlands) versus closed (i.e. gallery forests) environments at this site, as well as ambient temperature, sun exposure, and behavioral context, were included as factors in this study. This study will enhance our knowledge of chimpanzee thermoregulation and our interpretation of early models regarding the evolution of bipedalism in hominins.
Summary

Fongoli is considered a mosaic landscape, consisting of grassland, woodland, gallery forest, and bamboo woodland (Pruetz & Bertolani, 2009). This research examines the relationship between positional behavior and heat stress in the Fongoli chimpanzees. The various postural and locomotive modes employed by chimpanzees are expected to differ in their exposure to UV radiation, thereby altering the experienced thermal load. Therefore, it was hypothesized that body temperature will vary with positional behavior. Arguments regarding the evolution of bipedalism in hominins suggest that a bipedal stance lowers the body’s surface area in contact with the sun (Wheeler, 1984); additionally, this upright posture increases contact with wind, thus acting as an effective means of thermoregulation. With this, bipedal posture and locomotion are hypothesized to impact body temperature differently than quadrupedal positions, which are predicted to be associated with a higher body temperature when compared to bipedalism.

Shifting use of microhabitat is a probable means of thermoregulation throughout the day and over seasons, as different habitat types vary in their degree of sun exposure. Chimpanzees at this site exhibit nocturnal behavior significantly more during the dry season (Pruetz, 2018). A higher occurrence of nighttime behavior during the hottest time of year indicates a behavioral shift to compensate for increased thermal stresses in this savanna mosaic environment. Therefore, habitat type as well as ambient temperature and behavioral context were recorded important factors when assessing effects of positional behavior on body temperature. Together these elements will bolster our understanding of behavioral thermoregulation, as well as our interpretations of bipedal evolution in hominins.
References


CHAPTER 2

THERMO-IMAGING BIPEDALISM ON THE SAVANNA: CHIMPANZEE LOCOMOTION AT FONGOLI, SENEGAL AND IMPLICATIONS FOR THE EVOLUTION OF HOMININ BIPEDALISM

Introduction

Questions on what makes human beings unique continue to intrigue anthropologists and other scientists. One such question relates to the origins of habitual bipedalism in the hominin lineage, something regularly debated by anthropologists. Selective pressures connected to savanna habitats, such as thermal stress, are interpreted as essential drivers of adaptive traits in hominins. Arguments regarding the evolution of bipedalism in hominins suggest that a bipedal stance acts as an effective means of thermoregulation, as it lowers the body’s surface area in contact with the sun as well as increases contact with wind (Wheeler, 1984, 1985, 1991a, 1991b; Ruxton & Wilkinson, 2011).

Research suggest that early hominids throughout the Plio-Pleistocene existed in a more open savanna environment, characterized as a mosaic of both grassland and woodland habitats (Kappelman et al., 1997; Reed, 1997; Cerling et al., 2010; Domínguez-Rodrigo, 2014). This study focuses on chimpanzees in the Fongoli community in Senegal, as they inhabit a similar environment (Pruetz & Bertolani, 2009). Fongoli chimpanzee’s home range consists of woodland, grassland, bamboo and gallery forest habitats (Pruetz, 2006; Pruetz et al., 2008), and they are thus far the only community occupying a savanna woodland habitat that are fully habituated to observers. With their close evolutionary relationship to humans, chimpanzees are commonly used as referential models in examining hypotheses regarding hominin evolution.
(Moore, 1996). Parallels in habitat, however, make savanna chimpanzees an even better model for this research, as they offer use of a referential model based on both homology and analogy (Moore, 1996). Studying chimpanzees occupying a savanna mosaic environment provides a unique opportunity to assess these questions, such as the thermoregulatory advantages of bipedalism and how thermal stresses impact furred apes in a hot, dry and open environment. This thesis addresses the array of positional behaviors used by West African chimpanzees in relation to body temperature through use of a thermo-imaging camera.

This study looks to examine the relationship between positional behavior and heat stress in the Fongoli chimpanzees by using a thermo-imaging camera (FLIR E75bx IR). Claims concerning hominin bipedal evolution suggest that this upright posture lowers the body’s surface area in contact with the sun (Wheeler, 1984); in addition, a bipedal stance heightens contact with wind, fostering a thermoregulatory advantage. As follows, bipedal posture and locomotion were hypothesized to reduce heat load in savanna chimpanzees.

This hypothesis led to following predictions: (1) body temperature will vary with positional behavior, (2) bipedalism will differentially effect body temperature, (3) bipedalism will reduce body temperature relative to quadrupedal positions, and (4) body temperature will vary with chimpanzee habitat type. I expected that the various postural and locomotive modes employed by chimpanzees would differ in their relative exposure to UV radiation, which in turn would alter their experienced thermal load. Moreover, should Wheeler’s (1984) hypotheses hold true, bipedalism was expected to influence body temperature differently than quadrupedal positions, with higher body temperatures predicted to be associated with quadrupedal positions than with bipedalism.
This study examined how the various habitat types in the Fongoli chimpanzee home range influenced exposure to heat stress. Captive chimpanzees have been recorded displaying a sun-avoidance strategy, particularly during the hottest hours of the day, suggesting the importance of shade use in thermoregulation (Duncan & Pillay, 2013). Habitat types at Fongoli differ in their degree of sun exposure, as this site is a mosaic landscape, consisting of grassland, woodland, gallery forest, and bamboo woodland (Pruetz & Bertolani, 2009). Chimpanzees here exhibit behavioral adjustments linked to heat stress (Pruetz & Bertolani, 2009; Pruetz, 2018; Wessling et al., 2018), such as cave use, water use and nocturnal behavior, and were recently found to show seasonal variation in stress and dehydraation levels, with levels peaking when dry season temperatures were highest and with water scarcity (Wessling et al., 2018). Chimpanzees at Fongoli likely also make use of the mosaic landscape to avoid intense sunlight during the hottest times of day and of year. However, not enough data were available per microhabitat to accurately assess the individual effects of each habitat type on body temperature, though habitat type was still included as a factor in the models as it enhanced model fit. Ambient temperature, sun exposure and behavioral context were also recorded as relevant factors when assessing how positional behavior impacts body temperature. Amalgamating these components will deepen our understanding of behavioral thermoregulation, as well as our interpretations of bipedal evolution in hominins.

**Bipedal evolution and thermoregulation**

Hypotheses put forth to explain the evolution of habitual bipedalism in hominins are extensive, though likely not all mutually exclusive. Freeing the hands for efficient load carrying (Videan & McGrew, 2002; Gebo, 1996; Washburn, 1968; Bartholomew & Birdsell, 1953),
bipedal threat displays (Jablonski & Chaplin, 1993), predator defense (Walter, 2004), or to aid more efficient feed and foraging (Hunt, 1996; Hunt, 1994; Wrangham, 1980; Rose, 1976; Jolly, 1970) have all been proposed as factors shaping the evolution of bipedalism. This research, however, focused on hypotheses linking bipedalism to thermoregulation, looking to this posture as a means to overcome heat stress (Wheeler, 1984, 1985, 1991a, 1991b, 1992; Dávid-Barrett & Dunbar, 2015).

A shift in habitat from one of closed canopy rainforest to a more open woody-savanna (Kappelman, et al. 1997; Reed, 1997; Cerling et al., 2010; Domínguez-Rodrigo, 2014) is often linked with the origin of habitual bipedalism in hominins (Wheeler, 1991b). This shift would intensify exposure to direct solar radiation, which can induce hyperthermia (Wheeler, 1984, 1991b); therefore, it is suggested that adaptations lessening heat stress or enhancing heat dissipation would have faced strong selective pressures (Wheeler, 1984, 1991a, 1991b, 1992). To overcome challenges of existing in a hot, dry and open environment, Wheeler (1984) proposes that bipedalism would have been a favored mode of locomotion. With a lack of an efficient selective cooling mechanism in primates (e.g. primates lack a carotid rete; Hayward & Baker, 1969; Wheeler, 1991b), hominids would rely on other means to protect the brain from thermal stress, such as behavioral shifts (Wheeler, 1984, 1991a, 1991b). Bipedalism not only reduces surface area exposed to direct sunlight, but also increases exposure to airflow by raising body surfaces above the ground (Wheeler, 1984, 1985, 1991a, 1991b, 1992).

Wheeler’s models were not without criticism. Ruxton and Wilkinson (2011) report that any gained thermoregulatory advantages would be negated by the endogenous heat load incurred by bipedal locomotion in an open environment. They argue that bipedalism would not benefit thermoregulation unless hominids had already undergone hair loss. This new model was
challenged by Dávid-Barrett and Dunbar (2015), as neither altitude of early hominins or activity budget were taken into account, indicating instead that hominins were moving steadily throughout the day. With altitude and activity budget included in their updated model, Dávid-Barrett and Dunbar (2015) conclude that there is a substantial thermal advantage to being bipedal in an open habitat, even for a furred ape; however, such benefit does not come through in a shaded environment.

**Behavioral thermoregulation**

Primates rely on both physiological (e.g. evaporative cooling) and behavioral (e.g. microhabitat selection) means of thermoregulation (Kosheleff & Anderson, 2009; Duncan & Pillay, 2013; Chaplin et al., 2014; Lopes & Bicca-Marques, 2017). Behavioral strategies combatting thermal stresses are efficient when an animal is beyond its thermoneutral zone, as these strategies can lessen the energetic demand of physiological thermoregulation (Hey, 1975; Brain & Mitchell, 1999; Hill, 2006; Terrien et al., 2011; Lopes & Bicca-Marques, 2017). In addition to microhabitat choice, research on these behavioral strategies to combat a high thermal environment tend to examine changes in positional behavior.

Shifting positional behavior is thought to alter rate of heat dissipation due to the modification of the body’s surface-to-volume ratio exposed to the sun (Lopes & Bicca-Marques, 2017). Titi monkeys (*Callicebus bernhardi*) were found to amplify use of heat-dissipating postures and avoid areas of high sun exposure when temperatures exceeded the thermoneutral zone (Lopes & Bicca-Marques, 2017). Additionally, yellow baboons (*Papio cynocephalus*) in Amboseli National Park changed postures and body orientation with changes in their microclimate (Stelzher & Hausfater, 1986), as well as spent more time resting in the shade.
(Stelzher, 1988). To avoid heat loss in the morning, the baboons maintained hunched postures and oriented their trunks away from the wind (Stelzher & Hausfater, 1986).

**Thermo-imaging chimpanzees**

The altering of positional behaviors in response to thermal environment by other primate species lends credence to the idea that early hominins also employed such behavioral shifts. Using a thermo-imaging camera to evaluate this idea, this study explores the relationship between positional behavior and body temperature in chimpanzees occupying a savanna environment. Chimpanzees are frequently bipedal during male displays, vigilance and feeding, and bipedal behavior is observed significantly more in the Fongoli community than at other sites (Tourkakis, 2009). Moreover, the home range of the chimpanzees at Fongoli is within a savanna mosaic environment (Pruetz & Bertolani, 2009), similar to that of early hominins (Kappelman, et al. 1997; Reed, 1997; Cerling et al., 2010; Domínguez-Rodrigo, 2014). Thermo-imaging bipedal chimpanzees at this site with a FLIR E75bx IR camera, one can assess the associated heat load through use of point temperature measurements on individual dorsum.

Thompson et al. (2017) demonstrated the reliability of infrared thermography using a FLIR E60bx IR camera in examining primate body temperature. Using infrared thermography and subcutaneous measures, they assessed the relationship among temperatures and temperature gradients in the peripheral tissues between furred and bare areas in mantled howling monkeys (*Alouatta palliata*). Results showed that surface temperatures of furred areas still held a relationship with subcutaneous temperatures (Thompson et al., 2017), supporting use of a FLIR camera as a non-invasive means to assess body temperature of wild primates. Following similar methodology to evaluate chimpanzee body temperature in relation to positional behaviors, this
study will enhance our knowledge of chimpanzee thermoregulation as well as our interpretation of early models regarding the evolution of bipedalism in hominins.

**Methods**

**Study site**

This study was performed at the Fongoli field site (12°39’ N, 12°13’ W) in southeastern Senegal. This site is composed of savanna woodland vegetation containing a mosaic of grassland, woodland, gallery forest, bamboo woodland and ecotone forest habitats (Pruetz, 2006; Lindshield et al., 2017). Gallery forest understory is distinguished by diverse herbaceous-level plants, while a grass understory predominates woodland, grassland and bamboo woodland areas (Pruetz & Bertolani, 2009). Woodland accounts for the greatest percentage (46%) of habitat type in the Fongoli chimpanzee home range (Pruetz, 2006). Rainfall averages 900mm annually (Ba et al., 1997; Pruetz & Bertolani, 2009). The longer dry season typically spans seven months (October–May), with the shorter wet season persisting from June–September. Little rainfall, if any, occurs during the transitional months of October and May; however, erratic rainfall patterns have recently been recorded, with rainfall data occurring in May (Pruetz, 2018; Lindshield et al., 2017). Daily temperatures average 28.4°C, though in the late dry season the maximum temperature often exceeds 40°C (Pruetz & Bertolani, 2009; Lindshield et al., 2017). The chimpanzees at Fongoli have a home range of approximately 110 km² (Boyer, 2017), 4% of which includes croplands (Pruetz & Bertolani, 2009; Lindshield et al., 2017). Permanent and seasonal settlements, roads, croplands, foot trails, free ranging cattle, annual bush fires, seasonal sheep herding, wood collection for timber and fuel, and artisanal gold mining are other
anthropogenic factors characterizing the Fongoli chimpanzees’ home range (Pruetz & LaDuke, 2010; Pruetz & Kante, 2010; Lindshield et al., 2017).

**Study subjects and behavioral data collection**

Adult male chimpanzees (*Pan troglodytes verus*, at least 14 years of age and/or integrated into the adult male dominance hierarchy; n=12) were the focus of this study per the Fongoli Savanna Chimpanzee Project’s (FSCP) protocol. Focal male subjects were followed from night nest to night nest, with behavioral data collected opportunistically using a thermo-imaging camera. If during a day’s data collection period the focal male disappeared and could not be relocated within 20 minutes, a new focal male was chosen (per FSCP protocol). Females were not subjects of focal follows, as adult females may be targets to gain infants for the pet trade, and though the risk is slight, it is not trivial (1 case in 15 years; Pruetz & Kante, 2010). While females are fully habituated when in association with adult males, they remain nervous around people when met in small all-female parties or in isolation. The Fongoli community has been studied since 2001, and averages 32 individuals annually (2005-2018). In 2005, after adult males became accustomed to researcher presence, systematic all-day follows of individual males began (Pruetz & Bertolani, 2007). Individuals’ unique physical appearances, such as facial scarring or ear notches, were used in focal identification.

The field season began May 27, 2018, lasting through July 20th; data collection took place from June 6, 2018 through July 16, 2018. Data collection followed an every-other-day schedule, that is after one day of data collection, one rest day was set aside in order to charge camera batteries, summarize data and to avoid researcher fatigue. Instantaneous focal animal sampling was used at 5-minute intervals to record the various positional behaviors used by
subjects throughout their daily activities and to capture thermo-images using the FLIR E75bx IR; however, due to behavioral, habitat, and camera constraints, certain positional behaviors and habitat types were more challenging to obtain in data collection. The open nature of the Fongoli study site during most of the year promotes excellent visibility of study subjects; however, some barriers still exist when taking proper thermo-images. Obtaining appropriate images requires more flexibility than exists using instantaneous sampling methods due to visibility barriers and observation protocols, so image capture followed a rough, rather than strict, 5-minute sampling schedule. Images were taken opportunistically if behaviors or habitats of interest, or those more difficult to obtain at each interval (e.g. bipedal posture or locomotion, suspensory behaviors, etc.), were observed outside of the rough 5-minute sampling schedule. With this rough sampling schedule, measures could be recorded up to one-minute prior or past the 5-minute mark to accommodate the specificities in capturing thermo-images. This allowed for a more well-rounded sample.

Included in this study were recordings of positional behavior and habitat type, assessing how these factors relate to body temperature and thermoregulation. Recorded positional modes were consistent with those described by Hunt et al. (1996) to maintain uniformity with other positional behavior studies. Locomotor modes are defined as the positional behaviors employed during movement, while postural behaviors are relatively motionless positions. Knuckle-walk/run, bipedal walk, assisted bipedal walk, brachiation, and vertical climb are but a few behaviors that comprise the modes of locomotion (Hunt, 1991; Hunt, 1992; Doran, 1993; Hunt et al., 1996; Stanford, 2006; see Appendix A for behavioral catalog). Postural modes involve positions such as sit, squat, quadrupedal stand, bipedal stand, supported bipedal stand, lie, and forelimb suspend.
To assess the effects of thermal stress for apes generated in open (grassland, woodland, bamboo woodland) versus closed (gallery forest) environments, habitat type was recorded. I also noted the behavioral activity of the focal individual (i.e. forage/feed, travel, rest, social). Other collected data included: (1) adult male identity, (2) date, (3) time of day, (4) degree of sun to which subject is exposed (0%, 25%, 50%, 75%, or 100% of body's dorsal surface), (5) substrate (arboreal, terrestrial), and (6) ambient temperature. Abiotic factors, such as ambient temperature and sun exposure, were included, as Thompson et al. (2017) found that these variables increased the explanatory value of their predictive models. In the late dry season at Fongoli, when most trees lose their leaves, temperatures are characteristically higher, regularly exceeding 40º Celsius (Pruetz, 2007). These high temperatures are above the thermal neutral zone for chimpanzees (17-29 ºC: Bruhn & Benedict, 1936) and are beyond their mean core body temperature of 37.25 ºC (Jensen, 2009; Morrison, 1962), and were consequently anticipated to amplify stresses due to UV radiation. Moreover, wild chimpanzees in the Budongo Forest of Uganda, a semi-deciduous tropical rain forest (monthly temperature range of 19-32 ºC: Reynolds, 2005), adjusted activity levels in accordance with ambient temperature and sun exposure (Kosheleff1 & Anderson, 2009). Ambient temperature was recorded using Kestrel Drops placed throughout the Fongoli landscape with temperature measurements taken every hour. Battery life of the Kestrel Drops, however, prevented the collection of hourly ambient temperatures on certain dates during the study. To ensure these data were collected on an hourly basis, the Weather Underground database supplemented climatic data. Therefore, hourly ambient temperature data were obtained by mining temperature points from both the Kestrel Drops and Weather Underground. The degree to which chimpanzees were exposed to the sun (0%, 25%, 50%, 75%, or 100% of body's dorsal surface) was estimated visually by the observer.
Thermo-imaging data

Thermo-imaging data were collected with a FLIR E75bx IR camera. Methods in taking thermo-images followed the Thompson et al. (2017) study of mantled howling monkeys (*Alouatta palliata*), in which they related surface temperatures to subcutaneous temperatures using a FLIR 60bx IR camera and internal telemeters. Their study demonstrated the reliability of infrared thermography when examining primate body temperatures, and found that the furred dorsum (i.e. the back) was a better gauge of subcutaneous body temperature than hairless areas (i.e. the face). Reliable, non-invasive measures are necessary for endangered or critically endangered species, like chimpanzees, as their status limits use of more invasive methods like implanted telemeters.

Each captured photo included both a high-resolution image and a thermo-image. Images are taken from both directly behind and at a side angle of the dorsum of the focal subject, provided the surface is clearly visible and obliquely oriented to the observer. Variables such as body temperature, positional behavior, habitat type, date, time, and distance to focal are apparent based on the photos obtained. Specifics of these variables were recorded in a field notebook immediately following photo capture along with the minimum and maximum temperatures unique to each image. For instance, as these are still images, it was indicated whether the individual was engaging in a postural (e.g., quadrupedal stand) or locomotor (e.g., quadrupedal walk) behavior, as well as specified the microhabitat, behavioral context, and sun exposure, among other variables. While much of this information is apparent based on the images alone, recording the real-time data corroborates given scores. These recordings help convey the thermal load faced by the chimpanzees by providing their body temperature in different postures, microhabitats, and times of day.
Data analysis

A linear mixed effects model was created in the statistical computing software Rstudio to test the hypothesis that positional behaviors differentially impact body temperature. Residual plots of the model were indicative of a good model fit. Chimpanzee body temperature obtained from the FLIR E75bx IR camera (see temperature in upper left corner of Figure 2.1) was used as the response variable, and individual focal chimpanzee was included as a random effect. Model reduction using Akaike’s Information Criterion (AIC) was used to reduce the model from the full model, initially including all variables of interest (i.e., positional behavior, ambient temperature, date of data collection, habitat type, behavioral context, sun exposure, substrate, individual chimpanzee). The final model (AIC: 3168.603, DF: 16) included the fixed effects of positional behavior, ambient temperature, sun exposure, the date data were collected and habitat type, and focal chimpanzee as a random effect:

\[
\text{Chimpanzee body temperature} \sim \text{positional behavior} + \text{ambient temperature} + \text{sun} \\
+ \text{date} + \text{habitat type} + (1|\text{individual})
\]

The absolute value of t-values > 1.96, p-values < 0.05, and 95% confidence intervals were used to determine significance of variables in relation to the outgroup. As bipedalism is the positional behavior of interest, it was used as the outgroup for comparison.
Figure 2.1: Sample FLIR E75bx IR image. Individual chimpanzee (BN) feeding in terrestrial bipedal stand.

It was prudent to combine postures and locomotor behaviors that most resembled one another, particularly in relation to sun exposure, for analyses. For instance, suspensory postures like “quadrumanous” and “forelimb suspend” were reduced to single identifier of “suspensory” during analysis. This enhanced the number of suspensory samples and reduced the number of levels within positional behavior, allowing for a more meaningful analysis. Similarly, the category of “bipedalism” (n=160) included all variations of the position (e.g., bipedal walk, n=22; bipedal stand, n=19; assisted bipedal stand, n=119).
Results

I collected a total of 239.42 hours of instantaneous focal animal sampling (19 sampling days, 2873 data points) over the course of this study. After removing outliers and data points not containing a thermo-image, 67 hours of data (804 data points) remain for final analysis. Of those 804 thermo-images, 19.9% (n = 160) were of chimpanzees in a bipedal position (Figure 2.2). The thermography dataset comprised a minimum of 23 photos per day with a maximum of 67 (n = 804 total photos). Only three data collection days contained less than 30 thermo-images. These lower numbers can be explained by rainfall (n = 2 days) and a high percentage of chimpanzee resting behavior (n = 1 day), which either limited visibility or use of the FLIR 75bx IR camera.

Figure 2.2: Frequency of each positional behavior from June 6 – July 16, 2018
Body temperature
The AIC, best fit linear mixed model included body temperature from the FLIR thermo-image (Figure 2.1) as the response variable, with fixed effects of positional behavior, ambient temperature, habitat type, date of sampling, individual’s exposure to the sun, and the random effect of individual chimpanzee. Over the course of this study, chimpanzee surface body temperature ranged from 26.1 to 41.6 °C, and averaged 34.1 °C (median: 34.0 °C, IQR: 3.7; Figure 2.3). However, when controlling for time of day, chimpanzee body temperature averaged 32.83 °C before noon, 35.75 °C from noon to 5 PM, and 34.61 °C in the early evening (Figure 2.4). Body temperature had a positive and significant relationship with ambient temperature (β: 0.2716; t-value: 15.873; 95% C.I. [0.2368, 0.3047]).

![Range of Chimpanzee Body Temperatures](image)

*Figure 2.3: Range of chimpanzee body temperatures from June 6 – July 16, 2018*
Figure 2.4: Range of chimpanzee body temperatures across varying times of day from June 6 – July 16, 2018

The date of each sample had a significant and negative relationship with body temperature (Table 2.1). As the rainy season began during this study, ambient temperature tended to decrease as the study progressed. The negative estimate indicates that as date increased, or as the study moved forward, body temperature decreased by 0.0334 °C. This may be indicative of how the cooler rainy season impacts body temperature and thermoregulation; however, this estimate is very small.

Ambient temperature averaged 29.8 °C throughout the study (median: 30.1 °C, IQR: 5.9), and ranged from 19.4 to 36.5 °C. However, when controlling for time of day, the ambient temperature averaged 27.32 °C before noon, 32.23 °C from noon to 5 PM, and 31.97 °C in the early evening.
Table 2.1: Effect of abiotic factors on chimpanzee body temperature

<table>
<thead>
<tr>
<th></th>
<th>Difference in body temperature</th>
<th>Std. Error</th>
<th>t-value</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ambient Temperature</td>
<td>+0.2716</td>
<td>0.0171</td>
<td>15.873 *</td>
<td>[0.2369, 0.3047]</td>
</tr>
<tr>
<td>Degree of Sun Exposure</td>
<td>+0.0490</td>
<td>0.0029</td>
<td>16.736 *</td>
<td>[0.0433, 0.0547]</td>
</tr>
<tr>
<td>Date of Thermo-image</td>
<td>-0.0334</td>
<td>0.0072</td>
<td>-4.666 *</td>
<td>[-0.0478, -0.0195]</td>
</tr>
</tbody>
</table>

*indicates significance at p < 0.05

Positional behavior and body temperature

In comparing the effect of bipedalism on body temperature to quadrupedal positions, bipedalism was used as the comparative outgroup in the linear mixed model. A t-value of +/-1.96 was used in assessing significance, as well as 95% confidence intervals and a significance threshold of p < 0.05. Summary statistics suggest a significant difference in body temperature between bipedalism and quadrupedal stand (t-value: 1.983; p-value: 0.04; 95% C.I. [0.0109, 1.1078]). Chimpanzee body temperature was on average 0.559°C higher when the individual engaged in quadrupedal stand as opposed to a bipedal position. These data are summarized in Table 2.2. However, this trend did not hold with quadrupedal walk. While the model estimate shows a higher average body temperature when walking quadrupedally, the difference from bipedalism is not significant (p-value: 0.058; Table 2.2).
Table 2.2: Effect of positional behavior on body temperature relative to the bipedal position

<table>
<thead>
<tr>
<th>Position</th>
<th>Difference in body temperature</th>
<th>Std. Error</th>
<th>t-value</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quadrupedal Stand</td>
<td>+0.5588</td>
<td>0.282</td>
<td>1.983 *</td>
<td>[0.0109, 1.1077]</td>
</tr>
<tr>
<td>Quadrupedal Walk</td>
<td>+0.3698</td>
<td>0.195</td>
<td>1.895</td>
<td>[-0.0082, 0.7524]</td>
</tr>
<tr>
<td>Sit/Squat</td>
<td>+0.4499</td>
<td>0.175</td>
<td>2.577 *</td>
<td>[0.1116, 0.7916]</td>
</tr>
<tr>
<td>Lie</td>
<td>-0.9063</td>
<td>0.258</td>
<td>-3.509 *</td>
<td>[-1.4060, -0.3987]</td>
</tr>
<tr>
<td>Vertical Climb/Cling</td>
<td>+0.1968</td>
<td>0.365</td>
<td>0.539</td>
<td>[-0.5136, 0.9086]</td>
</tr>
<tr>
<td>Suspensory</td>
<td>+0.7180</td>
<td>0.547</td>
<td>1.312</td>
<td>[-0.3433, 1.7881]</td>
</tr>
</tbody>
</table>

* indicates significant difference at p < 0.05

Upon examining other positional behaviors in relation to bipedalism, sit/squat also showed significantly increased body temperature (p-value: 0.009; Table 2.2). When comparing sit/squat to quadrupedal positions, however, there was no significant difference in impact on body temperature (quadrupedal stand: $\beta = 0.109$, t-value: 0.420, p-value: 0.67, 95% C.I. [-0.3975, 0.6129]; quadrupedal walk: $\beta = -0.08$, t-value: -0.483, p-value: 0.63, 95% C.I. [-0.4026, 0.2436]). Chimpanzees in a lying position consistently maintained a significantly lower body temperature than when in all other positions. Figure 2.5 depicts the sample means and standard errors of each positional behavior’s corresponding body temperature from the model, while Figure 2.6 plots the observed values of these data.
Figure 2.5: Sample means of the effect of positional behavior on body temperature

Figure 2.6: Observed values of the effect of positional behavior on body temperature
**Habitat Type**

Habitat type was examined regarding its impact on body temperature; however, samples sizes were too small regarding the different habitat types (i.e., woodland, grassland, bamboo woodland, gallery forest) for detailed analysis. Even when condensing levels into “open” (i.e., grassland, woodland, bamboo forest habitat) vs. “closed” (i.e., gallery forest), there was not enough data in closed habitat (less than 10%) for further analysis (Figure 2.7). Habitat type was still included as a factor in the linear mixed model, as it improved the fit of the model; however, there was no significant difference between microhabitats within the model.

**Figure 2.7: Frequency of open vs. closed habitat types from June 6 – July 16, 2018**
Discussion

Positional behavior and bipedalism

With this research, I provide novel data on thermal-imaging of savanna chimpanzees to investigate the hypothesis that the evolution of bipedalism in the hominin lineage is related to reducing heat stress. Wheeler (1984) suggested that with a shift in habitat to a more open, woody savanna, adaptations lessening heat stress or enhancing heat dissipation would have faced strong selective pressures. By reducing the surface area exposed to direct sunlight, as well as increasing the exposure of the body’s surface to airflow, bipedalism was proposed as a favored mode of locomotion in early hominins. When including altitude and activity budget in this model, Dávid-Barrett and Dunbar (2015) also indicate a substantial thermal advantage of bipedalism when in an open habitat.

To assess these claims, this research focused on the positional behaviors of chimpanzees occupying a hot, dry and open environment at Fongoli, Senegal while using a FLIR E75bx IR thermo-imaging camera. I examined the following in their relative exposure to heat stress in chimpanzees: (1) how various postural and locomotor behaviors differ, (2) the effects of bipedalism, (3) the difference in effect of bipedal and quadrupedal behaviors, and (4) how habitat types vary. In testing the effects of positional behavior on chimpanzee body temperature, my model accounted for the influence of ambient temperature, sun exposure, date, habitat type, and focal chimpanzee.

The results give support to the hypothesis that body temperatures will vary with positional behavior. When altering the outgroup in the model (i.e., changing the model reference category from bipedalism to the lie position), each tested positional behavior differed significantly with the lie posture. With bipedalism as the referent, it also significantly differed in
its effect on body temperature with quadrupedal stand and sit. Lying behavior consistently resulted in a significantly lower body temperature. Brain and Mitchell (1999) study on chacma baboons (Papio hamadryas ursinus) found that periods of inactivity were correlated with drops in body temperature. Moreover, chimpanzees at Fongoli are recorded to rest more and travel less during the hottest times of day and year to minimize energy expenditure (Pruetz & Bertolani, 2009). Therefore, this reduction in body temperature is expected, as this positional behavior is associated with periods of inactivity or resting.

When looking closer at the relationship between bipedalism and quadrupedal positions, there is a significant difference in the effect of bipedalism on chimpanzee body temperature when compared to quadrupedal stand, though interestingly not when compared to quadrupedal walk. When an individual engaged in quadrupedal stand, body temperature was significantly higher compared to bipedalism. In addition, body temperature also increased when individuals engaged in quadrupedal walk, but the effect did not significantly differ from that of bipedalism. This surprising result may be attributable to the movement of the focal individual during photo capture, which could have influenced the camera reading or perhaps the stationary posture of quadrupedal stand led to higher temperature readings. It may be useful to re-examine this trend across a broader seasonality range. It is possible that observations during the hotter dry season would reflect stronger differences between the various positional behaviors, specifically between bipedal and quadrupedal positions. This could provide additional backing for the trends observed here. However, as these data were collected in the transitional months leading into the cooler wet season, discerning significant differences between positional behaviors, particularly relative to bipedalism and quadrupedal stand, at all provides stronger evidence in support of Wheeler’s (1984) claims.
The effect of bipedalism significantly differed from that of lie and sit/squat, while quadrupedal stand significantly differed only from that of lie. In each of these cases, other than lie, bipedalism resulted in a lower body temperature. The reduction of body temperature while in a bipedal position, particularly when compared to a quadrupedal position (i.e., quadrupedal stand), is consistent with the hypotheses laid out by Wheeler (1984, 1985, 1991a, 1991b) and Dávid-Barrett and Dunbar (2015), and therefore offer support to the notion that bipedalism may offer a thermoregulatory advantage over quadrupedal positions. I argue the cooler months in which these data were collected offer stronger support for Wheeler’s hypotheses. One would expect a greater difference in effect on body temperature between bipedalism and quadrupedalism during the hottest times of year; however, evidence of this trend nearing the wet season when ambient temperature has cooled provides greater support to these claims.

**Abiotic factors**

Following Thompson et al. (2017), chimpanzee sun exposure and ambient temperature were expected to increase the explanatory value of the predictive models. Including these abiotic factors in the model improved model fit. Exposure to direct sunlight or hotter ambient temperatures were predicted to significantly impact body temperature. As expected, chimpanzee sun exposure (0%, 25%, 50%, 75%, 100%) and ambient temperature both maintained positive and significant relationships with body temperature. That is, the more exposure an individual chimpanzee had to the sun in a sample, the higher their body temperature (as sun exposure increased, body temperature increased by 0.049 °C; additionally, as ambient temperature increased, chimpanzee body temperature was raised by 0.273 °C). Wheeler’s hypothesis on how bipedalism would benefit thermoregulation of early hominins credits life in a hot, dry and open...
habitat as a substantial piece in this puzzle. These data give evidence of how a hotter environment can significantly impact the body temperature of the individuals living there, corroborating Wheeler’s assertion.

**Habitat Type**

An objective of this study was to examine microhabitat and its influence on chimpanzee body temperature. The Fongoli field site is comprised of woodland, grassland, bamboo woodland and gallery forest habitats (Pruetz, 2006; Lindshield et al., 2017). The data reflect a higher occurrence of woodland habitat collected during the course of this research. In addition to being the most abundant habitat type, and one that chimpanzees use in proportion to its availability (Pruetz & Bertolani, 2009), woodland habitat facilitated easier thermo-image capture when compared to the other habitat types at this site. Often the distance from the chimpanzees prevented proper image taking while in grassland and gallery forest; moreover, the chimpanzees tended to move quickly through the open grassland and were often concealed by denser foliage while in gallery forest, making image capture more challenging.

The present model shows no significant difference between the effect of habitat type (neither separate habitat types nor combined as “open” vs. “closed” habitats) on chimpanzee body temperature; however, the small sample size of each habitat type (grassland, n = 42; bamboo/bamboo woodland, n = 61; gallery forest, n = 66), save for woodland (n = 635), makes these data less informative, particularly when considering not all positional behaviors were accounted for within each habitat type. Adjusting to a more open environment from one of more closed canopy is considered a significant shift over the course of hominin evolution, as it likely imposed important selective pressures concerning the behavioral ecology of early hominins.
(Wheeler, 1991a; Pruetz & Bertolani, 2009). One would expect more open environments to impose higher heat stress than those that are more shaded, particularly when considering the significant impacts of ambient temperature and sun exposure on body temperature outlined above. An open habitat would impose increased exposure to the sun, which was shown to have a positive relationship with body temperature. Additionally, chimpanzees at Fongoli have been previously recorded utilizing its mosaic landscape in times of thermal stress (Pruetz & Bertolani, 2009), and exhibit behavioral adjustments linked to heat stress (Pruetz & Bertolani, 2009; Pruetz, 2018; Wessling et al., 2018), such as cave use, water use and nocturnal behavior.

Conclusions

The findings of this thesis support the hypothesis that positional behaviors differ in their effects on body temperature. Additionally, Wheeler’s (1984) hypothesis concerning hominin bipedal evolution has gained support through these findings. Wheeler (1984) suggests that a bipedal stance fosters a thermoregulatory advantage and considers heat stress a major selective pressure in the evolution of bipedalism in hominins. The results presented here suggest bipedalism is associated with reduced body temperatures in chimpanzees occupying a savanna mosaic habitat, particularly relative to the quadrupedal stand posture. Hypotheses concerning bipedal evolution in the hominin lineage are numerous; with support for Wheeler’s hypothesis, these results hold significance in our consideration of how and why bipedalism in hominins evolved.

Future analyses are encouraged to include both seasonality and a heavier focus on the effects of habitat type. This study was carried out during transitional months (June-July 2019) going into the wet season, and tree crowns in more open woodland habitats were denser than
would be throughout the dry season. J. D. Pruetz (personal communication) is conducting a larger study using the FLIR E75bx IR thermo-imaging camera year-round at the Fongoli field site. This will garner a greater sample of each positional behavior within each type of habitat throughout both wet and dry seasons, allowing deeper consideration into the questions posed throughout this study. The hotter dry season may introduce a greater effect of positional behavior on body temperature, expressly between bipedal and quadrupedal positions. Adding seasonality as a component in the dataset will allow for more comprehensive analyses, ultimately advancing our understanding of bipedal evolution in the hominin lineage.

References


CHAPTER 3
CONCLUSION

The research presented in this thesis examined the relationship between positional behavior and heat stress in the Fongoli chimpanzees by using a thermo-imaging camera (FLIR E75bx IR) as an indirect measure of ape body temperatures. My findings support the hypothesis that chimpanzee positional behaviors differ in their effects on body temperature. What is more, my results provide support for Wheeler’s (1984) hypothesis concerning hominin bipedal evolution. Wheeler (1984) suggests that a bipedal stance fosters a thermoregulatory advantage, as it would reduce the body’s surface area in contact with the sun while also amplifying its contact with the wind. Therefore, Wheeler looks to heat stress as the ultimate selective pressure explaining the evolution of bipedalism in hominins. Chimpanzees occupying a savanna mosaic habitat (Pruetz, 2006; Pruetz & Bertolani, 2009) were used to test these claims, as their close evolutionary relationship to humans and similarities in habitat to early hominins (Kappelmann et al., 1997; Reed, 1997; Cerling et al., 2010; Domínguez-Rodrigo, 2014) allow their use as a referential model based on both homology and analogy (Moore, 1996). Results show that chimpanzee body temperature is lowered while in a bipedal position when measured against quadrupedal positions, significantly so against the stationary quadrupedal stand. There are many hypotheses surrounding the evolution of bipedalism in the hominin lineage, though not all mutually exclusive. With support for Wheeler’s hypothesis, these results hold significance in our consideration of how and why bipedalism in hominins evolved.

A more inclusive, follow-up analysis can incorporate both seasonality and effects of microhabitat. The shift from a closed canopy to a more open environment is deemed significant
in the course of hominin evolution due to the selective pressures we expect it imposed on the behavioral ecology of early hominins (Wheeler, 1991a; Pruetz & Bertolani, 2009). This study intended to examine the effects of open versus closed habitat types on body temperature, but sample size was not conducive for further analyses. Data were also collected during transitional months (June-July 2019) going into the wet season, and trees within characteristically open habitats maintained denser foliage cover than would be seen throughout the dry season. Future analysis will focus more exclusively on the effects of microhabitat, with field seasons covering both the wet and dry seasons (J. D. Pruetz, personal communication). The longer study on this subject will ensure all positional behaviors are more equally represented in the data across both the dry and wet seasons, as well as throughout all habitat types. Representation of seasonality in the dataset will allow more comprehensive analyses, granting a deeper understanding of evolution in the hominin lineage.

References


### APPENDIX A

**BEHAVIORAL CATALOG**

Behavioral Catalog is taken from Hunt et al. (1996), Hunt (1992) and Doran (1993) with modifications by N.W.

<table>
<thead>
<tr>
<th>Type of Pattern</th>
<th>Code</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Behavioral Context</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foraging</td>
<td>Fo</td>
<td>Grasping food source and placing in mouth followed by masticating and ingesting substance; face relaxed and eyes open; bout includes stationary position or movement within a food patch, such as a tree crown.</td>
</tr>
<tr>
<td>Traveling</td>
<td>Tv</td>
<td>Any combination of hindlimb or forelimb use to propel body in a swinging or forward motion between tree crowns or forward on the ground; face relaxed.</td>
</tr>
<tr>
<td>Resting</td>
<td>RE</td>
<td>Body relatively motionless, but can include small movements, such as shifting body weight; face relaxed and eyes open or closed; breathing regular with or without the presence of yawning.</td>
</tr>
<tr>
<td>Social</td>
<td>Sc</td>
<td>Behavior involving more than one individual; includes both affiliative and agonistic behaviors, such as grooming, play, displays, or sexual behavior.</td>
</tr>
<tr>
<td>Vocalization</td>
<td>Vo</td>
<td>Communicative noises made by individuals, such as pant-hoots, pant-grunts, pant-barks, screams, “waaa”-barks, etc.</td>
</tr>
<tr>
<td>Other</td>
<td>Ot</td>
<td>Any activity functionally discrete from Tv, Fo, RE, Sc, or Vo.</td>
</tr>
<tr>
<td>Postural Behavior</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sit</td>
<td>St</td>
<td>Weight supported by ischia and one or two legs; hips and knees either tightly flexed (sit-in) or extended out (sit-out); ischia bear most of the weight.</td>
</tr>
<tr>
<td>squat</td>
<td>SQ</td>
<td>Body weight is borne solely by the feet, both hip and knee are strongly flexed. Substantial body weight not borne by forelimbs or ischia. The trunk is orthograde or suborthograde and the back is typically flexed</td>
</tr>
<tr>
<td>---------</td>
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<td>----------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>lie</td>
<td>Ly</td>
<td>Reclining on a relatively horizontal weight-bearing structure; body weight borne by back, stomach or side</td>
</tr>
<tr>
<td>vertical cling</td>
<td>VCI</td>
<td>Adhering to a vertical support via strongly flexed forelimbs and hindlimbs; feet may grasp or may be used as partial support; no weight bore by ischia</td>
</tr>
<tr>
<td>stand</td>
<td>QS</td>
<td>Three or four-limbed standing on horizontal or subhorizontal supports; elbow and knee are (relatively) extended and trunk is near horizontal</td>
</tr>
<tr>
<td>bipedal stand</td>
<td>BS</td>
<td>Standing on the hindlimbs with no significant support from any other body part; hips and knees may be flexed or extended</td>
</tr>
<tr>
<td>supported bipedal stand</td>
<td>SB</td>
<td>Standing on the hindlimbs while hands grasp foliage to maintain balance</td>
</tr>
<tr>
<td>forelimb suspend</td>
<td>FS</td>
<td>Unimanual or bimanual suspension with either no other part of body contacting weight-bearing structure or with support from ischia, feet (with flexed hindlimbs), side, back or elbow of contralateral arm; elbows extended, humerus abducted, trunk orthograde; this posture combines Hunt (1992) arm-hang and arm-hang-support</td>
</tr>
<tr>
<td>forelimb-hindlimb suspend</td>
<td>FH</td>
<td>Suspension by a forelimb and a hindlimb with limbs typically extended</td>
</tr>
<tr>
<td>quadrumanous-suspend</td>
<td>QM</td>
<td>Suspension with all four limbs contributing relatively equal support</td>
</tr>
<tr>
<td>other suspensory</td>
<td>SO</td>
<td>Miscellaneous suspensory modes such as quadrupedal suspensory bodily progression below and along or across supports with regular or irregular gaits</td>
</tr>
<tr>
<td>Type of Pattern</td>
<td>Code</td>
<td>Description</td>
</tr>
<tr>
<td>----------------------</td>
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<td>---------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td><strong>Locomotor Behavior</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quadrupedal Walk</td>
<td>QW</td>
<td>Forelimbs contact weight bearing structure via knuckles or palms/volar surface while feet either grasp substrate or contact via volar surface; includes quadrupedal knuckle-walk and quadrupedal palmar-walk</td>
</tr>
<tr>
<td>Bipedal Walk</td>
<td>BW</td>
<td>The hindlimbs provide support and propulsion, with only insignificant contributions from other body parts. The hip and knee may be flexed (flexed bipedal walk) or extended (extended bipedal walk)</td>
</tr>
<tr>
<td>Assisted Bipedal Walk</td>
<td>AB</td>
<td>The hindlimbs provide support and propulsion while hands grasp foliage to maintain balance</td>
</tr>
<tr>
<td>Quadrupedal Run</td>
<td>QR</td>
<td>Wrist and hand bear weight in knuckled orientation; volar surface of foot contacts weight bearing support; fast locomotion using asymmetrical or irregular gaits and with a period of free flight</td>
</tr>
<tr>
<td>Bipedal Run</td>
<td>Bin</td>
<td>Only hindlimbs used in support and propulsion, but with a period of free flight</td>
</tr>
<tr>
<td>Brachiation</td>
<td>Br</td>
<td>Hand-over-hand orthograde suspensory locomotion with forelimbs bearing over half the body weight; effectively no hindlimb contribution in locomotion or support; humerus abducted and elbow extended</td>
</tr>
<tr>
<td>Clamber</td>
<td>Cb</td>
<td>Body displacement in various directions on and across multiple, diversely oriented supports with no particular gait; all appendages attach to substrates in different ways; maintaining the body either pronograde or orthograde</td>
</tr>
<tr>
<td>Vertical Climb</td>
<td>VC</td>
<td>Ascending and descending locomotion on a weight bearing structure angled &gt;45°</td>
</tr>
<tr>
<td>Leap/Drop</td>
<td>Lp</td>
<td>Propulsion involving an extended period of free flight with more horizontal than vertical displacement (leap); “dropping” involves</td>
</tr>
</tbody>
</table>
slight propulsion downward with little force onto a lower stratum
with mainly vertical bodily displacement
## APPENDIX B

### LIST OF STUDY SUBJECTS

<table>
<thead>
<tr>
<th>Age-Class</th>
<th>Sex</th>
<th>Name</th>
<th>Rank</th>
<th>Notes</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult</td>
<td>Male</td>
<td>Jumkin</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Luthor</td>
<td>2</td>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bo</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mike</td>
<td>4</td>
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<tr>
<td></td>
<td></td>
<td>Dawson</td>
<td>5</td>
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<tr>
<td></td>
<td></td>
<td>Lupin</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>K.L.</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Diouf</td>
<td>8/10*</td>
<td></td>
<td>Does not pant-grunt to Bilbo or Lex</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lex</td>
<td>9*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bilbo</td>
<td>10/8*</td>
<td></td>
<td>Does not pant-grunt to Diouf, but observed pant-grunting to Lex when no other chimpanzees are around</td>
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</tr>
<tr>
<td>Bandit</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Siberut</td>
<td>12</td>
<td></td>
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</tbody>
</table>