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Savanna chimpanzees (*Pan troglodytes verus*) as a referential model for the evolution of habitual bipedalism in hominids

by

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

Major: Anthropology

Program of Study Committee:
Jill Pruetz, Major Professor
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Abstract

Observations of the bipedal behavior of wild savanna chimpanzees (*Pan troglodytes verus*) can provide insight into the evolution of habitual bipedalism in early hominids. This study provides data on the bipedal behavior of eight adult male chimpanzees at the Fongoli field site in southeastern Senegal. Data were collected during transition months at the end of the dry season and beginning of the wet season. Focal instantaneous data on positional and locomotor behavior indicate that bipedalism in Fongoli chimpanzees is a rare, infrequent behavior, accounting for only 2.3% of all positional and locomotor behaviors. Focal all-occurrences data provides a more detailed look at ecological and behavioral variables favoring bipedal behavior here. Fongoli chimpanzees exhibited bipedal postures and locomotion in both arboreal and terrestrial contexts. Bipedal postures were most frequent during feeding and foraging in either context. All bipedal feeding and foraging postures involved forelimb assistance. Bipedal locomotion occurred most often terrestrially during agonistic bipedal threat displays, which often included using hands to throw rocks, and drag or wave branches and loose leaves. In particular, the results of this study indicate that Fongoli chimpanzees are significantly more bipedal than chimpanzees at other sites, exhibiting a rate of 1.05 bipedal bouts per observation hour. These findings suggest that both postural and locomotor bipedalism should be considered in scenarios seeking to reconstruct the evolution of bipedalism in a variety of arboreal and terrestrial contexts. In addition, the mosaic savanna-woodland habitat shared by Fongoli chimpanzees and recent reconstructions of the paleoenvironment of early hominids may have been an important variable in favoring the evolution and origin of habitual bipedal behavior.

Chapter 1. Introduction

1.1 Background and Significance

Many animals, from birds to lizards to cockroaches, adopt bipedal postures and/or move bipedally in certain contexts (Alexander 2004). Likewise, it is not surprising that nonhuman primates will adopt bipedal postural and locomotor behaviors under some conditions. The bipedal behavior of nonhuman primates is typically considered facultative, not habitual, meaning they lack specific morphological specializations related to extended bouts of habitual bipedalism. At the same time, they exhibit behavioral flexibility in adopting this postural and locomotor mode in certain contexts. Despite this difference, nonhuman primates can provide insight into the context in which erect, habitual bipedalism evolved (Rose 1991).

The origins of hominid¹ bipedalism remain one of the great questions of paleoanthropology, and this question is thought to be central to understanding hominid evolution (Stanford 2006). This debate has been organized around two main issues: what traits characterized the last common ancestor of the genera *Homo* and *Pan* and what selective pressures favored a transition to habitual bipedalism in the earliest hominids (Stanford 2006). The hypotheses that have been proposed to explain the origin of bipedalism are extensive and varying. However, there is still little agreement regarding the selective forces that shaped its evolution in the hominid lineage. Bipedalism has been characterized as an adaptation for everything from predator defense (Walter 2004) to thermoregulation (Wheeler 1984; Falk

¹ Hominid is defined here as a “habitually bipedal ape.” See Chapter 1.3 for discussion of this definition.

1990). It is likely that many hypotheses are not mutually exclusive, and that in fact, several selective forces were at work in shaping the evolution of bipedalism. However, which hypotheses are most valid in explaining the evolution from a nonbipedal prehominid ancestor to habitually bipedal hominids is an area of contention in paleoanthropology. Despite the continually changing interpretation of fossil evidence in regards to early hominids, studies of nonhuman primates and, in particular, our closest living relatives, the chimpanzees of the genus *Pan*, offer an excellent opportunity to shed light on the context and selective pressures under which habitual bipedalism evolved.

Although some work has been undertaken studying savanna chimpanzees (Suzuki 1969; McGrew et al. 1981; Kortlandt 1983; Hunt 1994, 1996), study of habituated individuals at long-term study sites (Pruetz et al. (2002) in southeastern Senegal) allow comparisons to forest dwelling chimpanzees for a better, more comprehensive model for human evolution (Moore 1996). In addition, because referential models are typically based on either analogy or homology but rarely both, savanna chimpanzees potentially provide a “best of both worlds” approach to understanding the context in which human bipedalism evolved (Moore 1996). Chimpanzees in Senegal live in savanna-woodland mosaic habitats that are ecologically similar to the paleoenvironments that have been reconstructed for early hominids (Pruetz 2006; Pruetz & Bertolani 2007; Reed 1997; Kappelman et al. 1997; Pruetz & Bertaloni, in press). These conditions enable the study of possible selective pressures leading to the evolution of habitual bipedalism in both arboreal and terrestrial contexts and a more comprehensive approach to understanding the evolution of habitual bipedalism in our own lineage. Observations of savanna chimpanzees can help us to understand the

morphological, social, and behavioral differences imposed on apes by both habitats (Moore 1996).

1.2 Objectives and Hypotheses

Here, I propose a holistic approach to studying variables relevant to the context in which habitual bipedalism evolved in early hominids, using savanna chimpanzees as a referential model. The objective of this study is to elucidate the context in which savanna chimpanzees adopt bipedal postures and locomotion. In addition to describing the bipedal behavior of savanna chimpanzees, this study is aimed at two main objectives:

1. To determine the degree to which ecological and behavioral context predicts the frequency, duration, and rate of postural and locomotor bipedal behavior in savanna chimpanzees.
2. To examine the bipedal behavior of savanna chimpanzees at Fongoli in relation to other studies of the bipedal behavior of chimpanzees at other sites, particularly Stanford (2006) and Hunt (1994, 1996).

Because of the similarities between the environment of extant savanna chimpanzees in Senegal and the paleoenvironment of early hominids (Pruetz 2006, Pruetz & Bertolani 2007; Pruetz & Bertolani, in press; Reed 1997; Kappelman et al. 1997) as well as the close evolutionary relationship between chimpanzees and *Homo* (Chen & Li 2001), similarities are also expected in the way that chimpanzees and early hominids may have responded to environment pressures in terms of their bipedal behavior. Using this information, I will evaluate the plausibility of existing hypotheses in terms of the behavioral and ecological contexts that may have promoted the adoption of habitual bipedal behavior in early hominids.

1.3 Habitual Bipedalism in Hominids

Defining the term “hominid” is essential to any inquiry into the origins of habitual bipedalism. Currently, the taxonomic definitions of the Hominidae in the literature contrast with the colloquial usage of the term “hominid,” which is often used to describe bipedal apes. However, there is a vast array of inferred definitions for “hominid.” In particular, there is disagreement in the literature in terms of whether hominids are expected to have been habitually or only facultatively bipedal. Habitual bipedalism is associated with specific morphological specializations that relate directly to the compulsory use of bipedalism as the main mode of postural and locomotor behavior. For example, Prost (1980) reconstructed the earliest hominids as facultative bipeds, with bipedal behaviors adopted occasionally without morphological specialization rendering bipedalism compulsory. Others (Tuttle 1981; Stern & Susman 1983) have reconstructed these hominids as bipeds with substantial arboreal adaptations. Finally, some (Johanson & Edey 1981; Lovejoy 1981, 1988) have defined the earliest hominids as terrestrial habitual bipeds. Although reconstructions of hominids as facultative bipeds have received the least support in the literature, only a minority of scholars supports a reconstruction of the earliest hominids as habitual bipeds (Hunt 1994). The greatest difficulty seems to exist in the apparent lack of consensus as to what defines a hominid. Implicit in many of these examples is a definition of “hominid” as a species within our own lineage, or as an eventual out-group of *Homo sapiens* (i.e. the robust australopithecines), post-split from the genus *Pan*.

As the fossil record grows, it becomes even more difficult to loosely define “hominid.” Recently, it has been suggested that during the Plio-Pleistocene there was an adaptive radiation of “hominids” in the fossil record (Foley 2001). In addition, Wolpoff

(1999) suggests that rather than one morphological form of habitual bipedalism, a diversity of biomechanical forms may have characterized the earliest hominids, within and outside of our own lineage, according to particular ecological contexts. In this case, the defining feature of a “hominid” is habitual bipedalism, rather than taxonomy or the other factors mentioned above. In light of this new interpretation, I adopt this definition for “hominid.” In doing so, I will maintain habitual bipedalism as the key defining characteristic of hominids. For this reason, I will not focus strictly on the hominid lineage that led to the genus *Homo*, but on the selective pressures involved in the evolution of habitual bipedalism in the earliest hominids in general.

1.4 Our Last Common Ancestor

Reconstructions of the last common ancestor of *Pan* and *Homo*, which are thought to have split from each other an estimated 5-6 million years ago (Chen & Li 2001), have often been central to the debate in the literature regarding the evolution of habitual bipedalism in hominids (Stanford 2006). In defining this last common ancestor, scholars seek to define the suite of traits it displayed (See Table 1.1 for summary). Keith (1923) was one of the first to attempt to reconstruct the evolution of habitual bipedalism and characterize the last common ancestor. He argued that human evolution was characterized by four phases of posture and locomotion (Keith 1923). The first stage was a pronograde catarrhine monkey-like ancestor, followed by the second, or “hylobatian” stage, which he defined as a small, brachiating gibbon-like ancestor (Keith 1923). The third stage posited a larger, great ape-like ancestor who displayed not only suspensory behavior but also terrestrial knuckle-walking, and finally, the culminating hominid stage, terrestrial bipedalism (Keith 1923). The ability to brachiate was at the center of Keith’s (1923) theory as he felt it explained many of the similarities in

human and ape upper limb and torso morphology. Gebo (1996) argues that Keith's (1923) four stages of human evolution have largely been discredited, although the idea that the last common ancestor may have had some suspensory ability has not been completely abandoned in more recent reconstructions.

Table 1.1 Summary of reconstructions of last common ancestor of *Pan* and *Homo*.

Reconstruction	Supporters	General Description of Traits
Hylobatian Ancestor	Keith 1923; Morton 1926; Tuttle 1974	Small bodied climber and arboreal biped with long, extensible fore- and hindlimbs similar to extant gibbons
Arboreal Quadruped	Prueschoft 2004	Small to medium sized above-branch pronograde quadruped
Vertical Climber	Stern 1971, 1975; Prost 1980; Fleagle et al. 1981	Vertical climber characterized by mix of traits related to brachiation and bipedalism, adapted to climbing as well as fore- and hindlimb suspensory related locomotion and posture
Terrestrial Quadrupedal Knucklewalker	Washburn 1968; Richmond et al. 2000, 2001	Considered a more parsimonious explanation given the close evolutionary relationship between the African apes, chimpanzees, bonobos, and gorillas, and the only extant habitual biped, humans. Evidenced by similarities in pedal, carpal, limbs, and trunk features in living apes, humans, fossil hominids

Several reconstructions of the last common ancestor involve a primarily arboreal context: an arboreal quadruped ancestor, a hylobatian ancestor, and a vertical-climbing ancestor. The first, the arboreal quadruped reconstruction, involves an adaptation to above-branch, pronograde quadrupedalism, similar to that observed in extant anthropoids (Richmond et al. 2001). According to this reconstruction, the earliest bipeds would have retained some of the characteristics necessary for an emphasis on above-branch

quadrupedalism including: a small to medium body size, short limbs relative to body size, intermediate finger and toe lengths as well as long first digits, a narrow rib cage, anteriorly facing scapula, and morphological characteristics indicating stability in the wrist and shoulder (rather than mobility or flexibility) (Richmond et al. 2001). Prueschoft (2004) argues that many of the characteristic traits of all hominoids are functionally related to arboreal quadrupedalism, and that divergences in morphology between great apes and humans lie more in morphological traits related to human habitual bipedalism.

The hylobatian ancestor reconstruction (Morton 1926; Tuttle 1974) has been more readily supported in the literature. Tuttle (1974) argued that the last common ancestor was a small-bodied climber and arboreal biped with long, extensible forelimbs and hindlimbs similar to those of the hylobatids. He emphasizes arboreal bipedal posture and locomotion as a precursor to terrestrial bipedalism (Tuttle 1974). One of the strengths of the hylobatian reconstruction is that there is a straightforward mechanism for the transition from arboreal bipedal postures and locomotion to terrestrial habitual bipedality (Hunt 1996; Richmond et al. 2001). However, Richmond et al. (2001) argue that this model is not distinct from the vertical climbing model and is weakened by the expectation of small body size in the ancestor of early hominids, which unlikely considering the body sizes of the earliest hominids.

Stern (1971, 1975) reconstructed the last common ancestor as a vertical-climber on the basis of the similarities between human and ateline (in particular *Alouatta*) hip and thigh musculature. He posited that these similarities related to “antipronograde” behavior, including climbing, as well as fore- and hindlimb suspensory-related locomotion and posture.

Based on field observations of chimpanzees, Probst (1980) argued that human bipedalism was more similar to chimpanzee vertical climbing than chimpanzee facultative bipedal postures or locomotion and that the development of traits relating to vertical climbing were more likely to be attributes of the last common ancestor (Probst 1980). In particular, Probst (1980) argued that this model accounted for the mix of morphological traits often related to brachiation and bipedalism found in the Australopithecines by classifying them as adaptations to arboreal vertical climbing. Likewise, Fleagle et al. (1981) also concluded that the forelimb muscles of atelines and apes were more important during climbing and hoisting as opposed to brachiation, supporting this reconstruction. Gebo (1996) criticized this reconstruction, arguing very few living primates, including the African apes, emphasize vertical climbing as a main locomotory mode or display traits specifically adapted for it.

The last common ancestor of the genera *Pan* and *Homo* has been reconstructed generally as a terrestrial quadruped based on evidence of terrestrial weight support in the skeletal evidence of fossil hominids, extant African apes, and modern humans (Gebo 1996). The terrestrial knuckle-walker reconstruction (Washburn 1968; Richmond et al. 2000, 2001) has received much attention and support in the literature (Richmond et al. 2001). Although Sarmiento (1994) and Gebo (1996) argue that there is no evidence that one mode of terrestrial quadrupedalism should be favored over another in reconstructions of the last common ancestor, Gebo (1996) considers knuckle-walking a more parsimonious explanation as it is seen in both the genera *Pan* and *Gorilla*, close living relatives of humans. Richmond et al. (2001) argue that pedal features, as well as limb and upper trunk features of extant anthropoids and fossil hominids are consistent with a terrestrial ancestor and also suggest

knuckle-walking. In addition, they posit that much of the evidence used to support the vertical climbing hypothesis is fully consistent and better explained with an African ape-like ancestor that knuckle-walked terrestrially and climbed trees (Richmond et al. 2001).

1.5 Hypotheses for the Evolution of Habitual Bipedalism

Like reconstructions of the last common ancestor of the genera *Pan* and *Homo*, hypotheses relating to the selective pressures shaping the evolution of habitual bipedalism in hominids are numerous and contentious. While it might be argued that environmental (or habitat and niche) change in equatorial Africa is one of the major ultimate causes of the evolution of bipedalism, little resolve has been made in outlining the actual proximate causes (See Table 1.5 for summary) for the evolution of this unique postural and locomotor adaptation (Jablonski & Chaplin 1993). Here, I focus on those hypotheses that most closely relate to the behavioral and ecological contexts that may have favored the evolution of habitual bipedalism.

Perhaps one of the most simplistic but important proximate causes of the evolution of bipedalism was a pre-adaptation to bipedal posture in the apes (Jablonski & Chaplin 1993; Sigmon 1971). Habitual bipedalism does not occur in any nonhuman primates except in some rare cases (Napier & Napier 1976; Bauer 1977; Ogihara et al. 2005). For example, Bauer (1977) observed an adult male chimpanzee adapt habitual bipedalism as his predominant postural and locomotor mode after paralysis of the arms. Despite these rare cases in which extreme conditions such as disease or injury demand adoption of habitually bipedal behavior, the “compromise” morphology of nonhuman primates makes them generally ill-adapted for long bouts of bipedalism, or habitual bipedalism. Still, many nonhuman primates are

facultative bipeds under some conditions (Rose 1991). Therefore, Rose (1991) argued that the unique, habitual bipedalism of hominids, including our species has its origins from the more typical compromise morphology of higher primates. The pre-hominid pattern suggested by these origins would have included occasional bouts of bipedal behavior despite a flexible morphology more adapted toward the performance of other activities but allowing some behavioral plasticity in postural and locomotor mode (Rose 1991). Similarly, Sigmon (1971) argues that bipedal behavior similar to that common in most of the higher primates, in particular the great apes, could have easily been present in pre-hominids. As the environment changed and favored bipedalism, it became an increasingly more valuable advantage shaped by natural selection (Sigmon 1971).

Many researchers have suggested that maximizing locomotor efficiency was an important selective force in the evolution of habitual bipedalism (Rodman and McHenry 1980; Pilbeam 1986; Foley 1992; McHenry 1991). This explanation suggests that bipedalism is less energetically costly than quadrupedalism (Sayers & Lovejoy 2008). Despite the continuing popularity of this argument, Taylor and Rowntree (1973) argued that neither quadrupedalism or bipedalism relates to locomotor “efficiency” in the way the hypothesis’ supporters have suggested, i.e. relating locomotor efficiency to the rate of energy consumed in travel per unit time or distance. Many authors suggest that, in fact, human bipedalism may be relatively inefficient compared to quadrupedalism like that in chimpanzees (Rose 1991; Jablonski & Chaplin 1993; Carrier 1984). Some studies (Carrier 1984; Rodman & McHenry 1980) suggest that humans are inefficient runners as compared to quadrupedal animals. In general, habitual bipedalism as it is manifested in the human form is at least as

efficient as the quadrupedalism, or other forms of locomotion in other animals. This is not surprising, considering that 75 to 90% of total locomotor cost is wrapped up in balancing the body's center of mass above the ground, regardless of locomotor mode (Kram & Taylor 1990).

Feeding and foraging hypotheses have often been considered as potential explanations for the evolution of bipedalism. Leutenegger (1987) argues that feeding hypotheses are the best-supported explanations, as this activity takes up a larger portion of daily time budget of the typical primate than any other behavior. Stanford (2006) argues that bipedal posture originated as an adaptation for foraging in an arboreal context, similarly to Tuttle (1975) who points to bipedalism as an adaptation to life in the trees as a large-branch locomotor mode as well as an arboreal feeding posture. Rather than focus on an arboreal context, Jolly (1970), Rose (1976), and Wrangham (1980) proposed that bipedal posture was initially favored on the ground as a terrestrial feeding posture. Rose (1976) added that as bipedalism was favored, it might have been incorporated and preferred in many other situations, thus emphasizing that different selective pressures would have been involved in the evolution of human bipedalism (Rose 1976). Together, Jolly (1970), Wrangham (1980), and Rose (1976) argue that natural selection would have favored both postural and locomotor bipedalism, with the former utilized within food patches for gathering food and the latter as the most efficient means of travel between food patches.

Based on field observations of chimpanzees, Hunt (1994, 1996) suggested the "small tree feeding" hypothesis, which links the evolution of bipedal behavior and arboreal arm-hanging in hominids with feeding adaptations for small fruit gathering in both arboreal and

terrestrial contexts. According to this hypothesis, postural bipedalism would have been favored over locomotor bipedalism in terrestrial contexts as a preadaptation to “fully realized” locomotor bipedalism in *Homo erectus* (Hunt 1994; 1996). Hunt (1994, 1996) maintains that this interpretation is consistent with the fossil anatomy of *Australopithecus afarensis*, which he argues would have exhibited chimpanzee-like “bent-knee, bent-hip” locomotor bipedalism. Although Stern and Susman (1983) support this interpretation, re-evaluation of the bipedal locomotor mode of *A. afarensis* compared to chimpanzees by Crompton et al. (1998) using computer simulation showed that chimpanzee-like bipedalism was not compatible with the morphology and proportions of *A. afarensis*. Instead, the limb proportions of *A. afarensis* were more compatible with either human erect bipedal posture or that of humans simulating a “bent-hip, bent-knee” gait making it possible that *A. afarensis* had walked in an erect, human-like bipedal manner (Compton et al. 1998). Kramer & Eck (2000) also supported the conclusion that *A. afarensis* could have been an efficient, erect biped despite not having modern limb proportions.

Efficiency in load carrying has also been put forward as an important selective pressure shaping the evolution of bipedalism. Gebo (1996) and Videan and McGrew (2002) argued that bipedalism freed hominid hands from the “burden of support,” making carrying a key ecological adaptation to more openly dispersed resources and to carry and efficiently transport items, from food to tools to babies. Washburn (1968) suggested that carrying tools of “defense,” or weapons would have been an essential consequence of moving from the safety of an arboreal context, to the ground, when hominids could no longer escape danger by climbing a tree. Bartholomew and Birdsell (1953) also placed importance on habitual

bipedality allowing locomotion to be unimpeded during the transport or use of a tool. However, tool use as a key component to habitual bipedalism is contentious (Hewes 1961). Hewes (1961) argued first that the difficulty of transporting tools is overemphasized and that while freeing hands for tool use may be central to human evolution as a selection pressure, it would not be strong enough to elicit the evolution of habitual bipedalism. He focused particularly on food carrying and transport as an essential component of the evolution of bipedality arguing that this is the only locomotor mode that could achieve “maximal transportational efficiency” in the transport of food resources over significant distances (Hewes 1961).

Another hypothesis often offered as an explanation for the evolution of bipedalism involves the use of bipedal postural behavior in display and defense contexts. Jablonski and Chaplin (1993) argued that the bipedal-threat display shared by African great apes and humans is particularly important in reconstructing the origins of habitual bipedalism. These bipedal-threat displays can be long in duration and persistent, and the bipedal stance makes the individual appear larger and frees the hands to display with objects (Jablonski & Chaplin 1993; Fifer 1987). Likewise, Fifer (1987) proposed that the origins of habitual bipedal posture and locomotion arose from the development of defense via stone throwing. Based on this, Jablonski & Chaplin (1993) suggest that as habitats became more open and resources more patchy and widely dispersed in the late Miocene, intraspecific competition between protohominids over these resources would have greatly increased causing bipedal displays and appeasement to become essential for success in these harsher environments.

Recently, Walter (2004) has hypothesized that bipedalism originated as an adaptation for predator defense and was a preadaptation for bipedal locomotion. He argues that bipedal posture was an adaptation for defense against predators, specifically as an inhibitor of ambush predation, in more open habitats, and particularly, savannas (Walter 2004). Bipedal posture would have deterred predators from attacking by not only alerting the predator that its intended prey was vigilant and aware of its presence, but also by giving the potential hominid prey the appearance of “standing up to” or “standing firm” against the potential predator (Walter 2004). This could signal to the coursing predator that its chances of making the catch decreased significantly enough that it should abandon its prey item in search for another easier, unaware catch. Walter (2004) argues that this interpretation is supported by the literature on chimpanzee defense in more open habitats with many predators. Although he does not test this hypothesis himself using chimpanzees as a referential model, several aspects (particularly vigilance) lends themselves to testing through both field observations and experimental trials.

Table 1.2 Summary of the main hypotheses relating to the evolution of habitual bipedalism.

Hypothesis	Supporters	General Summary
Preadaptation to Upright Posture	Jablonski & Chaplin 1993; Sigmon 1971; Rose 1991	Suggests that habitual bipedalism originated in the compromise morphology that is seen in extant higher primates. Compromise morphology would have allowed facultative bipedal behavior to be increasingly favored by natural selection.
Feeding/Foraging Hypothesis	Leuttenegger 1987; Rose 1976; Tuttle 1975; Jolly 1970; Wrangham 1980; Hunt 1994, 1996; Standford 2006	Suggests that habitual bipedalism was favored first as an feeding and foraging adaptation. Hypotheses vary in terms of where this feeding was most likely to occur first, i.e. in arboreal or terrestrial contexts.

Table 1.2 (*continued...*) Summary of the main hypotheses relating to the evolution of habitual bipedalism.

Hypothesis	Supporters	General Summary
Load Carrying Hypothesis	Bartholomew & Birdsell 1953; Washburn 1968; Hewes 1961; Gebo 1996; Videan & McGrew 2002	Suggests that habitual bipedalism evolved to facilitate the freeing of hands for carrying and transporting items (food, tools, infants, etc.) as an ecological adaptation to more openly dispersed resources during Miocene.
Display Hypothesis	Jablonski & Chaplin 1993	Suggests that habitual bipedalism was favored as a primary adaptation for bipedal threat displays used in increased intraspecific competition over patchy resources in harsher environments during Miocene.
Defense Hypothesis	Jablonski & Chaplin 1993; Walter 2004	Suggests that habitual bipedalism originated as an adaptation for ambush predator defense in open, exposed savanna habitats.
Locomotor Efficiency Hypothesis	Rodman & McHenry 1980; Pilbeam 1986; Foley 1992; McHenry 1991	Suggests that habitual bipedalism evolved in order to maximize locomotor efficiency. This hypothesis assumes that habitual bipedalism in the human form is more efficient than the quadrupedalism of other animals, such as chimpanzees. Despite its popularity, this hypothesis has been largely questioned.

1.6 Early Hominid Paleoenvironments

Reconstructing the paleoenvironment inhabited by early hominids is essential to gaining insight regarding many aspects of hominid evolution (Kappelman et al. 1997; Reed 1997). These reconstructions can also inform comparisons with extant apes in efforts to produce useful referential models, such as the savanna chimpanzee model focused on here (Pruetz & Bertolani 2007 and see Chapter 2). In particular, these reconstructions provide important information on the selective pressures that led to the evolution of adaptations to habitual bipedal behavior in early hominids. These selection pressures may also exist for

extant chimpanzees living in similar habitats (Pruetz & Bertolani 2007). Therefore, the evaluation of the hypotheses put forth to explain the evolution of habitual bipedalism in early hominids is made possible by comparisons with closely-related savanna chimpanzees who live in environments analogous to the hominid paleoenvironments in which habitual bipedalism would have been first favored.

The first reconstructions of the paleoenvironments of early hominids were typified by an emphasis on open savannas (Reed 1997). More recent research has suggested a mosaic habitat interspersed with wooded, closed and more open habitats (Kappelman et al. 1997; Reed 1997). Kappelman et al. (1997) base these descriptions on a detailed breakdown of habitat subtypes, including forest, heavy cover (defined as bush, woodland, swamp, close to water), light cover (light bush, tall grass and hilly areas), and plains (edge or ecotone, open country, arid country) (Described in relation to Fongoli habitat subtypes in Table 1.3). These habitat subtypes are reflective of decreasing vegetative cover and terrestrial obstacles, from closed (heavy cover) to open (light cover or open country) conditions (Kappelman et al. 1997). In addition to this, they use a gradient to describe canopy cover, from open to closed conditions (Kappelman et al. 1997). Using fossil fauna, in particular bovid indicators, known to inhabit particular types of habitats, as well as an understanding of the selective pressure of habitat structure on body mass with regard to predation and diet, Kappelman et al. (1997) reconstruct early hominid East African paleoenvironments at Koobi Fora, Kenya and Olduvai Gorge, Tanzania. Their reconstruction includes a habitat range of open (light cover and open country) to more closed (heavy cover) conditions, with little evidence for forest-type conditions (Kappelman et al. 1997).

Reed (1997) compiles data on modern African habitats based on a detailed gradient of closed, vegetative habitat types (forest, closed woodland, woodland-bushland transition, and medium density woodland) to more open habitats (bushland, open woodlands, scrublands, grasslands, plains, and deserts). These modern habitat types also represent a gradient of seasonality, from well-watered habitats to seasonal or arid habitats, which show decreasing vegetation density and rainfall similar to Kappelman's et al. (1997) habitat gradient. His focus is on eight habitat types: forest, open woodland, closed woodland, scrubland, bushland/woodland, grassland, bushland, and desert (Reed 1997; Described in relation to Fongoli habitat subtypes in Table 1.3). He combines this information with a similar approach to Kappelman et al. (1997) using fossil macromammal indicators to reconstruct a range of East African hominid site paleoenvironments (Reed 1997). This allows him to correlate the number of hominid finds at particular sites with possible "preferred habitats" of early hominids such as the australopithecines (Reed 1997). For example, Reed (1997) suggests that paleohabitats at a particular East African site, Tulu Bor, which has produced few hominid species, is characterized by more open habitats (i.e. scrubland and flood plain) than other east African sites where hominid finds are more abundant. This suggests that the paleoenvironment at this site was "too open" and therefore, not preferred by early hominid species such as *Australopithecus afarensis*. Reed (1997) suggests that later *Homo* species, such as *Homo erectus*, were the first hominids to inhabit these more open habitats such as grassland habitats. While these open country grassland habitats of later *Homo* may be analogous to savanna habitats that lack trees, savannas can range from very open conditions, such as grasslands where trees are absent, to grassland habitats that contain trees but lack continuous canopies. This range of savanna habitats as well as woodland habitats

characterized by “light cover” is likely to have made up the paleoenvironment of early hominids (Kappelman et al. 1997) and is also analogous to the chimpanzees’ range at Fongoli (Pruetz et al. 2008).

Table 1.3 Habitat subtypes at Fongoli in relation to Reed (1997) and Kappelman et al. (1997) descriptions of hominid paleoenvironments.

Habitat Subtypes at Fongoli (Pruetz & Bertolani, in press)	Occurrence at Fongoli (Pruetz & Bertolani, in press)	Habitat Classification (Reed 1997)	Vegetation Gradient* (Kappelman et al. 1997)
Gallery Forests	<3%	Forest	Closed canopy, “heavy cover” habitats
Ecotone Forests	<3%	Forest	
Bamboo Woodland	12%	Open Woodland	Intermediate-Open canopy, “Light Cover” habitats
Woodland	46%	Open Woodland; Woodland/Bushland**	
Grassland With/Scattered Trees	36%	Grassland	

*This vegetation gradient relates to a decreasing degree of vegetative cover as well as terrestrial obstacles from “closed” to “open” conditions (Kappelman et al. 1997).

**Reed (1997) describes woodland/bushland similarly to an open woodland in terms of tree density, but includes a bush/scrub rather than grass understory. This is analogous to a “thicket” habitat subtype at Fongoli, which is subsumed under the woodland habitat category (Pruetz, pers. comm.)

Habitat structure at Fongoli suggests a similar gradient of vegetative cover across habitats utilized by chimpanzees as that described by Kappelman et al. (1997) and Reed (1997). Pruetz et al. (2008) found that closed habitats at Fongoli were typically characterized by larger trees averaging almost double the height (12.5m) of trees found in more open habitats such as woodland (7.6m) (Pruetz et al. 2008), which may relate to differing degrees of canopy cover from more closed to more open habitats. Fongoli is described as a woodland-savanna mosaic, including primarily open-canopy habitats potentially similar to what Kappelman et al. (2007) described as “light cover” to open habitats, such as woodland, bamboo woodland, grassland with scattered trees, and grassland without trees (Pruetz et al. 2008; Table 1.3). In addition, some closed canopy habitats exist, with small patches of gallery and ecotone forest (Pruetz 2006, Pruetz et al. 2008; Table 1.3). Importantly, Reed (1997) suggests that the australopithecines may have “preferred” or been more abundant in habitats with available water. Gallery forest habitats, closed habitats characterized by continuous canopy around water sources, are rare at Fongoli but are considered an important habitat to chimpanzees (Pruetz & Bertolani, in press).

It is likely that early hominids were living in increasingly open environments throughout the Plio-Pleistocene (Kappelman et al. 1997; Reed 1997). Rather than being strictly open savanna habitats (i.e. grasslands), these paleoenvironments would have been typified by patches of more wooded, closed habitats as well as more open country savanna-like conditions (Kappelman et al. 1997). Based on estimated day and home ranges calculated in terms of the body size of early hominids, it is probable that hominids utilized all of these habitats as part of their day or home ranges (Kappelman et al. 1997). This is similar to the

types of habitats utilized by Fongoli savanna chimpanzees, which inhabit a mosaic savanna-woodland habitat (Pruetz & Bertolani 2007). Based on these similarities, savanna chimpanzees at Fongoli offer the unique opportunity to gain insight into the selective pressures at work on early hominid behavior and adaptation.

Chapter 2. Nonhuman Primates as Referential Models Hominid Bipedalism

2.1 Introduction

Nonhuman primates adopt bipedal behaviors in a variety of contexts. However, some important differences exist between bipedalism in nonhuman primates and the habitual bipedalism of humans, making them, in some ways, kinematically and morphologically distinct from each other (Alexander 2004). Rose (1991) relates these distinctions to the “lack of commitment” to bipedalism in the morphology of nonhuman primates. He argues that while the “compromise morphology” of nonhuman primates allows facultative bipedalism, it is poorly and inefficiently adapted for prolonged bouts of bipedalism (Rose 1991). Because of these differences, Alexander (2004) argues that meaningful comparisons of kinematic measurements, such as stride length, are increasingly difficult. Despite the differences in morphology and therefore “type” of bipedalism, nonhuman primates provide excellent insight as to the context in which erect, habitual bipedalism evolved (Rose 1991). In this way, research utilizing nonhuman primates as a referential model for understanding early hominid behavior may provide key insight for the evaluation of existing hypotheses relating to the evolution of habitual bipedalism in early hominids.

2.2 Nonhuman Primates as Referential Models

Reconstruction of the behavior of early hominids has been a central problem for biological anthropologists. This is due to the fact that behavior in large part does not “fossilize” and can be difficult to interpret in the fossil record, as well as the many, often conflicting and mutually exclusive, scenarios that have been posited regarding diverse

aspects of human evolution (Stanford 1991). Using nonhuman primates as referential models for these various questions regarding human evolution has been one solution to this problem.

Referential models employ the behavior, ecology, and social systems of a nonhuman primate species in order to frame and reconstruct the behavior of early hominids (Stanford 1991). In these models, a particular nonhuman primate species is chosen discreetly based on either homology (“similarity due to common descent”) or analogy (“similarity due to common adaptation”) to the referent (Moore 1996). Often, comparisons are made between different species of the nonhuman primate model in order to inform interpretations. This type of model can be particularly useful in examining paleoanthropological questions by showing what is possible as far as what scenarios or hypotheses may actually have been feasible when describing or understanding different aspects of evolution. These models function as part of a narrow focus comparative approach to a particular paleoanthropological question, suggesting new ideas or directions for interpretation, and generating useful, detailed hypotheses or scenarios that can then be tested and evaluated (Moore 1996).

Even in the absence of appropriate paleontological and archaeological data, hypothesized “scenarios” can be tested via experimental or observational data in order to evaluate the plausibility of different hypotheses (Videan & McGrew 2001). This is particularly important in examining the origins and evolution of bipedalism, as there is little paleontological evidence of a potential last common ancestor of chimpanzees and humans as well as much contention over which of the many, various hypotheses regarding the selective pressures shaping the evolution of bipedalism were most valuable or important in it’s development. While there are some dangers inherent in referential modeling, if care is taken

to avoid oversimplified analogies or the masking of important variation, referential modeling can test potential descriptive scenarios relating to human evolution or early hominid behavior specifically, through experimentation or observation of nonhuman primates (Moore 1996).

Despite the benefits of using nonhuman primates as referential models for gaining insights to questions regarding human evolution, the merits of particular referential models versus others have been rigorously debated. What nonhuman primate should be used to model particular aspects of human evolution is often a point of contention. Many different species of primate have been used as referential models for exploring the origins and evolution of human habitual bipedalism, from baboons (Rose 1976; Rose 1984; Wrangham 1980) to more recently, orangutans (Thorpe et al. 2007). Chimpanzees and bonobos have also often been used as referential models; however, the validity of both models has been questioned and debated in the past (Zihlman 1996).

2.3 Old World and New World Monkey Models

Westergaard et al. (1998) suggested tufted capuchins (*Cebus apella*) as a potential model for the origins and evolution of human bipedalism. Similar to Hunt (1994, 1996) and Stanford (2006), Westergaard et al. (1998) suggest that bipedalism may have originated in the trees, reaching in an upright bipedal posture for food items in above-head and peripheral branches. This bipedal feeding may have been a preadaptation to fully recognized locomotor bipedalism later in the hominid lineage (Westergaard et al. 1998; Hunt 1994).

Hirasaki et al. (2000) used experimental observations on another New World primate, black-handed spider monkeys (*Ateles geoffroyi*) to gain more insight into potential

preadaptative kinematics of vertical climbing that may have been important in the origins and evolution of human bipedalism. Hirasaki et al. (2000) suggested that spider monkey climbing may provide a good model for the necessary vertical climbing preadaptations that would favor bipedal posture, as spider monkey “hindlimb driven” vertical climbing strengthens hindlimb muscles important in bipedal posture and locomotion. Although they avoided suggesting that their results support an arboreal vertical climbing model for the potential last common ancestor (Prost 1980), Hirasaki et al. (2000) argue that their results do suggest that the spider monkey-type climbing seems to have “potential to develop into human bipedalism.”

Japanese macaques (*Macaca fuscata*) have been used frequently in experimental and captive studies of the kinematics of human bipedalism. Hirasaki et al. (2004) compared the bipedal walking of macaques highly trained to walk bipedally to the bipedal walking of ordinary macaques and found important implications for the earliest stages of hominid bipedalism. First, they argue that training can improve bipedal walking in macaques without the necessary morphological changes for erect human-like bipedalism (Hirasaki et al. 2004). Therefore, the earliest bipeds may have been able to walk bipedally in a human-like fashion without these necessary morphological changes as well (Hirasaki et al. 2004). Second, Hirasaki et al. (2004) contend that their results support the hypothesis that the human gait is in fact advantageous and important to human bipedalism.

Based on field observations of olive baboons (*Papio anubis*), Rose (1976) argued that hominid bipedalism most likely evolved as an adaptation in feeding situations and that as it evolved it may have become incorporated into other contexts, such as social contexts. He

emphasizes that while feeding might have been a major component in the origin and evolution of bipedalism in early hominids, many different selective pressures were probably involved in the development of habitual bipedalism as seen in humans (Rose 1976). This echoes Sigmon (1971) who argued that a variety of bipedal situations are important and should be considered.

In his study of gelada baboons, Wrangham (1980) observed the adoption of both bipedal postures and locomotion within the course of daily activity, particularly within the context of foraging. Based on these observations, he argued that bipedal behavior would have been initially favored in habitats with fruiting bushes and open undergrowth, which made bipedal postures an advantageous adaptation for feeding (Wrangham 1980). Second, bipedalism would have been favored as a more efficient form of travel between food patches (Wrangham 1980). In summary, Wrangham (1980) argues that bipedalism might have originated as a feeding and foraging posture and then into locomotion for energetic efficiency.

2.4 Ape Models

The Lesser Apes, in particular gibbons, have long been used as a model for human habitual bipedalism. Gibbons are a highly arboreal species, whose locomotion is characterized by speed and mobility (Vereecke et al. 2005). Observations of gibbons using terrestrial locomotion are often infrequent and typically occur when crossing gaps in fragmented forests (Satie & Alfred 2002). In the trees, they exhibit forelimb-dominated locomotion, while their hindlimbs are kept flexed at the hip and knee (Jungers & Stern 1976). This is punctuated by short, fast bouts of bipedal locomotion on large branches, as well as

jumping and quadrumanous climbing (Tuttle 1972). Therefore, the function and form of their hindlimbs is of interest in terms of their comparison with habitually bipedal humans.

For these reasons, many of the first hypotheses regarding the evolution of habitual bipedalism were based in comparisons to the hylobatians, gibbons and siamangs. Before being overshadowed by the vertical climbing hypothesis for the reconstruction of the last common ancestor of chimpanzees and humans, Keith's (1923) reconstruction included a brachiating gibbon-like ancestor, followed by an arboreal ape-like ancestor and finally the hominid biped (Gebo 1996). This focus on a brachiating ancestor explained the retention of morphological features relating to arm-swinging and suspension shared by extant apes and humans (Gebo 1996). Using experimentally based comparisons of human bipedalism to gibbon bipedalism, Prost (1980) found that gibbon bipedalism is more similar functionally and morphologically to chimpanzee bipedalism than human bipedalism. Likewise, Shapiro and Jungers (1988) found more consistency in the musculature of the back in relation to its function in bipedalism in gibbons and chimpanzees than in either species compared to humans. Although not eliminating the hylobatids as a potential referential model, these studies dispel any special or unique similarities between gibbon bipedalism and human bipedalism in form or function as compared to the other apes.

Grehan (2006) has made a morphologically-based argument for consideration of the orangutan as the best potential model for hominid evolution. He identifies 28 morphological traits shared between humans and orangutans as well as the presence of "orangutan-related" traits in early hominids that he argues suggest a different evolutionary scenario than one that puts humans most closely related to the genus *Pan* (Grehan 2006). Few of these traits can be

tied to bipedalism. For example, Grehan (2006) suggests similarities between the shape of the navicular tubercles of the foot in both orangutans and humans. The navicular may be important in that as one of the tarsal bones of the foot, its features (i.e. relative orientation of the bone, orientation of articular areas as well as curvature of the navicular facets) can provide important information in terms of the tarsal complex and the movement it would allow as well as information regarding load bearing (Sarimiento & Marcus 2000).

Information gained from knowledge of similarities in tarsal bones from humans and orangutans could be applied in paleontological contexts with success, as tarsal bones often preserve well and are often found at early hominid sites (Sarimiento & Marcus 2000).

However, Grehan (2006) fails to explain the degree to which this trait might be similar in both apes and provides little in terms of the implications that exhibiting this particular trait may have on their behavior. In general, the argument Grehan (2006) presents may be questioned in terms of the traits he provides, many of which could potentially be the product of individual variation in morphology or ancestral traits retained from a common ancestor that were lost in the African apes (Grehan 2006).

Harmon (2007) presents the case that similarities exist between the shape of the proximal femur in orangutans and humans, which may have important implications for the evolution of habitual bipedalism in general. Orangutans, humans, and gibbons share a relatively long femoral neck, a short greater trochanter, and a superiorly projecting head, which Harmon (2007) suggests could be the result of retention of ancestral traits in humans, orangutans, and gibbons. Alternatively, Harmon (2007) suggests these similarities may be the result of convergence in these three apes, because of a locomotor repertoire in each with

the same skeletal demands. This would equate the leaping and bipedal walking found in gibbons and the arboreal quadrupedalism in orangutans with hominid terrestrial habitual bipedalism (Harmon 2007). The hypothesis presented by Thorpe et al. (2007), discussed at length below, also seems to support this conclusion. Despite these similarities, orangutans are typically thought to be distinct in terms of their morphology (Begun 2006).

Recently, Thorpe et al. (2007) has suggested orangutans (*Pongo pygmeaus*) as the best ape model for understanding the evolution of bipedalism. Based on paleoanthropological evidence, Thorpe et al. (2007) argue that bipedalism arose in an arboreal context. In order to understand the adaptive benefits of bipedalism in the trees, Thorpe et al. (2007) then look to the orangutan, who uses bipedal postural and locomotor behavior in order to access flexible supports that would be too unstable to access otherwise. In fact, the orangutan may be more bipedal than other species of nonhuman primate according to the results of Thorpe and Crompton's (2006) study of positional behavior in this species (Table 2.1). However, these authors focus on orthograde standing, which they argue subsumes bipedal, monopodal, and compression postures, that they suggest are more important than narrowly defined bipedal postures in terms of the evolution of hominid bipedalism (Thorpe & Crompton 2006). They argue that this orthograde stand posture may be a distinctive feature shared by apes (Thorpe & Crompton 2006). In terms of locomotor bipedalism, Thorpe et al. (2007) posit that orangutans navigating flexible branches to move through the trees is similar to humans running bipedally on "springy tracks" increasing knee and hip extension, which differs from other primates like monkeys and the other apes who have a flexed-limb bipedal gait. Based on this, they conclude that instead of being a new or

innovative behavior, human bipedalism is linked to orthograde postural and locomotor behavior exhibited by a common ancestor to all of the apes (Thorpe et al. 2007).

Bonobos (*Pan paniscus*) have often been used as a model for the evolution of hominid bipedalism (Videan & McGrew 2001). Vereecke et al. (2005) describes bonobos as gracile and arboreal apes who typically travel using arboreal quadrupedalism, quadrumanous climbing, and scrambling performed at a slow pace, rather than moving swiftly like gibbons. However, they also include fast-paced locomotor behaviors in their locomotor repertoire, such as diving, leaping, and semi-brachiating, of a different type than that displayed by gibbons (Vereecke et al. 2005). In addition to arboreal behaviors, bonobos also often travel terrestrially, where they typically exhibit quadrupedal knuckle-walking, as well as infrequent bouts of bipedalism and tripedalism (Vereecke et al. 2005).

Based on comparisons of skeletal and morphological characteristics between bonobos, common chimpanzees, and humans, Zihlman (1978) argued that bonobos provided the best model for understanding the evolution of bipedalism because of their more generalized, less sexually dimorphic morphology. Despite the common perception of bonobos as “scaled down chimpanzees,” Zihlman (1996) evidenced that bonobos have a qualitatively different body and limb morphology than do chimpanzees. Based on comparisons of skeletal and morphological characteristics between bonobos and common chimpanzees of similar size, Zihlman (1996) found that the former consistently displayed a statistically significant difference in humerus/femur ratio, additionally demonstrating that the bonobo has relatively shorter arms and longer as well as more robust legs than the common chimpanzee. In light of this investigation, Zihlman (1996) argued that the bonobo’s distinct

body proportions may have important implications for choosing bonobos over chimpanzees as a model for human bipedalism in terms of skeletal morphology and function.

In contrast to Zihlman's arguments regarding bonobo morphology as important in terms of the study of bipedalism, D'Aout et al. (2002) presented experimental data comparing the bipedal walking of bonobos and humans that may suggest that an efficient inverted pendulum type bipedalism as seen in humans is not expected for bipedal bonobos. Although D'Aout et al. (2002) evidenced similarities in the angle profiles of the hip in both humans and bonobos, they found that bonobos differed from humans markedly in the angle profiles of the knee and ankle during bipedal movement. Therefore, while hip-knee coordination appears similar to the human pattern, the knee-ankle coordination differs significantly from the human pattern. This suggests relative inefficiency in bonobos in terms of bipedal locomotion, although D'Aout et al. (2002) argue that this would not necessarily correlate with less efficient quadrupedalism.

In terms of behavior, it has often been suggested that bonobos display bipedal behaviors more frequently than common chimpanzees, because their longer and heavier hindlimbs make them predisposed to bipedalism (Zihlman 1996). Zihlman (1996) suggested that this preadaptation for bipedal behavior coupled with a lower center of gravity may have allowed for an easier transition between quadrupedal ape to bipedal hominid than previously expected via other models. Behavioral differences between common chimpanzees and bonobos have also been cited with possible implications for understanding the selective pressures involved in the evolution of bipedalism (Videan & McGrew 2001). Although some caution should be taking in interpreting the consequences of these differences, Stanford

(1998) argued that in general, differences have been exaggerated in their relation to the evolution of bipedalism. Likewise, Videan and McGrew (2002) contend that the rates of bipedalism in both species are not significantly different. Despite this, the bonobo model has been used to shed light on questions related to the evolution of human habitual bipedalism (Videan & McGrew 2001).

2.5 The Chimpanzee Model

Many of the models for the evolution of bipedalism focus on chimpanzees (Videan & McGrew 2001). Much of the popularity of the chimpanzee model may spring from the knuckle-walking hypothesis for the last common ancestor of chimpanzees and humans. During quadrupedal knucklewalking, the African apes, chimpanzees, gorillas, and bonobos flex their fingers and bear weight on the dorsal surface of their middle phalanges (Richmond & Strait 2000). This reflects a compromise that allows them to walk quadrupedally using their hands and upperlimbs while at the same time retaining long, curved phalanges for movement arboreally (Richmond & Strait 2000). During this movement, the wrist is held in a locked position via a complex of traits in the carpal bones, including a distal projection of the dorsal ridge, a distinct size and dorsal orientation of the scaphoid notch, and the relative disto-medial orientations of the lunate and scaphoid articular surfaces (Richmond & Strait 2000). Richmond & Strait (2000) and others have argued that evidence of this knuckle-walking wrist locking mechanism appears in early hominids as well as humans and suggests a knuckle-walking ancestor.

Behavioral evidence has also been cited frequently as support for the use of a chimpanzee model for the evolution of habitual bipedalism in early hominids. As with other

primates, chimpanzees adopt bipedal postures and locomotion more frequently in some habitat types than others as well as in a variety of behavioral contexts (Sigmon 1971). For instance, Goodall (1965) noted chimpanzees at Gombe National Park in Tanzania used bipedal postures in a spectrum of contexts, including looking over tall grass, or scanning the surroundings for a conspecific, observing novel things in their environment, when carrying objects, during displays, and when greeting conspecifics. Bauer (1977) has even reported near-habitual bipedalism in a wild chimpanzee at Gombe, in Tanzania, as a result of forearm paralysis. Comparisons between the frequencies of bipedal behavior exhibited by chimpanzees and other nonhuman primates also reveal that they may be more bipedal than many other species (Table 2.1). This variation in the context and frequency of bipedalism may lend some insight into the varied selective pressures that shaped the evolution of habitual bipedality.

While Goodall (1965) only notes observations of bipedal posture and locomotion in a terrestrial context, Hunt (1994, 1996) observed chimpanzees in Mahale Mountains and Gombe National Parks adopting bipedal postures in both arboreal and terrestrial contexts during foraging in small fruit trees in open forests. During these feeding bouts, chimpanzees often assisted bipedal postures by grasping overhead branches using a forelimb for stabilization (Hunt 1994, 1996). Based on these observations as well as comparisons to australopithecine anatomy, Hunt (1994, 1996) developed the “small tree feeding” hypothesis. This hypothesis posits that the origins of bipedalism lie in arboreal arm-hanging and bipedal postures coupled with terrestrial bipedalism as adaptations for foraging for fruit in small trees, either from the ground or within the tree (Hunt 1994, 1996). He argues that bipedal

postural feeding and foraging may have been a preadaptation to terrestrial bipedal locomotion (Hunt 1994, 1996).

Like Hunt (1994, 1996), Stanford (2006) focuses on bipedal posture as important in the origins of bipedalism. Recently, he has renewed interest in a hypothesis reconstructing the origin of bipedalism as a postural adaptation to foraging in the trees via field observations of chimpanzees in the Bwindi Impenetrable National Park in Uganda (Stanford 2006). He observed that the Bwindi chimpanzees moved fluidly between four-legged, three-legged, and two-legged postures while utilizing the three dimensional space of the canopy for foraging for fruit (Stanford 2006). Stanford (2006) suggests that this fluidity between quadrupedal and bipedal postures may have occurred in early hominids as well. While this is counterintuitive if a definition of “hominid” implies habitual bipedalism, it may be an important aspect of the postural behavior of the last common ancestor of chimpanzees and humans. Despite this potential problem, Stanford (2006) asserts that the origin of bipedal posture lies in the last common ancestor adopting arboreal bipedal postures foraging in fruiting trees and that these origins preceded the evolution of bipedal locomotion. Unlike Hunt (1994, 1996), Stanford (2006) reports no terrestrial bipedalism in the Bwindi chimpanzees, although this may be indicative of a difference in habitat leading to a difference in frequency of certain bipedal behaviors (as suggested by Sigmon 1971) rather than an absence of it.

As Goodall (1965) observed, chimpanzees often use bipedal postures and locomotion during displays. Jablonski and Chaplin (1993) expanded this noting that all of the African apes exhibit both stationary and moving bipedal terrestrial displays. Jablonski and Chaplin

(1993) add that our species shares this trait with the African apes, although bipedal threat displays are often masked in humans by our extensive culture. They argue that these displays were important in the evolution of habitual terrestrial bipedalism (Jablonski & Chaplin 1993). According to Jablonski & Chaplin (1993), bipedal postures were adopted for social control in the prehomnids, as increasingly open and harsh habitats in the late Miocene caused increased intraspecific competition for resources. Because this new environment would have also favored bipedal locomotion, the common elements between the locomotor behavior and the display postures would have favored the evolution of habitual terrestrial bipedal locomotion (Jablonski & Chaplin 1993). Similarly, Walter (2004) recently explored bipedal postures in chimpanzees as a defense mechanism against coursing predators rather than in aggressive competition with conspecifics. He argued that erect stature alone may also confer some advantage in deferring predators through intimidation by giving the appearance of not only vigilance and awareness of the predator but also of “standing up to” the potential predator (Walter 2004).

Videan and McGrew (2001) used experimental manipulations to examine the differences in frequency of bipedal behaviors (both postural and locomotor bipedalism) in captive common chimpanzees and bonobos. They tested several hypotheses regarding the selective pressures postulated to be involved in the evolution of bipedality (Videan & McGrew 2002). The hypotheses tested by Videan and McGrew (2002) were the “vigilance” hypothesis as outlined by Day (1986) with similar elements to Walter (2004), the “carrying” hypothesis outlined by Hewes (1961), the “display” hypothesis described by Kortlandt (1980) and Jablonski and Chaplin (1993), and the “foraging” hypothesis postulated by Rose

(1984) and Hunt (1994, 1996). Videan and McGrew (2002) did find behavioral differences in which experimental manipulations favored bipedal behavior in chimpanzees versus bonobos. Both bonobos and chimpanzees adopted bipedal locomotion in the “carry” hypothesis manipulation (Videan & McGrew 2002). Neither the “display” nor “vigilance” manipulations changed the bipedal behavior of either species (Videan & McGrew 2002). Chimpanzees increased their bipedal postural behaviors in the “forage” manipulation (Videan & McGrew 2002). Videan and McGrew (2002) concluded that both the “carry” hypothesis and the “foraging” hypothesis are well supported by their experimental bonobo and chimpanzee referential model and are plausible mechanisms that may have shaped the evolution of bipedalism.

Table 2.1 Comparisons of bipedal behavior in species of wild nonhuman primates.

Species	Study Site	% Overall Postures and Locomotion	Average Rate of Bipedalism (bouts/hour)	Primary Behavioral Context	Type of Bipedalism Observed
Chimpanzee <i>(Pan troglodytes verus)</i>	Fongoli, Senegal (this study)	2.2	1.05	Feed/Forage (postural); Intraspecific displays (locomotor)	Postural and Locomotor
Chimpanzee <i>(Pan troglodytes schweinfurthii)</i>	Bwindi, Uganda (Stanford 2006)	—	0.73	Feed/Forage	Primarily Postural

Table 2.1 (*continued...*) Comparisons of bipedal behavior in species of wild nonhuman primates.

Species	Study Site	% Overall Locomotion	Average Rate of Bipedalism (bouts/hour)	Primary Behavioral Context	Type of Bipedalism Observed
Chimpanzee <i>(Pan troglodytes schweinfurthii)</i>	Mahale & Gombe, Tanzania (Hunt 1994, 1996)	0.3	0.17	Feed/Forage	Primarily postural
Chimpanzee <i>(Pan troglodytes versus)</i>	Tai Forest, Ivory Coast (Doran 1993)	1.2	_____	Feed/Forage	_____
Bonobo <i>(Pan paniscus)</i>	Lomako Forest, Zaire (Doran 1993)	1.2	_____	Feed/Forage; Travel	Postural and Locomotor
Orangutan <i>(Pongo pygmaeus)</i>	Ketambe Research Station, Sumatra (Thorpe & Crompton 2006)	6.0**	_____	Look/Scan	Postural ^o
Orangutan <i>(Pongo pygmaeus)</i>	Ketambe Research Station, Sumatra (Thorpe & Crompton 2006)	0.7•	_____	Travel; Feed/Forage	Locomotor ^o

Table 2.1 (*continued...*) Comparisons of bipedal behavior in species of wild nonhuman primates.

Species	Study Site	% Overall Locomotion	Average Rate of Bipedalism (bouts/hour)	Primary Behavioral Context	Type of Bipedalism Observed
Gelada baboon <i>(Theropithecus gelada)</i>	Simien National Park, Ethiopia (Wrangham 1980)	_____	4.2 (during feeding on grass)	Travel during Feeding on grasses*	Primarily locomotor*
Olive baboons <i>(Papio anubis)</i>	Gombe, Tanzania Hunt (1996)	0.0	_____	_____	_____
Olive baboon <i>(Papio anubis)</i>	Gilgil (Rift Valley), Kenya (Rose 1976)	0.8	_____	Feed/Forage	Primarily Postural
Redtail Guenon <i>(Cercopithecus ascanius)</i>	Kibale Forest Reserve, Uganda (Gebo & Chapman 1995)	4.0 (of total postural behaviors during feeding/ foraging and travel contexts)	_____	Feed/Forage	Postural
Blue Guenon <i>(Cercopithecus mitis)</i>	Kibale Forest Reserve, Uganda (Gebo & Chapman 1995)	3.0 (of total postural behaviors during feed/ forage and travel contexts)	_____	Feed/Forage	Postural

Table 2.1 (*continued...*) Comparisons of bipedal behavior in species of wild nonhuman primates.

Species	Study Site	% Overall Locomotion	Average Rate of Bipedalism (bouts/hour)	Primary Behavioral Context	Type of Bipedalism Observed
White-cheeked mangabey (<i>Cercocebus albigena</i>)	Kibale Forest Reserve, Uganda (Gebo & Chapman 1995)	1.0	_____	Feed/Forage and Travel	Postural and Locomotor
Red Colobus (<i>Colobus badius</i>)	Kibale Forest Reserve, Uganda (Gebo & Chapman 1995)	<1.0	_____	Feed/Forage	Postural and Locomotor
Black and White Colobus (<i>Colobus guerza</i>)	Kibale Forest Reserve, Uganda (Gebo & Chapman 1995)	<1.0	_____	Feed/Forage	Postural and Locomotor
White-Face Capuchin (<i>Cebus capucinus</i>)	La Suerte Biological Field Station, Costa Rica (Garber & Rehg 1999)	<1.0	_____	Feed/Forage	Postural+

*Wrangham (1980) equates bipedal behaviors as defined here (standing or locomoting with body weight supported primarily on the legs, see Table 3.2 for detailed definitions) with bipedal shuffling by gelada baboons. Bipedal shuffling is defined by Wrangham (1980) as slow-paced locomoting while in an upright sitting posture rather than standing, with buttocks possibly touching ground over short distances with the knees bent. The degree to which this behavior is similar to bipedal behavior defined by this study as well as others is unclear and complicates comparisons to other studies.

**Thorpe and Crompton (2006) subsume bipedal, monopedal and compression postural behaviors together under orthograde stand. Therefore, this percentage represents the percentage of overall time engaged in orthograde stand behaviors, not solely bipedal postures.

°Study by Thorpe and Crompton (2006) includes only postural behaviors and considers locomotor behaviors of orangutans separately so they are included here as separate categories.

•Thorpe and Crompton (2006) report bipedal locomotion as a percentage of total locomotor behaviors (7.3%) rather than lumping postural and locomotor behaviors into one analysis as is the case with the rest of the studies reported. Therefore, the percentage reported here was calculated based on the total observations of all postural and locomotor behavior for comparison to other nonhuman primates.

+Garber and Rehg (1999) refer to a specific type of tail-assisted bipedal posture that they call a tail-assisted bipedal crouch. This may not be analogous to assisted bipedal postures in chimpanzees.

2.6 The Importance of the Savanna Chimpanzee Model

Sayers and Lovejoy (2008) recently criticized the common use of the chimpanzee model in understanding early hominid behavior. The authors suggest that the “australopithecines-are-like-chimpanzees” view that has often accompanied such investigations into early hominid behavior via referential modeling is ill founded. Sayers and Lovejoy (2008) also criticize attempts at using chimpanzee models on the basis of “homology and analogy” as Moore (1996) suggested. Finally, they take issue with chimpanzee referential models, which focus on similarities between chimpanzees and hominids when greater insight is found in differences in terms of evolutionary divergence of species (Sayers & Lovejoy 2008). Despite these criticisms, the inclusion of savanna chimpanzees provides a stronger referential model that can provide important insight into the behavior of early hominids.

Three issues exist with these criticisms. First, there are few chimpanzee referential models that have been produced based both on analogy and homology. This type of referential model implies that the chimpanzees studied must be both similar in “homology,”

or biology, which is answered by the close evolutionary relationship that we assume between humans, hominids, and chimpanzees, and “analogy,” or common adaptation to a particular habitat. In terms of both analogy and homology, savanna chimpanzees provide the best choice for gaining insight into early hominid behavior; however, few chimpanzee studies have incorporated analogy in terms of understanding early hominid behavior (Suzuki 1969; McGrew et al. 1981; Kortlandt 1983; Hunt 1994, 1996; Pruett et al. 2002). Of these few, none except Pruett et al. (2002) have been long-term studies of habituated individuals. Therefore, the critique that Sayers & Lovejoy (2008) produce regarding the use of homology and analogy in referential modeling is based on studies that do not actually employ references utilizing both aspects.

A second key issue seems to be a focus on the substitution of chimpanzees *as* a replica of early hominids in referential models to date, rather than an argument that chimpanzees may be similar to early hominids in the ways that they utilize a particular type of habitat. This is a danger of any referential model, regardless of the species or question considered. Even cautiously chosen models run the risk of being based on oversimplified analogies (Strum & Mitchell 1987). Taking this interpretation to its logical extreme, referential models can be easily mistaken as the extant version of an extinct hominid, rather than recognizing both the model and referent as each represents a unique biological position (Tooby & DeVore 1987; Moore 1996). Similarity does not necessarily imply a particular degree of exactness, and insights into both the similarities *and* differences among savanna chimpanzees and the behavior expected of early hominids may produce insight into their evolution that are not yet answered or are unanswerable by fossil evidence.

Finally, Sayers and Lovejoy (2008) overlook the context in which referential models can be most helpful in terms of gaining insight into early hominid behavior. While Sayers' and Lovejoy's (2008) criticisms of particular studies is important, a referential model can be strengthened when taking a more holistic approach to evolutionary questions. First, referential models based on savanna chimpanzees can help us to define human uniqueness through the identification of similarities among hominoids versus differences between humans and the other great apes (Pruetz & LaDuke, submitted). Likewise, comparisons across study sites and habitats are essential for the most holistic referential model. It is in the differences that chimpanzees exhibit across habitats and study sites that the most insight can be gained in terms of early hominid behavior. In other words, no one chimpanzee referential model stands alone in explaining hominid behavior. The similarities *and* differences in the ways that chimpanzees behave in different ecological contexts and under different pressures can help us to understand the ways in which these unique conditions affect behavior. For this reason, study of savanna chimpanzees as part of long-term studies of habituated individuals not only provides the best referential model for early hominid behavior in terms of both analogy and homology, but also contributes important insight to comparisons with chimpanzees at other study sites.

Chapter 3. Methods

3.1 Introduction

I used a holistic approach to studying savanna chimpanzees as a referential model for hominid evolution to better inform our understanding of the context in which habitual bipedalism may have evolved in early hominids. The objective of this study is to elucidate the context in which savanna chimpanzees adopt bipedal postures and locomotion. Beyond describing the bipedal behavior of savanna chimpanzees at Fongoli, this study is aimed the following objectives:

1. To determine the degree to which the ecological and behavioral context predicts the frequency, duration, and rate of postural and locomotor bipedal behavior in savanna chimpanzees.
2. To examine the bipedal behavior of savanna chimpanzees at Fongoli in relation to studies of the bipedal behavior of chimpanzees at other sites, particularly Stanford (2006) and Hunt (1994, 1996).

Because of the similarities between the environment of extant savanna chimpanzees and the paleoenvironment of early hominids as well as the close evolutionary relationship between chimpanzees and *Homo*, similarities are also expected in the way that chimpanzees and early hominids utilized the environment in terms of bipedal behavior. Using this information, I will evaluate the plausibility of existing hypotheses promoted as explanations for the evolution of habitual bipedalism in terms of the behavioral and ecological contexts that may have promoted the adoption of habitual bipedal behavior in early hominids.

3.2 Study Site



Figure 3.1 Map of Senegal. Study site located in southeastern part of the country.

Research was conducted at the Fongoli study site in southeastern Senegal ($12^{\circ}40'N$ $12^{\circ}13'W$, Pruetz 2006), at the northern geographical limits of chimpanzees' range in West Africa (Carter et al. 2003). The rainy season in this region spans June through September, with May and October as transitional months between the rainy and dry seasons (Pruetz & Bertolani 2007). The chimpanzees at Fongoli inhabit primarily open woodland and grassland habitats as well as small patches of gallery forest and seasonally cultivated fields (Pruetz 2006), and the site can be considered a savanna-woodland mosaic (Pruetz & Bertolani 2007). The Fongoli chimpanzee community has been under study since 2001 by Dr. Jill D. Pruetz. Fongoli is located in an area where the range of the chimpanzees overlaps with that of humans (Pruetz 2006). Despite this overlap, humans do not generally hunt chimpanzees for food (Pruetz & Bertolani 2007).

3.3 Study Subjects

During this study, 35 individuals made up the Fongoli community, including ten adult males, seven adult females, and 17 immature chimpanzees. As per habituation protocol, eight of ten males were used as focal subjects. One adult male, Mamadou, was excluded because of possible problems with his postural and locomotor behavior due to an injury sustained to his left leg (Pruetz, pers. comm.). Another adult male, Foudouko, was excluded, as he was not seen during the duration of the study. Most adult females are also timid around observers, and so were also excluded from the focal sampling (Pruetz, pers. comm.). Opportunistic ad libitum data was recorded on the bipedal behavior of adult females, as well as adolescent and juvenile males and females, which may provide insight or future direction for study of these age-sex classes (Appendix 2).

3.4 Methodology

Data was collected from May 15th thru June 15th 2008, 3-4 days per week. According to protocol, eight of ten adult male chimpanzees were used as focal subjects, observed at a distance of 10-20 meters. Efforts were made to collect data on each focal individual equally, so that no individual biases will be reflected in the results (Table 3.1). Data was analyzed according to individual as well to confirm and correct any potential individual biases.

Focal data was recorded at five-minute intervals using instantaneous sampling method. At each interval, maintenance behavior (Appendix 1), postural/locomotor state (Appendix 1), and ecological context, arboreal (any height above the ground on branches or vines) or terrestrial (on the ground), was recorded. This allowed me to determine percentage

of overall time spent engaging in bipedal behavior in relation to other positional/locomotor behaviors.

Table 3.1 Number of observation hours per focal subject according to instantaneous scan data.

Focal Subject	# Observation Hours
Yopogon (YO)	22.65
K.L. (KL)	15.5
Diouf (DF)	15
Bilbo (BI)	14.4
Bandit (BN)	12.6
Karamoko (KM)	8.2
Siberut (SI)	14.8
Lupin (LU)	12.1
Total	115.25

Following Doran's (1992) recommendations regarding data collection on rare or infrequent positional and locomotor behaviors, focal data was recorded on all occurrences of bipedalism. In order to understand the context in which bipedalism occurs, data was recorded according to several categories. Bipedalism was recorded as terrestrial or arboreal, postural or locomotor, as well as unassisted or assisted following Hunt (1996) (Table 3.2). Terrestrial bipedalism was divided into categories according to slope and quality of the terrain (Tables 3.3 and 3.4). Following Garber & Pruetz (1995), arboreal bipedalism was divided by supporting branch size in relation to the anatomy of the focal subject (Table 3.5) and angle (Table 3.6). Finally, behavioral context or maintenance behavior was also

recorded (Appendix 1). A bout was defined as starting when a focal individual rose to a bipedal posture or in bipedal locomotion to the time when that individual began a new postural or locomotor behavior, such as quadrupedal walking or standing. Bout duration will be recorded for all bipedal locomotion and postures lasting ≥ 1 second using a hand-held watch.

Table 3.2 Categories of bipedalism (Adapted from Hunt 1994, Hunt et al. 1996, Doran 1992).

Behavior	Categories of Behavior
Bipedal Posture	<i>Unassisted (UBP)</i> : chimpanzee stands with most of its weight supported by hindlimbs with trunk vertical for at least 1 second
	<i>Assisted (ABP)</i> : chimpanzee uses one or both hands to grasp overhead substrate to provide balance but most of its body weight is supported by hindlimbs with trunk vertical for at least 1 second
Bipedal Locomotion	<i>Assisted (ABL)</i> : chimpanzee uses one or both arms to grasp overhead substrate to provide balance during locomotion with weight borne on hindlimbs with trunk vertical for more than 1 second
	<i>Unassisted(UBL)</i> : chimpanzee moves with weight borne on hindlimbs, with trunk vertical, for more than 1 second

Table 3.3 Terrestrial bipedalism: terrain slope (Adapted from Doran 1992, Garber & Pruetz 1995).

Category	Slope
Vertical (V)	Approximately 76° to ≤ 90°; terrain is near or completely vertical, requires climbing to move up or down; denoted by a + when chimpanzee is oriented up vertical plane and by – when chimpanzee is oriented down the vertical plane
Oblique (O +/-)	Approximately 46° to ≤ 75°; indicates marked positive or negative slope in terrain; denoted by + when chimpanzee is oriented up incline and by – when chimpanzee is oriented down incline
Horizontal (H)	Approximately 0° to ≤ 10°; indicates relatively level terrain, little to no incline

Table 3.4 Terrestrial bipedalism: terrain quality (Adapted from Pruetz, pers. comm.).

Category	Definitions
Rocky (RCK)	Terrain is characterized by uneven, rocky terrain, including large boulders (>0.5 meters in diameter)
Loose Soil (LS)	Terrain is characterized by loose soil, gravel, or sand that can shift underfoot. Little or no moisture in soil.
Smooth (SMT)	Terrain characterized by firm, compacted, dry soil; lacks rocky obstacles.
Muddy (MD)	Soft, watery, and loose soil; saturated with water to point of becoming sticky, slippery, and thick. May inhibit easy movement over terrain.
Water (WA)	Standing water on terrain, as in pools, streams, creeks, lakes, rivers, etc. that focal individual can traverse without swimming.
Plateau (PL)	Terrain that is characterized by flat stones. Rocky but relatively flat terrain.
Slippery (SLP)	Terrain characterized by flat stone, leaves, or flattened grasses that are wet causing terrain to be slick

Table 3.5 Arboreal bipedalism: substrate diameter (Adapted from Garber & Pruetz 1995; Pruetz, pers. comm.).

Category	Substrate Diameter in relation to anatomy of focal individual
Small (Sm)	Substrate can be encircled with hand or foot
Medium (Md)	Substrate can be encircled with both hands or both feet
Large (Lg)	Substrate can be encircled with arms.
Extra-Large (XL)	Focal individual unable to encircle substrate.

Table 3.6 Arboreal bipedalism: substrate angle (adapted from Garber & Pruetz 1995).

Category	Substrate Angle
Vertical (V)	Approximately 76° to $\leq 90^\circ$; substrate is near or completely vertical
Oblique (O)	Approximately 46° to $\leq 75^\circ$; indicates marked positive or negative angle in substrate
Horizontal (H)	Approximately 0° to $\leq 10^\circ$; substrate is oriented parallel to ground, assumed to be a horizontal plane

3.5 Data analysis

Analyses were performed using the JMPTM statistical program (Copyright © 2007 SAS Institute Inc.). Simple descriptive statistics based on instantaneous scan sampling data at five-minute intervals were used to determine the overall breakdown of postural and locomotor behavior for Fongoli chimpanzees. All occurrences data was analyzed in terms of two dependent variables: the frequency of bipedal behavior and the duration of bipedal behavior. The rate of bipedal behavior was calculated based on the number of bipedal bouts observed during focal all-occurrence sampling (the frequency of bipedal behavior) and the number of observation hours. The results were then put into context via comparison to other

chimpanzee sites (i.e. Bwindi, Stanford [2006] and Gombe/Mahale, Hunt [1994, 1996]). The possibility of a particular focal individual being more bipedal than other individuals and biasing the data set was assessed using multiple regression analysis, by including focal subject as an independent variable. Because focal subject did not correlate significantly with frequency, duration, or rate of bipedal behavior, the focal subject data was pooled into an overall analysis of the behavioral contexts favoring bipedalism.

Stepwise Multiple Regression analysis was used to determine the “best” model for predicting both the frequency and the duration of bipedal behavior using the ecological and behavioral categories recorded as independent variables. Fisher’s Exact Tests were used to determine whether or not bipedal behavior differed across categories. Fisher’s Exact Tests were favored over Pearson’s Tests because of the small sample size in some categories. Bivariate analysis was also used to determine effects of independent variables that contained two categories (i.e. general context, which includes an arboreal category and a terrestrial category). Ninety-five percent confidence intervals were used in cases when independent variables included more than two categories to determine whether any category differed statistically in terms of eliciting bipedal behavior.

The rate of bipedal behavior per each observation hour was determined to calculate the average rate of bipedal bouts. These rates were then averaged to produce the mean rate of bipedal bouts for Fongoli chimpanzees. A 95% confidence interval was calculated using the JMP™ statistical package and then used to determine whether or not the rate differed statistically from the rates of bipedal bouts reported at Bwindi (Stanford 2006) and Gombe/Mahale (Hunt 1994, 1996). Additional calculations determined how the rate of

bipedal behavior differed across categories, including arboreal or terrestrial contexts and during feeding and foraging. These rates were calculated using the frequency of bipedal bouts in a particular context divided by the number of observed hours in that context.

3.6 Methodologies at Other Sites

In order to build a stronger referential model based on savanna chimpanzee behavior and to contribute to what Moore (1996) calls a relational model that considers how bipedal behavior differs across chimpanzee sites, the results of this study are analyzed and interpreted in comparison to studies of chimpanzee bipedal behavior at Bwindi (Stanford 2006) and Mahale and Gombe (Hunt 1994, 1996). First, differences in degree of habituation exist across chimpanzee sites. Both this study and the study by Hunt (1994, 1996) utilized observations of habituated focal individuals. In contrast, Bwindi chimpanzees were not habituated during Stanford's (2006) study. The result was that Bwindi chimpanzees could not be approached terrestrially and were typically observed in treetops (Stanford 2006). Chimpanzees at Bwindi were observed by researchers sitting on steep opposite-facing slopes 20 to 50 meters across narrow ravines from where chimpanzees were foraging in an arboreal context (Stanford 2006).

In terms of sampling methods, Stanford (2006) utilized a focal subject all occurrences method for recording bipedal behavior, similar to the method used for exploring the ecological and behavioral contexts of bipedal behavior in this study. This allowed for more direct comparisons of data on Bwindi chimpanzees and Fongoli chimpanzees. In contrast, Hunt (1994, 1996) used instantaneous focal scans at two minute intervals for recording the positional and locomotor behavior of Mahale and Gombe chimpanzees, though his analysis is

consistent with this study as it focuses on occurrences of bipedal behavior resulting from these scans. While Stanford (2006) observed focal subjects of all age and sex classes, Hunt (1994, 1996) focused on adult individuals of both sex classes. Both Stanford (2006) and Hunt (1994, 1996) examined ecological and behavioral variables that may influence bipedal behavior in chimpanzees, including maintenance behavior, forelimb assistance, fruit size (for feeding and foraging contexts) and general context (arboreal or terrestrial), which is consistent with this study. Stanford (2006) and this study follow Hunt's (1994) definitions for forelimb assistance as well as fruit size during feeding and foraging contexts. Specific ecological variables such as substrate size and angle are utilized by Stanford (2006) in terms of arboreal bipedalism and expanded upon here to include terrain slope and quality specific to terrestrial bipedal bouts. Stanford (2006) estimates branch diameter to the centimeter, in contrast to this study where several categories of branch diameter are defined in terms of the focal subject's anatomy and body size (Table 3.5). While Hunt (1994, 1996) focuses on frequency of bipedal behaviors, data on the duration of bipedal bouts is included in this study and in Stanford (2006).

Chapter 4. Results

4.1 Data Collected

A total of 129 bipedal bouts of one second or more duration were observed during 115.25 focal observation hours of eight adult male chimpanzees at Fongoli, in May and June 2008. The possibility that a particular focal individual biased the data set was explored using regression analysis. In this analysis, the focal individual was the independent variable. Results showed that no individual was significant in terms of predicting models for the frequency, duration, or rate of bipedal behavior. Therefore, focal subject data was pooled for analysis of frequency, duration, and rate of bipedal behavior.

Using an instantaneous scan sampling method, 1334 intervals were recorded each five minutes during focal observation sampling. These data was used to determine the overall frequency of postural and locomotor behavior for Fongoli chimpanzees (Figure 4.1 and Table 4.1). Fongoli chimpanzees engaged most often in inactive postures ($n = 1054$), accounting for 79.0% of overall postural and locomotor behaviors. Quadrupedal locomotion was also frequent ($n = 199$), accounting for 14.9% of overall postural and locomotor behavior. Bipedal behaviors, including assisted and unassisted bipedal postures and locomotion ($n = 31$) accounted for 2.3% of postural and locomotor behavior observed. Additional analyses were performed using data obtained via focal all-occurrences of bipedal behavior sampling method, which allowed a more detailed look at the ecological and behavioral contexts of bipedal behavior.

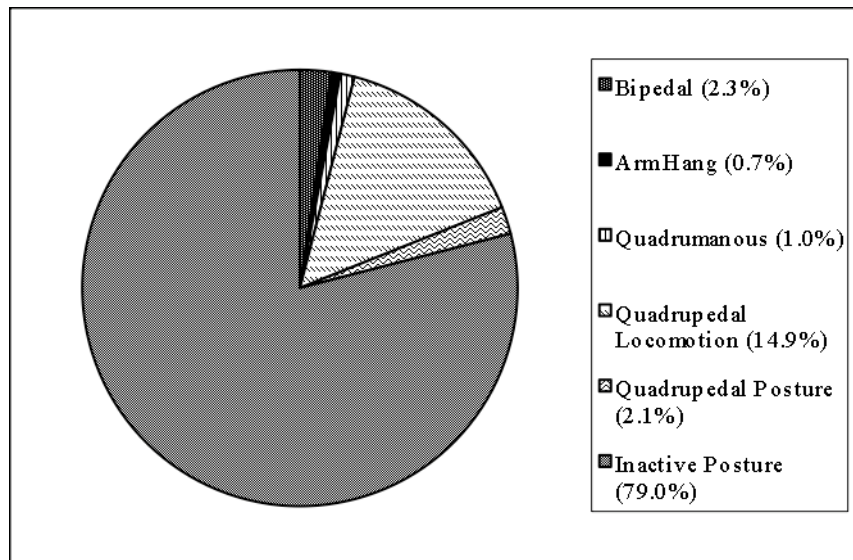


Figure 4.1 Overall breakdown of postural and locomotor behavior exhibited by Fongoli chimpanzees from instantaneous focal subject data.

Table 4.1 Summary of overall frequencies of postural and locomotor behavior for Fongoli chimpanzees, $n = 1334$, from instantaneous focal subject data. Intervals when the focal subject was not visible are excluded.

Postural/Locomotor Behavior	Bout Frequency (n)	% Frequency Overall
Bipedal	31	2.3
Arm Hang	9	0.7
Quadrumanous	14	1.0
Quadrupedal Locomotion	199	14.9
Quadrupedal Posture	27	2.1
Inactive Posture	1054	79.0

Fongoli chimpanzees engaged in both terrestrial ($n = 86$) and arboreal ($n = 43$) bipedalism. Overall time spent in terrestrial contexts was 81% versus 19% time spent in arboreal contexts. Therefore, when the frequency of terrestrial and arboreal bipedal bouts

were weighted by the percentage of time spent in each context respectively, Fongoli chimpanzees were significantly more bipedal in arboreal contexts than terrestrial contexts (Confidence Interval: 3.17 bouts/hour to 2.14 bouts per hour; see Section 4.4 for rates of bipedalism). In addition, chimpanzees engaged in both bipedal locomotion ($n = 30$; 23.3% of total occurrences) and bipedal postures ($n = 99$; 76.7% of total occurrences). Bipedal locomotion occurred terrestrially in all occurrences but one, where an adult male engaged in an agonistic threat display on a large (substrate could be encircled by individual's arms), horizontal (angle $< 10^\circ$) branch. Bipedal postures were both arboreal ($n = 43$) and terrestrial ($n = 56$).

4.2 Frequency of Bipedal Behavior

The frequency of bipedal bouts recorded for adult male chimpanzees at Fongoli did not differ significantly by focal subject ($t = -0.25$, p -value = 0.8067). Therefore, the frequency data on each focal subject was pooled for an overall analysis. Stepwise Multiple Regression Analysis was used to determine the best model for predicting the frequency of bipedal behaviors by type (postural or locomotor). Several independent variables were considered in this analysis: maintenance behavior, forelimb assistance (whether or not the forelimbs assisted in weight support during bipedal behavior), general ecological context (arboreal or terrestrial), substrate size and substrate angle for arboreal contexts, and terrain quality and terrain slope for terrestrial contexts. None of these ecological variables significantly correlated with the frequency of bipedal behavior (p -value > 0.05) in terms of the best model.

The best model for predicting bout frequency of bipedal behavior by type included the variables “maintenance behavior” and “forelimb assistance” ($r^2 = 0.672928$, p -value < 0.0001). In the best model, maintenance behavior was significantly correlated with the frequency of bipedal behavior by type, postural or locomotor ($t = 7.43$, p -value < 0.0001) (Table 4.2). Sixty-one percent of bipedal bouts occurred in the context of feeding and foraging. In addition, feeding and foraging was markedly associated with postural bipedalism (98.7% of bipedal bouts). Twenty-eight percent of bipedal bouts occurred in the context of agonistic social displays by males (Figure 4.2). During these displays, bipedal locomotion was favored (in 72.2 % of display occurrences) and was typically observed in concurrence with males using freed hands to drag or wave branches and leaves and to throw rocks as part of the display. Other maintenance behaviors associated with bipedal behavior included vigilance, social play, and copulation, which together accounted for less than 9.3% of all bipedal bouts.

Table 4.2 Frequency of bipedal behavior in terms of behavioral context and habitat.

	N				TOTAL	%
	Arboreal		Terrestrial			
Context	Postural	Locomotor	Postural	Locomotor		
Feed/Forage	39	1	38	0	78	61
Copulate	0	0	2	1	3	2
Play	0	0	2	1	3	2
Scan	1	0	8	1	9	7
Display	3	0	7	26	36	28
TOTAL	42	1	57	29	129	100

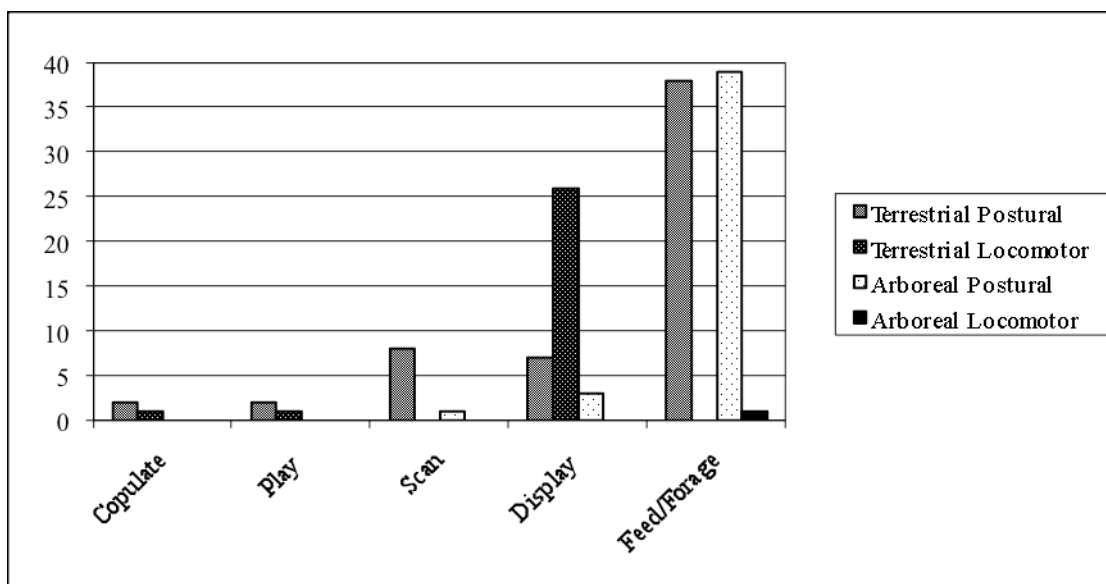


Figure 4.2 Frequency of bipedal behavior in terms of behavioral context.

In addition to maintenance behavior, forelimb assistance was also significantly correlated to the frequency of postural versus locomotor bipedalism ($t = -7.21$, $p\text{-value} < 0.0001$). Bipedal behaviors were recorded as assisted when an individual used his arms to partially support body weight (See Table 3.2 for definition). Bipedal locomotion was typically unassisted (93.3% of total occurrences), whereas bipedal postures were typically assisted (86.7% of total occurrences). A Fisher's two-tailed test confirmed that the probability of forelimb assistance differed across bipedal behaviors ($p\text{-value} < 0.0001$). A Fisher's one-tailed test showed that the absence of forelimb assistance was significantly correlated with bipedal locomotion. Ninety-three percent of the bouts of bipedal locomotion ($n = 28$ of 30 total bouts) were unassisted. Therefore, forelimb assistance was more closely associated with bipedal postures. Only 13 postural bipedal bouts (total $n = 99$) were unassisted. This was regardless of general context, arboreal or terrestrial, of the bipedal postures. Figure 4.3 illustrates the frequency of assisted and unassisted bipedal postures

according to type of bipedal behavior (postural or locomotor) and general context (arboreal or terrestrial). Overall, 86.9% of bipedal postures were assisted.

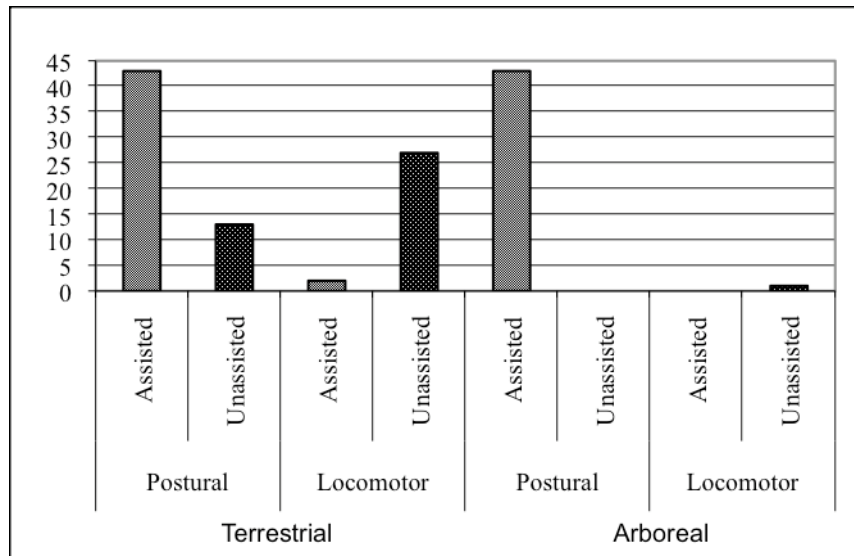


Figure 4.3 Frequency of assisted and unassisted bipedal bouts according to type of bipedal behavior (postural or locomotor) and context (arboreal or terrestrial).

4.3 Duration of Bipedal Behavior

The duration of bipedal bouts recorded for Fongoli adult male chimpanzees did not differ significantly by focal subject in either arboreal (F Ratio = 1.2852, p-value = 0.2853) or terrestrial contexts (F Ratio = 0.5753, p-value = 0.7739). Therefore, the duration data on each focal subject was pooled for an overall analysis of duration. Bipedalism was characterized by brief bouts of a few seconds or extended bouts that lasted up to half a minute in duration (Figure 4.4). Seventy-four of 129 bipedal bouts were brief, lasting less than five seconds. Fifty-five bipedal bouts ranged from five seconds to 39 seconds. Three bipedal bouts lasted more than 30 seconds. These longer bipedal bouts involved observations of adult male

chimpanzees feeding and foraging for *Saba senegalensis* fruit in an arboreal context using postural bipedalism.

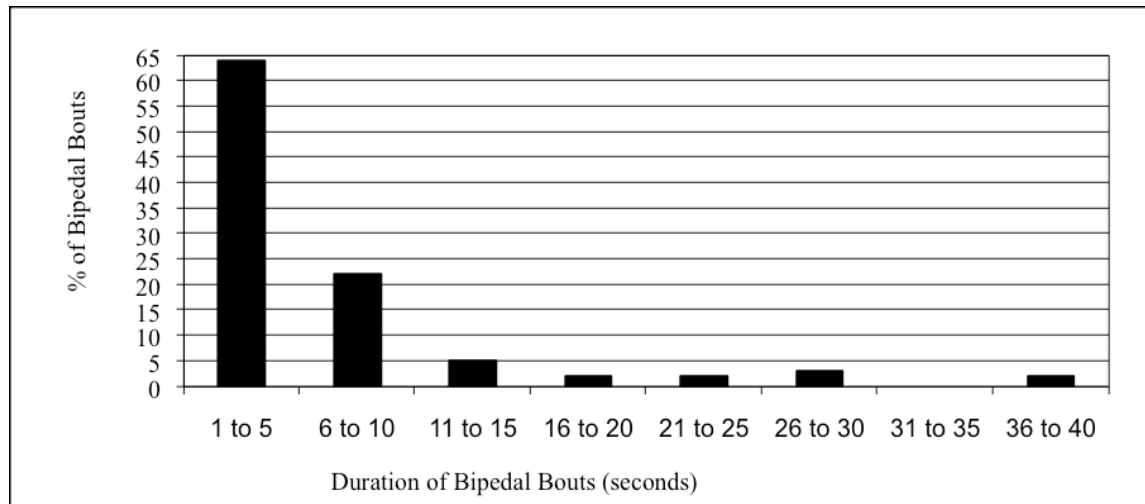


Figure 4.4 Percentage of bipedal bouts according to bout duration.

The average bipedal bout duration for Fongoli adult male chimpanzees was 6.54 seconds ($s = 0.658$). This is statistically shorter than the average duration observed by Stanford (2006) at Bwindi (11.9 seconds). However, Stanford (2006) limited his calculation of average bout duration to include only those lasting greater than or equal to five seconds. For comparison to Bwindi chimpanzees (Stanford 2006), average bout duration for Fongoli chimpanzees was calculated excluding bouts less than five seconds ($n = 53$). The average bipedal bout length for bouts lasting greater than or equal to 5 seconds was 12.073 seconds ($s = 1.184$). This is statistically similar to the duration of bipedal bouts observed at Bwindi (95% Confidence Interval: 14.445 seconds to 9.700 seconds).

Both postural and locomotor bipedal bouts were observed in arboreal and terrestrial contexts. The average bout duration for postural bipedalism was 7.35 seconds ($s = 0.74$).

The average bout duration for locomotor bipedalism was 3.83 seconds ($s = 1.35$). There was a statistically significant difference in the average bout durations of postural and locomotor bipedalism ($t = -2.294$, $p\text{-value} = 0.0234$). Maintenance behavior was not significant in determining the duration of bipedal behavior ($F \text{ Ratio} = 2.232$, $p\text{-value} = 0.0683$). Ninety-five percent confidence intervals were calculated in order to determine whether statistically significant differences in bipedal behavior existed across categories of the specific ecological independent variables involved in arboreal and terrestrial contexts. When 95% confidence intervals overlapped for these categories, they were deemed similar in terms of average duration of bipedal behavior and were not statistically different. According to the confidence interval analysis, the duration of bipedal bouts did not differ statistically by branch diameter (See Table 4.3 for summary), branch slope (Table 4.4), or food type (for bipedalism observed during feeding and foraging, Table 4.5) in arboreal contexts. Likewise, the duration of bipedal bouts did not differ statistically by terrain slope (Table 4.6), terrain quality (Table 4.7), or food type (during feeding and foraging, Table 4.8) in terrestrial contexts according to analysis of overlapping 95% confidence intervals. However, the duration of bipedal bouts did differ significantly by general context of bipedal behavior (arboreal or terrestrial) as illustrated by the “best” model for predicting the duration of bipedal behavior in Fongoli chimpanzees.

Table 4.3 Summary of 95% confidence intervals for duration of arboreal bipedal behavior according to branch diameter categories. Duration of arboreal bipedal bouts did not correlate significantly with branch diameter (F Ratio = 2.0183, p-value = 0.1108). Because the 95% confidence intervals overlapped in range for each category of branch diameter, the duration of bipedal behavior did not differ statistically for any branch diameter category.

Branch Diameter	Frequency of Bipedal Behavior (n)	Average Duration (sec)	Lower 95% CI	Upper 95% CI
Small	27	9.0741	16.21	55.794
Medium	11	11.2727	5.26	12.883
Large	4	11.7500	5.30	17.241
Multiple Branches	1	3.0000	-16.79	22.794

Table 4.4 Summary of 95% confidence intervals for duration of arboreal bipedal behavior according to branch angle categories. Duration of arboreal bipedal bouts did not correlate significantly with branch angle (F Ratio = 2.453, p-value = 0.7836). Because the 95% confidence intervals overlapped in range for each category of branch angle, the duration of bipedal behavior did not differ statistically for any branch angle category.

Branch Angle	Frequency of Bipedal Behavior (n)	Average Duration (sec)	Lower 95% CI	Upper 95% CI
Horizontal	15	11.8667	6.43	17.302
Oblique	28	9.5714	5.59	13.550
Vertical	0			
Multiple Branches	1	9.0000	-12.05	30.051

Table 4.5 Summary of 95% confidence intervals for duration of arboreal bipedal behavior that occurred during feeding and foraging according to food type categories. Duration of arboreal bipedal bouts did not correlate significantly with food type (F Ratio = 0.0239, p-value = 0.9764). Because the 95% confidence intervals overlapped in range for each category of food type, the duration of bipedal behavior did not differ statistically for any food type category.

Food Type	Frequency of Bipedal Behavior (n)	Average Duration (sec)	Lower 95% CI	Upper 95% CI
Leaves/Flowers	4	9.24000	-1.332	19.832
Saba Fruit	36	10.4444	6.917	13.972

Table 4.6 Summary of 95% confidence intervals for duration of terrestrial bipedal behavior according to terrain slope categories. Duration of terrestrial bipedal bouts did not correlate significantly with terrain slope (F Ratio = 0.2408, p-value = 0.7866). Because the 95% confidence intervals overlapped in range for each category of terrain slope, the duration of bipedal behavior did not differ statistically for any terrain slope category.

Terrain Slope	Frequency of Bipedal Behavior (n)	Average Duration (sec)	Lower 95% CI	Upper 95% CI
Horizontal	76	4.48684	3.452	5.522
Oblique	8	5.50000	2.310	8.690
Vertical	1	3.0000	-6.023	12.023

Table 4.7 Summary of 95% confidence intervals for duration of terrestrial bipedal behavior according to terrain quality categories. Duration of terrestrial bipedal bouts did not correlate significantly with terrain quality (F Ratio = 1.8835, p-value = 0.1214). Because the 95% confidence intervals overlapped in range for each category of terrain quality, the duration of bipedal behavior did not differ statistically for any terrain quality category.

Terrain Quality	Frequency of Bipedal Behavior (n)	Average Duration (sec)	Lower 95% CI	Upper 95% CI
Loose Soil	27	3.74074	2.054	5.427
Plateau	12	5.83333	3.304	8.363
Rocky	7	3.14286	-0.169	6.455
Slippery	6	8.50000	4.923	12.077
Smooth	33	4.36364	2.838	5.889

Table 4.8 Summary of 95% confidence intervals for duration of terrestrial bipedal behavior according to food type categories. Duration of terrestrial bipedal bouts did not correlate significantly with food type (F Ratio = 1.6579, p-value = 0.1680). Because the 95% confidence intervals overlapped in range for each category of food type, the duration of bipedal behavior did not differ statistically for any branch diameter category.

Food Type	Frequency of Bipedal Behavior (n)	Average Duration (sec)	Lower 95% CI	Upper 95% CI
Saba Fruit	8	7.3750	4.261	10.489
Flowers/Leaves	16	5.5000	3.298	7.702
Termite*	10	5.2000	2.415	7.985
Honey	1	7.0000	-1.808	15.808

* During bipedal bouts involving feeding and foraging for termites, focal subjects would select and modify fishing tools while standing bipedally. This appeared to give the focal subject a full view of the patch from which they selected the tool as well as freed the hands for making the tool.

Stepwise Multiple Regression Analysis was used to determine the “best” model for predicting the duration of bipedal bouts. A one-variable model including the general context of bipedal behavior (arboreal or terrestrial) was produced. This one-variable model was useful in predicting bout duration (F Ratio = 19.7990, p-value < 0.0001). However, the one-variable model only explains 13.487% of the variation in bipedal bout length. Despite this low degree of explained variability, the duration of bipedal bouts was statistically different for arboreal and terrestrial contexts ($t = 4.449611$, p-value < 0.0001). The average bout duration for terrestrial bipedalism was 4.565 seconds ($s = 0.758$). The average bout duration for arboreal bipedalism was statistically greater ($t = 4.450$, p-value < 0.0001) than the duration of bouts in arboreal contexts, with an average duration of 10.3401 seconds ($s = 1.0534$). The longer duration of bouts of postural bipedalism in arboreal contexts than in terrestrial contexts may contribute to this statistical difference. The average duration of bouts of bipedal posture in arboreal contexts ($n = 99$) was 10.302 seconds ($s = 1.579$) versus an average duration of 5.090 seconds ($s = 0.5961$) in terrestrial contexts ($n = 30$). In addition, bouts of bipedal locomotion occurred most often in terrestrial contexts and tended to be much shorter in duration than bipedal postures (mean duration = 3.552 seconds, $s = 0.828$), which may also contribute to the statistical difference in duration of arboreal and terrestrial bipedal bouts.

4.4 Rate of Bipedal Behavior

The average rate of bipedal behavior was first calculated as the number of bipedal bouts per each hour of observation (Figure 4.5). Multivariate analysis was run in order to determine whether or not the rate of bipedalism varied significantly by focal subject. This

analysis confirmed that focal subjects did not differ significantly in rate of bipedal behavior (F Ratio = 1.4438, p-value = 0.1941). Therefore, the rate of bipedal behavior data for subjects was pooled to produce an average rate of bipedal behavior for Fongoli chimpanzees. The average rate of bipedalism for Fongoli chimpanzees was 1.05 bouts/hour ($s = 0.148$). The 95% confidence interval calculated for this average rate of bipedalism ranged from 1.34 bouts/hour and a lower limit of 0.75 bouts/hour. Because this confidence interval did not include the average rate of bipedalism calculated by Stanford (2006) at Bwindi (0.73 bouts/hour), the average rate of bipedalism at Fongoli is statistically different. Fongoli chimpanzees are significantly more bipedal than chimpanzees at Bwindi.

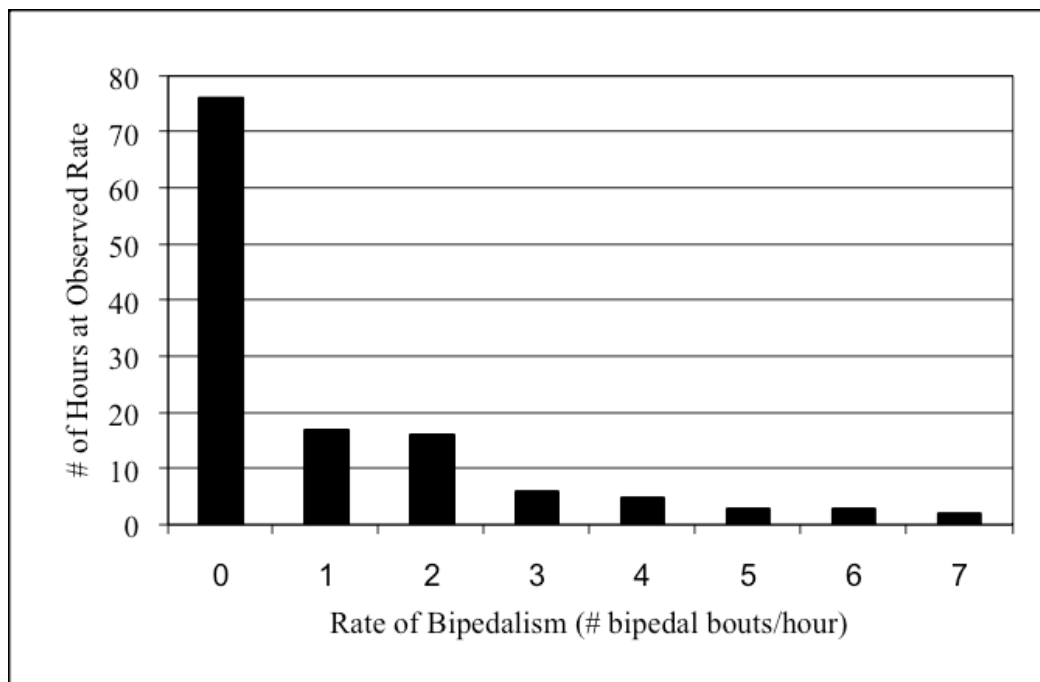


Figure 4.5 Summary of observation hours by rate of bipedalism observed during those hours.

The rate of bipedalism differed with regard to context (arboreal or terrestrial) for Fongoli chimpanzees. The average rate of bipedalism in arboreal contexts was 2.05

bouts/hour, while in terrestrial contexts the average rate was 0.95 bouts/hour. Fongoli chimpanzees were significantly more bipedal in arboreal contexts with respect to the amount of time spent in each context passed on analysis of the confidence interval calculated for the rate of bipedalism in arboreal contexts (Confidence Interval: 3.17 bouts/hour to 2.14 bouts/hour). The average rate of bipedalism for Fongoli chimpanzees was 2.7 bouts/hour during feeding and foraging, the behavioral context in which most bipedal behavior occurred.

4.5 Comparison of Results Across Study Sites

Table 4.9 Comparison of Fongoli chimpanzee bipedal bouts with those recorded by Hunt (1994, 1998) in Mahale and Stanford (2006) in Bwindi, adapted from Stanford (2006).

Study Site	Observation Hours (N)	Rate of Bipedalism (bipedal bouts/hour)	% Postural	% Locomotor
Bwindi (Stanford 2006)	246.7	0.73	99.4	0.06
Mahale (Hunt 1994, 1996)	571.0	0.17	84.8	15.2
Fongoli	115.25	1.05	76.7	23.3

In terms of the frequency of bipedal behavior, Fongoli chimpanzees engage in both locomotor and postural bipedalism in arboreal and terrestrial contexts. This is different from the bipedal behavior that Stanford (2006) observed in Bwindi chimpanzees, which engaged primarily in arboreal postural bipedalism. Hunt (1994, 1996) observed both postural and locomotor bipedalism at Mahale and Gombe, although he observed a lower frequency of bipedal locomotion (Hunt 1994, 1998) than was observed in the Fongoli chimpanzees. In terms of the mean duration of bipedal behavior, the Fongoli chimpanzees were statistically similar when bouts lasting under 5 seconds were excluded for direct comparison with Stanford (2006). Comparison of mean duration was not possible with Mahale and Gombe

chimpanzees because Hunt (1994, 1996) did not provide this information. Finally, in terms of the average rate of bipedal behavior, Fongoli chimpanzees engage in 1.05 bouts/hour on average. This is statistically different from chimpanzees at Bwindi, Mahale, and Gombe (95% Confidence Interval: 1.34 bouts/hour to 0.75 bouts/hour). These differences in the frequency, duration, and rate of bipedal behavior among chimpanzees at different sites (Table 4.9) suggest environmental differences underlying behaviors.

Chapter 5. Discussion

5.1 Introduction

While the results of this study are preliminary, they can help to evaluate the ecological and behavioral contexts favoring the evolution of habitual bipedalism in early hominids. In the past, referential models for the evolution of bipedalism have been based on either homology (“similarity due to common descent”) or analogy (“similarity due to common adaptation”) to the referent (Moore 1996). Fongoli chimpanzees provide a unique opportunity for a stronger referential model, based both on “analogy,” living in habitats similar to those reconstructed for early hominids, and “homology,” given the close phylogenetic relationship between chimpanzees and hominids (Moore 1996; Chen & Li 2001). Although Sayers and Lovejoy (2008) recently criticized referential models based on chimpanzees, I argue that a focus on this species can provide valuable insight into aspects of hominid behavior, including bipedalism. In particular, comparisons of Fongoli chimpanzee bipedal behavior to other sites, in particular Bwindi (Stanford 2006), Mahale, and Gombe (Hunt 1994, 1996), has important implications for understanding the evolution of this unique trait. These across-site comparisons allow the evaluation of hypotheses relating to the selective pressures at work in shaping habitual bipedalism that have been suggested in the literature. In addition, the results of this study shed light on methodological issues that limit these comparisons as well as provide important directions for future research.

5.2 The Ecological Context of Bipedal Behavior

Many of the hypotheses proposed to explain the evolution of bipedal behavior in early hominids exclusively cite either arboreal bipedalism (Tuttle 1975; Stanford 2006) or

terrestrial bipedalism (Jolly 1970; Rose 1976, 1984, 1991; Wrangham 1980) as being particularly important in the evolution of this behavior. To date, the exception has been Hunt (1994, 1996) who suggests that neither arboreal bipedal nor terrestrial bipedal explanations alone are satisfactory in reconstructing the adaptive scenario accounting for the evolution of habitual bipedalism in hominids. He argues that strictly arboreal hypotheses overlook the extent to which bipedal adaptations for terrestrial habitual locomotion has been perfected, citing refinements such as shock-absorption in the foot as unexplained and unnecessary in arboreal bipedalism (Hunt 1994). Likewise, he suggests that strictly terrestrial hypotheses lack the ability to explain the persistence of arboreal traits despite the evolution of habitual bipedalism in hominids (Hunt 1994). Hunt (1994, 1996) proposed the “small tree feeding” hypothesis, which centralized feeding and foraging for fruit in both terrestrial and arboreal contexts based on his observations of Mahale and Gombe chimpanzees. The lack of hypotheses that combine arboreal and terrestrial components for the evolution of habitual bipedalism in hominids may be the result of the ecological contexts on which these referential models have been based. For example, Stanford (2006) centralized arboreal bipedal postures during feeding and foraging in his hypothesis but evidenced his explanation using observations of Bwindi chimpanzees, which were unhabituated and lived in a dense rainforest type environment where they were rarely observed in terrestrial contexts. Likewise, Wrangham (1980) used observations of gelada baboons who are almost strictly terrestrial in the development of his upright posture and shuffling bipedalism hypothesis. Fongoli chimpanzees differ from the expectations of these hypotheses in their bipedal behavior and the ecological contexts in which these behaviors are favored.

Adult male chimpanzees at Fongoli engaged in bipedal behavior in a variety of ecological contexts. Both arboreal and terrestrial bipedalism are important in terms of the bipedal behavior of these savanna chimpanzees, although chimpanzees were significantly more frequent in their bipedal behavior in the trees. In contrast, Stanford (2006) primarily observed arboreal bipedalism in Bwindi chimpanzees of all ages and sex classes with no evidence of terrestrial bipedalism. This is a marked difference between the bipedal behavior of Fongoli chimpanzees and Bwindi chimpanzees. Fongoli chimpanzees do share similarities in terms of the occurrence and frequency of arboreal and terrestrial behavior with chimpanzees at Mahale and Gombe as demonstrated by Hunt (1994, 1996). The differences between Fongoli and Bwindi chimpanzees as well as similarities with Mahale and Gombe chimpanzees suggest the importance of general ecological context in determining the occurrence of bipedal behavior (discussed in detail in Chapter 5.5). Both arboreal and terrestrial bipedalism should be considered in scenarios that seek to explain the evolution of habitual bipedalism in hominids, as Hunt (1994, 1996) indicates.

A detailed look at the bipedal behavior of Fongoli chimpanzees reveals important differences across arboreal and terrestrial contexts, which may have important implications for the types of hypotheses favored in explaining the evolution of habitual bipedalism in hominids. In particular, type of bipedal behavior differed between substrates, with short bouts of bipedal locomotion occurring primarily in terrestrial contexts and bipedal postures occurring frequently in both contexts. Many researchers cite arboreal or terrestrial bipedal postures as an important part of the prehomimid behavioral repertoire (Tuttle 1975; Jolly 1970; Rose 1976, 1984, 1991; Wrangham 1980; Stanford 2006). This study brings attention to the

importance of short bouts of bipedal locomotion that have often been overlooked in the literature as an important part of the evolution of habitual bipedalism in early hominids. In particular, reconstructions of prehominids should consider bipedal locomotion in addition to the arboreal and terrestrial bipedal postures that are often part of these scenarios.

Incorporating arboreal and terrestrial components into hypotheses regarding the evolution of habitual bipedalism has been infrequent in the literature with the exception of Hunt (1994, 1996). However, specific ecological variables such as branch diameter and angle (in the case of arboreal bipedalism) have been included (i.e. Stanford 2006). Related hypotheses (Stanford 2006; Hunt 1994, 1996) seek to understand the particular conditions under which bipedal postures are exhibited. Stanford (2006) observed that both the frequency and duration of arboreal bipedal postures increased significantly with increasing branch sizes and branch angles. Likewise, Hunt (1994) cites terminal branch feeding in arboreal contexts and small fruit tree feeding and foraging in terrestrial contexts as being particularly important as well as fruit size. Interestingly, specific ecological variables were not important or significant in the frequency or duration of bipedal behavior in Fongoli chimpanzees. Bouts of arboreal bipedalism did not differ across categories of branch diameter or branch angle. Likewise, terrestrial bipedalism did not significantly correlate with terrain slope or quality. This may be the result of a lack of variation in these categories in terms of Fongoli chimpanzee overall substrate use in some cases, which may affect the ability of these categories to elicit differences in bipedal behavior. For example, Fongoli chimpanzees primarily use small substrates arboreally (47%), as well as medium (29%) and large (21%) with very little use of extra-large substrates (2%) (Pruetz, Tourkakis &

Linshield, in prep.; See Table 3.5 for definitions). In contrast, this lack of difference across categories may also suggest that Fongoli chimpanzees adopted similar bipedal behaviors in a wide variety of contexts, regardless of these specific ecological variables. It is possible that Fongoli chimpanzees are simply more behaviorally bipedal than other chimps as an adaptation to a savanna-mosaic environment. This behavioral emphasis on bipedal behavior results in the use of bipedal postures under a wide variety of ecological conditions in terms of substrates that is not seen at other sites, where chimpanzees use bipedal postures only under specific conditions or contexts. In order for habitual bipedalism to evolve, bipedal postures may have been favored in a wide variety of ecological and behavioral contexts. In addition to what appears to be a lack of specificity in terms of ecological variables related to bipedal behavior, the behavioral contexts of bipedal behavior exhibited by Fongoli chimpanzees (discussed at length in Chapter 5) suggest that bipedal postures and locomotion may have been causally-unrelated, being favored simultaneously in different behavioral and ecological contexts. Bipedal locomotion appears to be favored primarily during intraspecific displays in terrestrial contexts, while bipedal postures are more associated with feeding and foraging in arboreal contexts and, to a lesser degree, in terrestrial contexts. Evidence from Fongoli chimpanzees in particular seems to suggest that this is a plausible scenario and that the specific ecological factors cited in other hypotheses (i.e. Stanford 2006) are not as important in the evolution of habitual bipedalism as are the general ecological and behavioral contexts.

5.3 The Behavioral Context of Bipedal Behavior

Behavioral context correlated significantly with the type of bipedal behavior observed as well as the frequency and duration of bipedal behaviors in Fongoli chimpanzees. Feeding

and foraging behaviors significantly correlated with the occurrence of assisted bipedal postures observed in both arboreal and terrestrial contexts. Terrestrial bipedal locomotion was most frequently linked with aggressive displays, during which hands were often involved in throwing rocks or swinging and dragging branches. Both of these behavioral contexts have been centralized in hypotheses relating to the evolution of habitual bipedalism in hominids.

Feeding and foraging was associated with a significantly high rate of bipedal behavior at Fongoli (2.7 bouts/hour). In particular, the frequent occurrence of assisted bipedal postures during feeding and foraging may be relevant to a specific need for forelimb-assisted bipedal postures. This frequently adopted posture appears to be a feeding and foraging adaptation, aimed at freeing the hands and extending the reach for preferred food items. This explanation is well supported in the literature. Leutenegger (1987) argued that feeding and foraging explanations for the evolution of bipedalism were the most supportable scenarios, as this behavior takes up a large amount of the daily time budget of the typical primate. In addition, feeding and foraging has played a centralized role in many of the hypotheses related to the evolution of habitual bipedalism in early hominids (Jolly 1970; Tuttle 1975; Rose 1976, 1984; Wrangham 1980; Hunt 1994, 1996; Videan & McGrew 2002; Stanford 2006). Both Hunt (1994, 1996) and Stanford (2006) interpret feeding and foraging contexts as being particularly important in the evolution of bipedal behavior from their observations of chimpanzees at Bwindi (Stanford 2006), Mahale, and Gombe (Hunt 1994, 1996). Doran (1992) found that adult male chimpanzees at Tai Forest in the Ivory Coast exhibited increased bipedal behaviors during feeding as compared to traveling, where quadrupedalism

was most frequent. Likewise, Videan and McGrew (2002) cite experimental evidence that chimpanzees increased bipedal postures during “foraging” manipulations.

Bipedal locomotion at Fongoli was most frequently unassisted and occurred in the behavioral context of agonistic displays by adult male chimpanzees. These displays often involved chimpanzees using their hands to throw rocks, drag leaves, or drag and shake branches while engaging in a bipedal run. In addition to locomotor bipedal displays, male chimpanzees also engaged in postural bipedal threat displays. Both postural and locomotor bipedal displays occurred most frequently in terrestrial contexts, with locomotor displays occurring on the ground in 91.7% of bipedal bouts. These results provide support for several display hypotheses suggested in the literature (Kortlandt 1990; Jablonski and Chaplin 1993). Jablonski and Chaplin (1993) suggested that these bipedal-threat displays would have played an important role in intraspecific competition as resources became more patchy and dispersed in the late Miocene.

Walter (2004) suggested that bipedal defense postures would have been important in deterring attacks by coursing predators. Although not directly supported by these data, bipedal behavior in these displays demonstrates that this postural and locomotor mode is often adopted by chimpanzees under conditions when hands are freed to throw rocks, and drag and shake branches or leaves. Fifer (1987) centralizes this as an important aspect of bipedal behavior used in both defense and in intraspecific display behaviors. These behaviors may have been important in the past for deterring predators. In particular, these behaviors may give the chimpanzee the appearance of “standing up” or “standing firm” against potential predators, making an attack less likely as suggested by Walter (2004).

However, behaviors such as scanning the landscape, commonly associated with vigilance hypotheses for the evolution of bipedal behavior in hominids were not seen frequently in Fongoli adult male chimpanzees except in a few instances.

Many potential predators have largely been exterminated by humans at Fongoli (Pruetz 2008). Potential predators that remain include spotted hyenas (*Crocuta crocuta*) and leopards (*Panthera pardus*) (Pruetz 2008), in addition to threats such as black mambas (*Dendroaspis polylepis*), cobra species (*Naja*), puff adders (*Bitis arietans*) and rock pythons (*Python sebae*) (Pruetz, pers. comm.). Chimpanzees have been observed to react to side-striped jackals (*Canis adustus*) as if they were considered a threat (Pruetz, pers. comm.). Humans may also pose a threat to chimpanzees at Fongoli, although humans rarely hunt chimpanzees at this site (Pruetz 2006, 2008). Humans recently captured an infant chimpanzee at Fongoli, which was successfully returned to her mother, for example (Pruetz & Kante, in prep.). In general, there is relatively low predator pressure at Fongoli compared to some other sites, which may explain the lack of vigilance and defense behaviors exhibited by adult male chimpanzees. Despite the relatively low predator pressures on Fongoli chimpanzees, occurrences of bipedal scans and displays by one adult male, Diouf, after the group was approached by a “strange” human provides anecdotal evidence for such hypotheses. In the aftermath of the encounter, Diouf engaged in several bouts of bipedal behavior involving both scans of the landscape, presumably to confirm that the man was gone, and bipedal displays including leaf clipping, a behavior commonly associated with these displays in Fongoli adult males (Pruetz, unpublished data). While humans do not pose a significant threat to Fongoli chimpanzees, “strange” humans unknown to the group may be threatening

from the perspective of chimpanzees. Diouf exhibited vigilance and defense behaviors associated with bipedalism immediately following the chimpanzee group's encounter with the man, which left the group visibly nervous. The aforementioned behavior supports some aspects of these hypotheses by Walter (2004) and Jablonski & Chaplin (1993).

Although vigilance hypotheses are well supported in the literature (Day 1986; Walter 2004), they often involve using bipedal posture to scan the landscape, a behavior that was not frequently seen associated with bipedal behavior in Fongoli chimpanzees. The lack of observation of scan behaviors in Fongoli chimpanzees is congruent with observations by Hunt (1994) and Stanford (2006) who also rarely observed bouts involving vigilant scan behaviors. Videan and McGrew's (2002) experimental manipulations to test the plausibility of the "vigilance" hypotheses yielded similar results. Only three occurrences of bipedal behaviors in this study included vigilant scanning by an adult male, Diouf. These vigilant scans occurred after the encounter with a "strange" human discussed previously. Despite the infrequency of adult males engaging in vigilant scans of the landscape, data recorded *ad libitum* shows that adolescent and juvenile males were also observed engaging in bipedal behaviors occasionally in this behavioral context. This suggests that perceived threat or predation pressure may differ across age-sex classes in terms of its expression in vigilance behaviors. Therefore, differences in bipedal behavior may exist across age-sex class in this behavioral context.

Because only adult male chimpanzees were included in focal all-occurrences observations of bipedal behavior due to research protocol restrictions, the importance of behavioral contexts such as scan behavior as well as other behaviors (i.e. play) may be

skewed. Adult males are less likely to engage in such behaviors in general (Goodall 1986). Likewise, the frequent occurrence of bipedal locomotion in displays may result from important differences between adult male chimpanzees and other age-sex classes. Display behaviors do not occur as frequently in other age-sex classes (Goodall 1986). Bipedal locomotion may be more frequently incorporated into other behavioral contexts, such as play behavior in younger chimpanzees and carrying behaviors in adult female chimpanzees with young infants. Differences across age and sex class in terms of the behavioral contexts of bipedal behavior should be considered in developing a plausible scenario for the evolution of habitual bipedal behavior in hominids.

5.4 Forelimb Assistance in Bipedal Behavior of Chimpanzees

Both Stanford (2006) and Hunt (1994, 1996), as well as others (Tuttle 1975) place particular emphasis on the occurrence of forelimb assisted bipedalism. Forelimb assisted bipedal behaviors, defined as using one or both hands to grip a substrate in order to provide balance while most of the body weight is supported by the hindlimbs, was observed frequently at Bwindi (Stanford 2006) and Mahale and Gombe (Hunt 1994, 1996). In addition, forelimb assistance was significantly correlated to the frequency of bipedal behavior by type (postural or locomotor) for bipedal behavior observed in Fongoli chimpanzees. In fact, this variable was included in the best model for predicting the frequency of bipedal behavior by type for Fongoli chimpanzees. Likewise, it plays a dominant role in the hypotheses and reconstructions of the last prehomnids suggested by both Stanford (2006) and Hunt (1994, 1996, 1998).

Despite the predicting power of forelimb assistance in terms of the results of this study and its centralized place in the scenarios proposed by Stanford (2006) and Hunt (1994, 1996, 1998), other reasons for the occurrence of forelimb assisted behaviors in general could also be considered. Despite the frequency of assisted bipedal postures, it remains unclear in the literature and in the context of this study whether or not assistance by the arms in load-bearing in bipedal behaviors exhibited by chimpanzees is important in terms of its application to understanding the evolution of habitual bipedal behavior in hominids. This forearm assistance may simply be a result of the “compromise” morphology that Rose (1991) suggests is displayed by higher primates, including the apes. The “compromise” morphology exhibited by chimpanzees allows a certain degree of behavioral flexibility in terms of postural and locomotor behavior that would not have been possible given the specialized bipedal morphological adaptations exhibited by early hominids. This is supported by Vereecke et al. (2005) who suggest that the morphological features of the postcrania in some apes, such as the genus *Pan*, tend to reflect an adaptation for behavioral flexibility in positional behavior. This stands in contrast to humans, who exhibit morphological specializations, such as a rigid foot-ankle complex, that relate directly to habitual bipedalism rather than allowing for flexibility (Vereecke et al. 2005).

Forelimb assistance may be indicative of particular behavioral contexts, for instance feeding and foraging, in which the forelimbs are used more or less for balance during reaching for food items, particularly those that are chosen carefully. For instance, it was often observed ad libitum that Fongoli chimpanzees would not simply pick and eat each *Saba* fruit within proximity when foraging in trees. Rather, individuals would often choose fruits

by smelling and manipulating them, rejecting some fruits and choosing to pick and eat others. Forelimb assistance using one arm while the other remains free to grasp food items may serve to extend the reach of the foraging arm and hand, making picking preferred fruits or flowers and other food items that are dispersed in trees more efficient. This would suggest that forelimb assistance is not particularly important in terms of the frequency of actual bipedal behavior but rather a positional behavior particularly related to feeding and foraging, regardless of positional behavior. Bipedal behavior in this sense, would “free the hands” as has been suggested by Gebo (1996) and Videan and McGrew (2002) for more efficient foraging for food items in trees. It may be insignificant to consider divergence in forelimb assistance in terms of bipedal postures and locomotion, arboreally or terrestrially for these reasons. Hunt (1994) has also placed importance on the freedom of hands for efficiency in feeding and foraging, suggesting that harvesting fruit using both hands allows for more fruit to be gathered. However, Hunt (1994) suggests this specifically in relation to terrestrial bipedalism in which forearm assistance was less frequently seen in combination with bipedal postures.

Data indicating a divergence in the presence or lack of forelimb assistance during bouts of postural bipedalism may provide important information in terms of defining the suite of traits expected for the last common ancestor, particularly if this ancestor is assumed to be primarily arboreal. Similar to observations by Stanford (2006) on Bwindi chimpanzees, Fongoli chimpanzees frequently adopted forelimb assisted bipedal postures in arboreal settings. In fact, all arboreal postures exhibited by Fongoli adult male chimpanzees were assisted and this variable proved significant in determining the occurrence of bipedal

behavior by type (postural or locomotor). Although Stanford (2006) does not report terrestrial bipedalism, bouts of postural bipedal behavior demonstrated by Fongoli chimpanzees were significantly dependent on forelimb assistance in both terrestrial and arboreal contexts. Likewise, this may indicate a degree of morphological flexibility in terms of postural and locomotor behavior in the last prehomnids, similar to what we see in extant chimpanzees.

5.5 Comparisons Across Chimpanzee Sites

One of the main goals of this study was to contrast Fongoli chimpanzees with chimpanzees at other sites in terms of bipedal behavior, particularly at Bwindi (Stanford 2006) and Mahale and Gombe (Hunt 1994, 1996). The goal of this comparison is to evaluate to what extent ecological contexts influence bipedal behaviors across sites. In order to do this, descriptions of the habitats characterizing the chimpanzee ranges across field sites in Fongoli, Bwindi, Mahale, and Gombe are necessary. Fongoli chimpanzees inhabit a mosaic savanna-woodland habitat consisting of primarily open woodland and grassland habitat with small patches of gallery forests and seasonally cultivated fields (Pruetz 2006; Pruetz & Bertaloni 2007; See Chapter 2 and Chapter 3 for detailed description). Comparisons of descriptions of Bwindi (Stanford 2006), Mahale (Matsumoto-Oda 2002), and Gombe (Goodall 1986) to the habitats characterizing the Fongoli chimpanzee range suggest that the Fongoli chimpanzees inhabit the most open, savanna-mosaic type habitat of these three chimpanzee ranges. Fongoli particularly stands in contrast to the habitat of Bwindi chimpanzees. The Bwindi study site is located in the eastern region of Bwindi Impenetrable National Park in southeastern Uganda (Stanford 2006). Stanford (2006) describes the

Bwindi chimpanzees' range as being composed of rugged hills and deep ravines at high elevations with wet montane forest dominated by a variety of tree species as well as swamp and bamboo forests. Bwindi is characterized by two dry seasons, from May to July and late December to February (Stanford 2006). The Bwindi chimpanzees were not habituated for close terrestrial approaches by researchers, and very dense undergrowth inhibited Bwindi chimpanzees from being observed terrestrially (Stanford 2006).

Hunt (1994, 1996) observed chimpanzee bipedal behavior primarily at Mahale (N = 571.0 hours) and supplemented these observations with data from Gombe (N = 130 hours). Although Hunt (1994, 1996) does not provide detailed habitat description for either Mahale or Gombe, habitat information from Matsumoto-Oda's (2002) study of behavioral seasonality in chimpanzees at Mahale and Goodall's (1986) description of the habitat comprising the Gombe chimpanzee range allows comparison. The Mahale chimpanzee site is located in Mahale Mountains National Park, Tanzania, and is comprised of 70% gallery forests, with the remainder being woodland and tracts of land cleared by slash-and-burn agriculture (Matsumoto-Oda 2002). Mahale exhibits distinct wet and dry seasons, with fruit availability at its lowest level during the late wet season and at its peak in the early wet season (Matsumoto-Oda 2002). Matsumoto-Oda (2002) reported behavioral seasonality correlating with fruit availability in regards to daily group size, traveling behavior, and consumption of animal foods among Mahale chimpanzees. The Gombe field site, located in Gombe National Park, Tanzania, is also marked by dry and wet seasons (Goodall 1986). According to Goodall (1986), Gombe is generally characterized by rugged landscape with steep-sided valleys intersected by deep ravines. Goodall (1986) also provides information

regarding the habitat characterizing Gombe chimpanzees' range, which includes five major microhabitat types: subalpine moorland, open woodland, semideciduous forest, evergreen forest, and grasslands with scattered trees. During the dry season, conditions are ideal for observation while during the wet season, dense undergrowth can obstruct researcher views of chimpanzees (Goodall 1986). However, Hunt (1994, 1996) does not indicate during which season(s) observations on the bipedal behavior of chimpanzees at Mahale and Gombe were made.

Of these study sites, the Fongoli field site is characterized by microhabitats most analogous to those inhabited by early hominids. Reconstructions of the paleoenvironments suggest that early hominid ranges were typified by savanna and woodland habitats, with interspersed wooded and closed habitats as well as more open habitats (Kappelman et al. 1997; Reed 1997; See Chapter 2 for detailed discussion). Therefore, similarities and differences between the bipedal behavior demonstrated by Fongoli chimpanzees in comparison with chimpanzees at Mahale, Gombe, and Bwindi suggest important implications in terms of the evolution of bipedal behavior that occurred in similar paleoenvironments. Fongoli chimpanzees, like chimpanzees at other field sites, appear to use bipedal postures primarily as a feeding and foraging adaptation both arboreally and terrestrially. Despite this similarity, there were significant differences in the bipedal behavior of Fongoli chimpanzees and that of chimpanzees at other sites, particularly in terms of the frequency of both terrestrial and arboreal bipedalism and the overall rate of bipedalism.

5.5.1 Bipedal Behavior in the Feeding and Foraging of Chimpanzees

Feeding and foraging has often been suggested as a plausible behavioral context for the evolution of bipedalism (Jolly 1970; Tuttle 1975; Rose 1976, 1984; Wrangham 1980; Leutenegger 1987; Hunt 1994, 1996; Videan & McGrew 2002; Stanford 2006). This hypothesis was in fact strongly supported in terms of the bipedal behavior of Fongoli chimpanzees, as well as chimpanzees at Bwindi, Mahale, and Gombe. A comparison of the bipedal behavior of Fongoli, Bwindi, and Mahale and Gombe chimpanzees is summarized in Table 5.1. Both Stanford (2006) and Hunt (1994, 1996) centralize feeding and foraging as an important behavioral context favoring the evolution of bipedal postures and subsequently habitual bipedal locomotion. Stanford (2006) found that the bipedal behavior of Bwindi chimpanzees occurs significantly more often as bipedal postures during arboreal feeding and foraging. Likewise, Hunt (1994, 1996) observed Mahale and Gombe chimpanzees engaging in both arboreal and terrestrial feeding and foraging postures. Doran (1992) also cites feeding and foraging contexts as associated with increased bipedal behavior in chimpanzees at Tai, Ivory Coast, compared to traveling as well as in terms of overall locomotor behavior. Fongoli chimpanzees were no exception to this trend. Fongoli chimpanzees engaged in bipedal postures during feeding and foraging significantly more than in any other behavioral context. Bipedal postures were utilized by Fongoli chimpanzees in both arboreal and terrestrial contexts, regardless of ecological variables such as branch size or angle, terrain quality, and terrain slope. In contrast, both Hunt (1994, 1996) and Stanford (2006) outline specific ecological contexts of bipedalism, based on variables that they find significant in terms of bipedal behavior for Bwindi, Mahale, and Gombe chimpanzees, in the scenarios for

the evolution of habitual bipedalism in early hominids that they suggest. The lack of specificity in terms of these ecological variables demonstrated by Fongoli chimpanzee bipedal behavior highlights the importance of bipedal postures in feeding and foraging across microhabitats for Fongoli chimpanzees. While bipedal feeding and foraging postures are utilized under certain conditions across chimpanzee sites, they are more favored by the mosaic savanna-woodland habitat that makes up the Fongoli chimpanzee range. This stands in contrast to Bwindi, Mahale, and Gombe chimpanzees who may only engage in bipedal feeding and foraging postures in more specific contexts. Fongoli chimpanzees are also significantly more bipedal than chimpanzees at Bwindi, Mahale, and Gombe, which lends support to this interpretation.

Table 5.1 Bipedal behavior in feeding and foraging at Fongoli, Bwindi (Stanford 2006), Mahale and Gombe (Hunt 1994, 1996).

Study Site	Frequency of Bipedal Bouts during Feeding and Foraging	Total Frequency of Bipedal Behavior across Behavioral Contexts	% Total
Fongoli (this study)	78	129	60.5
Bwindi (Stanford 2006)	171	179	95.5
Mahale and Gombe (Hunt 1994, 1996)	78	97	80.4

5.5.2 Why are Fongoli chimpanzees more bipedal than chimpanzees at other sites?

Fongoli chimpanzees were significantly more bipedal than either Bwindi chimpanzees (Stanford 2006) or Mahale and Gombe chimpanzees (Hunt 1994). In addition, bipedal behavior accounted for a higher percentage of overall locomotor and postural

behavior at Fongoli (2.3%) than Doran (1993) reports for adult male chimpanzees at Tai (1.2%). Several hypotheses may account for this difference. Stanford cites observational conditions as a potential explanation for the frequent bipedalism of Bwindi chimpanzees, and this is also applicable to Fongoli chimpanzees. Because Fongoli chimpanzees live in a savanna-woodland mosaic habitat, trees are often short, averaging 12.5 m in height in closed habitats and 7.6 m in height in woodland habitats (Pruetz et al. 2008), making it possible for ready observation of arboreal bipedalism. Likewise, the open habitat with little undergrowth during the time of this study made observations of terrestrial bipedalism unobstructed. Observations were made during the end of the dry season and beginning of the wet season before tall grass and undergrowth was present, providing ideal conditions for observation of chimpanzee behavior. As Stanford (2006) suggests, this may mean that Fongoli chimpanzees are no more bipedal than chimpanzees at other sites, but that these behaviors are simply more easily seen due to observational conditions.

Age-sex differences in bipedal behavior may also account for the significantly higher rate of bipedalism in Fongoli chimpanzees. At Bwindi, both adult males and adult females were observed, as well as juveniles and infants (Stanford 2006). He reports no age-sex differences in the frequency of bipedal behaviors, although Bwindi adult male chimpanzees did differ significantly from other age-sex classes in the duration of bipedal bouts (Stanford 2006). Stanford (2006) also suggests that a few individuals may have had debilitating snare wounds that may have limited forelimb use, although he maintains this did not likely affect bipedal behavior overall at Bwindi. Hunt (1994) describes the Mahale and Gombe chimpanzees as healthy young-adult and middle-aged individuals. Both male and female

adult chimpanzees in their prime were part of this study group, spanning all social ranks (Hunt 1996). He reports no sex-class differences at Mahale or Gombe (Hunt 1994). At Fongoli, only adult male chimpanzees were included as focal subjects due to research protocol (Pruetz, pers. comm.). It is possible that adult male chimpanzees are more bipedal than other age-sex classes or that they perform bipedal behaviors in different ecological or behavioral contexts. Ad libitum data on adult females, adolescent males, and juvenile males suggests that Fongoli chimpanzees in general do engage in frequent bipedalism, but this evidence was not quantified systematically (Appendix 2). However, the contexts in which individuals of different age-sex classes engage in bipedal behavior may differ. For example, immature chimpanzees often used bipedal postures and locomotion in play behaviors. In only three occurrences of bipedal behavior, a low-ranking adult male, Karamoko was observed using bipedal postures and locomotion in play with juvenile and adolescent males. Further investigation is needed to determine whether age-sex differences in bipedal behavior exist and whether or not they affect the overall rate of bipedal behavior found in this study.

Seasonal differences in bipedal behavior may also account for the high rate of bipedalism observed in Fongoli chimpanzees. Fongoli chimpanzees were observed during this study only during the transition period (usually May-June) between the dry and wet seasons. Observational conditions were typical of the dry season, with no tall grasses or seasonal undergrowth. Because Fongoli chimpanzees were not observed in both wet and dry season conditions, it is difficult to know whether or not seasonal differences, such as visibility and grass height, as well as fruit availability, affected the rate of bipedalism observed during this study. Further investigation is needed to determine whether or not

seasonal differences in bipedality, in terms of frequency or ecological and behavioral context, exist and what these differences imply regarding of their application to reconstructions of the evolution of bipedal behavior in early hominids.

Larger ecological context may also explain the significantly higher rate of bipedalism observed in Fongoli chimpanzees compared to those at Bwindi (Stanford 2006) and Mahale and Gombe (Hunt 1994). The open savanna-woodland mosaic habitat inhabited by Fongoli chimpanzees may favor bipedal behavior more than the dense montane forest habitat of Bwindi chimpanzees or the more densely wooded and forested habitats utilized by Mahale and Gombe chimpanzees. Hunt (1994) suggests that Mahale and Gombe chimpanzees engaged in bipedal feeding most often in the open-forest habitats in their ranges, which may be similar to the habitat occupied by Fongoli chimpanzees. This would suggest that these types of mosaic savanna-woodland habitats are linked directly to increases in bipedal behavior compared to forested habitats inhabited by chimpanzees at other sites. The observation of both arboreal and terrestrial bipedalism in Fongoli chimpanzees, in contrast to Bwindi chimpanzees (Stanford 2006) in more densely forested habitats, may be indicative of the ecological differences between these two sites. This hypothesis is the most compelling explanation in regards to the significantly higher rate of bipedalism in Fongoli chimpanzees in comparison to Bwindi (Stanford 2006), Mahale, and Gombe chimpanzees (Hunt 1994; 1996) because of its implications for the evolution of bipedalism in early hominids. Current reconstructions of the paleoenvironments inhabited by early hominids suggest that these were typified by mosaic habitats interspersed with wooded, closed and more open microhabitats, analogous to the range inhabited by Fongoli chimpanzees. If the habitat of Fongoli

chimpanzees is in fact important in terms of the rate of bipedalism, then savanna chimpanzees provide key information in regards to constructing the most plausible scenarios for the evolution of habitual bipedalism in early hominids.

5.5.3 Methodological Issues

Comparisons between this study and those conducted by Stanford (2006) and Hunt (1994, 1996) are hindered by methodological differences used by each researcher. Hunt et al. (1996) suggests challenges in interobserver comparisons can result from differences in operational definitions of positional and locomotor modes. This is not an issue for comparison here, as both Stanford (2006) and this study follow Hunt (1994) and Hunt et al. (1996) in terms of standard terminology. However, differences in data collection across the sites made it difficult to evaluate whether or not chimpanzees at Fongoli were significantly more or less bipedal than chimpanzees at other sites. In addition, differences in data collection methods should be considered. Both instantaneous scan sampling and all occurrences data collection on focal subjects were utilized in this study. However, the bulk of analysis regarding the ecological and behavioral contexts of bipedal behavior was conducted on data produced by a focal subject all-occurrences of bipedal behavior sampling method. Stanford (2006) utilized a methodology similar to this study at Bwindi while Hunt (1994, 1996) relied primarily on instantaneous scan sampling for his study of Mahale and Gombe chimpanzee bipedalism (See Chapter 3 for detailed description of these methodologies).

Sampling methods are important given the nature of data collection on locomotor and postural modes in nonhuman primates (Doran 1992). Doran (1992) suggested three unique

aspects of locomotion that must be considered when selecting a sampling method for these behaviors, including the rare occurrence of most locomotor modes in terms of the nonhuman primate daily time budget, the relatively rapid duration of most locomotor bouts followed by longer bouts of inactivity, and the variety in duration and distance over which different locomotor behaviors occur. Bipedal behavior is consistent with each of these three considerations. According to the results of this study, bipedal bouts are typically short in duration, lasting only five to six seconds on average. They typically occur rarely in terms of the daily time budget and the locomotor and postural repertoire of chimpanzees. Finally, the duration and distance over which bipedal behaviors are performed appears to differ drastically and are shorter in most cases than other more common postural modes such as quadrupedal walking and pronograde inactive postures like lying, sitting, and reclining. Therefore, the differences between instantaneous scan sampling and all occurrences sampling in terms of chimpanzee positional and locomotor behavior has important implications for the results of a study focusing on bipedal behavior as well as comparison of such studies across chimpanzee sites, as is the case here.

Advantages and disadvantages exist for using both instantaneous and all-occurrences bout sampling methods for focal individuals in terms of their application to locomotor behavior (Doran 1992). Instantaneous sampling can be done at regular intervals, easing data collection and allowing for simultaneous collection of multiple types of behavioral and ecological data (Doran 1992). Doran (1992) tested both methods simultaneously and demonstrated that they yielded similar results when using a one-minute interval scan sampling. However, the time breadth of each interval may be important in terms of rarely

occurring behaviors that tend to be short in duration, conditions that appear to characterize both postural and locomotor bipedal behaviors. For instance, instantaneous scans utilizing one-minute or two-minute intervals may more successfully capture the frequency of these types of behaviors than an instantaneous scan sampling method using a five-minute interval for data collection. In addition, focal all-occurrences sampling may be of greater utility than instantaneous scan sampling under these conditions. While focal all-occurrences bout sampling may overestimate the frequency of locomotor and postural behaviors that occur relatively often, Doran (1992) suggested that this sampling method may be particularly useful in terms of sampling rare behaviors that are brief in duration. This supports the methods utilized by this study and Stanford (2006) to study the bipedal behavior of chimpanzees. Likewise, the use of similar methodology makes the results of this study more directly comparable to Stanford's (2006) study on Bwindi chimpanzees. Therefore, it is realistic to argue that Fongoli chimpanzees are significantly more bipedal than Bwindi chimpanzees based on the results of this study. However, because issues may exist in terms of the breadth of scan sampling intervals when comparing rarely occurring behaviors of short duration like bipedal behavior in chimpanzees, direct comparisons to Hunt's (1994, 1996) study on Mahale and Gombe chimpanzees may be confounded, particularly in terms of rate of bipedalism. It is possible that differences in methodology lead Mahale and Gombe chimpanzees to appear less bipedal than they actually are in comparison with Fongoli and Bwindi chimpanzees. Despite these confounding methodological issues in terms of the rate of bipedalism, comparisons of the frequency of bipedalism in particular ecological and behavioral contexts may be more or less comparable across all studies as they rely more broadly on the relative frequencies of bipedal behaviors under differing conditions.

Differing degrees of habituation across chimpanzee sites should also be taken into consideration regarding comparisons of the bipedal behavior of chimpanzees at Fongoli, Bwindi (Stanford 2006) and Mahale and Gombe (Hunt 1994, 1996). In particular, the habituation of focal subjects may be most important in terms of comparisons to Stanford (2006) (See Chapter 3 for description). Because Bwindi chimpanzees were not habituated, individual variation in bipedal behavior is not easily recognized or accounted for, which may skew Bwindi chimpanzees towards being more or less bipedal than reported. Likewise, it is difficult to know if Bwindi chimpanzees engage only in arboreal bipedal behavior or if they are more similar to Fongoli, Mahale and Gombe chimpanzees in engaging in these behaviors in both terrestrial and arboreal contexts. This may confound the use of interpretations based on these results in the evaluation of plausible scenarios regarding the evolution of habitual bipedalism in early hominids.

5.5.4 Sample Size Issues

Although the sample size for this study was small, statistical analysis on the ecological and behavioral contexts of bipedal behavior was still possible. However, the relatively small sample size of this study may complicate comparisons between chimpanzees at Fongoli, Bwindi (Stanford 2006), Mahale and Gombe (Hunt 1994, 1996) and should be noted in terms of the interpretations of these results. Comparisons in sample sizes across sites are summarized in Table 5.2. In terms of the number of bipedal bouts analyzed, this study is of comparable sample size to similar studies by Stanford (2006) and Hunt (1994, 1996). Therefore, comparisons of the results produced by statistical analysis of these bouts are supported. The three studies differed greatly in terms of number of observation hours, although the study presented by Stanford (2006) is not markedly larger. This study occurred

only during the end of the dry season at Fongoli, while Stanford (2006) collected data across wet and dry seasons in Bwindi. Hunt (1994, 1996) does not indicate during which seasons his study occurred. Differences in the rate, type, and context of bipedal behavior may differ seasonally and should be explored in future studies.

Age-sex class of focal subjects may also be important in elucidating the ecological and, in particular, the behavioral context of bipedal behavior in chimpanzees. Differences exist in terms of the focal subjects used for each study. Each of the studies compared here are characterized by relatively small sample sizes in terms of the number of focal subjects. The major difference exists in the age-sex classes characterizing focal subjects, which varies across these studies. Due to research protocol, only adult males were used as focal subjects in this study. This is contrasted with Hunt (1994, 1996) who included both adult males and adult females as focal subjects and Stanford (2006) who included focal subjects across age-sex classes. Neither Stanford (2006) nor Hunt (1994, 1996) cite significant differences in the bipedal behavior across age-sex classes. However, it is possible that including only adult males in this study may skew results, particularly in terms of the context of bipedal locomotion, which occurred primarily during agonistic bipedal-threat displays. Likewise, other differences in the behavioral and ecological contexts of bipedal behavior may exist that are not considered by this study.

Table 5.2 Sample size comparison for this study, Stanford (2006) and Hunt (1994, 1996).

Study Site	Duration of Study	Timing of Study	# Bipedal Bouts Observed	# Observation Hours	# Focal Subjects	Age-Sex Class of Focal Subjects
Fongoli	May-June 2008	Transition months at end of dry season/ beginning of wet season	129	115.25	8	Adult males
Bwindi (Stanford 2006)	May 2001-July 2003	Across field seasons	179	246.7	13	Across Age-Sex Classes
Mahale/Gombe (Hunt 1994, 1996)	Not specified	Across field seasons	97	Mahale – 571.0 Gombe- 130.0	21	Adult males and females

5.6 The Evolution of Habitual Bipedalism

The results of this study suggest striking similarities as well as differences between chimpanzees across habitats and study sites that may shed light on the evolution of habitual bipedalism in early hominids. These results can be considered in two ways. First, they function in terms of a referential model considering the behavior of savanna chimpanzees as a model for the evolution of habitual bipedalism. Second, these results contribute to a particular type of referential model, termed a relational model by Moore (1996), which is based on differences in behavior among populations of a highly variable species, chimpanzees. Sayers & Lovejoy (2008) have recently criticized the use of chimpanzees as a referential model for early hominid bipedalism (discussed at length in Chapter 2.6).

However, these authors misinterpret the extent to which current models utilize both analogy

and homology, conditions suggesting that savanna chimpanzees provide the best choice in terms of models seeking to reconstruct or evaluate evolutionary scenarios. Likewise, Sayers and Lovejoy (2008) overlook the contribution of a referential model based on savanna chimpanzees to a strengthened relational model as Moore (1998) suggests. Beyond these critiques, the use of savanna chimpanzees is not necessarily mutually exclusive from Sayers and Lovejoy's (2008) conceptual model, which would consider bipedal behavior across taxa in phylogenetic or cladistic analyses in order to identify and isolate character states of common ancestors. Thorpe et al. (2007) utilizes a similar approach in suggesting that orthograde postures shared by all great apes provides a more meaningful basis for the evolution of habitual bipedalism in hominids than does emphasis on the selective pressures that may have favored the trait in prehomnids. This study suggests a different conclusion, supporting a particular scenario or set of hypotheses related to these selective pressures but is no less useful in terms of the conceptual model that Sayers and Lovejoy (2008) suggest. In fact, compiled evidence for bipedal behavior across primate taxa suggests that savanna chimpanzees may be more bipedal than many other species and that feeding and foraging is markedly associated with bipedal behavior across taxa (Table 2.1).

Consideration of the bipedal behavior of savanna chimpanzees at Fongoli, comparisons of this behavior to chimpanzees living under different ecological conditions (i.e. at Bwindi, Mahale, and Gombe), and additional examination of this behavior across nonhuman primate species illuminate the evolution of habitual bipedalism in early hominids. In particular, the results of the study on their own and in terms of observations at other chimpanzee sites suggest that bipedalism is important in both feeding and foraging behaviors

and social behavior, or agonistic bipedal threat displays, which may also relate to vigilance and defense hypotheses. This sheds light on the contexts in which bipedalism may have been initially favored in early hominids.

These comparisons point particularly to feeding and foraging hypotheses for the evolution of bipedal behavior, which have long been suggested as plausible scenarios for the evolution of this unique hominid trait (Jolly 1970; Tuttle 1975; Rose 1976, 1984; Wrangham 1980; Hunt 1994, 1996; Videan & McGrew 2002; Stanford 2006). Feeding and foraging contexts were observed to be important across chimpanzee habitats in this study as well as research on the bipedal behavior of chimpanzees at Bwindi, Mahale, and Gombe (Hunt 1994, 1996; Stanford 2006). This trend across sites suggests that similar selective pressures may have favored bipedal behaviors in similar contexts in the evolution of habitual bipedalism in early hominids. In particular, bipedal postures appear to be important in this transition, occurring in feeding and foraging contexts both arboreally and terrestrially at two of the three chimpanzee sites (excluding Stanford (2006) at Bwindi).

Despite the importance of bipedal postures in terms of feeding and foraging, some hypotheses have also been suggested regarding contexts that would have favored bipedal locomotion in particular. The results from this study suggest that intraspecific bipedal threat displays commonly involve bipedal locomotion, potentially leaving the hands free for shaking or dragging branches and throwing rocks. This supports display and, to some extent, vigilance hypotheses that have been posited in the last three decades by Day (1986), Fifer (1987), Jablonski and Chaplin (1993), and Walter (2004). However, these hypotheses do not account for age-sex class differences, and therefore, may not fully explain the evolution of

habitual bipedalism. While the results from this study lend support to these hypotheses, more investigation is needed to determine how they impact our understanding of the evolution of habitual bipedalism. It is possible that bipedal behavior was first favored in feeding and foraging contexts and was then secondarily adopted into other activities such as intraspecific competition, as Rose (1976) suggested. Likewise, it should be noted that feeding and foraging hypotheses are not mutually exclusive with these other explanations and that bipedal behavior was favored in a wide variety of behavioral and ecological contexts in order to evolve into the habitually bipedal behavior of hominids. Several selective pressures were most likely at work in shaping the evolution of habitual bipedalism (Rose 1976).

The results of this study suggest a particular plausible scenario for reconstructing the evolution of habitual bipedalism in early hominids. Feeding and foraging appears to be central to the evolution of bipedalism. It is likely that feeding and foraging would have favored postural bipedalism, with forelimb assistance, in both arboreal and terrestrial contexts. However, bipedal locomotion cannot be overlooked. These locomotor bipedal bouts would have occurred simultaneously with bipedal postures, rather than postural bipedalism preceding and perhaps contributing to the more rapid evolution of bipedal locomotion, as has been suggested in the past (Stanford 2006). These locomotor bipedal bouts were likely causally unrelated to postural bipedalism during feeding and foraging, although once evolved into habitual bipedalism, may have proved useful in feeding and foraging contexts for transport. In particular, intraspecific displays as well as interspecific or predator defense behaviors may have provided the context for the evolution of these locomotor bipedal bouts. Bipedalism was likely favored in a wide variety of ecological

contexts, perhaps associated with some degree of behavioral flexibility in terms of postural and locomotor behavior being present in early hominids. This is supported by the findings of Bennet et al. (2009) that suggest a different form of bipedalism in these early hominids, distinct from the modern *Homo*-type habitual bipedalism. It is also possible that early hominids were characterized by a mix of arboreal and terrestrial traits similar to what is described in the australopithecines (Hunt 1994). Importantly, the results of this study suggest that savanna chimpanzees are a key model for providing insight into the evolution of habitual bipedalism, supported by analogies between the environment of Fongoli chimpanzees and reconstructions of the paleoenvironments of early hominids (Kappelman et al. 1997; Reed 1997; Pruetz 2008) as well as the significantly higher rate of bipedalism exhibited by Fongoli chimpanzees in comparison to other chimpanzee sites as well as across nonhuman primate taxa (Table 2.1).

5.7 The Last Common Ancestor?

The results of this study provide insight into the suite of traits that may have characterized the last common ancestor of early hominids. More than one lineage of habitually bipedal apes may have existed, and there may have been diversity in the modes of bipedalism that characterized these hominids (Wolpoff 1999; Leakey et al. 2001). The bipedalism that typifies humans today is likely to have differed both in morphology and in mechanics from the bipedalism exhibited by early hominids. In fact, the earliest evidence of human-like bipedalism in the fossil record are the recently described Ileret footprints in Kenya, which suggest that *Homo erectus/ergaster* exhibited human-like bipedal gait around 1.5 million years ago (Bennett et al. 2009). Comparisons between the Ileret footprints and

footprints at Laetoli described by Leakey & Hay (1979), associated with *Australopithecus afarensis*, suggest differences in the form and function of the foot important in bipedality between australopithecine and *erectus*-like bipedalism (Bennett et al. 2009). This evidence aligns the Ileret footprints and *Homo erectus* more closely with modern human bipedality and suggests that the australopithecines and other early hominids may have exhibited a starkly different type of primitive bipedalism that differs from its modern form in *Homo* (Bennett et al. 2009). The results of this study may provide insight into the traits that characterized early hominids and their last prehomimid ancestor.

The results of this study, in comparison with Stanford (2006) and Hunt (1994, 1996) suggest that bipedalism would have been favored in both arboreal and terrestrial contexts. It is likely that the last common ancestor of early hominids exhibited traits adapted to activities that took place in both arboreal and terrestrial contexts. Hunt (1994, 1996) suggests that this would explain the mix of arboreal and terrestrial traits seen in the australopithecines and may also be true of other hominids. It is also likely that some degree of behavioral plasticity in terms of locomotor and positional behavior existed in the last prehomimids, similar to what we see in chimpanzees today (Stanford 2006).

5.8 Conclusion and Future Directions

The results of this study suggest that savanna chimpanzees offer a key model for providing insight into the evolution of habitual bipedalism in early hominids. Savanna chimpanzees at Fongoli inhabit an environment that appears to be analogous to those inhabited by early hominids based on recent paleoenvironmental reconstructions (Kappelman et al. 1997; Reed 1997) and these chimpanzees were also significantly more bipedal than

chimpanzees at other sites as well as other primate taxa (Table 2.1). This study also provides the opportunity for comparison to previous work by Hunt (1994, 1996) and Stanford (2006) seeking to utilize chimpanzees as a referential model for the habitual bipedalism of early hominids. The differences and similarities existing between chimpanzees at Fongoli and other study sites (i.e. Bwindi, Mahale, and Gombe) stress the importance of a referential model based on comparisons of chimpanzees across study sites and habitat types in understanding the evolution of complex traits such as bipedalism. Likewise, these comparisons can be included in a phylogenetic or cladistic approach to the study of hominid evolution, as suggested by Sayers and Lovejoy (2008) (Table 2.1). In light of these comparisons, postural bipedalism in feeding and foraging contexts appear particularly important in terms of the selective pressures at work in shaping habitual bipedalism in early hominids. In addition, bipedal locomotion may have evolved simultaneously but under distinct behavioral contexts from postural bipedalism, being favored during display and defense behaviors on the ground. Hypotheses relating to the importance of bipedal threat displays in intraspecific competition and as predation defenses, as well as more weakly related vigilance hypotheses (as suggested by Day 1986; Fifer 1987; Jablonski & Chaplin 1993; Walter 2004) may also have played a direct role in the evolution of habitual bipedalism in early hominids. This suggests that it is likely several selective pressures were at work in shaping this unique trait and that the hypotheses that have been proposed to explain its evolution are not mutually exclusive.

While this study helps to provide a starting point for comparisons of savanna chimpanzees to those in forested habitats and thus provides a more holistic referential model

for understanding habitual bipedalism in early hominids, additional research is necessary to more thoroughly evaluate existing hypotheses seeking to explain the evolution of this unique trait. In particular, methodological differences inhibited to some degree cross-site comparisons of chimpanzee bipedal behavior. Additional research aimed specifically at investigating the bipedal behavior of chimpanzees should potentially involve the incorporation of focal all-occurrences of bipedal bout sampling method. Doran's (1992) suggestions may be particularly useful in examining locomotor and positional behaviors that are relatively infrequent and short in duration, both of which appear to characterize chimpanzee bipedal behaviors. Likewise, observations should occur across seasons, to discern whether or not seasonal differences affect bipedal behaviors and more specifically what ecological variables may elicit these differences. In a similar vein, observations of bipedal behavior across age-sex classes are necessary to explore whether or not bipedal behavior varies by these categories. If differences exist, they may shed light on the relevance of certain hypotheses, such as display hypotheses (Jablonski & Chapin 1993; Fifer 1987), which may in fact only be favored by particular age-sex classes, such as adult male chimpanzees. Finally, researchers seeking to adopt a more holistic approach to understanding the evolution of habitual bipedalism should continue to involve comparisons across chimpanzee study sites and habitats, as the differences and similarities between chimpanzee bipedal behavior at these sites may point to specific ecological contexts that were most likely to favor bipedal behavior in early hominids. The inclusion of research on chimpanzee bipedal behavior from more long-term study sites may provide additional insight into the evaluation of plausible scenarios for the evolution of bipedalism as well as what traits may have characterized the last prehomnids.

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Appendix 1. Ethograms

Table A1.1 Behavioral repertoire: daily maintenance activities (Adapted from Nishida et al. 1999).

Category	Modifier	Definition
Feed-Forage (FF)	No Modifier	Look for food; remove food from substrate; process, and consume food; includes movement while feeding
	Carry (FFC)	Use arm(s) and hand(s) to hold foodstuffs while feeding and foraging
Travel (T)	No Modifier	Move from one location to another; does not include movement while feeding/foraging
	Transport (TT)	Use arm(s) or hand(s) to hold object (tool, rock, stick, etc. does not include foodstuff) while moving from one location to another
Social Affiliative (SA)	No Modifier	Social behavior that includes groom, reassure, affiliative touch, and alloparental care. Does not include play (see Social Affiliative Play)
	Play (SAP)	Activity often associated with laughter, vocalization, play face; includes lone and social play, object play, locomotor play, etc.
	Mount (SAM)	Embrace another individual with both arms from behind; pelvic thrusts may occur; includes copulation with intromission
Social Antagonistic (SN)	No Modifier	Attacking or threatening another individual; includes push, kick, hit, grab, slap, bite, drag, charge, stamp, pinch, and scratch, head tip, arm wave, hit toward, throw at, branch wave, stamp, slap, charge, charging display, hunch, fixed stare, soft bark, waa bark, wraa call, compressed lip and scream; does not include display (see Social Antagonistic-Display)

Table A1.1 (*continued...*) Behavioral repertoire: daily maintenance activities (Adapted from Nishida et al. 1999).

Category	Modifier	Definition
Social Antagonistic (SN)	Display SND	Focal individual moves in a slow, rhythmic gait, run at moderate or fast speed, towards or past target individual if one exists; patterns can incorporate piloerection, throwing rocks, branches or other substrate, dragging and swaying branches, stamping, flailing, drumming, raking, chest beating, pant hoots, compressed lips and face, bipedal swaggering, charging, hitting, etc.
Observation (Obs)	n/a	Actively watching stimulus, includes scanning social group, landscape, or focusing on some point of interest
Rest (R)	n/a	Not moving; includes sit, lie, autogroom, and sleep
Not Visible (NV)	n/a	Focal individual cannot be seen by human observer; is hidden or obscured from view so that behavior cannot be identified

Table A1.2 Postural and locomotor behaviors (Adapted from Hunt et al. 1996, Hunt 1994).

Category	Behaviors	Definition
Locomotor	Bipedal	See categories and definitions in Table 1.
	Quadrupedal (Qu)	Walking or running on a horizontal plane using both hands and feet.
	Tripedal (3W)	Using three limbs to locomote in a quadrupedal fashion with fourth limb carrying/transporting object or grasping a support.
	Quadrumanous (QM)	Locomoting with at least one foot gripping a substrate. Includes vertical climbing and descent as well as movement in a horizontal direction.
	Semi-Brachiate (Br)	Locomoting under substrate using hands to grip substrate and rotating shoulders without assistance from feet.

Table A1.2 (*continued...*) Postural and locomotor behaviors (Adapted from Hunt et al. 1996, Hunt 1994).

Category	Behaviors	Definition
Postural	Bipedal	See categories and definitions in Table 1.
	Quadrupedal (QS)	Stand using both hands and feet.
	Tripedal (3S)	Standing on three limbs.
	Quadrumanous (QMS)	Pausing on substrate using with hands and feet grasping substrate.
	Arm-Hang (AH)	Hang from overhead substrate using at least one arm. Other arm may be used in foraging, eating, or supporting body weight, etc.
	Rest Posture (RP)	Includes sit, lie, etc. Limbs not used for supporting body.

Appendix 2. Ad Libitum Data on Female and Immature Age-Sex Classes

Fifty-two opportunistic ad libitum observations of adult females, adolescent males, and juvenile males and females were recorded. These observations are provided in the following tables.

Table A2.1 Frequency of bipedal behavior in terms of behavioral context and habitat according to ad libitum data on adult female and juvenile female chimpanzees.

N						
	Arboreal		Terrestrial			
Context	Postural	Locomotor	Postural	Locomotor	TOTAL	%
Feed/Forage	4	0	9	0	13	72.2
Travel- Carry	0	0	0	2	2	11.1
Scan	0	0	1	0	1	5.6
Play	0	0	1	1	2	11.1
TOTAL	4	0	11	3	18	100

*Only two observations of juvenile females were made, so they were pooled with observations of adult females in this table. Both of these bipedal bouts were observed during intraspecific play with adolescent and juvenile males.

Table A2.2 Frequency of bipedal behavior in terms of behavioral context and habitat according to ad libitum data on juvenile male chimpanzees.

N						
	Arboreal		Terrestrial			
Context	Postural	Locomotor	Postural	Locomotor	TOTAL	%
Feed/Forage	0	0	2	0	2	22.2
Play	2	0	2	2	6	66.7
Scan	0	0	1	0	1	11.1
TOTAL	2	0	5	2	9	100

Table A2.3 Frequency of bipedal behavior in terms of behavioral context and habitat according to ad libitum data on adolescent male chimpanzees.

N						
	Arboreal		Terrestrial			
Context	Postural	Locomotor	Postural	Locomotor	TOTAL	%
Feed/Forage	3	0	6	1	10	40.0
Copulate*	0	0	1	0	1	4.0
Play	2	0	3	1	6	24.0
Scan	0	0	5	0	5	20.0
Display	0	0	0	2	2	8.0
Social**	0	0	1	0	1	4.0
TOTAL	5	0	14	4	25	100

*Adolescent male solicits to adult female.

**Adolescent male, Bo seen to stand bipedally for several seconds and vocalize at adult male Diouf while stamping feet on ground. Adolescent male appeared as if exhibiting a “temper tantrum” (Nishida et al. 1999).