Chimpanzee (*Pan troglodytes verus*) Behavioral Responses to Stresses Associated With Living in a Savanna-Mosaic Environment: Implications for Hominin Adaptations to Open Habitats

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ABSTRACT

Anthropologists have long been interested in the behavioral ecology of nonhuman primates living in savannas given what we know of early hominin environments. As expected, chimpanzees in the Fongoli community in southeastern Sénégal show a unique suite of behavioral adaptations to stresses associated with their savanna habitat. While Fongoli chimpanzees are species-typical in certain regards, such as including ripe fruit in the diet during all months of the year, they also adjust their behavior to the particular stresses of this dry, hot and open environment. These behaviors include using caves as shelters during the dry season, soaking in pools of water during the hot, early rainy season, and traveling and foraging at night during maximum phases of the moon. Adult males of this 35-member community serve as focal subjects in a long-term study of the ecology and behavior of chimpanzees in a savanna-mosaic environment. Here, we report on Fongoli chimpanzee activity budgets, grouping behavior, and habitat use during the dry versus wet season based on over 2500 hours of observation from March 2005–July 2006. Findings support the hypothesis that ecological pressures associated with a savanna environment significantly affect great ape behavior. The Fongoli chimpanzees' large home range (>65km²) is sometimes used cyclically, with the community traveling as one large party, in contrast to the typical chimpanzee fission-fusion pattern. Combined with data on temperature in the various habitats within the savanna mosaic, results show that Fongoli chimpanzees minimize energy expenditure during the hottest months and at the hottest time of day by resting more and traveling less, in addition to selectively using small patches of closed-canopy habitats, such as gallery forest. They move significantly more during early hours of the hot, dry season specifically and range in smaller parties at this time compared to during the wet season. The stresses associated with a savanna-mosaic environment and chimpanzees' behavioral adjustments to them have important implications for understanding early hominin behavior in similar environments.

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INTRODUCTION

Environmental hypotheses have long been used to explain significant changes in hominin evolution (Dart 1925; Darwin 1871; Jolly 1970; Robinson 1954). In particular, the 'savanna hypothesis' has been used to explain such distinctive hominin features as bipedalism, tool use, and increased brain size (see Potts 1998 for review). Given their close kinship with humans, as well as the unique habitat in which they live, chimpanzees living in savanna-woodland environments have long been of interest to anthropologists (Suzuki 1969; Kano 1972; McGrew et al. 1981; Moore 1992; Sept 2002). Although the savanna hypothesis has been largely abandoned in its original form, a move from a closed to a more open environment over the course of hominin evolution remains a significant change that likely acted as an important selective pressure regarding the behavioral ecology of early hominins. With more detailed information on paleoenvironments associated with possible basal hominins such as *Sahelanthropus* (Brunet et al. 2002; Vignaud et al. 2002) and the Australopithecines in general (White et al. 2006), for example, anthropologists recognize the complexity of the environment inhabited by early hominins and the mosaic nature of the habitats specifically. Anthropologists have shifted from a tendency to associate major anatomical and behavioral changes in early hominins with a grassland savanna environment to the recognition that riverine and open and closed woodlands are perhaps more characteristic of these hominins' habitats (Potts 1998). This has resulted in a revised form of the savanna hypothesis, which focuses on the woodland-forest environment

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as the critical feature influencing hominin evolution (Potts 1998). This has important implications for reconstructing early hominin socioecology and makes the consideration of chimpanzees living in woodland-savanna mosaics pertinent to related questions.

A savanna-woodland habitat is thought to be associated with selective pressures operating on early hominin evolution, and hypotheses proposed to explain key adaptations in hominins look to environmental factors. However, Potts (1998) examined such habitat-specific hypotheses in light of the environmental records at key hominin localities and concluded that they do not adequately explain the key adaptive changes in the hominin lineage. Nonetheless, inferences continue to be made regarding the influence of open environments on early hominin behavior (Reed 1997; Spencer 1997; Vrba 1985; and, see Foley 1999) largely because ecology remains a key component to be considered in hominin evolution. The issue is far from resolved.

Given the difficulties in understanding the behavior of extinct hominins, extant apes of the Family Hominidae provide an opportunity to assess the effects of ecological variables on the behavior of our closest living relatives in similar habitats. However, little evidence exists regarding these habitats' effects on living hominins, chiefly because apes in this environment are notoriously difficult to habituate to researcher presence (McGrew et al. 2003). Although extensive data are available regarding the ways in which monkeys, such as baboons (Papionini), adapt and adjust to open environments (Dunbar 1998; Hill and Dunbar 2002; Kamilar 2006), the Fongoli site in southeastern Sénégal provides the first data on a habituated community of chimpanzees living in such an environment.

Chimpanzees in the Fongoli community in southeastern Sénégal show a unique suite of behavioral adaptations to stresses associated with their savanna environment. While chimpanzees at Fongoli are species-typical in certain regards, such as including ripe fruit in the diet during all months of the year (Pruetz 2006), they also adjust their behavior to the particular stresses of this dry, hot and open environment. Fongoli chimpanzees exhibit unique behaviors such as using caves as shelters during the dry season (Pruetz 2007), soaking in pools of water during the early rainy season, and moving and foraging at night during maximum phases of the moon in the dry season. They also exploit protein sources, such as prosimian primates, that chimpanzees at more forested sites ignore, and they use tools to hunt these prosimians (Pruetz and Bertolani 2007). Detailed behavioral data on our closest living relative that allows us to understand the responses of apes in a savanna mosaic can add to the comprehensive body of data used to make hypotheses about the behavior of early hominins in open, hot and dry habitats. Comparing chimpanzees in such a habitat to those living in more forested areas gives us insight into how apes respond to the selective pressures associated with such an environment (Moore 1996) and which variables should be considered most heavily in scenarios of early hominin evolution.

METHODS

STUDY SITE

Chimpanzees in Sénégal inhabit the area known as the Mandingue Plateau, which also constitutes part of southwestern Mali and northeastern Guinea (Carter et al. 2003). This area defines the northern and geographical limits of chimpanzees' range in West Africa. Due to drought during the 1970s and 1980s in the Sahel region of Africa, the intertropical convergence zone has moved southward to encompass part of Sénégal (Giannini et al. 2003; Zeng 2003), perhaps increasing the stresses acting on chimpanzees in this habitat. In southeastern Sénégal, savanna chimpanzees coexist with humans belonging to the Bédik, Malinké, Bassari, Diahanke, and Puhlar groups. Humans here compete with chimpanzees over wild plant foods, such as the fruit of *Saba senegalensis* (Pruetz and Knutsen 2003). Humans do not hunt chimpanzees for food, although chimpanzees are periodically targeted for the capture of infants that can be sold as pets (Pruetz and Kante in prep.). This region of southeastern Sénégal is Sudanian savanna and Guinean woodland, which can be envisioned as a savanna-woodland mosaic. Rainfall in this area averages 900mm annually (Ba et al. 1997). In southeastern Sénégal, the rainy season is from June through September. May and October may be considered transitional months, although virtually no rain falls in May in some years. November through April constitute the dry season, when rainfall does not occur. At this time, almost all trees lose their leaves, and natural and human-induced bush fires sweep through the area. Other animal species at the site include those associated with open environments, such as patas monkeys (*Erythrocebus patas*) and oribi (*Oribi oribi*), as well as species that typically use closed canopy habitats more extensively, such as green monkeys (*Cercopithecus aethiops sabeus*) and bushbuck (*Tragelaphus scriptus*).

The Fongoli site (12º40′ N, 12º13′ W) is at the junction of the Sudanian and Sudano-Guinean vegetation belts (Figure 1). The chimpanzee home range is estimated, minimally, to be 65km², which is from two to six times as large as ranges of chimpanzee communities living in more forested areas (Basabose 2005; Chapman and Wrangham 1993; Herbinger et al. 2001; Newton-Fisher 2003). The home range is predominantly open woodland and grassland, with small patches of gallery forest and seasonally cultivated fields (Pruetz 2006; Figure 2). Trees average around 10m in height in woodland habitat, while grassland includes few scattered trees (Figure 3; Pruetz et al. 2008). Small patches of gallery forest contain taller trees, and the canopy is often contiguous. Woodland, grassland, and bamboo woodland (Figure 4) are characterized by a predominantly grass understory, while gallery forest understory is characterized by a diversity of herbaceous-level plants. Fields may be completely cleared or characterized by some degree of regrowth of vegetation (Figure 5). Estimations of habitat types that constitute the Fongoli chimpanzees' home range were derived from transects oriented N-S (3km) and E-W (3km), which were placed at the approximate center of the Fongoli study site, plus one additional randomly-placed transect 1km

Figure 1. Map of Senegal and Fongoli study site (figure modified and used with permission from Projet Niokolo Badiar FED Number 4213/RED, DPNS, DNFF, ORTOM).

long. Each 100m along transects, a circular plot of a 5m radius was sampled for specific vegetative characteristics and classified as gallery forest, woodland (including bamboo woodland), field, or grassland.

Temperature data were collected using remote data loggers (Pruetz 2007). From 2001 to 2004, Hobo™ temperature loggers were placed in woodland, grassland, and gallery forest habitats so as to be fully shaded and were set to record ambient temperatures each 6–10 minutes (Pruetz 2007). Although battery failure resulted in data loss for some habitats in some years, temperatures were collected over at least one annual cycle for each of the different habitats (Pruetz 2007). Data were analyzed with Boxcar™ software, excluding nighttime temperatures (1801 to 0559 hours) in statistical analyses (Pruetz 2007). Temperature differences were analyzed with t-tests, using mean monthly temperatures in the different habitats as dependent variables (Pruetz 2007). Data on rainfall were collected using a rain gauge located at Fongoli village, within the chimpanzees' home range. Rainfall is presented as monthly averages based on data collected over the course of 3.5 years at Fongoli, from June 2005 through December 2008.

STUDY SUBJECTS

The Fongoli community contained 35 individuals during the study, which included 10 adult males, seven adult females and 18 immature chimpanzees. Nine of ten adult males served as focal subjects as part of a long-term study of the ecology and behavior of chimpanzees in a savanna-mosaic environment. One aged adult male was excluded due to his poor sight and hearing and resultant timidity around observers. Both focal animal and scan sampling with interval recording methods were used to collect data on activities such as resting, feeding, traveling, grooming, and other social behaviors as well as habitat use. Data on activity were collected during more than 2500 contact hours with chimpanzees from March 2005 through March 2006. Mean values for individual males were analyzed according to dry versus wet season and by hour so as to avoid problems with pooling of data and to control for seasonal effects and time of day, respectively. Additionally, we report on chimpanzee grouping behavior during dry versus wet seasons based on over 3000 hours of data collected from March 2005–July 2006. Party size is defined as all individuals encountered in a single day, following Boesch (1996).

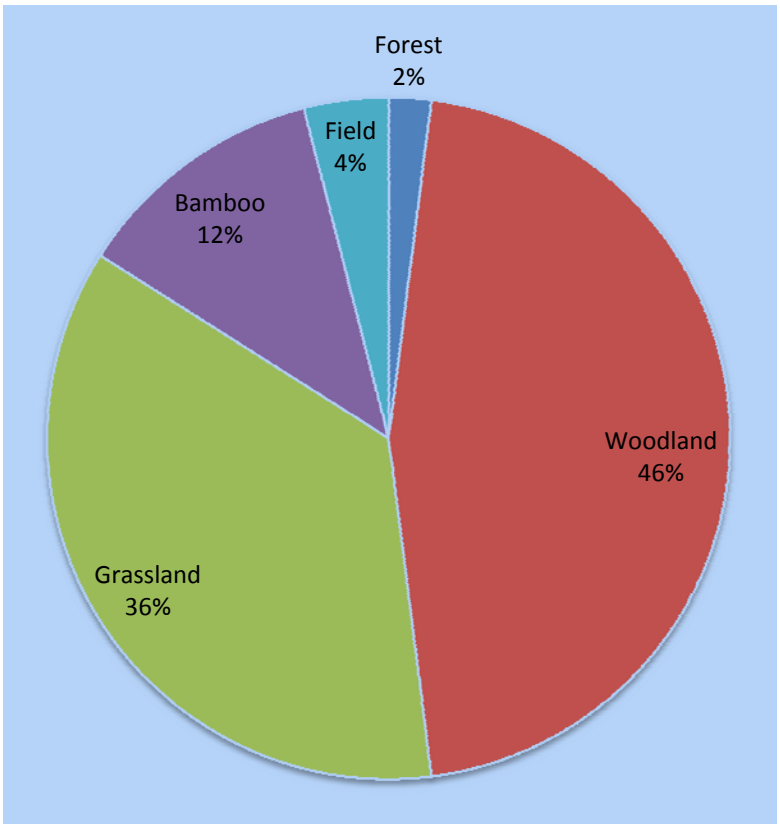

Figure 2. Habitat composition at Fongoli.

Figure 3. Adult male Fongoli chimpanzees in short grassland habitat, with woodland in background, dry season (photo by Paco Bertolani).

Figure 4. Adult male Fongoli chimpanzee in bamboo woodland habitat, dry season (photo by Paco Bertolani).

Figure 5. Party of chimpanzees at Fongoli crossing fallow field during dry season with research assistant Dondo Kante following (photo by Maja Gaspersic).

RESULTS

CLIMATIC DATA

Data collected on temperature in various habitats throughout the annual cycle reveal significant variation in temperature according to season, with certain habitats also being significantly cooler than others (Pruetz 2007; Figure 6). Maximum temperatures in the dry season exceed 40 degrees Celsius. Average annual rainfall at Fongoli over this period was 786mm per year.

HABITAT USE

Habitat use by Fongoli chimpanzees (the amount of time spent in the respective habitats) varied significantly from what was expected based on the availability of the different

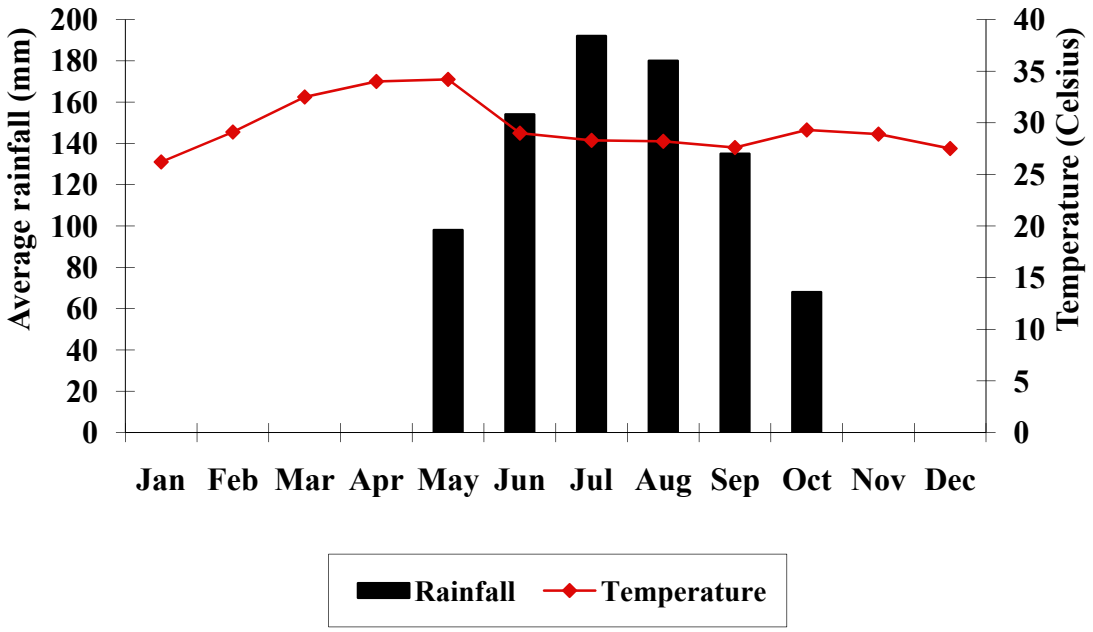

Figure 6. Rainfall and temperature by month at Fongoli.

habitats within their home range (X^2=18.47, df=4, p=0.001). Chimpanzees preferred small patches of closed-canopy habitats, such as gallery forest. Habitat use also varied with season. Fongoli chimpanzees especially preferred the small patches of forest during the dry season (X^2=34.101, df=4, p<0.010; Figure 7). During the dry season, Fongoli chimpanzees used forested habitat almost twice as much as during the wet season. These forest patches also are associated with the few continuously available sources of water during the peak of the dry season. During the wet season, chimpanzees used woodland habitat more often than would be expected based on its availability but used this habitat less than would be expected during the dry season.

ACTIVITY

Individual males differed significantly from one another regarding non-grooming social behavior (ANOVA: p=0.006, F=2.790, df=8) but were otherwise similar in the amount of time they spent resting, feeding, moving, and grooming. Fongoli chimpanzees' response to dry season pressures involved minimizing energy expenditure during the hottest time of day by resting more and traveling less. In general, time of day significantly affected activity, except for non-grooming social behavior (ANOVA: df=13; feeding: p=0.000, F=14.218; moving: p=0.000, F=8.215; grooming: p=0.000, F=7.103; resting: p=0.000, F=11.166). The difference was enhanced during the dry season, as chimpanzees traveled and fed significantly more during early morning hours (0600–0859 hours: X^2=25.48, df=1, p=0.001; 0900–1159 hours: X^2=11.23, df=1, p=0.001), while resting and grooming more during midday (Figure 8). When compared to chimpanzees studied at more forested sites, such as Kibale, Uganda (Ghiglieri 1984) and Gombe, Tanzania (Goodall 1986; Wrangham and Smuts 1980; Wrangham 1977, 1986), Fongoli in-

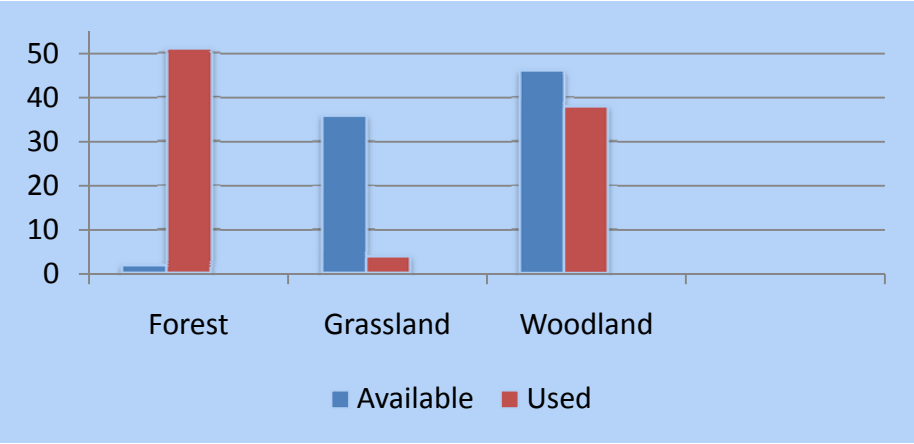

Figure 7. Habitat use (%) by Fongoli chimpanzees in relation to availability of habitat type.

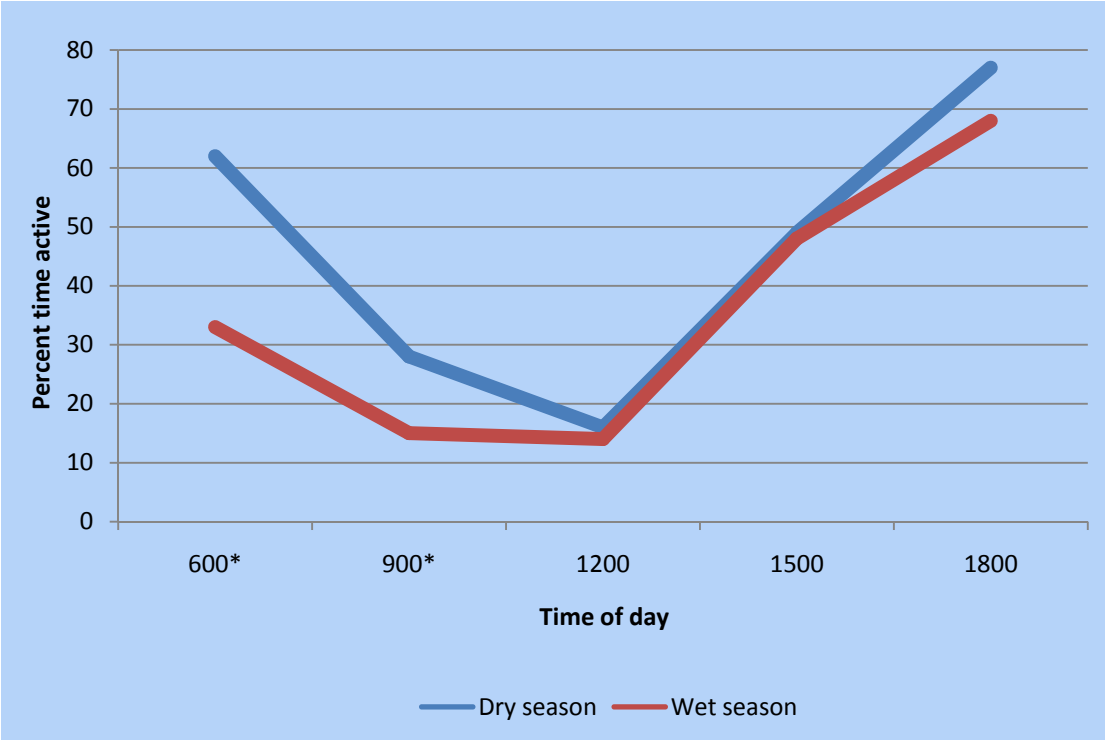

Figure 8. Activity of adult males according to time of day (denotes significant difference).*

dividuals rest significantly more (Figure 9; X^2=35.70, df=1, p=0.001). Conversely, they spend significantly less time feeding (see Figure 9; X^2=18.12, df=1, p=0.001), but they spend an almost equivalent amount of time traveling.

GROUPING BEHAVIOR

Chimpanzees at Fongoli are species-typical in exhibiting a fission-fusion social system, but they also use their home range cyclically, regularly moving around their range as a large, cohesive group. In general, Fongoli chimpanzees are found in larger parties than chimpanzees at other sites (X^2=19.275, df=1, p=0.001), even when community size is controlled (X^2=71.510, df=1, p=0.001). Average party size at Fongoli during this study was 15 (n=17 months; Figure 10). Party size during the dry season was significantly smaller than during the wet season (t=-2.220, df=10.853, p=0.049), irrespective of the fact that only a few dry season water sources existed, which served to unite smaller parties. Dry

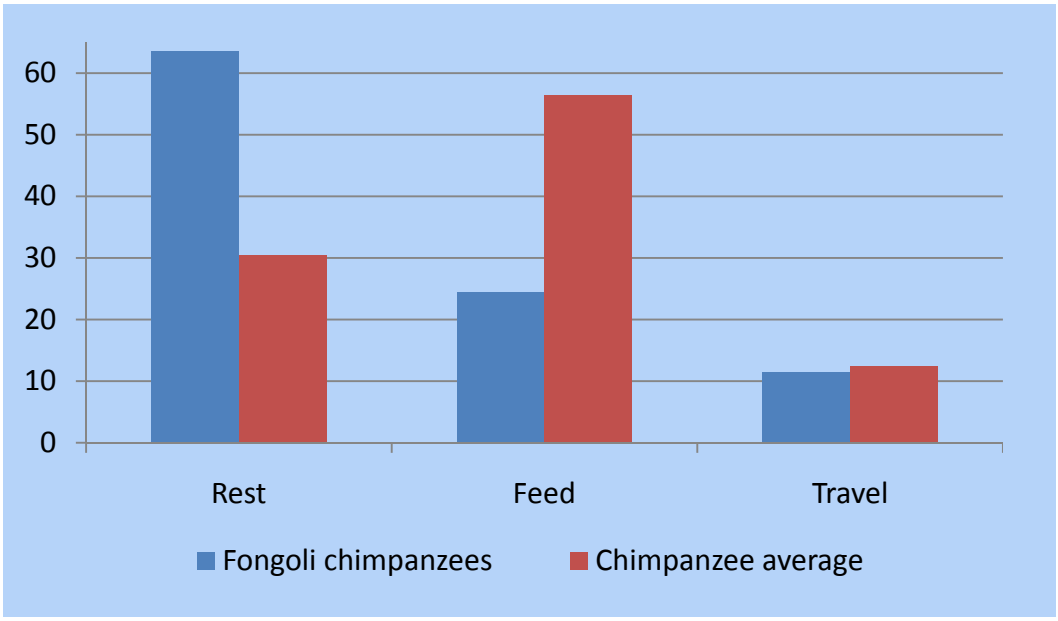

Figure 9. Fongoli chimpanzee activity (%) compared with other sites.

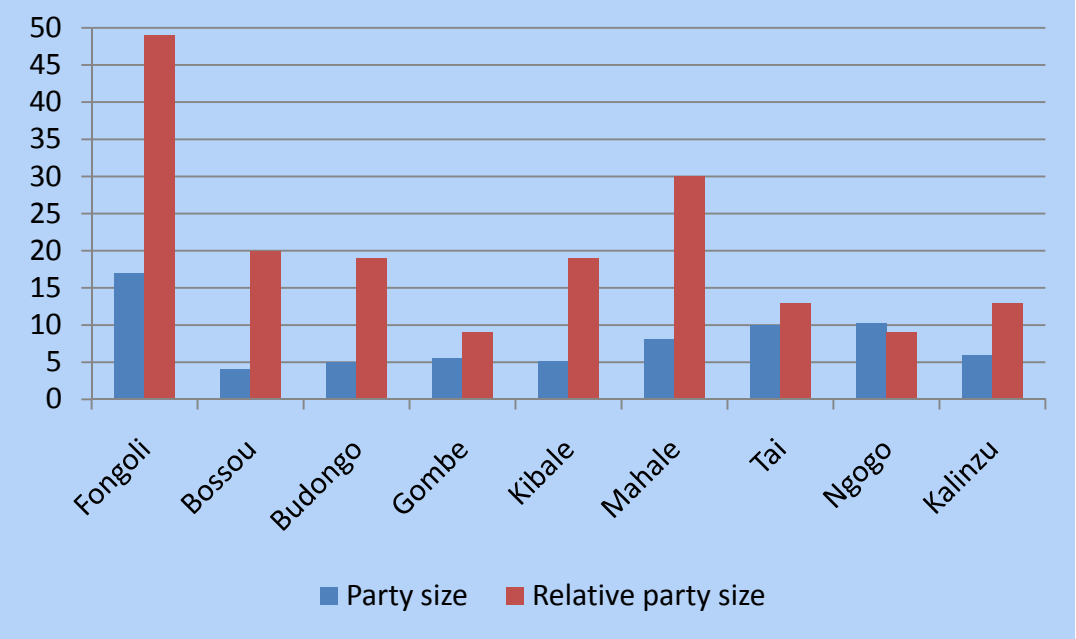

Figure 10. Party size (frequency) and relative party size (average party size divided by community size) compared across chimpanzee study sites.

season average party size was 12.1 individuals, while wet season average party size was 17.7 individuals. Analyses revealed that rainfall but not temperature significantly and positively correlated with party size (Pearson correlation, 2-tailed: party size and rainfall, r^2=0.678, N=14, p=0.008).

DISCUSSION

Climatic variables can affect chimpanzee behavior at all levels, ranging from habitat type to microhabitat areas used, activity levels, and even grouping behavior. Many aspects of what appear to be unique behaviors exhibited by Fongoli chimpanzees are linked to thermal stresses in their savanna environment. In general, the Fongoli chimpanzees might be termed energy minimizers when compared to chimpanzees living in more forested habitats. Specifically, in what appears to be a response to high heat stress, they prefer to use closed canopy forested habitat and move around and feed earlier during the dry season when temperatures are lower. Our results support the hypothesis that climatic pressures affected early hominins significantly in similar environments.

HABITAT USE

Fongoli chimpanzee behavior indicates they react significantly to pressures associated with seasonal changes in this hot, dry and open environment. During the dry season, Fongoli chimpanzees are selective regarding their use of gallery forest habitat in particular, using this habitat significantly more often than expected given its availability within their home range. Additionally, they used grassland habitat significantly less than expected given its availability within their range. Gallery forests at Fongoli provide the only permanent sources of water at the peak of the dry season but also provide shade in the form of evergreen trees and lianas. Other habitat types, such as woodland and grassland, are dominated by deciduous vegetation that provides virtually no shade during dry season months, and such open habitats are significantly hotter (Pruetz 2007).

ACTIVITY

Fongoli chimpanzees varied their activities according to season. Data on chimpanzee activity combined with temperature data show that Fongoli chimpanzees minimize energy expenditure at the hottest times of day. They rest more and travel less during the hottest times of day, which is a common primate pattern, but their level of inactivity exceeds that of the average chimpanzee.

Fongoli chimpanzees travel more during the cooler, early morning hours of the dry season. This increase in travel may also be a response to limited food availability at this time, which may in turn be a result of their restriction to only a few key forested areas in their home range associated with permanent water. The few permanent sources of water available at the end of the dry season may be likened to a pseudo-home base for Fongoli chimpanzees at this time, as they move outwards from these areas in a radiating fashion to forage, likely depleting available food resources in these areas.

GROUPING BEHAVIOR

Chimpanzees at Fongoli are significantly more cohesive than chimpanzees studied elsewhere, with an average party size of 15. When the party size is taken in the context of the community size, following Boesch's (1996) calculation of relative mean party size, Fongoli chimpanzees also form significantly larger parties. Fongoli chimpanzees exhibit an average party size of close to 50% of their community size, compared to the average of 15% seen at other sites.

Although Fongoli chimpanzees are significantly more cohesive than other communities, seasonal differences occur at the site. Average party size at Fongoli was significantly smaller during dry season months, even though the few available water sources were locations where parties regularly fused. Isbell and Young (1996) maintain that chimpanzee fission-fusion social organization differs from the social organization thought to characterize early humans (i.e., small, cohesive bands) because of the distribution and abundance of foods in forested versus savanna environments. The grouping behavior at Fongoli does not support this hypothesis, and indicates that patterns of food availability for apes in savanna versus forested environments should not be simply dichotomized as abundant versus scarce and widely scattered. The social nature of chimpanzees combined with an extremely large home range may mean savanna chimpanzee communities must range more cohesively in order to maintain their level of sociality. Fongoli chimpanzees are similar to chimpanzees elsewhere in terms of the amount of time they spend grooming (this study), for example, but fissioning into small parties in such a large home range may prove prohibitive to maintaining social bonds.

INFORMING HYPOTHESES OF HOMININ EVOLUTION

Differences between Fongoli chimpanzees and those living in more closed environments are especially informative regarding the behavior of early bipedal apes and their responses to what were likely similar selective pressures associated with an open environment. In order to better understand the behavior of savanna chimpanzees and perhaps the behavior of ancestral hominins, we examine our data according to what Moore (1996) has termed a relational model, a form of referential model. The behavior of chimpanzees within a savanna mosaic at the Fongoli site in southeastern Sénégal differs from that of chimpanzees at forested sites where they have been studied previously.

Temperature, food and water are three variables considered most important in affecting ape behavior in an open, hot and dry environment. Although the relationships among these three main variables are likely to be complex, even with these relatively preliminary data from Fongoli, hypotheses can be formulated based on associations between behavior and particular variables. The data presented here indicate that rainfall is a proximate factor affecting chimpanzee behavior in a savanna habitat. Although rainfall is commonly thought to correlate significantly and positively with food availability, at Fongoli the period of greatest fruit abundance is during the late dry season and early or transitional rainy season (Pruetz 2006). Fongoli chimpanzees form larger parties during the rainy or wet season, not during the period of greatest food abundance, indicating that water availability first and foremost affects grouping behavior.

The observation that Fongoli chimpanzees increase their activity during the coolest hours of the day during the dry season indicates that temperature should be considered a significant factor affecting hominin behavior in this environment as well. Fongoli chimpanzees' patterns of preferentially using gallery forest habitat might be explained by temperature stress or water stress, given these habitats are associated with the few water sources available throughout the year as well as the few sources of shade.

In addition to the findings of the current study, other aspects of the Fongoli chimpanzees' behavior indicate that temperature is significant for living great apes in a savanna environment. Chimpanzees here have been observed to forage and to travel up to one kilometer on brightly moonlit nights (Pruetz, unpublished data). This nocturnal movement is hypothesized to be a reaction to temperature stress during the dry season. Habitat types available to chimpanzees at Fongoli vary in temperature, and this has been linked to apes' cave use here (Pruetz 2007). Even slight changes in habitat use by early hominins, such as using more open habitats in addition to more forested areas, would have exposed early bipedal apes to some of the same pressures that affect savanna-dwelling chimpanzees today. Hypotheses that include climatic variables as important selective pressures on the behavior and adaptations of early hominins appear to be especially relevant. The influence of dry season water availability and its subsequent effects on patterns of food availability and distribution as well as the confounding effects of high temperatures on early hominin behavior should be emphasized in scenarios of hominin evolution.

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