STUDY DESIGN

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

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Introduction

Questions on what makes human beings unique have plagued 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). Chimpanzees are commonly used as referential models in examining hypotheses concerning hominin evolution due to their close evolutionary relationship to humans, but the parallels in habitat make savanna chimpanzees an even better model for this research. 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. I propose to examine chimpanzees at the Fongoli site in Senegal, as they are the only community occupying a savanna woodland habitat who are habituated to observers to date. I will address the array of positional behaviors used by West African chimpanzees in relation to body temperature through use of a thermo-imaging camera.

Fongoli is considered a mosaic landscape, consisting of grassland, woodland, gallery forest, and bamboo woodland (Pruetz & Bertolani, 2009). 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. Therefore, comparing chimpanzee heat signatures between habitat types will be pertinent to this study, as well. Chimpanzees at this site also 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. Activity scheduling during the day and at night will be examined for comparison in relation to heat stress; moreover, data will be collected on diurnal and nocturnal body temperatures of chimpanzees. Amalgamating these components will deepen our understanding of chimpanzee behavioral thermoregulation, as well as our interpretations of bipedal evolution in hominins.

Bipedal evolution and thermoregulation

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). 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 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,

australopith time budget models imply only 16% of the day was devoted to travel (Bettridge,

2010). Moreover, the altitude at which australopiths 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.

An informative method in behavioral reconstruction of early hominids 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

off 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 project sets forth to indirectly test the aforementioned hypotheses of hominin bipedal evolution by examining the heat load faced by chimpanzees in a savanna mosaic environment. I propose to thermo-image savanna chimpanzee posture and locomotion throughout their home range and across seasons. Doing so can enhance our models 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 (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; 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 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.

The altering of positional behaviors in response to thermal environment by other primate species lends credence to the idea that chimpanzees also employ such behavioral shifts. Using a thermo-imaging camera, I can evaluate the relationship between positional behavior and body temperature in chimpanzees occupying a savanna environment. Fongoli chimpanzees exhibit significantly more bipedal behavior than is observed at other sites (Tourkakis, 2009), and are frequently bipedal during male displays, vigilance and feeding. Thermo-imaging bipedal chimpanzees with a FLIR E75bx IR camera allows me to assess the associated heat stress by measuring per pixel temperature of individuals. Moreover, chimpanzees at Fongoli likely make use of its mosaic landscape to avoid intense sunlight during the hottest times of day and of year. 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 (Kosheleff1, & Anderson, 2009). Temperatures in the late dry season at Fongoli, when most trees lose their leaves, are characteristically higher, regularly exceeding 40 degrees Celsius (Pruetz, 2007). This is 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 37.25 C (Morrison, 1962). I, therefore, intend to examine thermal stresses associated with open (i.e. grasslands and open woodlands)

versus closed (i.e. gallery forests) environments at this site by comparing chimpanzee heat signatures in these different habitat types.

Wheeler's (1991b) physiological model suggests that hominin foraging behavior may be temporally limited by high heat stress associated with an open environment. Reducing heat stress by seeking shade may be beneficial during the day's hottest hours, but daily activities, like foraging, can be restricted when doing so. Fongoli chimpanzees are observed to exhibit nighttime behavior, particularly during the hotter dry season (Pruetz, 2018). Their nocturnal foraging and social behavior offers support for Wheeler's (1991b) physiological model, as this signifies a behavioral shift to cope with heat stress. Employing nocturnal behavior to expand foraging niches at the year's peak temperatures have many implications for human evolution. Early use and control of fire has been suggested as an antipredator strategy at night (Burton, 2009). With decreased heat stress at night and scarce data on wild chimpanzee nocturnal behavior, I propose to conduct nighttime observations to record the activity and body temperatures of focal subjects. I intend to compare daytime behavior in open and shaded habitats to nocturnal activity scheduling across seasons (dry vs. wet), as well as compare diurnal vs. nocturnal body temperatures. This study will enhance our knowledge of chimpanzee thermoregulation and our interpretation of early models regarding the evolution of bipedalism in hominins.

Objectives and Hypotheses

The objectives of this study are to:

(1) Examine whether different postural and locomotor behaviors differ in their relative exposure to heat stress

  H_o: Positional behavior will have no effect on chimpanzee body temperature

  H_1: Chimpanzee body temperature will vary with differing postural and locomotor behaviors

(2) Determine if open habitats exert significant thermal stresses on apes at Fongoli

  H_o: Open habitats will have no effect on Fongoli chimpanzee body temperature

  H_1: Open habitats will have an effect on Fongoli chimpanzee body temperature

(3) Observe differences between Fongoli chimpanzee diurnal and nocturnal body temperatures

  H_o: There will be no difference in diurnal vs. nocturnal chimpanzee body temperature

  H_1: There will be a difference in diurnal vs. nocturnal chimpanzee body temperature

(4) Difference in Fongoli chimpanzee diurnal body temperature on days with high nocturnal activity

  H_o: There will be no difference in chimpanzee diurnal body temperature when nocturnal chimpanzee activity is high

  H_1: There will be a difference in chimpanzee diurnal body temperature when nocturnal chimpanzee activity is high

(5) Difference in Fongoli chimpanzee diurnal activity scheduling on days with high nocturnal activity

H_o: There will be no difference in chimpanzee diurnal activity scheduling when nocturnal chimpanzee activity is high

H_1: There will be a difference in chimpanzee diurnal activity scheduling when nocturnal chimpanzee activity is high

(6) Difference in Fongoli chimpanzee nocturnal activity scheduling between the dry and wet seasons

H_o: There will be no difference in chimpanzee nocturnal activity scheduling between the wet and dry season

H_1: There will be a difference in chimpanzee nocturnal activity scheduling between the wet and dry season

Predictions

Chimpanzee positional behaviors within both open and closed microhabitats will be examined, as 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. I therefore hypothesize 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 predicted to be associated with a lower body temperature when compared to quadrupedal positions.

I also hypothesize that open habitats will impose significant thermal stresses on the chimpanzees, predicting a positive correlation between open habitats, such as grasslands, and chimpanzee body temperature. Behavior within an open environment increases chimpanzee exposure to the sun, whereas other area of their home range, such as woodland or gallery forest, offer more protection through patches of shade. Chimpanzees are expected to seek shade more frequently during the hotter times of day, particularly during the dry season.

Studies at Fongoli indicate an increase in chimpanzee nocturnal activity during the hotter dry season (Pruetz, 2018). This study proposes to examine the differences in body temperature during the day and at night throughout the seasons (wet and dry) at Fongoli. There is expected to be a difference in body temperature between daytime and nighttime, with higher thermal stress during the day than at night. One expects a positive correlation between daytime body temperature and nocturnal activity. Additionally, an increase in overall body temperature during the dry season is predicted to correlate with increased nocturnal activity. With high ambient temperatures during the day, particularly during dry season, chimpanzees will be likely driven to increase resting behavior during the day, which may limit other daily activities, such as foraging and social behavior. To offset these costs, I expect chimpanzees will expand their nocturnal activity schedule to more frequently include social and foraging behaviors. Additionally, the cooler wet season is predicted to be associated with a lower overall body temperature and decreased use of nocturnal activity scheduling.

Methods

  Study site

  This study will be 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). 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 90 km^2, 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 factors influencing 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*; n=12) will be the focus of this study per

the Fongoli Savanna Chimpanzee Project's protocol. Focal male subjects will be 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 disappears and cannot be relocated within 20 minutes, a new focal male will be chosen (Lindshield, 2017). Females are not subjects of focal follows, as adult females may be targets to gain infants for the pet trade. Though the risk is slight, it is not trivial (1 case in 15 years; Pruetz & Kante, 2010; Pruetz & Herzog, 2017). While females are fully habituated when in association with adult males, they remain nervous around people when met in small parties or in isolation. The Fongoli community has been studied since 2001, and averages 32 individuals annually (2005-2017). In 2005, once adult males became accustomed to researcher presence, systematic all-day follows of individual males began (Pruetz & Bertolani, 2007). Individuals will be recognized by their unique physical appearances, such as facial scarring or ear notches. Additionally, after two days of data collection, one rest day will be set aside to avoid researcher fatigue, to summarize data, and for charging of camera batteries.

One night a week will be devoted to nighttime follows. Behavioral data collection will be modified following Pruetz (2018) to account for visibility and protocol at night. Nighttime data collection will begin once light conditions require use of a flashlight (Pruetz, 2018). A red-light flashlight will be used to minimize disturbance of focal subjects. Fongoli chimpanzees frequently nest well past sundown (Pruetz, 2018), so light conditions rather than nesting behavior will initiate data collection on nocturnal behavior. I will place myself a conservative distance from the chimpanzees prior to nightfall so they are aware of and not disrupted by my presence.

Preliminary data collection will begin in May 2018, and last through July 2018. This time period will allow all methods to be validated and enhanced. Moreover, intra-observer reliability will be improved, as I will have the opportunity to use the thermo-imaging camera in a field

setting while also collecting behavioral data. August through December 2018 will be devoted to

making any necessary procedural adjustments to finalize all aspects of the methodology, and

preliminary data analyses will be conducted. Data collection will continue at the start of January

2019, lasting through July 2019. This 7-month period includes both the dry and wet seasons at

Fongoli, allowing a full range of data variables to be recorded. Results will be analyzed from

August-December 2019, and writing will continue to May 2020.

Thermo-imaging data

Thermo-imaging data will be collected with a FLIR E75bx IR camera opportunistically.

Grass growth in the late rainy season can hinder viewing, but the open nature of the Fongoli

study site during most of the year allows for excellent visibility. However, some barriers still

exist when taking proper thermo-images. Preliminary use of the camera at Fongoli indicates the

anticipated procedure of 5-minute intervals will be inefficient due to the specificity of the camera

angles. Images will be taken from both directly behind and at a side angle of the focal subject,

provided the surface is clearly visible and obliquely oriented to the observer. Obtaining

appropriate images will therefore require more flexibility than exists using instantaneous

sampling methods due to visibility barriers and observation protocols. Though instantaneous

sampling methods will be ineffective, opportunistic image capture will follow a rough 5-minute

sampling schedule. Methods in taking thermo-images follow the Thompson et al. (2017) study

of mantled howling monkeys (*Alouatta palliata*). They found that the furred dorsum (i.e. the

back) was a better gauge of subcutaneous body temperature than hairless areas (i.e. the face).

Each captured photo will include both a high-resolution image and a thermo-image. As

this study is examining the influence of positional behavior as well as microhabitat on body

temperature, images will be scored based on the variables they encompass. Variables such as body temperature, positional behavior, habitat type, date, time, and distance to focal will be apparent based on the photos obtained. I will record the specifics of these variables in my field notebook immediately following photo capture with the image number indicated (see Appendix A for sample data sheet). For instance, as these are still images, I will note whether the individual was engaging in a postural or locomotor behavior. I will also specify the microhabitat, behavioral context, and sun exposure, among other variables. While much of this information will be apparent in the images, recording the real-time data will corroborate given scores. These recordings will convey the thermal load faced by the chimpanzees by providing their body temperature in different postures, microhabitats, times of day, etc.

Measures and analysis

This study will include recordings of positional behavior, habitat type and nocturnal behavior, assessing how these factors relate to body temperature and thermoregulation. Recorded positional modes will be 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, palmar walk and 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 B 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 versus closed environments, habitat type (grassland, woodland, gallery forest, bamboo woodland) will be recorded. I will also note the activity of the focal individual (i.e. forage/feed, travel, rest, social, vocalize). Other collected data will include: (1) adult male identity, (2) date, (3) time of day, (4) degree of sun to which subject is exposed (0%, 25%, 50%, 100% of body's dorsal surface), (5) substrate (arboreal, terrestrial), (6) moon phase (fuller versus darker phases). Moon phases were found to be a significant variable in nighttime activity, as chimpanzees were more likely to be active when the moon was in a fuller phase (Pruetz, 2018).

With few studies on chimpanzee nocturnal behavior (Zamma, 2014; Pruetz, 2018), I intend to mirror the methods of these studies but with some modifications. Due to visibility at night, chimpanzee vocalizations and activity-related sounds (CVAs; Zamma, 2014; Pruetz, 2018) and some nonvocal behavior will be recorded. These categories include: movement (behavior that does not involve auditory communication, i.e. shifting in, building, modifying or exiting nest, locomotion within or between tree crowns or on the ground, feeding, and soaking in water), social behavior (affiliative or agonistic; this includes sexual behavior), social vocalizations (those indicative of interactions between chimpanzees, such as submissive pant-grunts, pant-barks, and screams), and long-distance vocalizations (common calls, such as pant hoots and "waaa" barks) (Pruetz, 2018). Pruetz (2018) judged movement, social behavior and social vocalizations as activities in which at least one chimpanzee has exited a nest, while long-distance vocalizations did not necessarily suggest that a chimpanzee has left a nest. Observations or noises from other animals, as well as abiotic factors, like rain, high winds or thunder, will be noted, as well, as potential disturbances can influence chimpanzee behavior. While visibility at night is a questionable matter, I will use the thermo-imaging camera to try to detect and confirm the focal

subjects and their general behavioral patterns, as well as record body temperatures. The preliminary data collection period will demonstrate the full range of variables that can be recorded at night.

Abiotic factors, such as wind, humidity, solar radiation and temperature, will be measured throughout the study, as Thompson et al. (2017) found that these variables increased the explanatory value of their predictive models. Therefore, temperature and humidity will be recorded using a Kestrel Drop during focal male subject follows. Wind speed will be recorded using a Kestrel, and rainfall is logged daily at Fongoli camp.

Analyses will be conducted in R and will include models such as Generalized Linear Mixed Models (GLMM) to extract the relative contribution of stated factors on ape heat stress in an open savanna environment.

Project Summary

This study will examine the thermal load faced by West African chimpanzees in relation to positional behavior and microhabitat, as well as at night. There have been few studies on wild chimpanzee behavioral changes associated with thermal environment (Kosheleff1 & Anderson, 2009; Pruetz & Bertolani, 2009; Koops et al., 2012; Pruetz, 2018). This study will expand how we view behavioral thermoregulation through use of a thermo-imaging camera in a hot, dry and open savanna habitat. Body temperature will be recorded as individuals exhibit varying positional behaviors, utilize microhabitats, and in their nighttime activities. Additionally, activity scheduling during the day and at night will be examined for comparison in relation to heat stress. Heat stress is considered a major selective pressure in the evolution of bipedalism in the hominin lineage, as bipedal posture is expected to reduce exposure to UV radiation (Wheeler, 1984). Due

to their close evolutionary relationship and similarities in habitat, savanna chimpanzees make good referential models in examining hypotheses regarding hominin evolution. Therefore, this study will examine a community of chimpanzees occupying a savanna woodland habitat at Fongoli, Senegal. Results will deepen our understanding of chimpanzee behavioral thermoregulation, as well as our interpretations of bipedal evolution in hominins.

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CODE BOOK

Appendix A – Sample data sheet

Individual:	Date:								
Time	Positional behavior	Context	Substrate	Habitat type	Sun	Temp	Temp Range (low)	Temp Range (high)	Notes
5:30	BW	Tv	T	WD	20%	34 C	31.2 C	35 C	
5:36									
5:42									
5:50									
↓									
19:35									

Legend	
BW	Bipedal Walk
Tv	Travel
T	Terrestrial
WD	Woodland
NA	Not Applicable

Appendix B – Behavioral Catalog

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

N.W.

Type of Pattern	Code	Description
Behavioral Context		
Foraging	Fo	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
Traveling	Tv	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
Resting	RE	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
Social	So	Behavior involving more than one individual; includes both affiliative and agonistic behaviors, such as grooming, play, displays, or sexual behavior
Vocalization	Vo	Communicative noises made by individuals, such as pant-hoots, pant-grunts, pant-barks, screams, "waaa"-barks, etc.
Type of Pattern	Code	Description
Postural Behavior		
Sit	St	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.
Squat	Sq	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
Lie	Ly	reclining on a relatively horizontal weight-bearing structure; body weight borne by back, stomach or side

Vertical Cling	VCi	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
Stand	QS	Three or four-limbed standing on horizontal or subhorizontal supports; elbow and knee are (relatively) extended and trunk is near horizontal
Bipedal Stand	BS	Standing on the hindlimbs with no significant support from any other body part; hips and knees may be flexed or extended
Supported Bipedal Stand	SB	Standing on the hindlimbs while hands grasp foliage to maintain balance
Forelimb suspend	FS	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
Forelimb-hindlimb suspend	FH	Suspension by a forelimb and a hindlimb with limbs typically extended
Quadrumanous-suspend	QM	Suspension with all four limbs contributing relatively equal support
Other suspensory	SO	Miscellaneous suspensory modes such as quadrupedal suspensory bodily progression below and along or across supports with regular or irregular gaits
Type of Pattern	Code	Description
Locomotor Behavior		
Quadrupedal Walk	QW	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
Bipedal Walk	BW	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)
Assisted Bipedal Walk	ABW	The hindlimbs provide support and propulsion while hands grasp foliage to maintain balance

Quadrupedal Run	QR	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
Brachiation	Br	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
Clamber	Cb	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
Vertical Climb	VC	Ascending and descending locomotion on a weight bearing structure angled >45°
Leap/Drop	Lp	Propulsion involving an extended period of free flight with more horizontal than vertical displacement (leap); "dropping" involves slight propulsion downward with little force onto a lower stratum with mainly vertical bodily displacement