THE RANGING BEHAVIOR OF BONOBOS IN THE LOMAKO FOREST

by

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DISSERTATION ABSTRACT

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The ranging behavior of an animal can reveal much about the social and ecological conditions it faces. Food availability, feeding competition, population pressures, metabolic requirements and human influences can all influence the ranging behavior of individuals. For modern humans, the manner in which we move about our world is limited only by access to technology and other cultural factors. Of course, it has not always been that way. Based on recent fossil discoveries, our earliest bipedal ancestors more closely resembled the living great apes in morphology. Consequently, studies of great ape behavior have been used to reconstruct scenarios of early hominin behavior. And while much has been written about chimpanzee (*Pan troglodytes*) ranging in this regard, less is known about bonobos (*Pan paniscus*).

Along with chimpanzees, bonobos are our closest phylogenetic relative, existing today as a descendant of a common ancestor the *Homo* and *Pan* genera shared sometime around six million years ago. Despite their close taxonomic relationship, however, there are a variety of behavioral differences between bonobos and chimpanzees. The aim of this dissertation is to better understand these differences within the context of ranging and social behavior and apply the results to models of early hominin behavior. More specifically, I used a Geographic Information Systems (GIS) approach to examine general bonobo ranging data, the differences in ranging behavior between males and females, and the manner in which neighboring groups interact. Compared with chimpanzees, bonobos at Lomako range over a much smaller total area, are not territorial, and differ in the composition of social parties. In general, female bonobos are more gregarious and cohesive, moving in semi-stable groups I call “cliques”, while males are less aggressive and more likely to move independently. These results likely reflect the high levels of food availability for bonobos at Lomako, reducing the level of feeding competition, and emphasizing social and mating strategies in group formation. Consequently, the spectrum of potential early hominin ranging behavior must be expanded from the current chimp-centric perspective.

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CHAPTER I

RANGING BEHAVIOR AND *PAN*

Introduction

If one regards our evolutionary lineage as a puzzle, then the bonobo (*Pan paniscus*) is a peculiar albeit important piece, the shape of which is not entirely clear. Along with the chimpanzee (*Pan troglodytes*), this ape is our closest phylogenetic relative, existing today as a descendant of a common ancestor that the genera *Homo* and *Pan* shared approximately six million years ago (Chen and Li 2001, Stone et al. 2002, but see Arnason et al. 2000). Several fossil hominids from the Miocene-Pliocene boundary have been discovered over the past decade with crania and post-crania that are similar to the living species of *Pan* (Zihlman et al 1978, Zihlman 1979, McHenry and Corruccini 1981, Lovejoy et al. 2009). The combination of the close genetic relationship shared between *Pan* and *Homo* with these recent fossil finds have spurred field studies across equatorial Africa in hopes of elucidating the potential behavior of our earliest ancestors and identifying the selective forces that may have shaped, defined, and distinguished human evolution (e.g. Wrangham and Pilbeam 2002). But while the overwhelming majority of research projects studying *Pan* have focused on chimpanzees, bonobos have received considerably less attention.

First described in 1933 (Coolidge), bonobos were the last of the four non-human great apes to be "discovered." Endemic to the Democratic Republic of the Congo (DRC) they are found primarily in the dense, primary rainforests of the Congo River basin, but also in the more open, mosaic environments in the southern portion of their geographic range (Thompson 2001, 2002). Based on genetic and paleoenvironmental analysis, bonobos were isolated from chimpanzees sometime between 800,000 and 1.8 mya

(Beadle 1981, Kaesmann et al. 1999, Yu et al. 2003, Won and Hey 2005, Caswell et al. 2008) when the Congo River grew to such a size that crossing the river was impossible for forest dwelling mammals, resulting in chimpanzees inhabiting the forests and other habitats north of the river and bonobos those to the south (Thompson 2003). Since that split, the two species of *Pan* have evolved a number of morphological and behavioral differences (White 1996, Parish, de Waal and Haig 2000, but see Stanford 1998a). These differences have become a primary focal point of research on *Pan* as the more well-known chimpanzee has become a template in which bonobo behavior and morphology can be compared and contrasted. This approach that has been widely successful in that the spectrum of behavioral differences seen within and between the *Pan* species has stimulated several debates as to the physical and behavioral characteristics of the last common ancestor the *Pan* species shared with humans. More specifically, studies of these apes have refined our view of the evolution of human tool use, culture, warfare, cooperation, intelligence and more. And while our knowledge on bonobos in these areas is growing, we have a long way to go.

The aim of this dissertation is to better understand the differences and similarities between bonobo and chimpanzee ranging and social behavior. In particular, I will use a Geographic Information Systems (GIS) approach (Chapter II) to examine general bonobo ranging data (Chapter III), differences in ranging behavior between males and females (Chapter IV), and intergroup interactions (Chapter V) and attempt to apply the results of these studies to matters of early hominin evolution (Chapter VI). To do this it is necessary to understand the forces that affect the way in which an animal moves. The remainder of this chapter will look at the ecological and social factors that affect the ranging behavior of primates with particular attention paid to the socio-ecological differences between chimpanzees and bonobos.

Factors Affecting Primate Ranging

The manner in which individuals and groups struggle to obtain, utilize, and defend home ranges has become one of the central pursuits in behavioral ecology (Börger et al. 2006). Taken as a whole, research has shown that the area an animal uses is determined by a complex set of morphological and behavioral traits that must factor the interplay between physiology, social conditions, life history traits, and ecology. The large number of definitions, expansive methodology, and debates over its usefulness (Borger et al. 2006, Gautestad and Mysterud 1995) hint further at the complexity with which animal ranging is endowed. Still, we know that animals do not wander about aimlessly. Rather, they tend to use a distinct area repetitively over time (Darwin 1859). In some species, the ranging area is vast. For example, Egevang and colleagues (2010) tracked Arctic Terns, migratory birds that travelled over 80,000 km annually. In other species, the home range may be small. Prairie voles (*Microtus ochrogaster*) were found to move over areas as small as 80 m^2 (Harvey and Barbour 1965).

Primates vary greatly in the ways in which they move about their environments. In an effort to quantify ranging behavior, studies have typically focused on two measurements: the annual home range (HR) and daily path lengths (DPL). The HR refers to those areas used most often (Burt 1943), are measured using a variety of techniques (see Chapters II & III), and can be interpreted conceptually or operationally (Powell 2000). Conceptual models of an animal’s HR are centered on familiarity and use. Operational models may more accurately reflect an individual’s cognitive map, which includes all areas an animal has traveled and can be an important consideration for conservation managers. Regardless, both of these models reflect the demography and ecological conditions vital for better understanding how an animal adapts to its environment (Börger et al. 2006) and may help explain the development of an individual's cognitive map (Peters 1978). Furthermore, an understanding of the way animals move through their habitat can help us more fully comprehend the manner in which they conceive and perceive their world (Powell 2000). A slightly more concrete concept, the DPL of an animal can also tell us much about the way in which individuals and groups must navigate their environment. It is often represented as an average or mean length moved throughout a day. Moreover, although DPL may mirror the more immediate conditions that drive animal movement, many of the social and environmental conditions that affect DPL also affect HR. Several studies have aimed to better grasp these conditions.

Individuals and groups must forage over an area that satiates their metabolic, nutritional, reproductive, and security requirements (Chapman and Chapman 2000). Accordingly, a species' place within its habitat influences the range area and daily distances travelled (Leonard and Robertson 2000). For example, early research on animals noted that larger animals typically have higher metabolic requirements (Kleiber 1932). As such, larger animals tend to have larger annual and daily ranges than smaller animals or must have access to richer habitats (Harvey and Clutton-Brock 1981, Swihart et. al 1988, Bassett 1995, Leonard and Robertson 2000). This general relationship, shown in several taxa (small mammals, McNab 1963; birds, Schoener 1968; lizards, Turner et al. 1969; and primates, Milton and May 1976, Clutton-Brock and Harvey 1977), hints at the greater affect of diet and food availability on ranging behavior.

Several studies have demonstrated the affect of food availability, trophic levels, and dietary niches on animal ranging (Clutton-Brock and Harvey 1977, Robinson and Redford 1986). In an effort to quantify these relationships, Harestad and Bunnel (1979) developed an equation, $H = RP^{-1}$, where H is home range, R is the metabolic energy requirements of an individual, and P is the productivity of the environment relative to trophic level. They found a strong correlation between home range size, body weight, and trophic level. Furthermore, general patterns confirmed the importance of diet on ranging as studies showed that carnivores have larger ranges than other animals while frugivores have larger ranges that folivores (Wrangham, Gittleman, and Chapman 1993). Furthermore, food distribution and abundance (Clutton-Brock 1977), forest structure (Gautier-Hion et al. 1981), and seasonality (Li et al. 2000) can affect ranging behavior.

Another factor is group size. In general, primates that range in groups typically have larger total home ranges than solitary individuals (Milton and May 1976) while bigger groups often range farther than smaller groups in order to find enough food (Altmann 1974, Takasaki 1981). Simply stated, individuals must travel greater daily distances over greater areas and expend more energy if they are part of a large group (Wrangham, Gittleman, and Chapman 1993). With an increase in energy and time spent traveling, a point may be reached at which time the energy gained from the environment is less than energy spent in transit. As a result, smaller groups should become advantageous, demonstrating a “constraint” on the size of a group that can efficiently exploit available resources. This model assumes that increased group size leads to increased within-group competition, which in turn, results in increased in DPL (Chapman and Chapman 2000).

No matter how available food may be, access is crucial. Primate groups often have home ranges that overlap with those of neighboring groups as well as other species. Subsequently, there are many strategies for insuring access and all of them influence movement patterns (Isbell 1983, Kinnaird and O'Brien 2000). Of these strategies, territoriality is the most extreme and most likely to occur when resources are in short supply, and in areas where those resources are economically defensible (Mitani and Rodman 1979, Lowen and Dunbar 1994). That is, territoriality should be seen when the benefits of defending an area outweigh the costs of defending it. When the costs of patrolling and territoriality are too high, groups may evolve other strategies such as avoidance, confrontation, or the use of long-distance calls to locate and notify neighbors of their presence (Kinnaird and O'Brien 2000).

Several other factors affect primate ranging. Parasite avoidance (Freeland 1979), predation (Isbell 1994), weather patterns (Clutton-Brock 1977), the previous day's movements (Fossey and Harcourt 1977), and the position of sleeping trees (Rasmussen 1979) have all been shown to play roles in primate ranging. Together, these factors illustrate the complex set of adaptations that must account for the interplay between ranging behavior and an individual's physiology, social conditions, life history traits, and ecology. Undoubtedly, many of these same factors influenced the ranging behavior of early hominins as well.

The Ranging Behavior of Extinct Hominins

Assessing the ranging behavior of extinct species has obvious limitations. Research on paleo-ecosystems, fossil morphology, and extant primate and mammal socio-ecology, however, can be used to create models of potential hominin behavior. For example, studies have demonstrated that primates (including humans) with larger brains require more high quality, nutrient dense diets to satiate their high metabolic requirements (Wolpoff 1980, Leonard and Robertson 1992, 1994). Consequently, the increases in hominin brain size throughout human evolution have likely been accompanied by changes in movement and foraging patterns that included larger daily and annual home ranges (Leonard and Robertson 2000).

It is also likely that ranging behavior changed as hominin body size increased. Estimates suggest that human ancestors average weight increased from 37 kg in *Australopithecus afarensis* to 58 kg in *Homo* erectus (McHenry 1994) To better understand the relationship between body size and ranging of hominins, Leonard and Robertson (2000) analyzed dietary quality, home range size, and body weight in 47 non-human primates and six groups of human foragers living in tropical habitats and found that individual home range size increased as body weight increased with a scaling component very similar to that found in the experiments of Harestad and Bunnell (1979). Leonard and Robertson (2000) showed that larger animals must work harder for food, expending more energy above their minimal basal metabolic rate. Furthermore, they used an “ape-model” and a “human-model” based on variation in dietary quality measured from extant apes and hunter-gatherers to predict home ranges for extinct hominins (Table 1.1). These and other studies have repeatedly demonstrated the usefulness of primates and living hunter-gatherers as models of extinct hominin behavior (Wrangham and Pilbeam 2002, Marlowe 2005) adding perspective to what would otherwise be a cloudy vision. And while all of the great apes have contributed to our understanding of early hominin behavior, the majority of research has focused on chimpanzees.

Table 1.1. Estimated body weight and home range size for fossil hominin species

Species	Male Weight (kg)	Female Weight (kg)	Avg. Weight (kg)	HR (individual) Ape model (km²)	Hr (individual) Human Model (km²)
A. afarensis	44.60	29.10	37.00	46	240
A. africanus	40.80	30.20	35.50	43	227
A. robustus	40.20	31.90	36.10	44	232
A. boisei	48.60	34.00	44.30	58	307
H. habilis	51.60	31.50	41.60	54	281
H. erectus	63.00	52.30	57.70	84	440
H. sapiens	65.00	54.00	59.50	86	451

[a] The "ape model" assumes a dietary quality similar to great apes while the "human model" assumes a dietary quality similar to modern tropical foragers (from Leonard and Robertson 2000).

Chimpanzees

The close relationship of humans to non-human primates (NHP) has undoubtedly been recognized for millennia. Baboons and langurs have been revered and kept as pets by ancient Egyptians and Indians and deemed to have human emotions and powers. African folklore often refers to NHP as “human-like” (Stirling, personal communication). In Senegal, for example, tribal people believed chimpanzees were former humans who cowardly fled to the forests in the face of war (Waller unpublished data). As early as the 7th Century BC, Greek poets were using primates as caricatures of humans (McDermott 1935) describing their mimicry of human nature as analogous to our own mimicry of the divine. It was not until centuries later that this relationship was formalized when Linnaeus, in his first edition of *Systema naturae* (1735), classified humans and monkeys within the same taxon. When Darwin published his theory of evolution via natural selection (1859) and speculated on the human/NHP evolutionary relationships (1871), interest in a scientific approach to studying NHP behavior was sparked.

Among the first primates investigated, chimpanzees have been studied extensively both in captivity and in their natural environment. Acclaimed psychologist Wolfgang Kohler spent several years during World War I at a primate reserve in the Canary Islands (Gould 2004). In his book, *The Mentality of Apes* (1925), Kohler detailed the manner in which chimpanzees solved complex problems dealing with obtaining food. In the 1920s, American psychologist Robert Yerkes began a similar series of investigations at his home and, later, at the Yale Laboratories of Primate Biology in Florida. His book *Almost Human* (1925) chronicles his experiences living with a chimpanzee and, what would only later be discovered, a bonobo (Coolidge 1984). Over the next 20 years, Yerkes and his colleagues demonstrated how very much like humans these nimble-minded apes behaved. A series of biochemistry and genetics studies would confirm just how phylogenetically close chimpanzees and humans are.

Beginning with a series of blood studies conducted by Nutall (1904), immunological research began to show how similar chimpanzees and humans and hinted at our shared evolutionary past. The culmination of this method of study occurred when Sarich and Wilson (1967 a, b) used the variability in the blood protein albumin to establish a molecular clock. Their results suggest that humans and chimpanzees split approximately five million years ago. Wilson and King (1975) made further protein structure comparisons and estimated that chimpanzees and humans share approximately 99% of their genetic material and confirmed the split date proposed by Sarich and Wilson (1967a, b). Both the percentage of shared DNA and the date for the *Pan*/*Homo* split have been refined as new techniques, including complete genome sequencing, have been developed. Since that time, a number of studies have generally confirmed these initial estimates and shown that chimpanzees and humans are very closely related based on their

DNA (Ruvolo et al. 1994) and that those differences that do exist are largely found in the genes that regulate expression rather than those that code for proteins (Enard et al. 2002). Furthermore, it is currently well accepted based on these studies and known DNA mutation rates, that chimpanzees and humans shared a common ancestor sometime around 5-6 million years ago (Chen and Li 2001, Glazko and Nei 2003, but see Patterson et al. 2006). Building from these impressive discoveries, however, a full perspective of human evolutionary scenarios will require information on the behavior of these apes within their natural environment.

Chimpanzee Field Studies

While the majority of his research focused on captive chimpanzees, Henry Nissen is thought to have been the first person to set out in an effort to study chimpanzees in their native habitat. Backed by Yerkes, Nissen (1931) spent nine weeks in what is today the country of Guinea remarking on basic behavior in his published field study. At the time, methods for studying wild apes were not developed and Nissen had few direct observations of chimpanzee behavior. Nonetheless, he pioneered a research approach that would illuminate chimpanzee behavior (Peterson 1998) and set the stage for Jane Goodall and Toshisada Nishida.

Beginning in 1960, the research conducted in Tanzania by Goodall at the Gombe Reserve and Nishida in the Mahale Mountains showed that the traits shared by humans and chimpanzees were not an artifact of chimpanzees having been raised in captivity. Their observations on social organization (Nishida 1968), social aggression (Goodall et al. 1979, Nishida et al. 1985), cooperative hunting (Goodall 1963), and the making and using of tools (Goodall 1964, have changed the way in which humans think about our ancient past and overturned speculation that one or the other of these traits are unique to humans. Furthermore, the results spurred dozens of long term field sites across equatorial Africa. What has emerged is a portrait of a species that behaves in a number of ways useful in constructing early hominid behavior (Wrangham and Pilbeam 2002).

All chimpanzees live in multi-male/multi-female communities, or “unit-groups,” where parties within the communities fluctuate in size and composition (Nishida 1968) based on factors such as food availability (Itani and Suzuki 1967, Goodall 1986, Wrangham 1986, Chapman et al. 1994, Mitani et al. 2002), predation pressure (Boesch 1991), the presence of females in estrus (Goodall 1986, Matsumoto-Oda 1999, Boesch and Boesch-Achermann 2000, Hashimoto et al. 2001, Mitani et al. 2002) and inter-group aggression (Wrangham 1999, Watts and Mitani 2001). Their daily lives are dictated by a rudimentary form of culture (McGrew 1992) that varies between groups and appears centered on obtaining food. For example, chimpanzees at the Fongoli site in southeastern Senegal combined their tool making abilities with their high regard for meat by modifying sticks into “spears”. The spears are then plunged into tree cavities in an effort to kill and eat galagos (Pruetz and Bertolani 2008). This behavior has not been found at any other chimpanzee site, suggesting it may be a cultural adaptation to an ecological challenge (acquiring animal protein). There are several other behaviors that vary between the different sites, all of which reflect the variable environmental and social conditions chimpanzees must face, providing insight into how behaviors are socially transmitted and ecologically driven (McGrew 1992, Boesch 1999).

Chimpanzees are primarily fruit eaters (Conklin-Brittain et al. 1998, Pruetz 2006) although they will supplement their diet with bark, flowers (pers. obs.), insects, eggs (Nishida and Uehara 1983, Stumpf 2007), and vertebrates hunted opportunistically or in a coordinated fashion (Stanford 1996). Still, the distribution of preferred fruits play the biggest role in their social organization (Wrangham 1980, Boesch 2002). Seasonality (Doran 1996), population density (Mitani 2006), habitat structure (Pruetz 2006), and inter-species competition levels (Waller 2005) have all been found to vary the amount of fruit available for each community. Areas with good food sources are highly coveted as access to more food can lead to higher reproductive success (Pusey et al. 1997, Williams et al. 2002, although see Riedel et al. 2011). As a result, chimpanzee females cannot afford to be very social, spend a considerable amount of time alone or with their dependent offspring, and must compete with each other over preferred areas (Nishida and Kawanaka 1972, Pusey 1979, Wrangham and Smuts 1980, Doran 1996, but see Newton-Fisher 2006, Wakefield 2008).

Male chimpanzees, on the other hand, are philopatric and constantly struggle for status within their community (Newton-Fisher 2002). From an evolutionary fitness perspective, highest-ranking males benefit from preferred access to females and food (Sugiyama and Koman 1979, Tutin 1979). Males stay within the community for their entire life and interact often (Goodall 1986). They make and break alliances relatively frequently which results in a fluid social hierarchy (de Waal 1982).

Despite fierce within-group competition, the fact that all the males within a community are related may be associated with strong male bonds (Watts 2002, but see Mitani et al. 2002 and Langergraber et al. 2007). These bonds are beneficial, directly or indirectly (via kin selection), in that they enable male community members to coordinate hunts (Stanford 1998b, Watts and Mitani 2001), patrol territories (Watts and Mitani 2001), and lethally raid neighboring communities (Goodall et al. 1979, Nishida et al. 1985, Manson and Wrangham 1991, Boesch & Boesch-Achermann 2000, Newton-Fisher 1999, Watts & Mitani 2001). These behaviors result in increased access to resources

(Williams et al. 2004) and mating opportunities (Nishida et al. 1985, Goodall 1986, Boesch et al. 2008). Simply stated, individual male chimpanzees benefit from grouping while the cost of grouping for individual females is generally higher. This basic premise is reflected in the way chimpanzees move about their habitat.

Chimpanzee Ranging

The area over which a community of chimpanzees ranges (Table 1.2) varies between populations and over time (Goodall 1986, Newton-Fisher 2002, Williams et al. 2004, Basabose 2005) and reflects many of the social and ecological conditions that they face. As mentioned above the temporal and spatial distribution of fruit plays an important role in chimpanzee ranging behavior. For example, chimpanzees in the Sahel region of Senegal live in a hot and arid environment where fruit-rich gallery forests are scattered within a predominantly wooded-grassland ecosystem (Baldwin et al. 1982, Waller 2005, Pruetz 2006). Additionally, the area experiences a prolonged dry season which results in relatively lower fruit availability and an increase in the importance of gallery forests to chimpanzees in this area (Baldwin et al. 1982). Consequently, estimates of home range at Mt. Assirik and Fongoli are amongst the highest recorded for chimpanzees at 37km^2 and 63km^2, respectively (Baldwin et al. 1982, Pruetz 2006). Meanwhile at sites like Gombe and Sonso, where there is higher fruit density and less seasonality, chimpanzee home ranges are much smaller (Newton-Fisher 2002, Williams et al. 2004).

Table 1.2. *Pan* Study Sites, modified from Stumph 2007

	Tai	**Bossou**	**Mt Assirik**	**Gombe**	**Mahale**	**Kanyawara**	**Ngogo**	**Budongo**	**Kahuzi-Biega**	**Wamba**	**Lomako**
Study Site Location	Ivory Coast	Guinea	Senegal	Tanzania	Tanzania	Uganda	Uganda	Uganda	DRC	DRC	DRC
Habitat	Tropical Rainforest	Tropical Forest	Savanna Woodland	Riverine Forest and Woodland	Riverine Forest and Woodland	Moist Evergreen Forest	Moist Evergreen Forest	Moist Tropical Rain Forest	Montane and Bamboo Forest	Dry, Swamp and Evergreen Forest	Primary Evergreen Forest
Annual Mean Rainfall (mm)	1829	2230	954	1775	1836	1671	1800	1842	1619	2000	1844
Elevation (m)	202	550	100-311	1137	1040	1500	1400	1100	2200	400	390
Provisioned	no	yes	no	until 2000	until 1987	no	no	no	no	until 1997	no
Community/Clique Size	29-82	16-22	>15	38-60	45-101	44	>140	>29	22	28	21-36
Home Range Size (KM²)	13-26	15-20	50	4-24	7 - 14	16	35	7	10	22	2.4*
Average Daily Range (m)	2400	1000	-	3450	4825	-	-	-	400	2608	1840*

***** This study

The effects of fluctuations in food availability have perhaps best been demonstrated at the Tai site in Cote d'Ivoire. A low-altitude, primary rain forest, the Tai forest experiences two significant dry seasons, one of which is accompanied by a significant reduction in fruit availability. Doran (1996) found that chimpanzees respond to seasonal changes in food availability in predictable ways. During extended periods of scarcity, chimpanzees reduced party size and day ranging, fed more frequently on lower quality foods, and increased the amount of time spent feeding. Despite these seasonal changes, fruit is widely scattered and females can move about the entirety of their community and without staking out independent core areas (Reidel et al. 2011).

Another factor affecting home range is community demographics. Larger communities tend to have larger home ranges than smaller communities, for the reasons described earlier in this chapter. For example, the atypical size of the Ngogo community (144 individuals) has a range similar in size to Mt Assirik even though its habitat more closely resembles that at Gombe. More specifically, there appears to be a link between the number of adult males and the extent of the community range (Herbinger et al. 2001, Lehmann and Boesch 2003), probably because males travel faster (Wrangham 2000)are have longer daily path lengths (Wrangham and Smuts 1980) than females. This is due in all likelihood to the costs of travel for females with offspring and the predominantly male behaviors that require longer travel times such as hunting, lethal raiding, and territorial patrols. Research has shown that these territorial patrols clearly demarcate boundaries (Watts and Mitani 2001, Newton-Fisher 2002) and inter-community aggression in the form of lethal raiding (Wrangham 1999) coupled with the threat of infanticide can also affect the manner in which chimpanzees are spatially distributed. Males at several sites have been found to attack and kill members of neighboring communities (Goodall 1986, Manson and Wrangham 1991, Boesche and Boesche-Acherman 2000, Watts and Mitani 2001). In some cases, this can result in the expansion of the community range resulting in increased access to food or mates (Williams et al. 2004, Goodall 1986). Lethal raiding can have an effect on the distribution of females as well. Inter-group killings means the threat of infanticide is greater on the periphery of chimpanzee community territories than at their core, so there is an overall tendency for females to avoid peripheral areas where they and their offspring are at greater risk of being attacked and killed (Arcadi and Wrangham 1999, Williams et al. 2004).

Like other species, the ranging behavior of chimpanzee communities is the result of a complex combination of climatic, ecologic, and social factors that change daily, seasonally, and annually. Still, a relatively clear picture of male kin groups patrolling large areas in order to envelope a maximum number of smaller female core areas and preferred feeding sites has emerged (Chapman and Wrangham 1993, Williams et al. 2004). Due in part to discoveries that have shown how similar chimpanzees and humans are genetically and behaviorally (i.e. tool use, cooperative hunting, and culture), one might be forgiven for assuming that our earliest ancestors lived in similar social systems with similar ranging behaviors. But there is another ape species that needs to be better understood. A species that is equally close to humans phylogenetically. A species that, when compared with chimpanzees, differs drastically in its social and ranging characteristics. That species is the bonobo.

Bonobos

As apes go, bonobos have many monikers. They have been called the “Last Ape” (Kano 1992) because they were the last of the great apes to be taxonomically classified. Mainstream media publications have often referred to them as the “hippy” or “make love, not war" ape for their eclectic sexual lifestyle. Despite the fact that their weight falls within the range of "common" chimpanzees, they have been called "pygmy," or "gracile," chimpanzees due to their smaller skeletal components (Coolidge 1984). Perhaps most accurately, they have been called the "forgotten ape" (de Waal 1998) as behavioral ecologists have ignored or dismissed them in favor of chimpanzees when modeling early hominid behavior. The term "bonobo" itself is troublesome as it is likely a misspelling of the town of "Bolobo", a port city where collected specimens were shipped abroad (Susman 1984). Interestingly, there is no universal Congolese name for bonobos, which may be due to the ethnic diversity of the country (White 1996). Regardless of what we call them, however, our perception of the potential spectrum of behavior of our earliest human ancestors is incomplete when they are disregarded. Thanks in no small part to long-term field research, that spectrum is becoming clearer.

First described as a separate species in 1933 (Coolidge) due to the juvenilized appearance of their skulls, bonobos are endemic to the Democratic Republic of the Congo (DRC-formerly Zaire) south of the Congo River. The separate taxonomic designation from chimpanzees has been debated (Stanford 1998, Parrish, de Waal and Haig 2000), but appears to be justified based on genetic and morphological research (Shea and Coolidge 1988, Ruvolo et al. 1994, Kaessmann et al. 1999, Stone et al. 2002, Yu et al. 2003). Estimated dates of divergence from chimpanzees range from .86 mya (Won and Hey 2005) to 2.5 mya (Morin et al. 1994). Although they show overlap with the four subspecies of chimpanzees in body weight and long bone lengths (Table 1.2), bonobos do have some juvenilized cranial traits. Their cranial capacity is slightly smaller (350 ml vs. 390 ml) as are their canines (Zihlman 1996). Additionally, bonobos have darker faces, hair parted down the middle (Kano 1992), and very different vocalizations (Hohmann and Fruth 1995). While these differences are important, it is behavior that most distinguishes bonobos from chimpanzees.

Bonobo Behavior

Even before Coolidge formally published his thesis that bonobos were a separate species from chimpanzees, others had speculated (Thompson 2001). Robert Yerkes wrote about a male he named "Prince Chim" who differed in personality and temperament from the male chimpanzees he had previously met. According to him (Yerkes 1925, pp 244), he had never met "…an animal the equal of Prince Chim in approach to physical perfection, alertness, adaptability, and agreeableness of disposition." And while some have claimed that the variability witnessed in bonobo behavior when compared with chimpanzees is a matter of degree and does not necessitate species distinction (Stanford 1998a, Newton-Fisher 2006), research on bonobos conducted in the field and in captivity since the time of Yerkes and Coolidge have overwhelmingly supported taxonomic separation.

Until more recently, the majority of information on wild-living bonobos came from field studies initiated at two sites: Wamba and Lomako. The Wamba site has been run by Japanese researchers since 1974 (Kano and Mulavwa 1984) with interruptions due to political instability and war from 1991-1994 and again from 1996-2002 (Idani et al. 2008). Research resumed there in 2003. Located in the northern section of the Luo Reserve, the 100 km^2 study area at Wamba includes five human settlements scattered amidst primary forest, old secondary forest, young secondary forest, swamp forests and agricultural fields (Kano and Mulavwa 1984, Kano 1992, Hashimoto et al. 2008). The majority of the observations at Wamba come from two groups, E1 and E2, with the E1 group provisioned until 1996 (Hashimoto et al. 2008).

The Ndeli site at the Lomako Forest Reserve, established by Noel and Allison Badrian from the State University of New York at Stony Brook, was established in 1973 and experienced similar disruptions due to war and civil unrest. The 40 km^2 study area consists of several forest types, but is principally climax evergreen and polyspecific primary rain forest (75.2% of study site) with smaller areas of second-growth, slope, and swamp forest (White 1992). While bonobos use all forest types, swamp and secondary areas are utilized less often and climax evergreen forest is used most often (93% of focal sampling-White 1992). The habitat at Lomako is less disturbed than at Wamba and the bonobos there have never been provisioned (White 1992). As a result, they are harder to follow and less is known about their behavior. Ecologically, the habitat at Lomako may be more indicative of the evolutionary environment that shaped bonobo behavior.

Today, as some semblance of normalcy returns to the once war-ravaged nation, both the Lomako and Wamba sites have reopened and research sites have been established at Salonga (Hohmann et al. 2006, Reinartz et al. 2008), Lac Tumba (Inogwabini et al. 2007), Lukuru (Thompson 2002) and Yalosidi (Coxe pers. comm.). Based on studies conducted at all of these sites, an idea of bonobo behavior that drastically differs from that of chimpanzees has emerged, with important consequences for our perception of our earliest ancestors.

Bonobo Social Organization

Instead of highly bonded males that are territorial and aggressive within and between communities, bonobo central social units consist of allied, unrelated females (Kano 1992, Parrish 1994), particularly those with infants (Chapter IV). Throughout this dissertation, I will use the term “clique” to describe groups of bonobos that are centered on a small number of core females, usually with infants. The females in these cliques appear to be relatively stable with greater turnover occurring among males and females without infants (Chapter IV). Consequently, male-female interactions are more numerous in larger parties while smaller groups reflect the bonds created by female-female affiliation (White 1992).

The female-female bonds are sustained through a homosexual behavior known as genito-genital (G-G) rubbing (White 1996) as well as through food sharing behaviors not seen in female chimpanzees (White 1994). Well known for their promiscuity, non-reproductive sex is not limited to females. Bonobos engage in sexual behavior across age categories and within and between sexes (Kano 1992) to build alliances (de Waal 1987), create paternity uncertainty (Williams et al. 2002) and diffuse rising tensions (Furuichi 1987, 1992, Kano 1992). The number of copulations may be increased in captivity or with provisioning (Kano 1992) and has been associated with feeding contexts suggesting that bonds are most important during feeding events. These bonds may help in creating relatively stable groups of females (Waller et al. 2008) that benefit by cooperatively defending food patches from others (White 1986, Idani 1991, Parrish 1994, Hohmann and Fruth 1996), group protection from infanticidal males (White and Waller 2008), and the nutritional rewards of coordinated hunts aimed at arboreal monkeys (Surbeck and Hohmann 2008). Having an infant may be necessary to be central members in the core female groups, suggesting that infanticide may drive females with infants together to cooperatively defend themselves (Chapter IV).

Males join cliques when food availability is higher (Waller et al. 2008) and may be most closely associated with their mothers, who may facilitate mating opportunities (Ihobe 1992, Furuichi 1997, Surbeck et al. 2010). Males are also more likely to be found ranging alone when compared with females (Kano 1992, White 1996) and may attempt to ingratiate themselves to female cliques by leading them to food sources (White et al. 2010). Compared to chimpanzees, there is much less male-male bonding among bonobos (Kano 1987, Kano 1992, White and Chapman 1994) and the dominance hierarchy is not as clear or aggressive (Furuichi 1997). They do not patrol territories or lethally raid neighboring communities, nor do females avoid the borders of their range (Chapter V, Waller et al. 2010) as expected given that males have not been found to commit infanticide (White and Waller 2008). In fact, inter-community bonobo interactions that have been observed usually consist of vocalizations that serve to announce the presence of each group with smaller groups tending to move away from larger ones (Badrian and Badrian 1984, Kano 1992). And although there are occasional violent acts between individuals (Kano 1992), bonobos are generally more peaceful compared with chimpanzees (Furuichi 1997). Several hypotheses have attempted to explain these behavioral differences, all of which focus on food availability.

Since the publication of Wrangham's (1980) ecological model of female bonding and competition, studies of primate social behavior have focused on the distribution of food and its effect on social structures. In that seminal paper, Wrangham proposed a strong link between the defendability of food, the costs of female bonding, and the corresponding dispersal of females. In species that eat food that is defendable such as fruit patches, groups of related females were predicted to cooperatively defend food sources from outside females within a hierarchical frame. In species who consumed non-defendable foods such as leaves, females would not experience the same level of bonding and cooperation and subsequently, their relationships would be loosely defined. Since then, primatologists have incorporated patch size (Janson 1988), intra and inter-group contest and scramble competition (Isbell 1991), and dispersal, tolerance, hierarchies, and kin dimensions (Sterck et al. 1997) that have further refined models of primate sociality based on female competition for food.

Three hypotheses based on these models have attempted to explain the social differences between bonobos and chimpanzees, all of which center on the assumption that the female-bonded social structure reported in bonobos is a species-specific trait allowed by high food availability and the subsequent low levels of feeding competition (Chapman et al. 1994), regardless of the fact that females are unrelated. The first hypothesis suggested that bonobo feeding competition is relatively low due to greater access to terrestrial herbaceous vegetation (THV), an abundant and ubiquitous food source (Wrangham 1986, Badrian and Badrian 1984). Eaten regularly by bonobos (Malenky and Stiles 1991), chimpanzees eat THV far less frequently (Wrangham 1986). For example, THV accounts for 33% of the overall food intake for bonobos at the Wamba site and only 7% of overall food intake for chimpanzees at Gombe (Wrangham 1986). Despite this fact, party size is smaller when bonobos are feeding on THV than other foods (White 1996). Furthermore, Malenky and Stiles (1991) found that although THV at Lomako was abundantly distributed, bonobos preferred particular plants (namely *Haumania liebrechtsiana*) to others, greatly reducing theotherwise seemingly ubiquitous distribution of THV patches. Consequently, Malenky and Stiles (1991) argue that it is unlikely that THV is responsible for the evolution of the bonobo social structure.

The second hypothesis proposed that food patch size was ultimately responsible for the reduced amount of feeding competition and larger party sizes of bonobos (White 1986, White and Wrangham 1988). According to White and Wrangham (1988), more bonobos (average party size = 7.21-7.26, White 1996) spent more time within a patch at Lomako while chimpanzee feeding parties at Gombe (average party size = 4.5, Goodall

1986) were smaller and remained within a patch for less time suggesting that patches at Lomako are bigger and allow for more sociality. Additional studies compared patches at Lomako and Kibale, a site that is ecologically more like Lomako than is Gombe, and found that patch size varied less at Lomako**.** This suggests that females are not prohibited from being social by fluctuating patch sizes (Chapman et al. 1994). Several methodological and definitional problems have been pointed out with regard to the results, however. For instance, there is little uniformity in the way patch size is measured across studies (Overdorff and Parga 2007). At Lomako, patch size was indexed based on the radius of the crown and tree diameter measured at breast height (DBH), while only DBH was measured at Kibale (White 1998) and no physical measurements were taken at Gombe (White and Wrangham 1988). Additionally, the density of patches, perhaps a more telling statistic (Chapman et al. 1994, Furuichi et al. 2008), is not included within these studies.

The third hypothesis, presented by Malenky (1990), suggested that the tree fruits eaten by bonobos in the Lomako region are consistently available year round as a result of decreased seasonality and high amounts of rainfall (1853 mm at Lomako vs. 750-1250 mm at Gombe). While rainfall is undoubtedly an important factor affecting the distribution of primate foods, several chimpanzee sites receive as much or more. Additionally, research challenging Malenky’s assumption that Lomako experiences less seasonality (described as the total number of months above or below 150 mm of rain) found that the Lomako Forest experiences two dry and two wet seasons and that there is no correlation between rainfall and total fruit abundance (White 1998).

Regardless of the problems associated with measuring food availability, it appears clear that bonobos live in areas with ample food resources. Several other behaviors have been observed that hint at the wealth of food options. For example, bonobos are not known to regularly use tools to access social insects such as termites (McGrew et al. 2007, Waller unpublished data) or to crack open hard-shelled seeds despite the availability of both resources within their range. This may be due to a lack of appropriate rocks for nut-cracking in their habitat or to an abundance of caterpillars, for which return rates are higher than for social insects (White et al. 2008). Regardless, it does not appear to be nutritionally necessary and/or economically viable for bonobos to spend time extracting hard to access foods.

Bonobo Ranging

Little has been published on the specifics of bonobo ranging. Studies at Wamba have been the most illuminating in this regard. Six communities have ranged at least in part within the Wamba study area, with the E group being the primary focus of research (Kitamura 1983, Hashimoto et al. 1998). According to Kano (1992), as much as 60% of the E group home range is shared by other groups resulting in a core range and an overlap range. Since the early 1980s, the E group split into two independent groups named E1 and E2 (Hashimoto et al. 1998). When researchers returned to the site in the late 1990s after political instability in the DRC interrupted research, they found that males had transferred into the E1 group from neighboring areas (Hashimoto et al. 2008). This suggests that, unlike chimpanzees, there is tolerance between and amongst males from differing groups. These findings combined with reportedly peaceful inter-group interactions (Idani 1991) hint at a reduced level of territoriality, an absence of lethal raiding, and a more fluid social group composition amongst male bonobos.

Past research at Lomako and Wamba used the grid square method to estimate annual home ranges. There are several problems with this technique, however, that make it less than ideal. For example, as each square visited has the same value regardless of the frequency of visits, home range may be overestimated if outlying peripheral areas are used only rarely, while core or habitually used areas may go unrecognized. Additionally, blocks that have not been used but were assumed to have been travelled through were included in home range estimates, further inflating the ranging area estimated. Finally, the range size is sensitive to grid size used by researchers as ranges decrease as grid square size decrease (Clutton-Brock 1975). Nevertheless, grid squares are easy to construct and can present a broad idea of areas frequented by groups or individuals. At Wamba, researchers used 500 m^2 grids and found that bonobos ranged between 12.3 and 31.5 km^2 during any one-year period (Hashimoto et al. 1998). The large size of these range estimates may be explained by the fragmented nature of the habitat, the location of provisioning sites within the study area, or bias favoring peripheral areas due to the grid square technique.

Thompson-Handler (1990) used 300m^2 grid squares to estimate the home ranges of three groups over four years at Lomako; Eyengo, Bakumba, and a “Splinter” group of immigrating females. These same groups will be the primary focus of research presented in this study. She found that the smaller Splinter group had a home range area of 8.1 km^2, while the larger Eyengo and Bakumba groups had home range areas of 12.0 km^2 and 13.8 km^2 respectively. She also noted that, like Wamba, there is a high degree of overlap between the group ranging areas. Approximately 30% of the Splinter range area overlapped with other cliques while nearly 50% of the Eyengo range and 41% of the Bakumba range overlapped with other cliques. As with Wamba, however, the same amount of bias towards peripheral areas and travel assumptions have influenced these measurements. In fact, based on frequency counts, 42 of 113 (37.2%) grids consisted of only one sighting while 25 of 113 (22.1%) of the grids had 5 or more sightings (range = 5-26) suggesting that nearly 40% of the estimated range is not habitually visited and that core areas are relatively small (Hashimoto et al. 1998, Hashimoto et al. 2008).

Although perhaps more indicative of immediate social and ecological conditions, even less is known about bonobo daily movement patterns. Again, Wamba has been most thoroughly studied. Furuichi and colleagues (2008), in an effort to better understand the relationships between food availability, ranging behavior, and social composition, used fruit fall clusters to estimate fruit abundance and daily follow data plotted onto a satellite image to estimate a daily mean ranging rate. Furthermore, they estimated daily ranging time based on the average times bonobos left their nests (07:26h) until they began constructing new ones (16:57h) resulting in a mean movement time of 9h, 31m. Applying mean movement time to travel distance calculated from follows, they concluded that bonobos at Wamba travelled approximately 2608 meters daily. The results showed positive correlations between party size and fruit abundance, as well as between party size and daily ranging distance, although the latter was not statistically significant. This is because, as food abundance goes up, more males join the female cliques. As these parties swell in size, they must travel further to satiate the needs of all party members.

Although Furuichi and colleagues (2008) show clear relationships between food availability, party size, and ranging, the methods used do have some issues. First, all-day follows of bonobos are notoriously difficult, particularly in primary and swamp forests or when bonobos are on the ground. Second, the measurement assumes that bonobos are moving constantly during the 9.5 hours of the day they are actively away from nests. The time spent feeding, resting, playing, and grooming is not factored into the equation.

Finally, the ranging rate of bonobos at Wamba rarely exceeded 600m/hr (Furuichi et al. 2008) meaning that bonobos would need to travel for approximately 4.3 hrs per day at that rate in order to cover 2608 meters daily, a length of time which exceeds the percentage of time spent traveling according to studies of bonobo activity budgets (Kano and Mulavwa 1984, White 1992).

The relationship between ranging behavior, food availability, and social organization is complex. If, as many believe, food availability in bonobo habitats is significantly higher compared with those areas inhabited by chimpanzees, bonobos should have less constrained party sizes and smaller annual and daily ranges simply because they need not expend as much energy traveling and can afford to be more social due to a lower degree of within group competition. Similarly, if competition from outside groups is not fierce, behaviors such as patrols or raids should not be seen, further contributing to smaller daily and annual ranges. Furthermore, as the area at Lomako has less human impact and higher percentages of undisturbed forests, bonobos there may be expected to range in even smaller areas than at Wamba. By more carefully examining the manner in which bonobos move about the Lomako Forest, we can better understand the differences in social organization between the *Pan* species. The remainder of this dissertation will attempt to do this.

CHAPTER II

GEOGRAPHIC INFORMATION SYSTEMS AND PRIMATE BEHAVIOR

Introduction

Data on the spatio-temporal locations of primates can be plotted using GPS (global positioning system) and GIS (geographical information system) technologies (Phillips et al. 1998). Once entered, one can analyze the influence of resource distribution on social organization, group cohesion, and issues related to conservation. For this dissertation, I take this approach with the bonobos of the Lomako Forest in the Equateur Province of the Democratic Republic of the Congo (DRC-formerly Zaire). Using the behavioral and spatial data collected during field seasons scattered between 1984 and 2009, combined with the analytical power of GIS software, a richer perspective on the manner in which individuals and groups of bonobos use their habitat emerges. In this chapter I detail the GIS methods used for this dissertation.

Research at Lomako

The history of bonobo studies at Lomako dates back to the early 1970s when preliminary studies were conducted (Badrian and Badrian 1977, 1978, 1980, Badrian et al. 1981, Susman et al. 1980). Long-term research, however, did not commence until 1980 when researchers from the State University of New York at Stony Brook (Susman 1984, White 1986) and Yale (Thompson-Handler 1990) maintained a semi-permanent presence throughout the decade. During the 1990s, research was carried out by White (1992, 1994, 1996, 1998) as well as researchers from the Max Planck Institute in Leipzig, Germany (Fruth and Hohmann 1994, Hohmann and Fruth 1995, Hohmann and Fruth 1996, Fruth and Hohmann 1996, Fruth and Hohmann 2002, Gerloff et al. 1995, Gerloff et al. 1999). Political instability in the form of warfare and coup d'états, however, put a halt to research beginning in 1996.

The recent political history of the DRC made long-term research on bonobos difficult. The 1990s saw hyperinflation, government corruption, and civil unrest as the economy collapsed. A military rebel movement that was supported by neighboring countries began in 1996 and led to the fall of the capital, Kinshasa, in 1997. Instability continued and a second war broke out in 1998. Despite a cease-fire in 1999, fighting within parts of the country continued. At Lomako, soldiers entered the area causing locals, including past project guides, to flee into the forest (Bosco, personal communication). The first truly democratic elections were held in 2006. Since the beginning of violence in 1996, estimates suggests that 5.4 million people starved or were killed and millions more were displaced (International Rescue Committee 2008). Political instability still characterizes the eastern area of Goma while the areas in and around Lomako are today considered peaceful.

In 2005 after a semblance of stability in the DRC emerged, Frances White again ventured into the Lomako Forest in an effort to ascertain the feasibility of resuming research at the site. In the summer of 2007, Dr. White, myself, Nick Malone, and Amy Cobden resumed research on the bonobos at Lomako. I conducted a second field season at Lomako during the summer of 2009.

The Site

Bonobos are the only Great Ape species confined to a single country: the DRC. The Great Apes Survival Project (GRASP), a partnership between the United Nations Environment Program (UNEP) and the United Nations Educational, Scientific and

Cultural Organization (UNESCO), identifies the scientific importance of the Lomako region, along with the Wamba site, because of their long-term scientific presence.

The Lomako Forest consists of the area between the Lomako and Yekokora Rivers and consists of approximately 3800 km^2 of polyspecific evergreen rain forest with some areas of dense undergrowth, permanently flooded swamps along the major rivers, and seasonally flooded swamp forest (Dupain et al. 2000). Before the civil war, access to the area was primarily via the road system although today the roads have deteriorated and most bridges are missing so that most are only passable by motorbikes that can be loaded into canoes. The river system, however, has become the major transportation access for the area, so that the best route into Lomako includes a flight into Basankusu and travel by canoe up the Maringa to the Lomako River. The Lomako Forest contains two main study sites: Iyema and N'deli. The Iyema study site has been home to the Bonobo in Situ project of Linda Van Elsacker and Jef Dupain of the Royal Zoological Society of Antwerp, Belgium since 1995. Research for this dissertation comes from the N'deli site.

Situated at 0°51' N, 21°5' E (Figure 2.1), the 40 km^2 N'deli area of the Lomako Forest includes a well-established trail system that transects a variety of forest types. Predominantly composed of primary evergreen and polyspecific rain forest (75.2% of study site) with smaller areas of swamp forest (12.6%), Bolafa (*Gilbertiodendron*) forest (9.9%) and secondary forest (2.3%), the bonobos use all forest types, but spend the vast majority of their time in the undisturbed primary forest (93.4% of focal sampling: White 1992). There is very little human impact in the form of development at the site, making it one of the "purest" bonobo study areas.

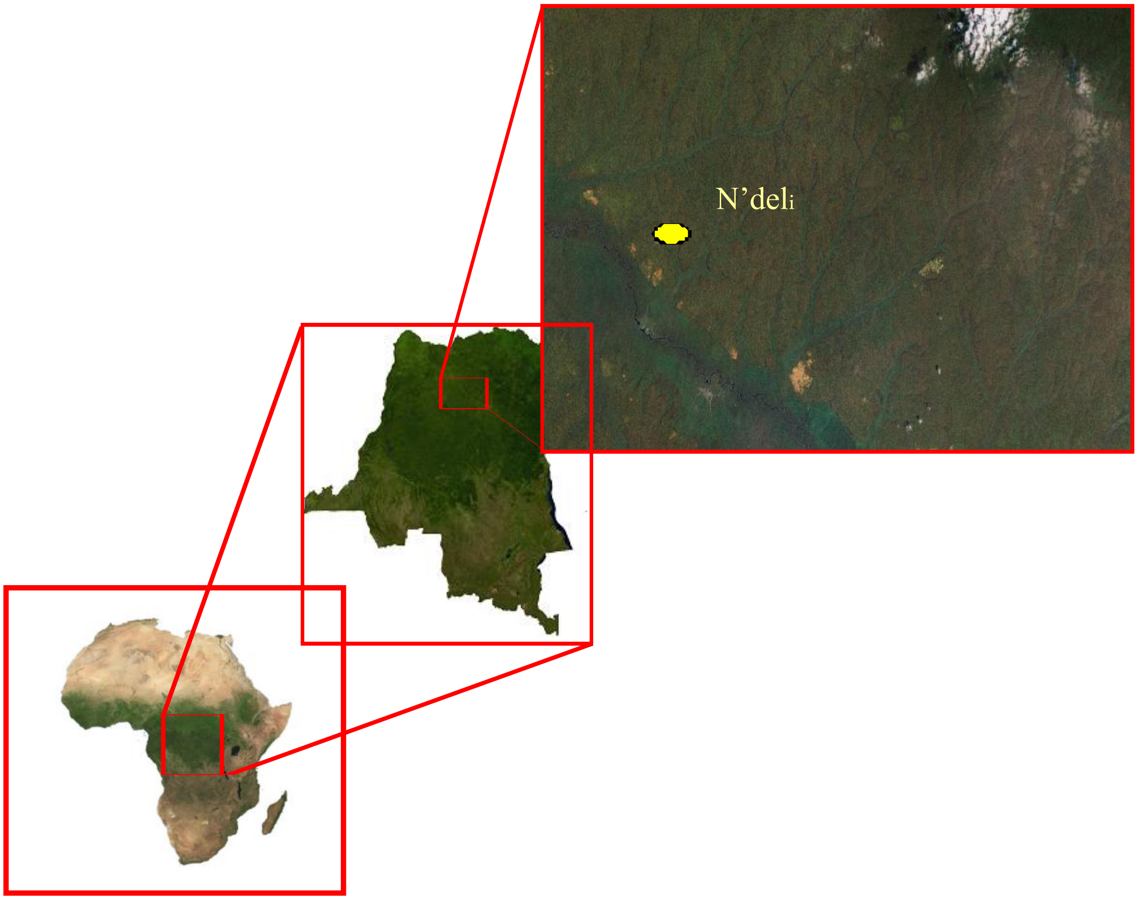

Figure 2.1. This map shows Africa, the DRC, and the N'deli field site in the Lomako Forest .

The Bonobos of Lomako

Since the 1970s, researchers working at Lomako have classified individuals as belonging to either the Eyengo or Bakumba communities (Badrian and Malenky 1984, White 1998, Hohmann and Fruth 2002). Named after the creeks that enter their respective ranges, the Bakumba group occupies the western portion of the study site while the Eyengo group occupies the eastern area. Additionally, White (1986) identified a “Splinter” group that consisted of four immigrating females and males (most likely from Bakumba) that followed them (Figure 2.2). Since studies conducted by White commenced in 1984, the composition for the Eyengo and Bakumba groups have fluctuated while the Splinter females became central figures within the Bakumba group by 1991. When research resumed in 2007, a group of bonobos living in the northeastern portion of the site were identified and called the NE group. Because of the long time span between field seasons, the relationship of the individuals living in the NE group to past groups remains unclear. One female with a particularly striking facial complexion was recognized by White as a former Eyengo community member, however as this study will show, membership in a group may be more fluid than previously believed. See Table 2.1 for a complete look at the group composition for each community.

Table 2.1. Group composition of bonobos at Lomako

Group	Sightings	Males	Females	Sub-adults	Infants
Splinter	69	4	4	0	0
Bakumba	36	4	11	8	5
Eyengo	76	11	10	4	5
NE	19	3	18	8	12
Combined	200	22	43	20	22

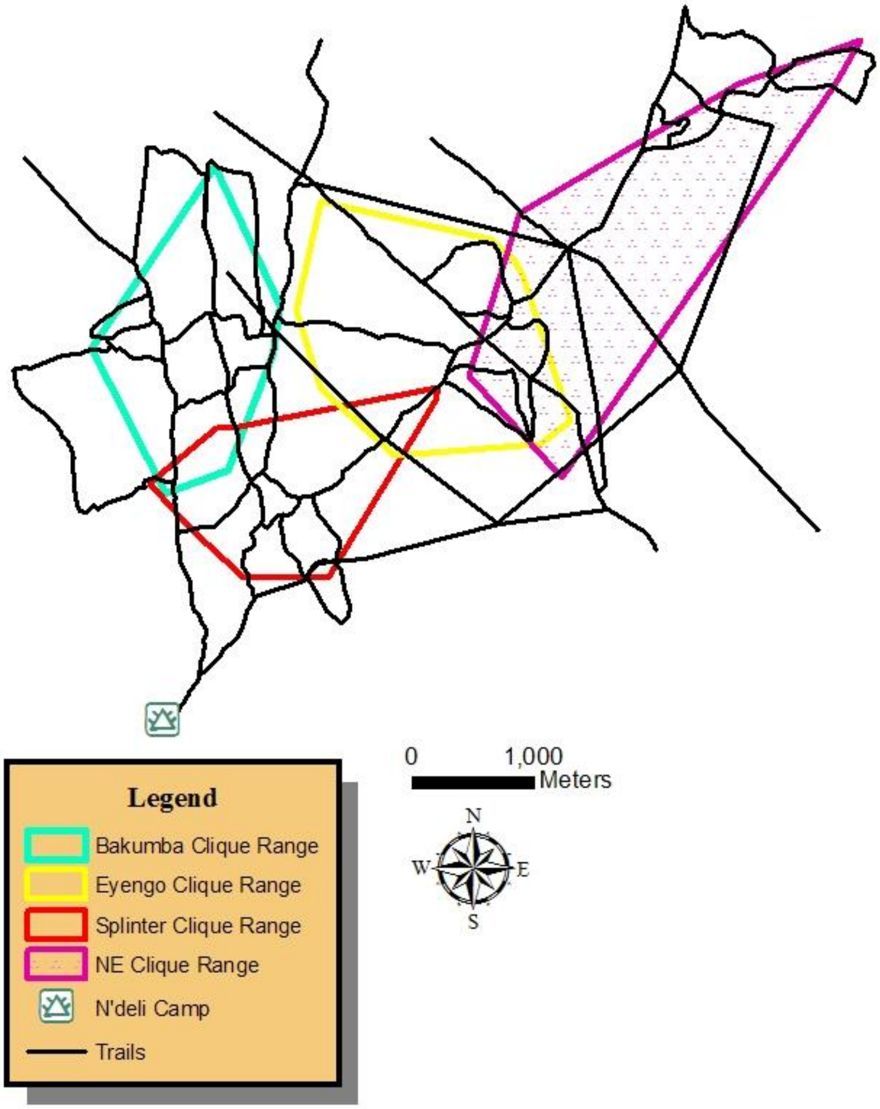

Figure 2.2. Trail system, location of the camp, and the home range as a minimum convex polygon of the Bakumba, Splinter, Eyengo, and NE bonobo communities.

Data Collection

The majority of the data analyzed for this dissertation comes from the field seasons conducted by Frances White from October 1984-July 1985, June-August 1991, and June-August 1995. More recent data comes from the field seasons conducted from June-August 2007 and June-August 2009. Analysis of home range estimates, daily path lengths, the differences between males and females, and inter-group relationships come from 200 sightings including 448 hours of focal animal observations. Focal sampling used methods established by Altmann (1974). Based on methods used by Mitani and Ansler (2003) we maintained statistical independence by typically recording one sighting each day. Multiple observations were recorded on the same days only in cases where sightings were separated by several hundred meters and party membership was clearly different. These observations were then entered into a GIS database for spatial analysis.

GIS/GPS

The means by which animals inhabit space is important for any ecological investigation and is central to ecological theory (Burt 1943, Dale 1999, Folt and Burns 1999). Spatio-temporal data has been collected and used to study foraging patterns (Nkurunungi and Stanford 2006), identify behavioral differences across groups (Bascompte and Vila 1997), and reveal effects of differing habitat regimes on populations (McDonald and St. Clair 2004). By utilizing GIS and GPS technologies, mapping accuracy and efficiency can be greatly improved (Dominy and Duncan 2001).

In its most basic form, GIS is a database format that keeps track of the location of events, activities, and things. Of course it is more than that. It is a spatio-temporal analytic tool, capable of answering a seemingly infinite number of questions on anything from advertising (Luke et al. 2000) to zoonotic diseases (Brownstein et al. 2002). The

ArcGIS suite (9.2) of software from ESRI is perhaps the most popular GIS program in North America. The RANGES8 software was created with animal ranging behavior in mind by Anatrak Ltd, a spin-off of the United Kingdom's Natural Environment Research Council's Centre for Ecology and Hydrology (NERC-CEH). Together, these software packages allow for the fast and reliable analysis of spatio-temporal data collected in the field. GPS units are important tools for collecting that data.

The GPS system was created in 1973 by the United States Department of Defense (DoD) and became fully operational in 1994. The system uses 24 satellites that orbit Earth every 12 hours on distinct trajectories at a height of 20,200 km (Longley et al. 2006). Each satellite transmits a unique "message" that identifies the satellite, its location, and the time at which the message was sent. These messages are then read by GPS receivers on the ground. When three or more satellites messages are read, the receiver uses the geometry of spheres and trilateration to determine its location. A fourth satellite is needed to account for all three dimensions (latitude, longitude, and elevation). The GPS satellites are timed and positioned in such a manner that insures that all areas of the Earth have at least four satellites visible at any given time (Dominy and Duncan 2001).

Despite the potential for sub-meter accuracy using GPS, several sources of error should be considered when analyzing GPS locations. Atmospheric effects, multipath issues, and clock errors are measured using Positional Dilution of Precision (PDOP), a function of receiver and satellite positions that determines accuracy based on vectors, positions, and the speed of the messages sent from each satellite. Lower PDOP values reflect greater positional accuracy as there is wider angular separation among the satellites used to analyze the GPS receiver location (Parkinson and Spilker 1996).

These sources of error are of particular concern under the canopy of primary rainforests. With few openings to the sky, obtaining location waypoints can be challenging. A study by Dominy and Duncan (2001) at the Kibale Forest in Uganda, highlight many of these problems once faced. They were regularly unable to receive four satellites, had high levels of PDOP, and were often forced to climb trees in order to increase accuracy. In 2000, however, the DoD turned off Selective Availability (SA), a program that limited the effectiveness of the system. Combined with innovations in GPS technology, the discontinuation of SA resulted in dramatically increased precision, giving personal handheld GPS units 10-meter accuracy (de Jong 2000).

For this project, I used a Garmin eTrex Legend during the 2007 and 2009 field seasons. Each point was projected in the World Geodetic System (WGS) 1984 Universal Transverse Mercator Zone 34N coordinate system and mapped using a Transverse Mercator projection. A total of 520 points were collected. Waypoints can represent a position on a trail, landmarks, feeding trees, bonobo observation, nest, or any other point of interest encountered (Figure 2.3). I did experience occasions when I could not get a reading due to extremely thick canopy. In these cases, I moved to a location where a point could be received and estimated the distance and direction to the location of the object of interest.

Once the points were collected, it was necessary to download them and import them into ArcGIS. To do this, I needed to access an import wizard from the Minnesota Department of Natural Resources web site (http://www.dnr.state.mn.us/mis/gis/index.) The wizard creates a table of attributes pertaining to each point that can be imported into ArcGIS. Once in ArcGIS, I added attributes to the table that described the various features. For example, a bonobo observation would include the *x,y* coordinates, number

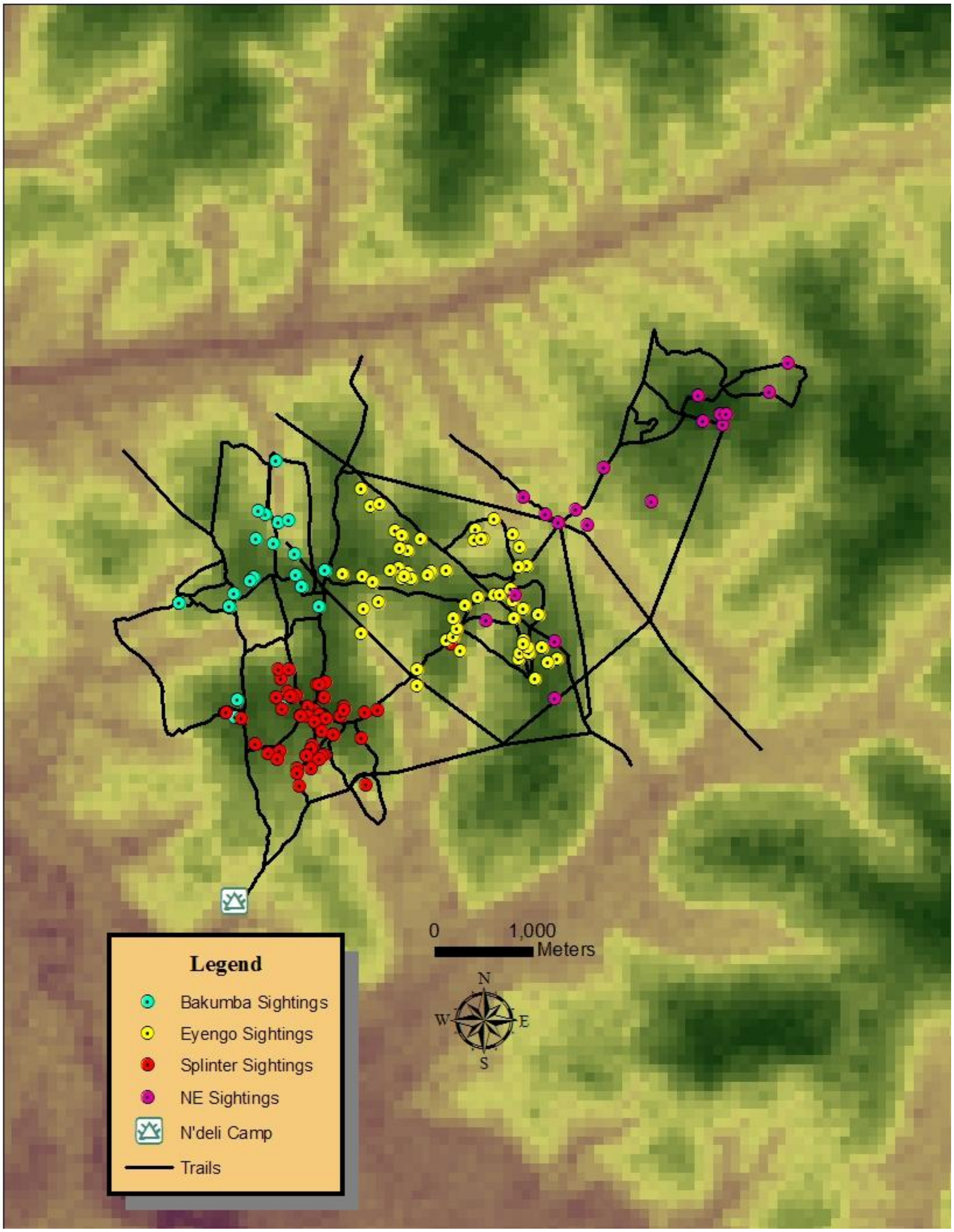

Figure 2.3. Trail system and the bonobo sightings in a Digital Elevation Model (DEM) map. When in the ArcGIS software, one can click on a point and all the information for that point is available.

of males, females, subadults and infants, and habitat type. Nest points include *x,y* coordinates, tree type, height, habitat, and number of neighbor nests. Additionally, the locations of observations and feeding trees recorded by White during earlier field seasons, were plotted onto the map using the location of transect markers as references. Once plotted, the same attributes recorded for the Garmin waypoints were applied. This type of database allows for a number of different types of analysis, many of which are used in the following chapters.

Summary

The use of GIS in studies of primate behavior, ecology, and conservation is only getting started. While the focus of this dissertation is the social and ecological factors that affect the ranging behavior of bonobos, I would be remiss not to point out the potential for applying GIS to conservation issues facing these apes. The International Union for Conservation of Nature (IUCN) has bonobos listed as endangered (IUCN *Redlist* 2010). In reality, however, little is known about the density and distribution of bonobos throughout their geographic range (Figure 2.4). Estimates of the population size of bonobos have ranged from 20,000-50,000 (Butynski 2001). GIS analysis and DEM maps (see Figure 2.3) can help those concerned with the welfare of bonobos to refine this estimate. Additionally, recent research has examined plots of trees in an effort to gain insights into patterns of seed dispersal and tropical tree diversity (Hubbell et al. 1999, Condit et al. 2000, Harms et al. 2000). Other studies have focused on conservation issues such as population density (Irvin et al. 2005), habitat suitability (Tores et al. 2010), and species reintroduction (Seddon et al. 2007). Consequently, the use of GIS technology with habitat use models is especially beneficial for conservation plans as habitat zones at risk of human encroachment are becoming more easily recognizable (Dominy and

Duncan 2001). Consequently, the increase in GPS receiver technology is allowing researchers to collect animal ranging data faster and far more accurately than in the past.

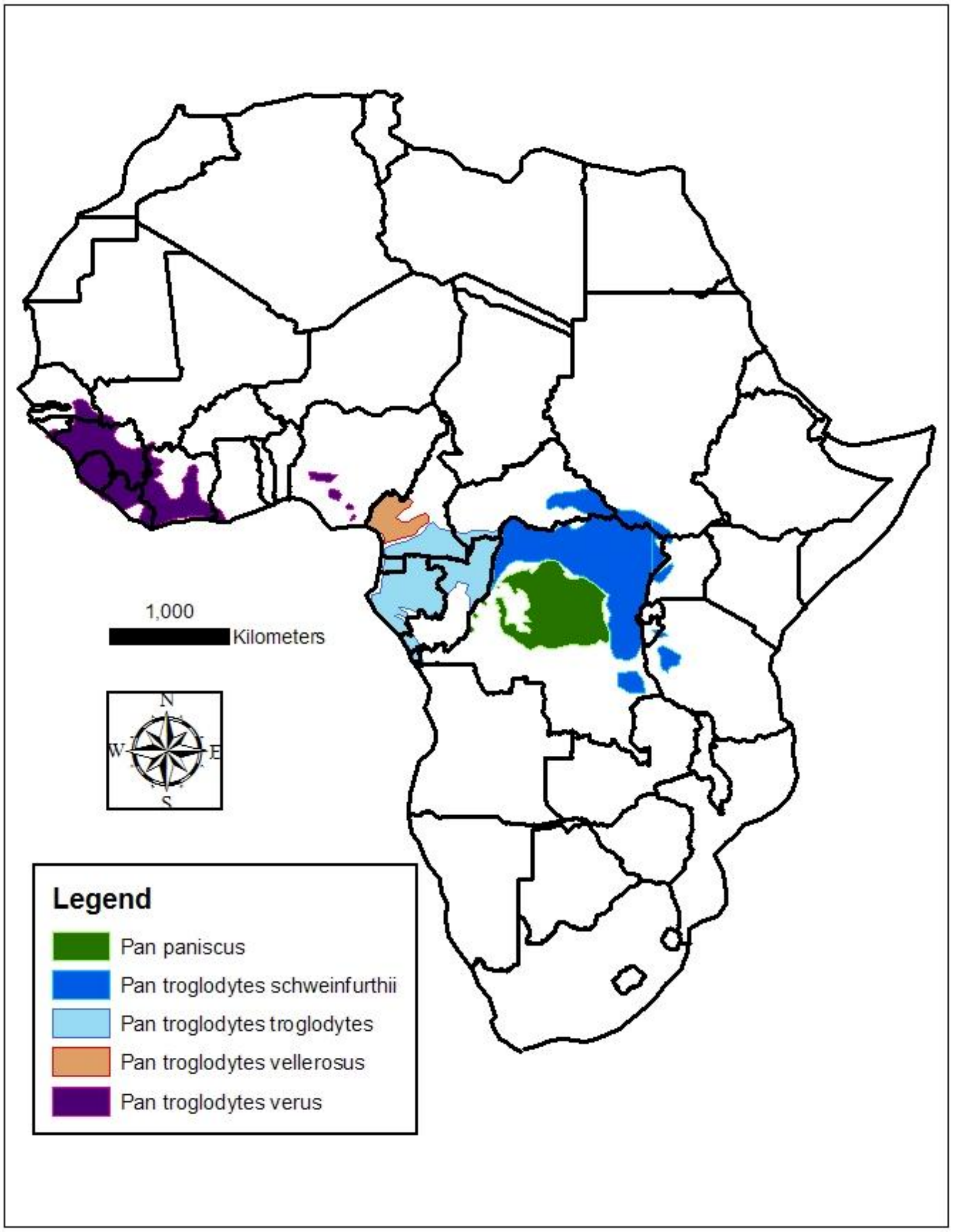

Figure 2.4. This map shows the entire geographic range of each of the *Pan* species and sub-species.

CHAPTER III

BONOBO RANGING BEHAVIOR AT LOMAKO

Introduction

The purpose of this study is to use GIS (Geographic Information Systems) software to examine spatial data collected during field seasons conducted intermittently over the past 27 years on three separate groups of bonobos in the Lomako Forest in an effort to more fully comprehend the ways in which these animals move about their habitat. Early studies of wild bonobos (*Pan paniscus*) in the Democratic Republic of the Congo (DRC) were only able to calculate rough estimates of ranging behaviors such as group home range (Thompson-Handler 1990, Kano 1992) and daily path length (Kano 1990) using approximate mapping methods. More accurate mapping using GIS shows that when compared with chimpanzees, bonobos at Lomako have smaller annual home ranges and daily path lengths. Furthermore, the swamp forests that border small creeks may act as semi-permeable barriers for bonobo groups as spatial analysis of habitat use shows that these swamp areas separate in part, the core areas of the three groups. Finally, changes in ranging behavior since wartime and the ensuing political instability show the potential affect of poachers and development on bonobo movements. When taken together, much of the spatial data suggests that bonobo female core groups may be stable in short term contexts, yet more fluid over longer time spans. As such, I suggest that bonobos do not live in clearly defined “communities” like chimpanzees, but rather live in more fluid associations I term “cliques.”

An animal’s ranging pattern reflects a complex adaptation to several physiological, social, and ecological factors. Body size (Harvey and Clutton-Brock 1981, Swihart et. al 1988, Bassett 1995), group size (Milton and May 1976, Takasaki 1981), food availability (Olupot et al. 1997, Barton et al. 1992, Li et al. 2000, Di Fiore 2003, Iwamoto 1992), predation risk (Boinski et al. 2000), and human interactions (Johns 1986, Decker 1994, Waller 2005) all combine to determine the costs and benefits associated with the size of home ranges, types of habitats favored, and distances traveled within a day. Those species that are ripe fruit specialists have a particular set of factors that affect their ranging behavior. The density of fruit trees as well as seasonal patterns affects the spatial and temporal availability of fruit. As such, annual home ranges, daily path lengths, and degrees of territoriality can be affected.

Chimpanzee "communities" consist of related, socially bonded males that control a clearly demarcated territory which envelope the separate but overlapping core areas of several independent females (Chapman and Wrangham 1993, Williams et al. 2002, but see Wakefield 2008, Reidel and Boesch 2011). In contrast, wild bonobos live in "cliques" (Chapter IV, Waller et al. 2011) that consist primarily of unrelated, allied females, their offspring, and related but independent males (Kano 1992, White 1996). Males do not form strong social bonds with each other, but their mothers may help them gain rank and facilitate entrance into the group (Ihobe 1992, Furuichi and Ihobe 1994, Furuichi 1997, Surbeck et al. 2010). Males have also been found to positively associate with infants, perhaps in an effort to gain favor with females (White et al. 2010). The differences in social organization between bonobos and chimpanzees have been attributed to differences in food availability. Larger food patches (White and Wrangham 1988, Chapman et al. 1994), more terrestrial herbaceous vegetation (Wrangham 1986), and less seasonality (Malenky 1990, White 1998) are all thought to contribute to increased and less variable food availability for bonobos, reducing the level of competition among females and allowing them to create bonds and form cliques which have potential benefits such as protection from infanticide (White and Waller 2008), cooperation during hunts (Surbeck and Hohmann 2008), or the defense of food patches from others (White 1986, Idani 1991, Parrish 1994, Hohmann and Fruth 1996).

This high level of food availability is also predicted to shape bonobo ranging. If food is more available compared with chimpanzee habitats, bonobos should have smaller home ranges and daily path lengths. Furthermore, increased food availability may prevent territoriality (see Chapter V) resulting in increased range overlap and more loosely defined social units. To date, however, little research has been published on bonobo ranging behavior. The purpose of this chapter is to use GIS in an effort to better comprehend the way in which bonobos at the N'deli site in the Lomako Forest range within their environment both on long-term and daily time scales. Additionally, I will look at the importance of habitat variation on group ranging behavior and report on changes in home ranges since the beginning of war and political instability in the DRC. Finally, I compare the results found at Lomako with other bonobo and chimpanzee sites.

Methods

The N'deli site in the Lomako Forest (0.7994° N, 21.143° E) is located in the Congo River Basin within the Equateur Province of the DRC. The 40 km² study area consists of several forest types, but is principally climax evergreen and polyspecific primary rain forest (75.2% of study site) with smaller areas of second-growth, slope, and swamp forest (White 1992). While bonobos use all forest types, swamp and secondary areas are utilized less often (White 1992, Hashimoto et al. 1998, this study).

Field studies of bonobo behavior began at Lomako in the 1970s and continued until 1998. and focused on two communities: Bakumba in the western portion of the study area and Eyengo in the east (Badrian and Malenky 1984, White 1998, Hohmann and Fruth 2002). Additionally, White (1986) identified a separate, “Splinter” group centered on four immigrating young sub-adult females and the four males who followed them in 1984-1985. The males were most likely from the Bakumba group, as by 1991, all eight individuals were central reproductive adults within the Bakumba clique.

A second set of data collected during field seasons conducted from June-August 2007 and June-August 2009 show the sightings for the northeast (NE) clique located in the northeast section of the study area and is thought to include former Eyengo group members although it is unclear exactly how many of the members were part of the original Eyengo group. As such, the ranging behavior of the NE group was used to look at changes in areas used since 1995 when research was halted due to political unrest. Each sighting during these field seasons was recorded using a handheld GPS unit (Garmin eTrex). Attempts to locate the Bakumba community during this time suggest that they have moved northwest of the study area. One sighting and several nests and feeding remains were found outside of the transect and trail system. The composition of all the cliques fluctuated and the data analyzed for this study (See Table 2.1) is limited to those individuals clearly identifiable within a designated group.

Data used for analyzing home range estimates and daily path lengths are from 200 sightings including 448 hours of focal animal observations recorded by White during field seasons conducted in October 1984-July 1985, June-August 1991, and June-August 1995 as well as the sightings recorded by Waller and White during the 2007 and 2009 field seasons. Based on methods used by Mitani and Ansler (2003) we maintained statistical independence by typically recording one sighting each day. Multiple parties were recorded on the same days in cases where sightings were separated by several hundred meters and party membership was clearly different.

To more accurately ascertain home range sizes, mean daily path length (DPL), and habitat use, the trail and transect system was mapped using the Garmin GPS unit and the sightings from each research season were plotted onto it (Figure 3.1). All maps were made using a Transverse Mercator projection and the WGS 1984 UTM Zone 34N coordinate system. Once plotted, the location data were entered into two GIS software programs for analysis. RANGES8 (Anatrak Ltd. 2010) was used to determine the home range of the three cliques for each field season and for all field seasons combined. ArcGIS (ESRI version 9.3) was used to analyze DPL, habitat use based on forest structure, and the shifts of the Eyengo/NE clique over time.

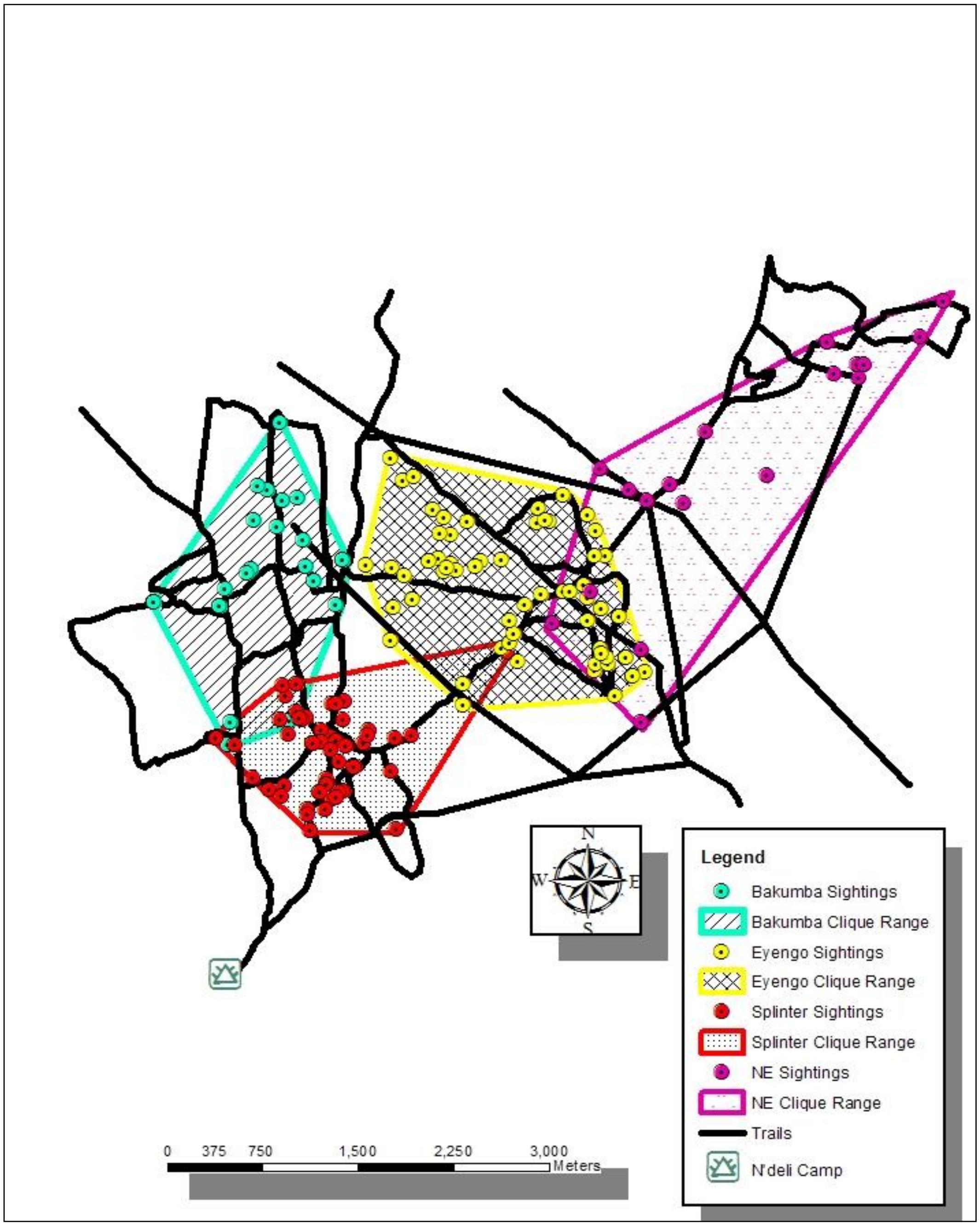

Figure 3.1. All sightings and total MCP for all field seasons for the Bakumba, Eyengo, Splinter, and NE cliques

Results

Home Range Areas

Minimum convex polygons (MCP), Fixed-Kernel Analysis (FKA), and Ellipses were used to determine the areas (home ranges) habitually used by the bonobos at Lomako. All results are reported in hectares (ha), with 1 km² = 100 ha. The MCP technique (Mohr 1947) completely encloses all location points recorded in such a way that the outer locations create a convex polygon. The area of a MCP is calculated using the following formula:

$$\hat{A} = \frac{x_1(y_n - y_2) + \sum_{i=2}^{n-1} x_i(y_{i-1} - y_{i+1}) + x_n(y_{n-1} - y_1)}{2}$$

where (x_i, y_i), $i = 1, 2, \ldots n$ are the coordinates of the locations.

The MCP technique is popular due to the ease with which these polygons can be constructed and for applications in conservation management (Nilsen et al. 2008). There are, however, a number of issues that render this form of home range measurement less than ideal. Because MCPs are completely non-parametric, they are somewhat uninformative in many situations as areas of high utilization have the same value as areas of low utilization. Additionally, MCPs are sensitive to outliers and ignore boundaries that exclude animal movements within the range (such as swamps, lakes, etc.) Furthermore, MCPs are sensitive to sample size, as an increase in the number of observations tends to result in larger areas. Therefore, one cannot compare two sets of data if they are based on different sample sizes (White and Garrott 1990). The MCPs reported here used 100% of the sightings observed.

Several studies have suggested that kernel analysis which uses least-squares cross validation (LSCV) is the best approach available to estimate range size (Seaman and Powell 1996, Kernohan et al. 2001). Using this technique, range area estimations are based on probability "kernels", regions surrounding each point location and containing some likelihood of animal presence. The width of the kernel is based on the smoothing parameter, or "bandwidth", which can be determined in a number of different ways. The main automated methods for smoothing parameter selection are reference (which is based on assumptions of bivariate normality) and least-squares cross validation (which is based on properties of the data). Kernel methods are either adaptive (where the kernel width increases as the distance between kernels increases) or fixed (always the same kernel width). Adaptive kernels tend to perform poorly, often over-estimating home range areas (Powell 2000, Kernohan et al. 2001). Fixed Kernel Analysis (FKA) was therefore used for this study. The kernel density estimator is mathematically determined as:

$$\hat{f}(x) = [1/(nh^2)] \sum_{i=1}^{n} K\left\{\frac{(x - X_i)}{h}\right\}$$

where n is the number of data points, *h* is the smoothing parameter (determined in this study by LCSV), *K* is a kernel density such as the one described below, *x* is a vector of x,y coordinates describing the location where the function is being evaluated, and X_i is a series of vectors whose coordinates describe the location of each observation *i* (Seaman and Powell 1996) .

According to Mitchell (2006), kernel estimators have a number of features that make them more useful than other methods. Namely, they perform better with smaller amounts of data, are more robust to autocorrelation, allow more than one center of activity, and result in a utilization distribution (UD) rather than a simple home range outline (Kernohan et al. 2001). A UD is a grid where the value for each cell represents the probability of the animal occurring in that cell. Among other uses, a UD allows for a more precise estimate of home range overlap than a simple outline (Mitchell 2006) and more readily identifies core areas.

Finally, the ellipse method uses a bivariate normal distribution of the locations to create a simplistic representation of the home range (Anatrak 2010). Nevertheless the analyses supply useful estimates of home range size and acentricity with a limited number of locations and can be estimated using different percentages of all points. Mathematically, the areas of ellipses are defined as:

$$A_e = \pi s_x s_y$$

where $s_x s_y$ are the standard deviations for the x and y coordinates (Anatrak Ltd. 2010). For this study, 95% of sightings were used to estimate this basic range pattern.

Ranging areas were measured for each clique and are presented for each field season using each of the three techniques mentioned above (Table 3.1, Figures 3.2, 3.3, and 3.4) Additionally, a total clique range was estimated based on all of the field seasons combined (Table 3.2, Figures 3.5, 3.6 and 3.7).

Table 3.1. Clique home ranges (ha) for each field season.

Clique	Field Seasons	# of months	# of sightings	MCP	95% FKA	95% Ellipsoid
Splinter	1984-1985	11	69	196.65	99.75	180.07
Bakumba	1984-1985	11	27	194.09	198.85	364.71
Bakumba	1991	2	9	144.65	110.48	533.24
Eyengo	1984-1985	11	39	215.8	222.58	365.22
Eyengo	1991	2	25	199.95	216.51	414.97
Eyengo	1995	2	13	158.29	197.32	423.75
NE	2007	2	8	130.26	91.49	446.38
NE	2009	2	10	121.09	294.49	256.85

Table 3.2. Total clique home ranges (ha) using data from all field

Clique	Clique Size	MCP	95% FKA	75% FKA	50% FKA	95% Ellipsoid
Splinter	8	196.65	99.75	63.03	38.21	180.07
Bakumba	28	280.32	247.4	152.12	97.06	434.71
Eyengo	30	294.92	225.95	185.14	86.56	590.8
NE	41	365.16	480.67	306.65	166.43	819.17

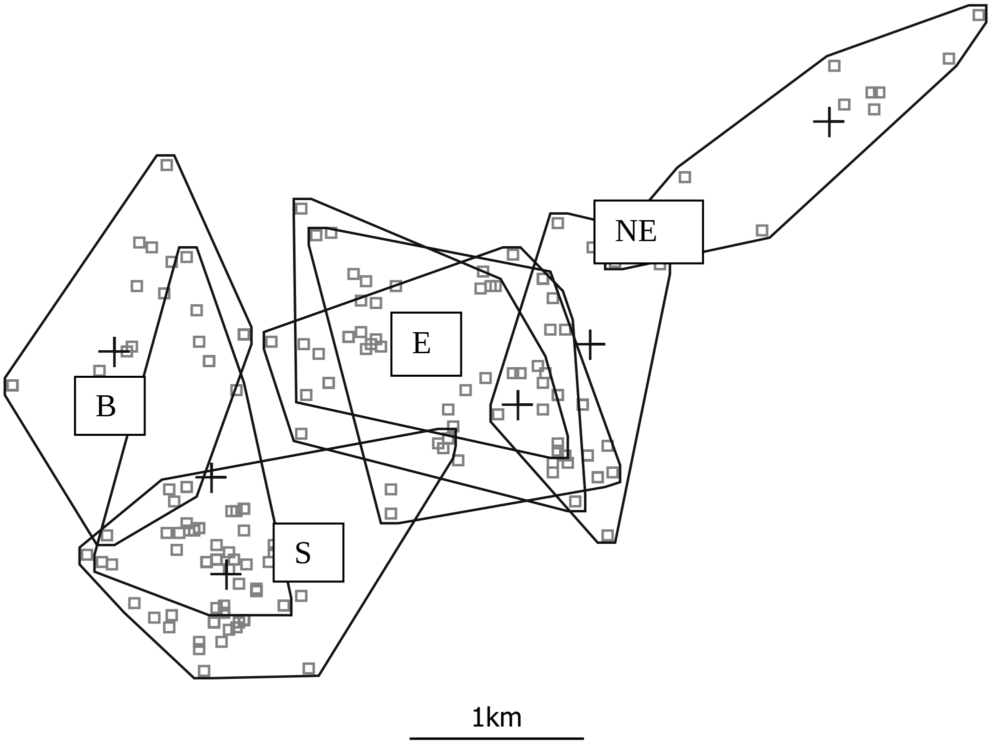

Figure 3.2. This map shows the MCP home ranges for each field season (Bakumba = B, Eyengo = E, Northeast = NE, Splinter = S).

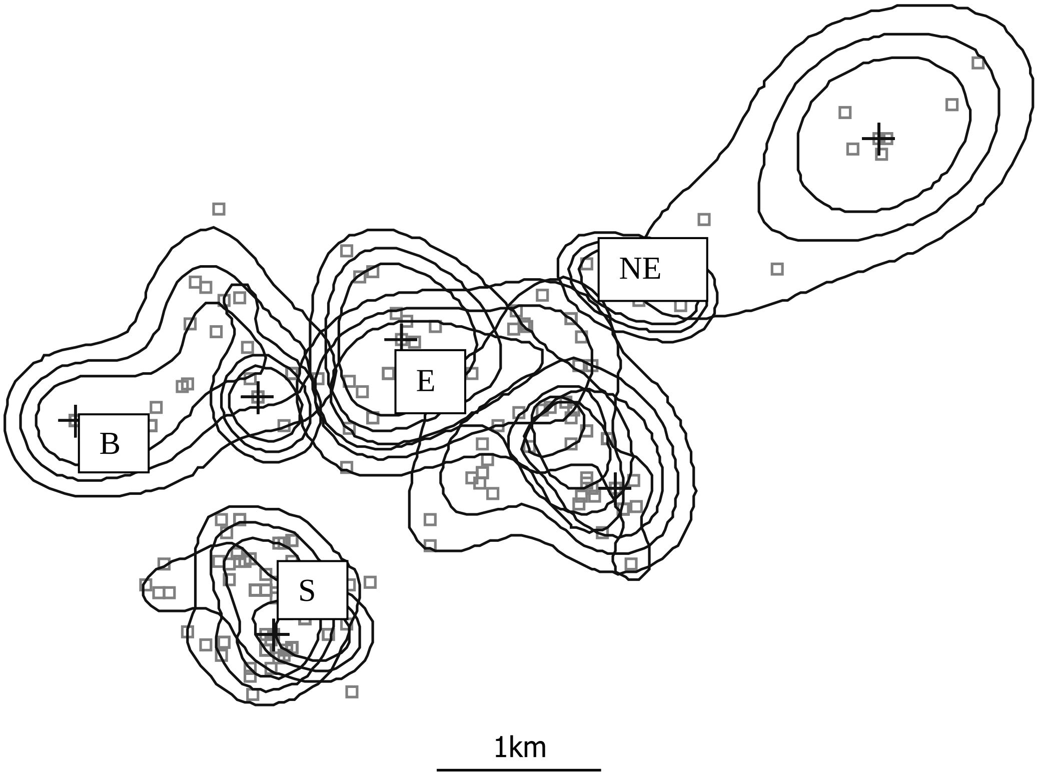

Figure 3.3. This map shows the 95% FKA home ranges for each field season (Bakumba = B, Eyengo = E, Northeast = NE, Splinter = S).

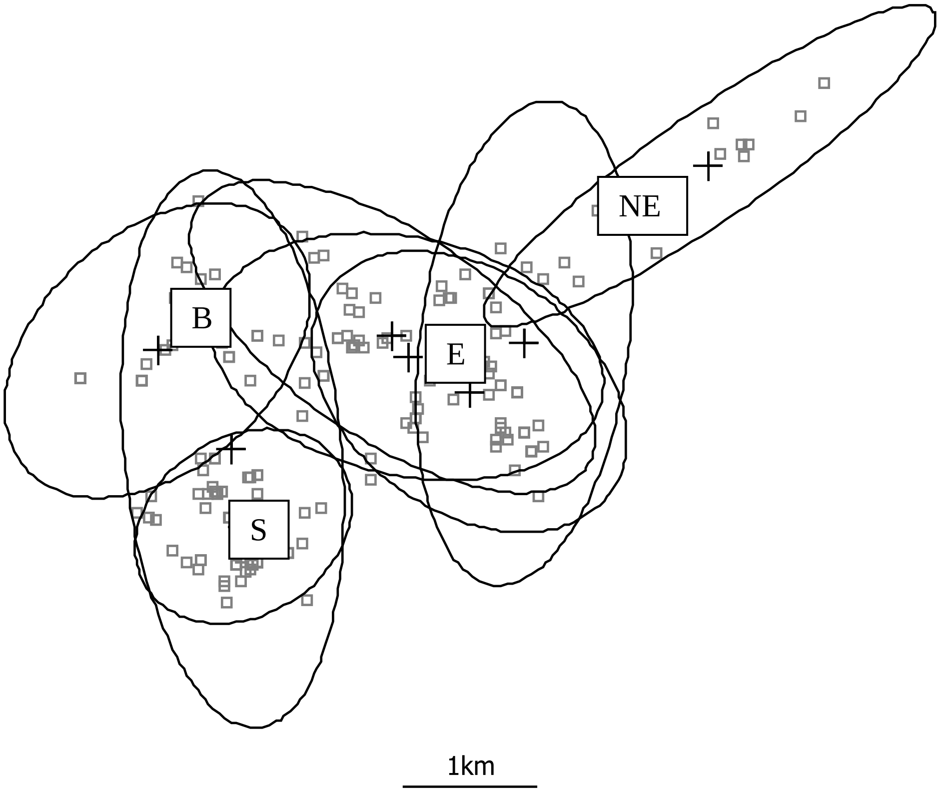

Figure 3.4. This map shows the 95% Ellipse home ranges for each field season (Bakumba = B, Eyengo = E, Northeast = NE, Splinter = S).

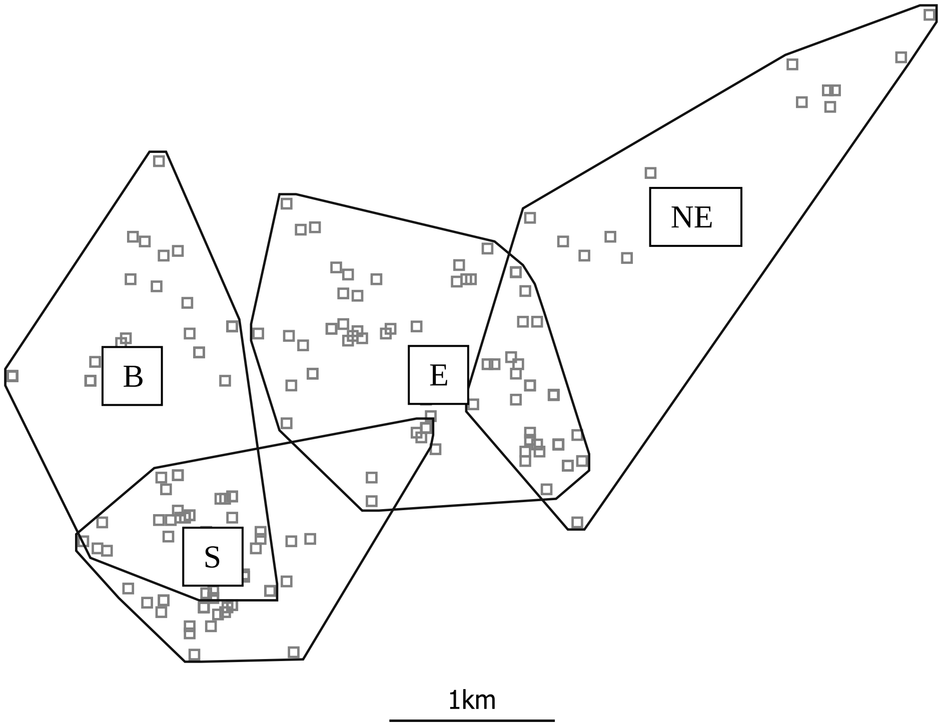

Figure 3.5. This map shows the MCP total home range for all field seasons combined (Bakumba = B, Eyengo = E, Northeast = NE, Splinter = S).

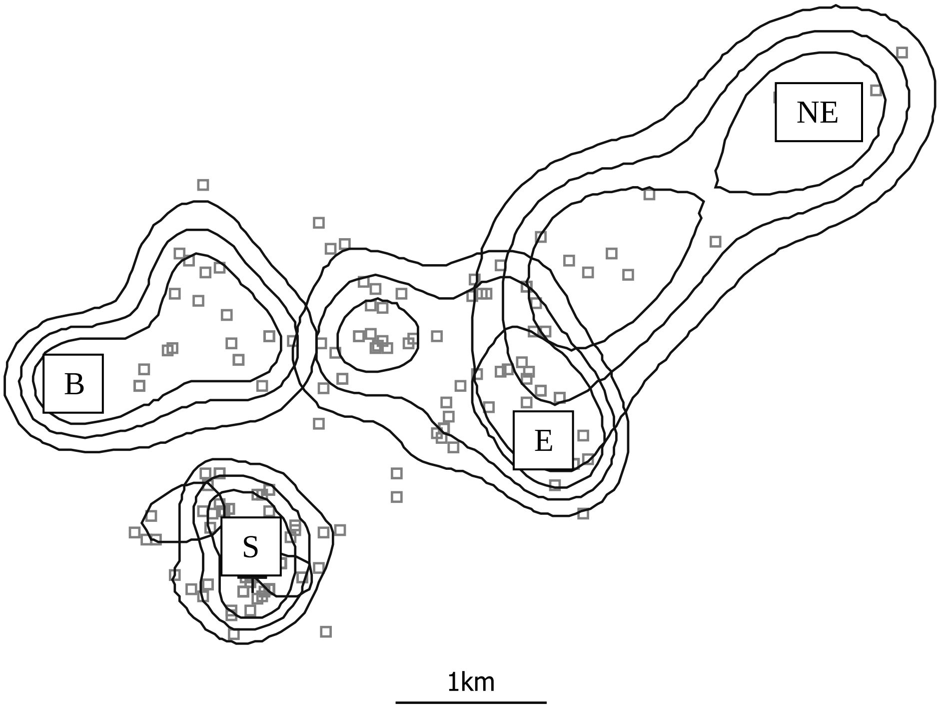

Figure 3.6. This map shows the 95% FKA total home range for all field seasons combined (Bakumba = B, Eyengo = E, Northeast = NE, Splinter = S).

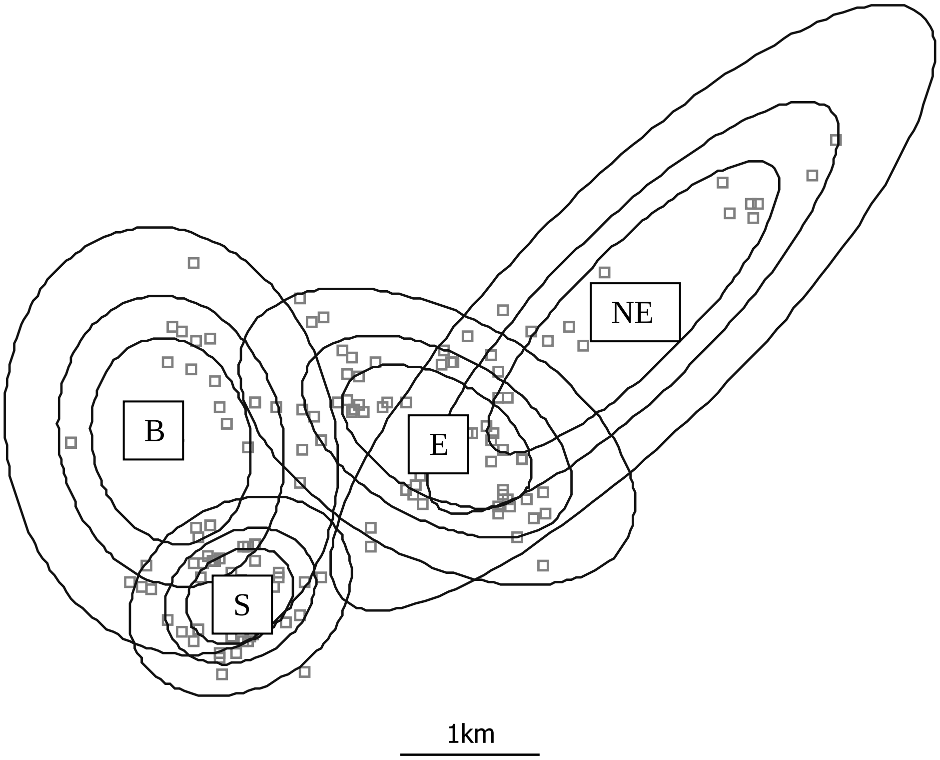

Figure 3.7. This map shows the 95% Ellipse total home range for all field seasons combined (Bakumba = B, Eyengo = E, Northeast = NE, Splinter = S).

Not surprisingly, the Splinter clique had the smallest range of each of the groups as it consisted of the fewest individuals. The ranging areas for the Eyengo clique ranged from 225.95 - 434.71 ha and the Bakumba clique ranged over an area between 247.4 - 590.8 ha, depending on the technique used. Somewhat surprising based on the limited number of sightings, the NE clique was estimated to have the largest range of the four groups measured. Their MCP is 365.16 ha, 95% FKA is 480.67 ha, and their 95% ellipse range was estimated at 819.17 ha. This may be due to the larger clique size or to human intervention, as the NE group is very likely the remnants of the Eyengo clique that was forced to abandon its core range when soldiers entered the area during the political instability of the late 1990s and early 2000s.

All together, these ranges differ significantly from those measured at Lomako in the past. Thompson-Handler (1990) used 300m^2 grid squares to estimate the home ranges of the Eyengo, Bakumba, and Splinter cliques over four years. She found that the Splinter group had a home range area of 810 ha, while the larger Eyengo and Bakumba groups had home range areas of 1200 ha and 1380 ha respectively. These ranges are unlikely to be indicative of the bonobo's true use of their habitat as the grid square method is less than ideal and tends to overvalue peripheral and infrequently visited locations (see critique in Chapter I). Conversely, the range area estimates presented in this study are most likely too small to represent a lifetime range and are more emblematic of frequently used core areas, which may best be represented by the 50% FKA. These methodological issues combined with variables such as the number of sightings, changes in food availability, and human influence make analyzing the discrepancies between the range estimates difficult in this long-lived species. For that reason, range areas should use the best method for the habitat and may best be contemplated as snap-shots of a particular time period.

Clique Overlap

The Eyengo and Bakumba cliques ranged over 14 and 39% of the Splinter home range, respectively (Table 3.3). The splinter group used 14% of the Bakumba range and only 9% of the Eyengo area. Perhaps not surprisingly, the Splinter group became central members within the Bakumba clique sometime between 1985 and 1991. Our data does not show overlap of the ranging areas between the Eyengo and Bakumba cliques, although others have noted overlap and direct contact between the groups (Badrian and Badrian 1984, Thompson-Handler 1990). See Chapter 5 for more information on inter-community ranging behavior.

Table 3.3. Percentage of home range overlap of each clique.

Clique	**% of range overlapped by other cliques**
Splinter	23
Bakumba	14
Eyengo	9

Daily Path Length

All day follows are difficult, especially when bonobos are on the ground, due to the thick vegetation within the forest. In order to determine the mean DPL of bonobo parties, their movements were mapped and measured using recorded route markers and ArcGIS and are shown on Figure 3.8. Only sightings with over 60 minute observations were included. The number of observation days with follow data is 74 and the mean tracking time per day is 182.73 minutes. Several of the follows include sightings when the bonobos spent entire days at one feeding location. One such example included a fig tree used near continuously for over three days. Once the distances were calculated, the DPL of bonobos was estimated by using the following formula:

$$\mathrm{DPL} = D \times (\mathrm{T}_a / T_o)$$

where D is the distance measured, T_a is the time the animal is active during the day and likely to move, and T_o is the total time of the sighting. I assume based on observed waking and nesting behavior that the daily movements occur during a 12 hour activity time per day. The means of all DPL were then calculated for all Lomako bonobos as well as each clique (Table 3.4). Estimates of DPL ranged from 0 - 17,650.5 (Figure 3.8) with an overall mean of 1839.73 meters/day. As at Wamba, observations under 120 minutes may skew the results. If only those sightings over 120 minutes (n = 44) are used, the mean DPL of bonobos at Lomako is 1213.46 meters.

Table 3.4. Mean DPL for each clique as well as for all follows combined.

Group	**# of follows**	**Mean DPL**
Splinter	15	1840.55
Bakumba	16	1088.34
Eyengo	34	2192.94
NE	9	1644.32
Combined	74	1839.73

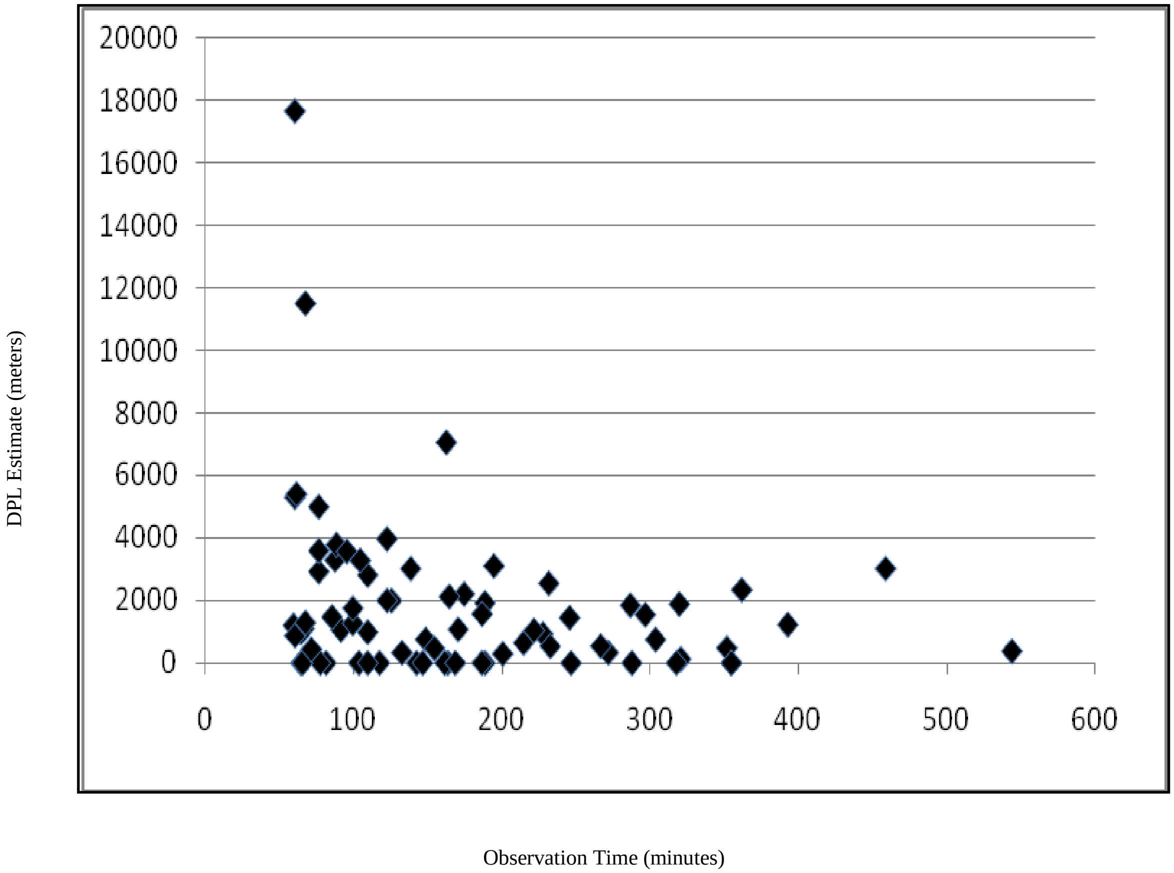

Figure 3.8. Relationship of DPL estimates (meters) and Observation Time

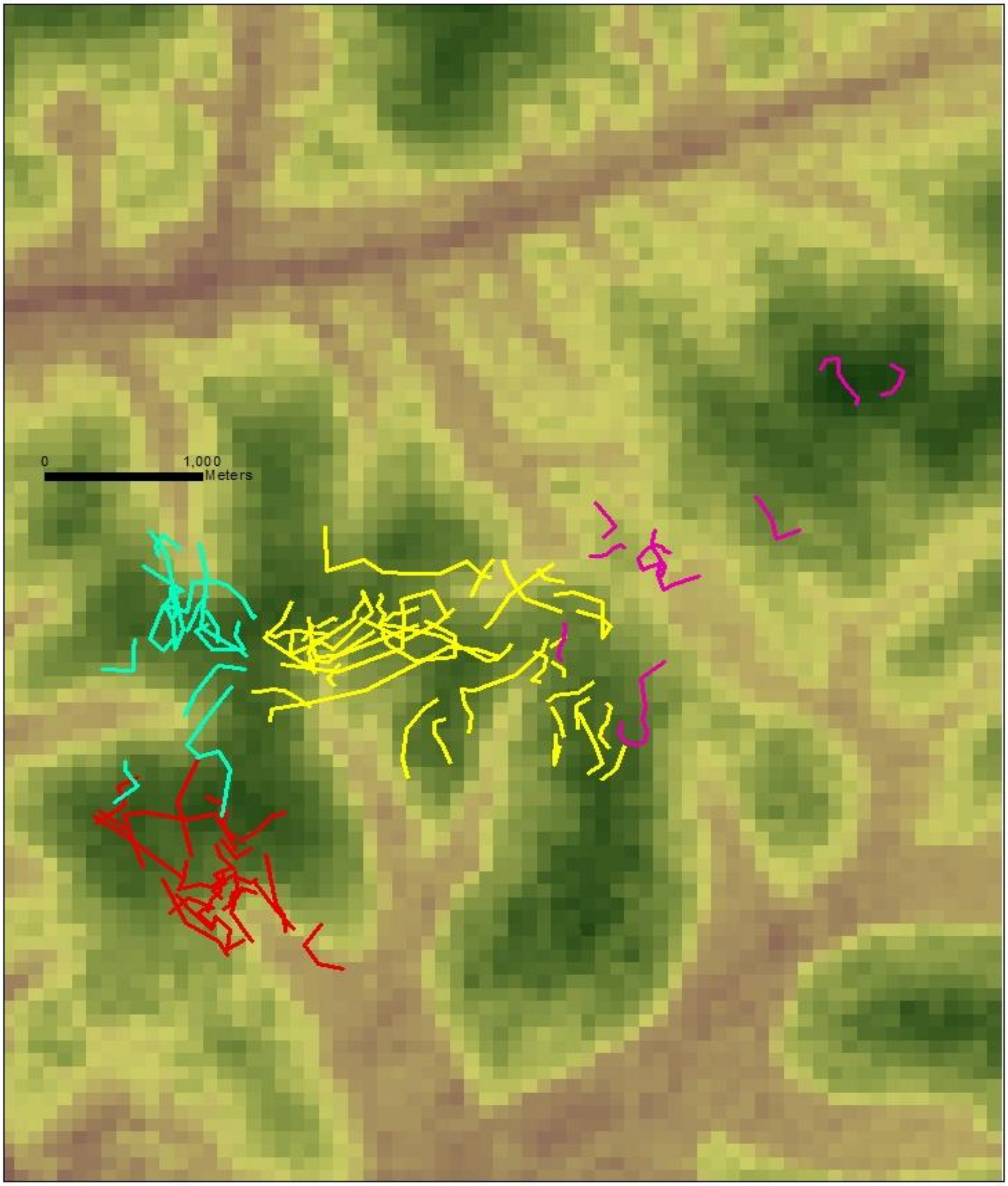

Figure 3.9. This map shows the measured DPL for bonobos at Lomako (Bakumba = Blue, Eyengo = Yellow, NE = Magenta, Splinter = Red).

The results show that Lomako bonobos not only have smaller home ranges than chimpanzees, but also move less during the average day. As bonobo male (45 kg) and female (33.2 kg) average weight falls within the range of male (42.7 – 59.7 kg) and female (31.5- 45.8 kg) chimpanzees, it is unlikely that body weight is a determining factor in explaining the variance. The absence of patrolling males and lethal raids may explain some of the differences, however, it is most likely the variation in food abundance that account for the primary differences between bonobos at Lomako and chimpanzees. Likewise, the difference between DPL of Lomako and Wamba bonobos may be due to habitat differences as Wamba has seen more human disturbance within the study area than Lomako, causing food to be less available. In general, the ranging behavior of bonobos at Lomako supports the notion that animals will move shorter distances and over smaller areas when food availability is high in an effort to conserve energy.

A series of linear regressions were used to determine if the estimated DPL was influenced by party composition and size. Counter to expectations, as party size increased, DPL decreased (Figure 3.10). A similar relationship was seen with number of females and DPL (Figure 3.11). This may suggest that bigger groups are formed when ample food sources such as fig trees are available and that these resources are large enough so that bonobos utilizing them need not move. Smaller parties occur in the absence of such large food depots forcing the smaller groups to have to move further in search of adequate resources.

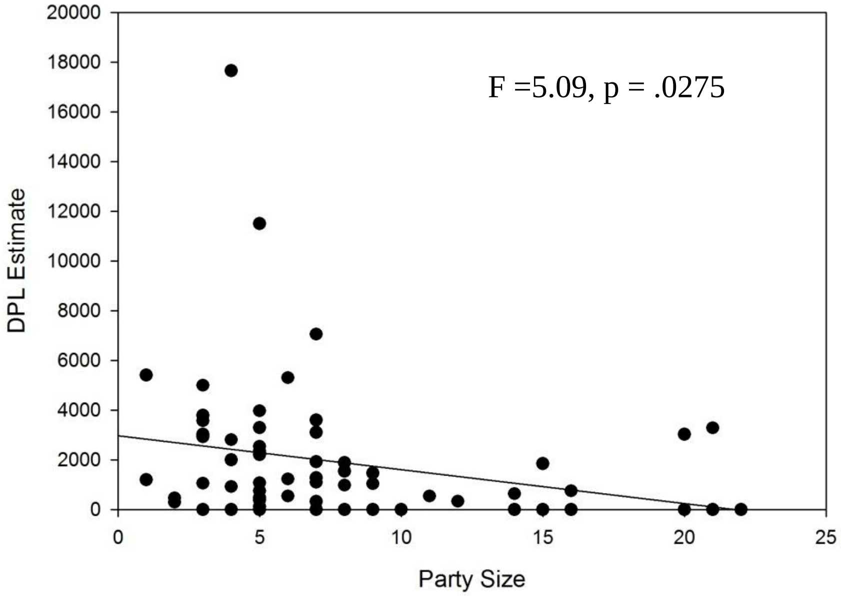

Figure 3.10. Effect of party size on DPL estimates.

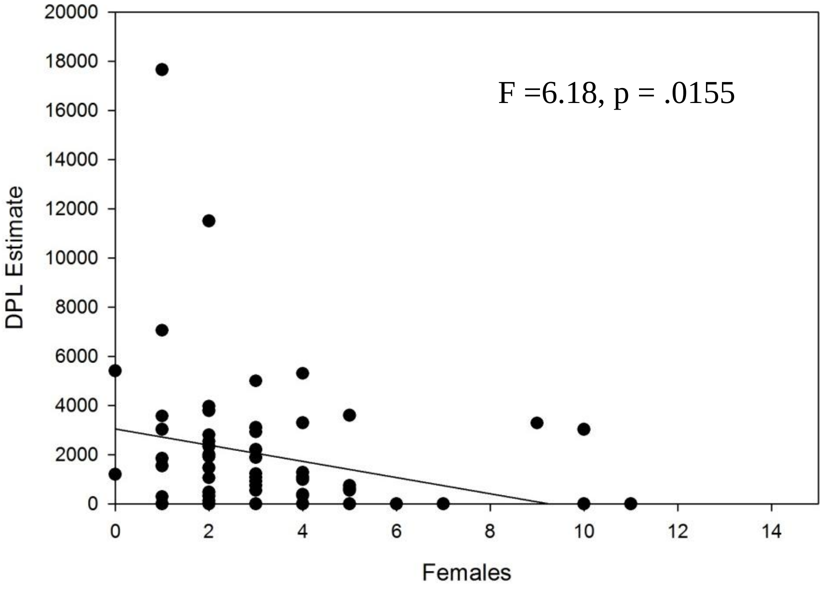

Figure 3.11. Effect of number of females in a party on DPL estimates.

Forest Variation

ArcGIS was used with satellite photos (Google Earth) and Digital Elevation Maps (DEMs) of the forest (NASA - shuttle radar topography mission) in an effort to look at the role forest variation plays in determining bonobo range use. Changes in the shades of the forest were matched with GPS mapped habitat structures exposing differences within the satellite image between the poly-specific primary forest and the swamp forests that border the creeks that flow through the area (Figure 3.12). Additionally, Flow Accumulating Analysis (FAA), which analyzes the slope of an area to figure out surface hydrology, was used to more thoroughly illuminate the forest structure. This slope reflects the differences between swamp areas, sloped forest, and primary polyspecific forest.

An analysis of bonobo ranging behavior within the habitat as displayed by satellite imagery (Figure 3.13) confirms that, while bonobos may occasionally move through swamp areas, they do not regularly occupy them. Equally noteworthy, the swamp areas and the homogenous *Gilbertiodendron* forests that surround them may act as semi-permeable buffers separating the various cliques’ core areas which consisted almost exclusively of primary polyspecific forests. These divisions may explain the lack of interactions between groups at Lomako as the pockets of primary forests match the FKA core range maps for each clique.

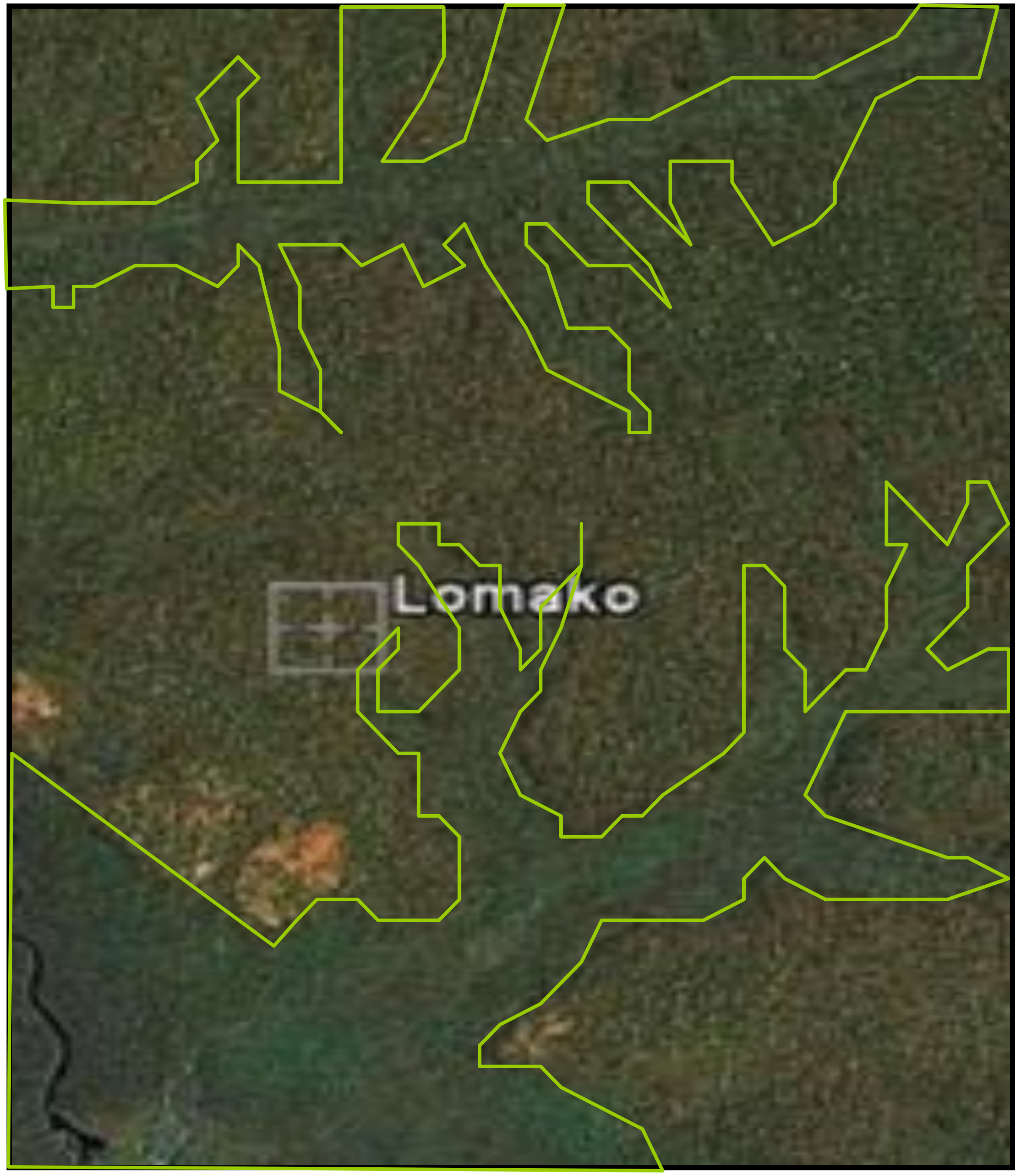

Figure 3.12. Satellite Image of Lomako Forest from Google Earth. Swamp forests are outlined in green. The brown areas is where the camp guides and their families live.

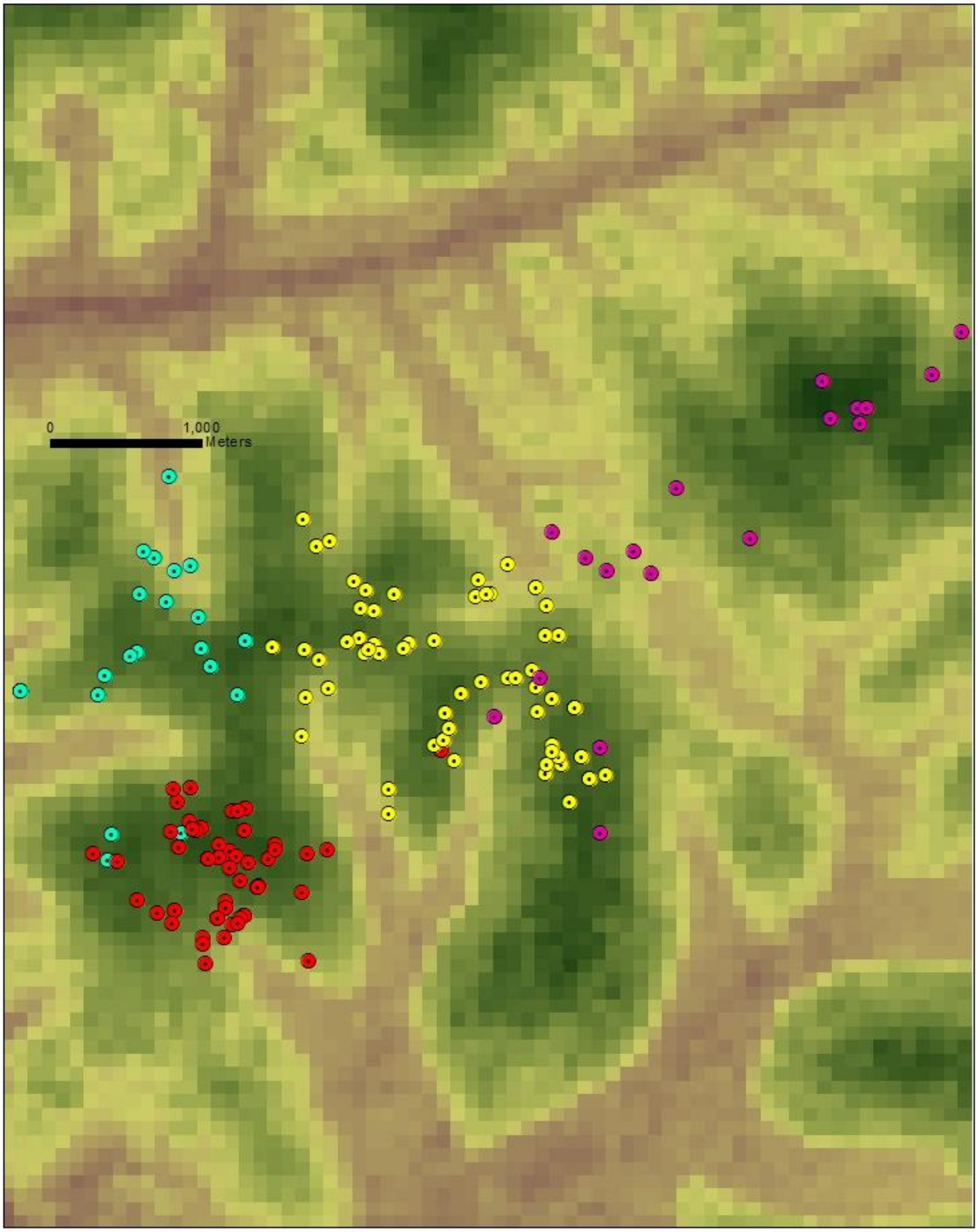

Figure 3.13. Clique sightings on FAA - DEM Map

Changes Since the War

Throughout the early phase (1984-1995) of field research at Lomako, the Eyengo and Bakumba communities did not significantly shift home range areas. When research recommenced in 2007, however, it became clear that the bonobos that once ranged throughout the study area had abandoned their former core ranges. According to the guides who worked for the project before and after the war, soldiers occupied the area on several occasions and may have hunted bushmeat within the study zone. Furthermore, many of the local people were forced to live in the forest to hide from the soldiers (Bosco personal communication). To analyze the shifts in core ranges, I measured the weighted mean centers (WMC) of each clique based on party size.   WMC is measured using the following equation:

$$\bar{x}_{wc} = \frac{\sum f_i x_i}{\sum f_i} \qquad \bar{y}_{wc} = \frac{\sum f_i y_i}{\sum f_i}$$

where *f* is the frequency of the points, *wc* is the weighted center, and *x* and *y* are the coordinates of each point. For this analysis, the party size (*i*) of each sighting was used to weigh the central tendency of bonobo sighting distribution within the study area.

In particular, I focused on the Eyengo and NE cliques (Table 3.5, Figure 3.14). One female currently in the NE clique was recognized based on facial characteristics to have once belonged to the Eyengo clique. This suggests that the NE group is made up at least in part of members from the former Eyengo group and that they were pushed away from their traditional core range during the war. More specifically, the results of the

WMC analysis show that during the early phase of research, the WMC for the Eyengo clique never shifted more than 1050 meters and remained within the overall core range as measured using a MCP. Between 1995 and 2009, however, the WMC of the Eyengo/NE clique shifted 2400.34 meters to the northeast outside of the former home range.

Table 3.5. Change in WMC (based on party size) for the Eyengo/NE cliques in between field seasons.

Field Seasons	Change in WMC Location
1985 - 1991	1050 meters
1991 - 1995	834 meters
1995-2009	2400 meters

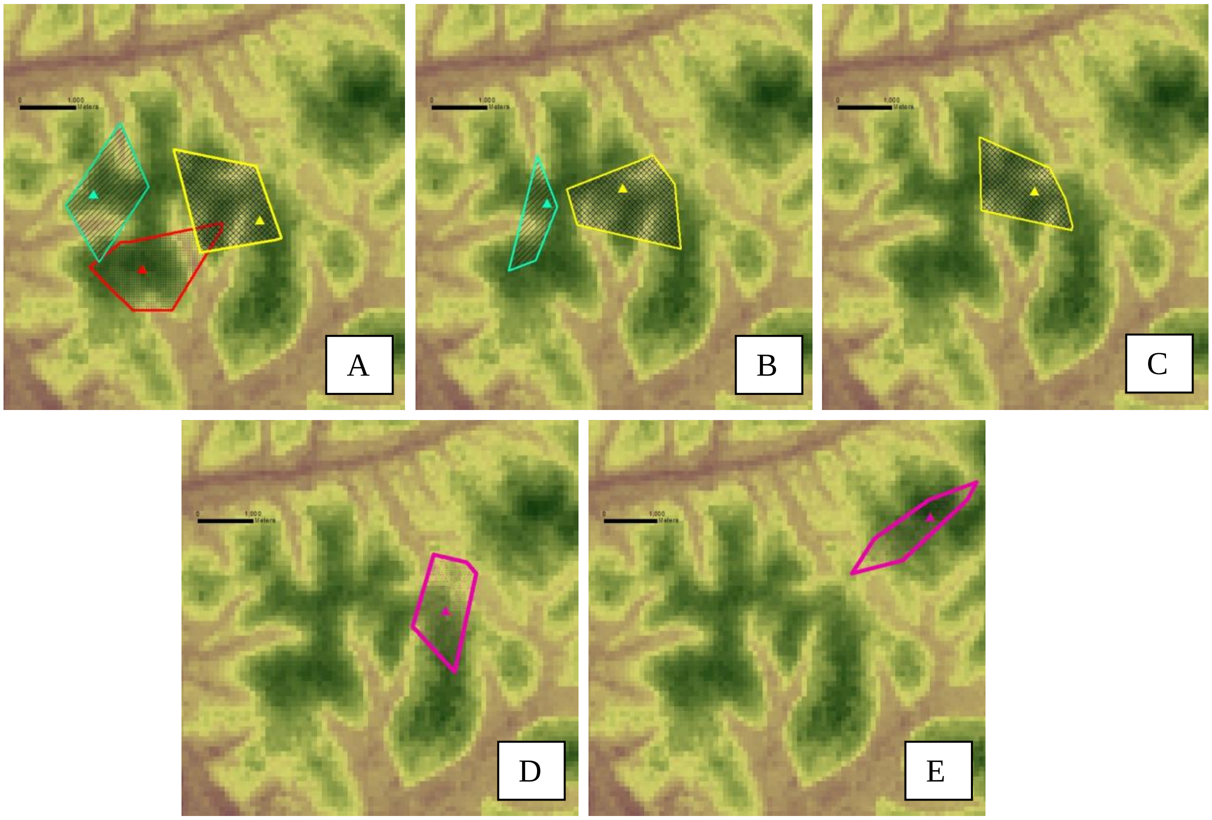

Figure 3.14. MCP ranges and WMC for each Field Season (A = 1984-1985, B = 1991, C = 1995, D = 2007, E = 2009).

As mentioned above, this may have resulted in a decrease in habitat quality as the bonobos in the NE group now range further than what the Eyengo group had done in the past. Surveys of the Bakumba former range showed little activity in the form of nests or feeding remains suggesting that the clique no longer habitually uses that area and may have moved to the northwest based on reports from guides and other locals. Between 1985 and 1991, however, their WMC only changes 811.14 meters, suggesting that their absence from the area is most likely due to increased human activity in the area during the war.

It is difficult to determine exactly why the ranges of these cliques shifted. Food availability may have changed or predation may have increased. Reports from local inhabitants, however, suggest that the soldiers, tired, hungry, and looking for food, entered the forest using the same trails used by researchers and began hunting. It is not too difficult to imagine a scenario where the sound of rifles and perhaps an actual encounter, scared the bonobos to retreat to locations outside of the study area where there were no trails and transects to facilitate easy human maneuvers. Conversely, this should be a lesson for those contemplating the creation of field study sites that include habituating subjects in states that are unstable.

Discussion

Research at the Wamba site has used grid squares of 500 x 500 meters to estimate an annual home range in the past. There are several problems with this technique as each square visited count the same regardless of frequency, meaning outlying areas may be over represented and core or habitually used areas go unnoted. Nevertheless, grid squares can present a broad idea of areas frequented by groups or individuals. At Wamba, bonobos from the E groups ranged in areas measured between 12.3 km^2 (1230 ha) and 31.5 km² (3150 ha) during any one year period (Hashimoto et al. 1998). This relatively large range may be further explained by the fragmented nature of the habitat or the location of provisioning sites within the study area. As provisioning has been stopped at the site, future research may discover differences in ranging behavior at the site.

More sophisticated research has looked at daily movement patterns at Wamba. Furuichi and colleagues (2008) used fruit fall clusters to estimate fruit abundance and daily follow data plotted on a satellite image to estimate a daily mean ranging rate in an effort to better understand the availability of food, ranging, and social organization. They found positive correlations between party size and fruit abundance, party size and daily ranging rate, and fruit abundance and daily ranging rate although the latter was not statistically significant. They further went on to estimate a daily ranging time based on the average times bonobos left their nests (07:26h) and began constructing new ones (16:57h) for a total of 9h 31m. Using the ranging rate calculated from follows and this activity time they concluded that bonobos at Wamba travelled an average of 2608 meters daily. Furthermore, they show that as food abundance goes up, more males join the female core cliques. Unlike at Lomako, however, as parties swell in size at Wamba, they must travel further to satiate the needs of all party members. Like the variation seen in total home range area, the difference between DPL estimates at Lomako and Wamba may be explained by habitat quality and varying levels of human habitat disturbance. and demonstrates the complex relationship between ranging behavior, food availability, and social organization. If, as most studies suggest, food availability in bonobo habitats is significantly higher, bonobos should have smaller annual and daily ranges simply because they need not expend as much energy traveling. Similarly, if competition from outside groups is not fierce, behaviors such as patrols or raids would not be seen, further contributing to smaller ranges when compared to chimpanzees. Finally, as the area at Lomako has less human impact and higher percentages of undisturbed forests, bonobos there may be expected to range in even smaller areas when compared with sites such as Wamba. The research presented here supports these concepts although it is based on relatively few sightings compared with other long term research projects. Still, these results suggest that the bonobos at Lomako may have the smallest annual ranges of any of the *Pan* study sites lending credence to the concept that high levels of food availability have significantly shaped bonobo socio-ecological behavior. To more fully appreciate bonobo ranging, the next chapter will focus on the differences between males and females in terms of ranging behavior and social cohesion.

CHAPTER IV

DO BONOBOS LIVE IN COMMUNITIES?

Introduction

The term “community” when applied to chimpanzees (*Pan troglodytes*) has come to be defined as a multi-male/multi-female, fission-fusion social system where members form temporary parties that fluctuate in size and composition within a delineated territory. Male chimpanzees are philopatric, closely bonded, actively patrol the borders of their home range, and are hostile to unknown males while female chimpanzees disperse from their natal group into a new community shortly after menarche. Once immigrated, the females are predicted to compete with each other for food and respond by establishing small core areas for themselves and their offspring, joining to form larger parties only during times of resource abundance or peak fertility. Thus, the home range of the community is predominantly determined by the area patrolled by males and can expand or contract based on male movement patterns. Female chimpanzees are expected to range over a much smaller percentage of the community territory than do males.

Bonobos (*Pan paniscus*) are also said to live in “communities”. When analyzing bonobo ranging behavior more closely, however, notable differences between the two species emerge. Female dyads are more cohesive than are male dyads or male/female dyads. Additionally, females with infants form the central core of bonobo social groups and are more likely to be in contact with other females than are females without infants. Females also range over a significantly larger percentage of the total group range when compared with chimpanzees. Unlike with chimpanzees, male bonobos are more loosely associated and employ a variety of tactics that aim to win acceptance from the female core groups. They do not form the patrol groups or lethal raiding parties seen in chimpanzees. Taken together, the results show that the structure of bonobo society differs from chimpanzee communities to a degree that warrants a distinguishing name. For reasons discussed, I suggest "cliques."

The relationship between an animal's environment and social system has become a central pursuit in primatology (Newton-Fisher et al. 2000). Models proposed by Wrangham (1980), van Schaik (1989), and Sterck and colleagues (1997) assume that female ranging behavior will be dictated by the availability, density, and distribution of food. Male movements will be determined by their ability to find and defend females. Seasonal changes in tropical environments are minimal compared with temperate zones (Whitmore 1986). Nevertheless, food availability, especially for frugivores, can fluctuate in both space and time (Peres 1994, Doran 1996, Conklin-Brittain et al. 1998, Knott 1998) and has been found to effect group size, levels of competition, aggression between and within groups, daily path lengths, total home range size, and reproductive rates (see Chapter I and Isbell 1991 for reviews). Females with offspring are particularly sensitive to the distribution of resources (Wrangham 1980). Because females are typically saddled with the high costs of raising infants (Trivers 1972), they are more likely to compete with other females for access to resources such as food, water, and nesting sites. Males, on the other hand, typically increase their reproductive fitness by attempting to increase their number of mating opportunities and are likely to compete amongst themselves for females. As our closest phylogenetic relatives, studies of chimpanzees and bonobos are vital for understanding the socio-ecological behavior of early hominins and can shed light on the manner in which males and females competed over resources. While both species are ripe fruit specialists, there are several differences in the way in which chimpanzees and bonobos move about their habitats.

Chimpanzees live in a variety of habitats across equatorial Africa. Although they inhabit primary rainforests (Sugiyama and Koman 1992, Boesch and Boesch-Achermann 2000), in general they are thought to occupy areas where fruit is patchily distributed across temporal and spatial scales (Wrangham 1977, Pruetz 2006). The patchy nature of fruit is thought to be responsible for the development of the fission-fusion social system seen in chimpanzees (Wrangham 1977, Wrangham 1979, Ghiglieri 1984, Isabyre-Basuta 1990, Boesch 1996). During periods of fruit scarcity, females and their offspring are typically less social, often retreating to their established core (Chapman and Wrangham 1993, Williams et al. 2002, but see Lehmann and Boesch 2005, Wakefield 2008, Reidel and Boesch 2011). These core ranges are competed over with females that occupy higher quality areas having higher reproductive fitness due to greater access to resources (Pusey et al. 1997, Williams et al. 2002).

Chimpanzee males, on the other hand, are philopatric and increase their reproductive fitness both directly and via kin selection by cooperatively patrolling their territory and excluding non-related males (Goodall 1986, Boesch and Boesch-Achermann 2000, Herbinger et al. 2001, Watts and Mitani 2005). Additionally, male chimpanzees at several sites lethally raid neighboring communities, resulting in the death of unrelated males, greater genetic representation within the overall area, and the expansion of the raiding males' overall territory (Goodall 1986, Manson and Wrangham 1991, Watts and Mitani 2001, Wilson et al. 2004, Boesche et al. 2008). This expansion increases access to preferred feeding sites for resident females and their offspring (Williams et al. 2002) and potentially increases access to previously peripheral females for the raiding males (Goodall 1986, Boesch et al. 2008). In terms of ranging behavior, it can be said that males delineate the groups' territory during their border patrols and lethal raids while females typically range over a much smaller percentage of the overall group home range (Williams et al. 2004). Those groups of patrolling males and the females they envelop that are affiliated exclusively with each other are called “communities” or, less frequently, “unit groups” (Goodall 1968, Nishida 1968).

Bonobos live in areas with high annual rainfall (Mulavwa et al. 2008), low levels of seasonality (White 1998), and high levels of fruit abundance (Hohmann et al. 2010) when compared to chimpanzee habitats. Furthermore, protein-rich terrestrial herbaceous vegetation (THV) is more readily abundant (Malenky and Wrangham 1994). In combination, these factors greatly reduce the degree to which bonobos need to compete over food (Malenky and Wrangham 1994, White 1996, Furuichi 2001). Consequently, groups can be larger and relatively more stable and may be less influenced by fluctuations in food availability (Kuroda 1979, Kano 1992, White 1988, White 1996, Mulavwa et al. 2008). Bonobo parties can also consist of larger percentages of the total group. At Wamba, the mean party size consisted of 51% of the total E1 group (Mulavwa et al. 2008) while at Lomako parties average 27% of all group members. Chimpanzee party sizes range between an average of 9 and 30% of the total community size (Hohmann and Fruth 2002).

Perhaps most notable, bonobo females form the core of their social groups despite not being kin (White 1988, Furuichi 1989, Kano 1992, Gerloff et al. 1999). Females leave their natal group around menarche (Idani 1991) and attempt to establish bonds with neighboring females (Furuichi 1989). These bonds are established through homosexual behaviors known as genito-genital (GG) rubbing (Kuroda 1980, Thompson-Handler 1990) as well as fruit sharing (de Waal 1989, White 1994). These bonds allow females to cooperatively defend food patches (White 1986, Idani 1991, Parrish 1994, Hohmann and

Fruth 1996) and protect themselves from infanticidal males (Waller et al. 2010) by having greater power when it comes to which males are allowed to enter the group (Furuichi 1997, Surbeck et al. 2010). Additionally, data collected at Lui Katol suggests that affiliated bonobo females benefit from coordinated monkey hunts at this site (Surbeck and Hohmann 2008).

Male bonobo ranging behavior also differs from chimpanzees as males rather than females are more likely to range independently, are less likely to join mixed parties (White 1992, Mulavwa et al. 2008), and do not patrol territories or lethally raid (Waller and White 2010, Chapter V). Consequently, less is known about their behavior when away from the female core groups. All together, bonobo parties are larger than those of chimpanzees both in terms of absolute numbers and in percentages of the total group. The purpose of this chapter is to further identify and illuminate the differences between bonobos and chimpanzees in the way in which males and females move through their habitat and form their social groups. Additionally, I will hypothesize as to how these social movements may reflect male and female strategies aimed at increasing their respective reproductive fitness.

Methods

The N’deli site in the Lomako Forest (0.7994° N, 21.143° E) is located in the Congo River Basin within the Equateur Province of the DRC. The 40 km² study area consists of several forest types, but is principally climax evergreen and polyspecific primary rain forest (75.2% of study site) with smaller areas of secondary growth, slope, and swamp forest (White 1992). While bonobos use all forest types, swamp and secondary areas are utilized less often (Hashimoto et al. 1998, see Chapter III).

Field studies of bonobo behavior began at Lomako in the 1970s and researchers have identified two distinct groups: Bakumba in the western portion of the study area and Eyengo in the east (Badrian and Malenky 1984, White 1998, Hohmann and Fruth 2002). Additionally, White (1986) identified a separate, “Splinter” group centered on 5 presumably immigrating young sub-adult females and the four males who followed them in 1984-1985. The males were most likely from the Bakumba group, as by 1991, all eight individuals were central reproductive adults living within the Bakumba range.

Table 4.1. Group composition for bonobos at Lomako.

Group	Sightings	Males	Females	Sub-adults	Infants
Splinter	69	4	5	0	0
Bakumba	36	4	11	8	5
Eyengo	76	11	10	4	5
Combined	181	19	26	12	10

Data used for analyzing ranging and social behavior was gleaned from 200 sightings including 448 hours of focal animal observations recorded by White during field seasons conducted in October 1984-July 1985, June-August 1991, and June-August 1995. Additional data on infants per females is presented from research conducted by Waller and White in 2007. Based on methods used by Mitani and Ansler (2003), I maintained statistical independence by typically recording one sighting each day. Multiple sightings were recorded on the same days only in cases where observations were separated by several hundred meters and party membership was clearly different.

Analysis of the data focused on five aspects of bonobo ranging and social formation; (1) the differences between male and female ranging behavior, (2) social cohesion based on spatial arrangements, (3) the effects of infants on female core group membership, (4) male strategies aimed at increasing mating opportunities, and (5) the differences between bonobos and chimpanzees in social construction. ArcGIS (ESRI 9.2) and RANGES 8 software were used to analyze ranging behavior (See Chapter II for more info).

Results

Ranging Behavior

There have been relatively few studies of female chimpanzee ranging behavior. At Gombe, where data on chimpanzees has been collected since the 1950s, females are not typically social, instead carving out individual core range areas that are significantly smaller than the range of the resident, highly-bonded males (Williams et al. 2002). Similar patterns have been found at Kibale (Chapman and Wrangham 1993), Mahale (Nishida et al. 1985), and Fongoli (personal observation). Females are more cohesive at Tai and Ngogo, where females range over a larger percentage of the community range (Boesch 1996) and form relatively stable parties (Wakefield 2008). Still, males at both of these sites delineate the community boundaries by forming patrol groups (Watts and Mitani 2001) and make up the core social units (Watts 2000, Boesch 1996). To look at male and female bonobo ranging, I used the *x,y* coordinates of each sighting to determine group (see Chapter III) and individual ranges. Because it is a better technique for comparing multiple range areas (Kernohan et al. 2001, Mitchell 2006, Powell 2000), the 95% Fixed Kernel Analysis (FKA) results are used here to represent the individual ranges of identified males (n = 3) and females (n = 6) with more than 10 observations from the

Eyengo group during the field seasons listed above (Table 4.2). The mean individual male home range was 158.77 hectares (ha) and ranged from 68.12-218.88 ha. The mean individual female home range was 98.37 ha and ranged from 54.50-168.16 ha. The male mean range equals 70% of the total Eyengo group range (225.95 ha) while the female mean covers 43.5 %. Additionally, females with infants inhabit the central core areas of the group range (Figure 4.1) and had ranges (mean = 67.01 ha) that were smaller than females without infants (mean = 114.06 ha).

Table 4.2. Individual ranging areas for Eyengo group members.

Individual	# of Sightings	95% FKA Range (ha)
F1 w/infant	13	68.24
F2 w/infant	14	65.77
F3	14	65.41
F4	12	54.5
F5	10	168.16
F6	11	168.16
M1	12	218.88
M2	10	189.32
M3	10	68.12

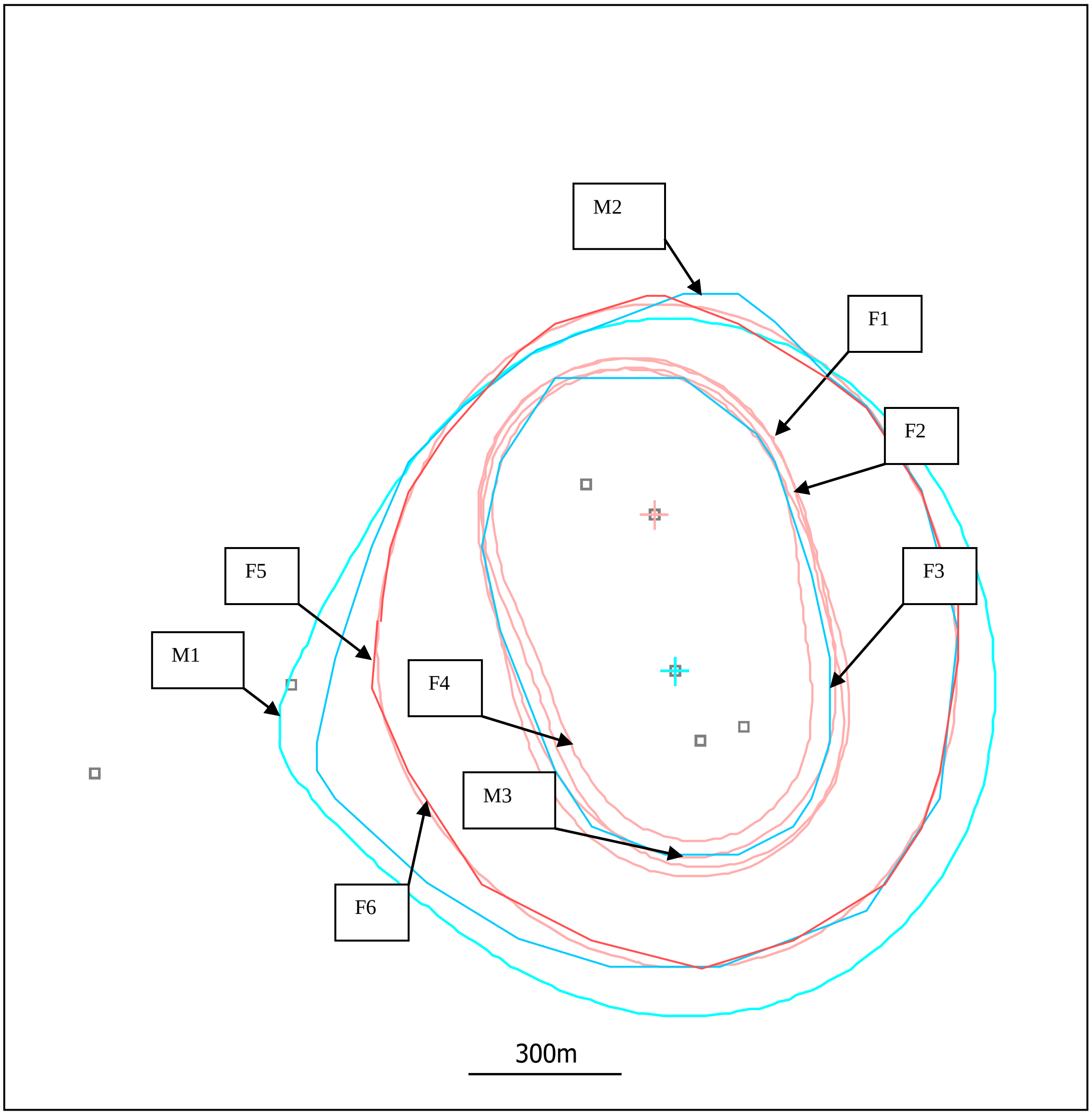

Figure 4.1. This map shows the 95% FKA ranges of the males (blue) and females (red) in the Eyengo group.

These results suggest that females with infants occupy the central portion of the entire group range while females without infants range over greater areas utilizing the peripheral zones of the total group range. Less can be said about the size of male ranging as males are not observed as easily as females. At least one male has been seen associated with the Bakumba, Eyengo, and Splinter groups suggesting that male membership in a group may be more fluid and could be based on acceptance by the core females rather than kin bonds as is seen in chimpanzees. To better understand how males may enter into female groups, I will look at the behavioral data collected during focal sampling.

Male Social Behavior

While chimpanzee males gain reproductive fitness by competing within their community (Watts 2000, Newton-Fisher 2002) as well as competing with neighboring communities (Goodall et al. 1979, Nishida et al. 1985, Manson and Wrangham 1991, Boesch & Boesch-Achermann 2000, Newton-Fisher 1999, Watts & Mitani 2001), less is known about male bonobos. Several studies have shown that mothers of adult males may facilitate membership into female groups (Ihobe 1992, Furuichi 1997, Surbeck et al. 2010) perhaps increasing mating opportunities. Other studies have shown that males are more affiliative with infants than are non-related females, perhaps in an attempt to expedite inclusion into the female core groups by appearing paternal or forming “friendships” (White and Waller 2010). Data presented here looks at the manner in which males move when near female core groups, particularly in feeding contexts.

Data was collected by White using 2 minute focal animal sampling from 1984 to 1985, and 5 minute focal sampling until 2007 (Altmann 1974). Interactions were recorded ad lib. The activity, height, and party size were recorded for the focal animal as well as location relative to the trail system and food sources. The location and context of the focal animal relative to a food patch was recorded. Individuals were classed as in a patch if they were in a food tree or vine canopy that contained food that was eaten by at least one party member. THV was not patchy in distribution and was not recorded as a food patch. Individuals were classed as near a food patch if they were in the immediate vicinity of a food patch, usually the adjacent tree or in the understory or on the ground below the food patch canopy. Individuals who were travelling into a food patch, typically on a main access branch, were classed as entering and those travelling out of a food patch were classed as leaving a food patch. The order of entry, timing, and interactions of individuals entering food patches was recorded whenever possible. Changes in party composition from individuals leaving or joining were recorded as they occurred (White 1992).

The frequency of activities was compared between males and females using G tests of Independence (Sokal and Rohlf 1995). Observed frequencies were compared to expected frequencies using G test of Goodness of Fit (Sokal and Rohlf 1995). Travel was the least frequent major activity, accounting for 16% of total focal sampling Males and females did not differ significantly in focal animal heights during locomotion for most contexts except when in the immediate vicinity of food patches. In these cases (Table 4.3), males were observed travelling more frequently in the lowest height categories, including on the ground, when next to food trees whereas females remained in higher height categories as in other food patch contexts. Lone individuals arriving on the ground at a food patch were most likely to be male. Males in parties arrived at food patches through the trees significantly more often than lone males which were equally likely to be in the trees or on the ground ($G=4.059$, $p < 0.05$). There was no significant dependence between arriving at a food patch on the ground or in the trees and whether females were in parties or alone (G=0.277, ns). Females arrived most often through the trees.

Table 4.3. Percentages of males and females at various levels in the forest showing that, as groups near food patches, males are more likely to be found at lower heights perhaps in an effort to control access to patches.

Food Patch Context	Sex	< 5 Meters	6-20 Meters	> 20 Meters	n	Significance
Outside	M	9	11	81	45	G = .056, ns
	F	9	10	80	102	
Near	M	42	52	8	12	G = 26.587, p<.001
	F	0	20	80	46	
Entering	M	0	29	71	7	G = 2.468, ns
	F	0	4	89	27	
In	M	0	19	81	16	G = 2.301, ns
	F	0	4	96	27	
Leaving	M	6	31	63	32	G = 3.994, ns
	F	6	15	79	121	
Total		6	17	77	435	

Because the majority of agonistic interactions and copulations occurred during the relatively rare observations of individuals entering food patches (White and Minton in prep) patch access points appear to be competed over by males. This study shows that males position themselves at patches in a manner termed here "tree-guarding" in hopes of mating with females attempting to enter. Together with positive infant interactions and the assistance of established mothers, male bonobos employ a number of individual strategies aimed at increasing reproductive fitness that differ from the intense inter- and intra-group competition that define chimpanzee males.

Social Cohesion

As mentioned above, bonobo females have been found to be more cohesive than males based on observations of party composition and nearest neighbor distances (White 1986, White and Burgman 1990). Here, I look to measure social cohesion using *x*,y coordinates from individuals in the Eyengo (5 females, 3 males) and Splinter (4 females, 4 males) groups (Tables 4.4 and 4.5) to determine whether there is a spatial component to this cohesion. These coordinates were entered into the RANGES8 software program in an effort to identify the degree to which individuals moved together. To do this, RANGES8 uses Jacobs' Index (Jacobs 1974), an analytical method which gives a single "cohesion" score based on the tendency of pairs of animals to be close together. Animals in fission-fusion social groups may seldom encounter each other because they rarely visit the same place at the same time. As such, Macdonald et al. (1980) called the analysis of overlapping range outlines "static interaction". To examine "dynamic interaction" it is necessary to look at locations taken within the same general time period in order to see if individuals were attracted to each other or whether they tended to avoid each other. The original tests of this method depended on two assumptions. First, that locations are statistically independent and second, that their distribution fit a parametric model. RANGES8 avoids assumptions about independence and distributions of locations between single pairs of individuals and provides a single statistic for each range as described in Kenward and colleagues (2001). To get these statistics, the observed and possible distances between animals are compared.

The mean, geometric mean and median distances are estimated between each observed pair for locations for animal 1 and 2. Then the equivalent values are estimated for the n x n possible distances if animal 2 could be at any of its n used positions when animal 1 was at each of its used positions. The observed and possible distances are compared using Jacob's Index (Jacobs 1974). This gives a value of 0 if the observed and possible distances were the same, rising towards +1 if observed distances were small relative to possible distances (because the animals were usually together) or falling towards -1 if animals tended to avoid each other. This gives a single index for each pair of animals, which tends to be most consistent if based on the geometric mean distances (Walls & Kenward 2001).

In general, the results (Tables 4.4 and 4.5) confirm that females were more cohesive (total mean score of .251) than were males (.0527) or males and females (.118). Additionally, these results were applied to an algorithm based on the Unweighted Pair Group Method with Arithmetic Mean (UPGMA, from Sneath and Sokal, 1973) to create cluster analyses (Figures 4.2, 4.3) on the inter-individual Jacobs' Index similarity matrices that produce graphic representations of the relationships among individuals. Moreover, the Eyengo females were more closely bonded than were the Splinter females.

Table 4.4: Jacobs' Index results for dyadic cohesion for six females and three males from the Eyengo group.

	F1	F2	F3	F4	F5	F6	M1	M2	M3
F1	■								
F2	0.7925	■							
F3	0.5993	0.5515	■						
F4	0.3641	0.3641	0.5815	■					
F5	0.0767	0.1794	0.0677	-0.0797	■				
F6	0.0767	0.1794	0.0677	-0.0797	1	■			
M1	0.0019	-0.0057	0.0281	-0.0463	-0.0029	-0.102	■		
M2	0.1092	-0.0057	0.1842	-0.145	0.2082	0.2082	0.8895	■	
M3	-0.0947	0.4217	0.1624	0.1867	0.5163	0.5163	0.2082	-0.102	■

Table 4.5. Jacobs' Index results for dyadic cohesion for four females and four males from the Splinter group.

	SF1	SF2	SF3	SF4	SM1	SM2	SM3	SM4
SF1	■							
SF2	-0.0976	■						
SF3	0.014	0.0103	■					
SF4	0.0612	-0.0091	0.0639	■				
SM1	-0.046	0.0067	0.4609	0.0306	■			
SM2	-0.1433	-0.087	-0.0374	0.0882	-0.0568	■		
SM3	0.0067	-0.0356	0.1552	0.0136	0.1107	-0.0913	■	
SM4	-0.0736	-0.0018	-0.0108	0.0241	0.0099	0.0201	0.1029	■

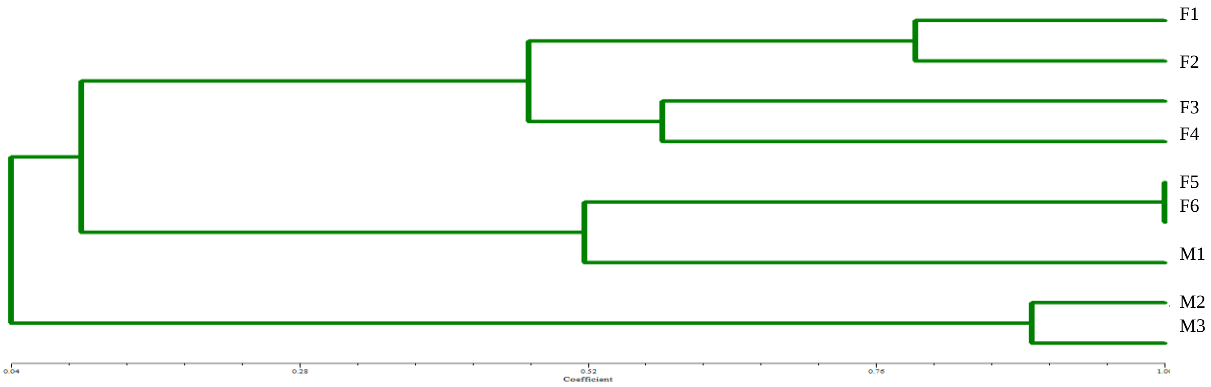

Figure 4.2. UPGMA cluster analyses on the inter-individual Jacobs’ Index spatial relationships for the Eyengo group.

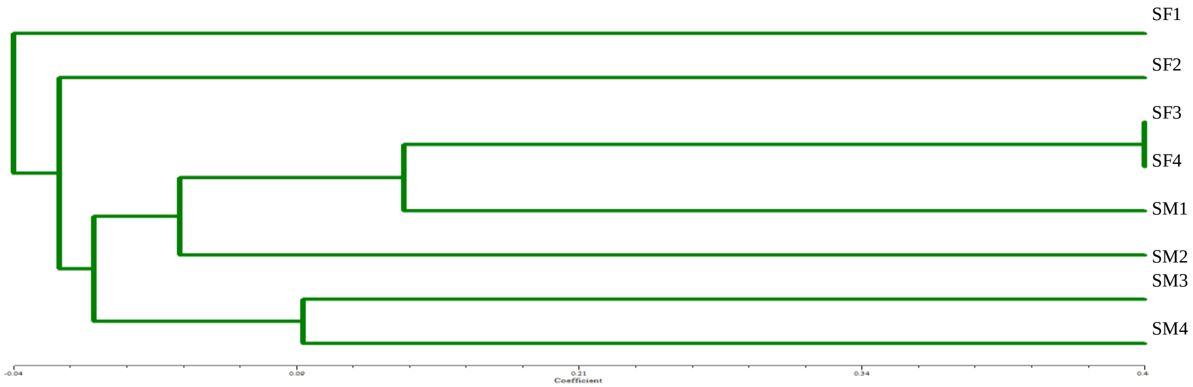

Figure 4.3. UPGMA cluster analyses on the inter-individual Jacobs’ Index spatial relationships for the Splinter group.

Effect of Infants on Social Behavior

To further investigate the role of females with infants in the formation of core groups, nearest neighbour data was analyzed for patterns. Statistical analyses of nearest neighbour data are difficult as distances at one point in time are dependent on the distance at the previous time point (White and Chapman 1994). Standard tests assume independence and, therefore, cannot be used (Sokal and Rolf 1995). Subsequently, it is necessary to calculate a transition matrix that contains the probabilities of nearest neighbours moving between distance classes (White 1986). After that, sampling can be used to determine the distance between a focal animal and its neighbours.

This technique has been used in the past to highlight the differences between bonobos and chimpanzees regarding social cohesion. White and Chapman (1994) found that male bonobos at Lomako were more likely to eat further away from each other compared to male chimpanzees at Kibale. Additionally, they found that female bonobos were more likely to feed together at close distances (1-2 meters) than were female chimpanzees. To better understand the nature of female core groups, neighbour distances (Table 4.6) were calculated for female members of the Eyengo, Bakumba, and Splinter groups using focal sampling (n = 1208 time units). The results show that females with infants are particularly cohesive. Females with infants spent more time in contact with other mothers than they did with females without infants suggesting that infants may be a requirement for adult female membership into the core of a group. Additionally, females without infants moved closer to females that do have infants and associated less with those that do not. All together, females with infants are attractive to other females, both with and without infants, as it is mothers that seem to bond together to defend food patches or repel infanticidal males.

Table 4.6. Nearest neighbors percentages of time spent by females with and without infants. This data shows that females with infants were more attractive to other females than were females without.

Focal Animal/Neighbor	**Contact**	**2 Meters**	**5 Meters**	**10 Meters**	**15 Meters**	**20 Meters**	**25 Meters**	**30 Meters**	**35 Meters**	**40 Meters+**
Females With Infants/Females Without Infants	14.02	14.63	53.66	12.2	0	5.49	0	0	0	0
Females With Infants/Females With Infants	23.17	18.73	38.1	17.14	2.86	0	0	0	0	0
Females Without Infants/ Females With Infants	12.35	20.99	36.42	26.54	0	0	0	3.7	0	0
Females Without Infants/Females Without Infants	9.43	14.58	46.83	22.53	6.48	0	0	0	0	0.15

The relationship amongst females appears to be a successful adaptation as the gregariousness of females may have a direct effect on reproductive fitness. Females at Lomako have a higher ratio of infants to females (.953 mean, 1.06 in 2007) when compared with published studies that report the number of infants per female for chimpanzees (range .743-.841, Figure 4.4). The difference between bonobos and chimpanzees in this regard may reflect the costs and benefits associated with varying degrees of female cohesion.

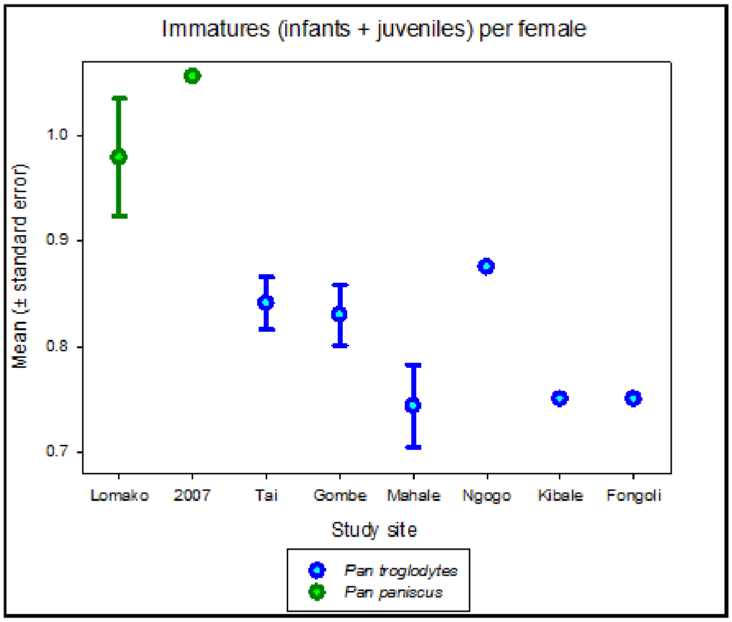

Figure 4.4. Comparison of the number of infants and juveniles per female from Lomako and chimpanzee study sites

Discussion

Many diurnal primates show female gregariousness (Sterk et al. 1997) although the majority of these female groups consist of related individuals. Because bonobo females leave their natal groups shortly after menarche (Furuichi 1989), the bonds they form and the subsequent cooperative behavior (shared food, assurance of female feeding priority, cooperative hunting) cannot be explained by kin selection (White 1992, White and Wood 2007). Previous attempts to elucidate these female bonds have centered on the need for cooperative defense of food patches, however, ecological studies, ranging patterns, and social relations demonstrated by this and other studies suggest that competition over resources in this food rich environment is minimal at best. More likely, female sociality combined with the high level of promiscuity and the subsequent paternity uncertainty such high rates of copulations produce, evolved as mechanisms to prevent infanticide, the sexually coercive behavior prevalent in chimpanzees, where females are typically unable to bond due to the strains of feeding competition. Infanticide has not been observed at any bonobo site. Females may also benefit from gregariousness by increasing mate choice as females become more selective with whom they mate when in estrus or by reducing predation. More research is needed to better determine the relative impact of these different factors.

Regardless of the benefits gained, it appears clear that females, particularly those with infants, form the core of bonobo social groups. These core groups, which I call "cliques," may be relatively stable perhaps fluctuating when peripheral females have offspring or the core females' offspring become independent. These cliques are attractive to females without infants as they may represent a safe haven for producing offspring as well as protection from harassing males. Cliques are also attractive to males as that is where females congregate. One male strategy aimed at infiltrating a clique requires the maintenance of close bonds with ones mother in hopes that she may facilitate the son's presence, allowing them to interact more frequently with the females within that group (Surbeck et al. 2010). Moreover, the mother's presence within the group affected dominance relationships (Ihobe 1992) with mothers at Salonga going so far as to chase off rival males (Surbeck et al. 2010). Another tactic, identified by White and colleagues (2010), looks for males to ingratiate themselves to fertile females by interacting positively with nearby infants, perhaps displaying a modicum of paternal investment.

Undoubtedly, dominance relationships play a role both in female and male positions within a clique. Compared with chimpanzees, however, females have much more influence within a group while males rely on individual strategies designed to increase access to females. Similarities are seen in more gregarious chimpanzees such as inhabit Tai and Ngogo, hinting at the importance of food availability in facilitating these behaviors (Wakefield 2008, Riedel et al. 2011). Yet none of the chimpanzee sites have shown the same degree of female gregariousness nor the independent nature of males as is seen at Lomako. These behaviors are reflected in the manner in which bonobo females and males move about their forest and starkly contrast the ranging behavior of chimpanzees.

Understanding the factors contributing to the natural, sexual, and kin selection on the ranging behavior of chimpanzees and bonobos is important for modeling the behavior of our earliest ancestors. While much effort has been devoted to classification debates centered on degree vs. kind (Stanford 1998, Parish et al. 2000), it is the spectrum of *Pan* behavioral diversity that is the key to understanding the evolutionary processes that shaped our own lineage. The research presented here should force us to broaden our perceptions of male and female hominin behavior. For example, food availability certainly played a role in the manner in which social groups were constructed. In areas were food was difficult to obtain, could be monopolized, or population pressure was high, distinct, rigid dominance hierarchies and extreme inter-group competition likely ensued. Intra-group hierarchies and neighbor group interactions would be less hostile in high food availability contexts. Consequently, chimpanzees can tell us much about the nature of warfare in humans while bonobos can tell us more about our capacity for cooperation. Chapter V explores these concepts by looking at the way individuals range in relation to neighboring cliques.

CHAPTER V

ARE BONOBOS TERRITORIAL?

Introduction

Chimpanzees (*Pan troglodytes*), our closest phylogenetic relatives, show inter-community lethal raiding that enhances mating opportunities and increases the number of feeding locations within an encroaching communities' expanded range. Consequently, this behavior has been used as a starting point for the study of the evolution of war and aggression in humans and has historically shaped the manner in which human evolutionary scenarios are constructed. As phylogenetically close to humans and having split from chimpanzees between .8 and 2.5 million years ago, bonobos (*Pan paniscus*), however, have not been found to engage in inter-community lethal raiding and, with notable exceptions, their behavior has not been given equal attention when it comes to human evolutionary models.

This study compares and contrasts the size and ecology of the *Pan* species' community ranging areas, sex ratios and party sizes near ranging peripheries, and the social behavior that precludes or prevents inter-community lethal raiding. Unlike what is reported for chimpanzees, bonobo party sizes are not significantly larger nor are they more male-biased near a communities' border. This evidence, combined with observed peaceful interactions between neighboring community groups solidifies the notion that bonobos do not engage in lethal raiding and should aid those interested in refining the conflict/cooperation aspects of human evolution.

Before human warfare developed into power contests between various economic, political, social, and cultural ideologies, lethal raiding existed amongst territorial bands of hunter/gatherers where it functioned to improve access to food and mates (Divale 1972, Chagnon 1988, Gat 2000) suggesting that border patrols and the invasion of neighboring groups can function as adaptive evolutionary behaviors (Wrangham and Peterson 1996). Likewise, chimpanzees (*Pan troglodytes*), one of our closest phylogenetic relatives, show border patrol behavior (Watts and Mitani 2001) and inter-community lethal raiding (Goodall 1986, Manson and Wrangham 1991, Boesche and Boesche-Acherman 2000, Watts and Mitani 2001) that is thought to similarly enhance mating opportunities (Goodall 1986, Boesche et al. 2008) and increase access to feeding locations within an encroaching community's expanded range (Williams et al. 2002, 2004). Consequently, chimpanzee territoriality and lethal raiding has been used as a starting point for the study of the evolution of warfare in humans as reflected in the manner in which human evolution is modeled (Wrangham and Peterson 1996, Manson and Wrangham 1991, Goodall 1986, Lehmann and Feldman 2008). Humans also interact peacefully and cooperatively (Smith 2010), however, by forming complex associations and alliances, allowing "others" to travel within lands and actively seeking trade (Fry in press). Equidistant from humans phylogenetically (Chen and Li 2001), bonobos (*Pan paniscus*) show markedly different intra and inter-community behaviors that include extensive non-reproductive sex (Badrian and Badrian 1984), alliances of unrelated, socially-bonded females (White 1990, White and Lanjouw, 1992), low levels of male-male bonding (White 1989, White and Burgman 1990, Hohmann and Fruth 2003), amicable inter-community interactions (Kano 1992) and an absence of lethal raiding. Unlike chimpanzees, bonobos may shed light on the human capacity for inter-group peace. Here I use a geographic information systems (GIS) approach to better understand bonobo ranging behavior in an effort to compare ranging and inter-group behavior and examine the variation in territoriality between and within the *Pan* species. Furthermore, these differences have implications for models of the potential behavior of the earliest hominins, which will also be discussed.

Competition and Ranging

Social animals show variation within their spatial distribution as they compete over food, mates, and shelter both within and among groups. Competition over such resources has been categorized into two general types: contest and scramble (Nicholson 1954). Scramble competition (colloquially known as “first come, first served”) exists when individuals or groups are unable to exclude others as resources may be too plentiful, spaced too far apart, or population density is too large. In such cases, competitors adjust their distribution in relation to habitat quality so that each individual or group acquires resources at a similar rate. This spatial partitioning is known as the “ideal free” distribution (Fretwell and Lucas 1970) and can be characterized by a lack of territorial behavior while reproductive success reaches equilibrium due to crowding in the better habitats and fewer individuals in the poorer.

Contest competition arises when limited resources can be economically defended through exclusion or direct displacement leading to increased reproductive success for those individuals or groups capable of defending key resources (Brown 1964). Where contest competition is employed, individuals or groups are spatially arranged in a “despotic free” distribution (Fretwell 1972) meaning that the dominant individuals or groups have differential access to preferred resources. Consequently, in cases where there is an estimable amount of contest competition, definitive dominance hierarchies both within and between groups are expected (Wrangham 1980). It is also possible that individuals can experience one type of competition while groups can experience another.

While these two distribution models may represent ends of a spectrum of spatial arrangements, they are accompanied by behaviors that illuminate the relationship between the distribution of individuals within and among groups and the socio-ecologic drivers of the distribution pattern. These include habitat quality, dominance hierarchies, and ranging behaviors. More specifically, where spatial behavior resembles the ideal free distribution (1) scramble competition should be observed (2) dominance hierarchies should be weak or nonexistent, (3) reproductive success should reach equilibrium as (4) higher quality habitats (or patches) should support more individuals while lower quality habitats should support fewer. Furthermore, (5) interactions should be non-antagonistic and (6) territoriality is less likely. Conversely, when individuals or groups live in a despotic free distribution, there should be a (A) strong dominance asymmetry that results in those groups or individuals capable of excluding others enjoying (B) higher reproductive success and (C) preferential access to resources. Additionally, (D) interactions should be aggressive and (E) territoriality, behavior involved in actively preventing others from entering into an area, should be observable.

For those concerned with the evolution of our own competitive nature and how it may relate to spatial distributions, there is perhaps no more pertinent non-human genus available for study than *Pan*. These two species, chimpanzees and bonobos, are the closest genetic relatives to humans alive today. Using mitochondrial DNA analysis, Ruvolo and colleagues (1994) showed that the *Pan* genera and humans shared a common ancestor as recently as 5-6 million years ago. A separate study sequenced 53 autosomal intergenic nonrepetitive DNA segments, the results of which suggest that the *Pan*/*Homo* split occurred between 4.6 and 6.2 million years ago. That same study showed that chimpanzees and bonobos differ genetically from humans by approximately 1.24%

compared with a *Pan*/*Gorilla* difference of 1.63% (Chen and Li 2001). More recent studies have confirmed this general timeline and close phylogenetic relationship (i.e. Patterson et al. 2006). Perhaps of equal interest, these two species, separated by as little as 900,000 years (Won and Hey 2005), behave in remarkably different ways.

Chimpanzees

Although endangered, chimpanzees have historically lived throughout equatorial Africa within a diverse array of habitats ranging from the dense rainforests of the Northern Congo Basin (Poulsen and Clark 2004) and the Ivory Coast (Boesche and Boesche-Achermann 2000) to the dry and hot mosaic environments of Senegal (McGrew et al. 1981, Pruetz 2006) and Tanzania (Hunt and McGrew 2002), the latter of which are thought to be similar in spatial and ecological landscape characteristics to those negotiated by early hominins (McGrew et al. 1981, Pruetz and Bertolani 2009). Despite the diversity of habitats in which chimpanzees find themselves, there are a number of behavioral characteristics that have come to typify the species. All chimpanzees are primarily fresh fruit eaters (Wrangham et al. 1998, Newton-Fisher 1999, Pruetz 2006) that live in multi-male, multi-female fission-fusion communities (or “unit-groups”), where parties within the communities fluctuate in size and composition (Goodall 1968, Nishida 1968) based on factors such as food availability (Itani and Suzuki 1967, Goodall 1986, Wrangham 1986, Chapman et al. 1994), predation pressure (Boesch 1991), the presence of females in estrus (Goodall 1986, Matsumoto-Oda 1999, Boesch and Boesch-Achermann 2000, Hashimoto et al. 2001) and inter-group relations (Wrangham 1999, Mitani and Amsler 2003). Females disperse from their native communities once they have reached sexual maturity (Nishida and Kawanaka 1972, Pusey 1979) and as adults primarily range alone or with their offspring in order to increase feeding efficiency and avoid male aggression (Williams et al. 2002). Females become more social during times of high food availability or during high fertility when individual females mate with several males (Goodall 1986) but do display rank and that rank is associated with reproductive success (Pusey et al. 1997).

Males in a community exist inside a hierarchy predominantly determined by aggressive competition with the highest ranking individuals enjoying increased access to fertile females and choice feeding trees (Goodall 1986). Social bonds as measured by grooming rates are strongest amongst the related males that remain within their natal groups. Additionally, bonds are stronger between males and females than they are among females (Watts 2000). These male bonds are thought to facilitate male-male cooperation such as is beneficial during monkey hunts (Stanford 1998, Watts and Mitani 2002, Newton-Fisher et al. 2002), political within-group maneuvering (de Waal 1982, Watts 2002), the exclusion of non-related males from community ranges via territorial boundary patrols (Watts and Mitani 2001), and lethal inter-community raids (Goodall 1986, Wrangham 1991, Boesch and Boesch-Acherman 2000, Watts and Mitani 2001).

Territorial boundary patrols in chimpanzees consist of the movement of several individuals, primarily males, towards the periphery of their community range (Goodall 1986, Boesch and Boesch-Achermann 2000, Watts and Mitani 2001, Mitani and Watts 2005). Movement is silent and intra-community competitiveness is temporarily suppressed (Boehm 1992) as the patrollers search for signs of members of neighboring communities (Mitani and Watts 2005). When neighbors are detected, patrol groups may retreat, respond with loud calls and charging displays (Mitani and Watts 2005), or launch coalitionary attacks against neighboring individuals which can be lethal (Goodall 1986, Manson and Wrangham 1991, Nishida and Hosaka 1996, Wrangham 1999, Fawcett and Muhumuza 2000, Watts et al. 2006, Boesch et al. 2008).

Conspecific coalitionary violence among animals in the form of lethal raids is rare with only a few species known to form aggressive coalitions of more than four individuals (for summary see van der Dennen 1995). While lions, hyenas, and cheetahs occasionally employ coalitional killing of conspecifics at rates that are currently unknown (Wrangham 1999), humans, wolves, and chimpanzees are the only species known to regularly kill adult members of neighboring groups during territorial disputes (Boehm 1992, Mech et al. 1998, Wrangham 1999). According to Wrangham (1999), chimpanzee lethal raiding occurs when coordinated border patrols infiltrate a neighboring community, find one or more vulnerable individuals, assess the probability of a successful attack, bite, kick and hit leaving the target dead or dying, and return to their own territory. Although seen at several long-term study sites, this behavior has been most dramatically described at Gombe. In the mid 1970s, two communities of chimpanzees, the Kahama and Kasekala, were the focus of researchers studying chimpanzee behavior and ecology at Gombe National Park in Tanzania (Goodall 1986). Each group had made incursions into the other’s territory, encountered lone opposing party members and called wildly forcing the smaller of the parties to retreat (Wrangham and Peterson 1996). This type of territorial defense is relatively common among animals. What is not common, however, is the behavior of the Kasekala community. They were not waiting for their rivals to encroach on their territory. Groups of at least six males and sometimes a couple of females would quietly move through border zones into Kahama turf and systematically kill lone males caught unaware. One by one, the six males and four adult females that once comprised the Kahama group were beaten and disappeared while the youngest females were integrated into the Kasekala group. By the end of 1977, the Kahama group was gone (Wrangham and Peterson 1996).

Originally described by Goodall (1986) and developed more fully by Wrangham (1999), the Imbalance of Power hypothesis proposes that the evolutionary function of unprovoked lethal raiding by chimpanzees is intercommunity dominance over the opposing party which has the potential to increase the fitness of the aggressors through increased access to resources such as foraging areas and females. Two conditions were originally deemed necessary in order for coalitional killing to occur in chimpanzees; the first being hostility between two communities and the second being a significant power difference between the two groups such that one community can attack the other with relative ease or at a low cost (Wrangham 1999). Males that successfully take over a portion of a neighboring territory are thought to benefit in a number of possible ways although there is little consensus as to which potential benefit is the prime driver of coalitional killing. Early observations from Gombe and Mahale suggested that males gained access to additional mates by expanding their territory and enveloping the smaller core ranges of the neighboring females (Nishida et al. 1985, Goodall 1986). This model has been criticized for its emphasis on the male-only community structure as recent studies have shown that encroaching males can be aggressive to resident females who in turn contract their core areas away from changing boundaries and remain in their original communities even if some resident males are killed or disappear (Boesch and Boesch-Achermann 2000, Boesch et al. 2008, Williams et al. 2002, 2004). More recent data from Gombe (Williams et al. 2002) and Kibale (Watts et al. 2006) suggests that males benefit by expanding their territory which in turn allows resident females increased access to food. This “food defense” hypothesis is currently more favored although data is still scant. Finally, a third potential benefit has been posited based on research at Tai. Boesch et al. (2008) suggest that lethal attacks may be male signals aimed at attracting female immigrants and that small communities will attack larger ones and take large risks to improve their reproductive success. In general, studies suggest that the social, ecological, and demographic conditions of the various communities can be important determinants affecting the level and frequency of lethal aggression (Boesch and Boesch-Achermann 2000, Mitani et al. 2002, Williams et al 2004).

Bonobos

With relatively few long-term study sites when compared with chimpanzees, the majority of bonobo data collected on wild living groups comes from Wamba (i.e. Kano and Mulavwa 1984, Kano 1992, Hashimoto et al. 2008) and Lomako (i.e. Badrian and Badrian 1977, Badrian and Malenky 1984, White 1986, White 1992, White 1996, Hohmann et al. 1999) in the Equateur Province, both of which have been focusing on the behavior and ecology of bonobos since 1973. Research at both sites was suspended when political instability caused by coup d'états and civil wars within the DRC during the late 1990s forced the sites to temporarily close. Today, as some semblance of normalcy returns to the once war-ravaged nation, both the Lomako and Wamba sites have reopened and new long term research sites have been established at Salonga (Hohmann et al. 2006), Lac Tumba (Inogwabini et al. 2007), Lukuru (Thompson 2002) and Yalosidi (Coxe pers. comm.).

The results of these studies have shown that bonobos, like chimpanzees, are omnivores that feed primarily on fruit (White 1994, Wrangham et al. 1998) and display a fission-fusion social system in which party size and composition change (Badrian and Badrian 1984, White and Wrangham 1988). Unlike chimpanzees, however, bonobos travel in relatively more stable associations, called cliques (see Chapters III and IV) where coalitions of unrelated females can have power over males (White 1990, White and Lanjouw, 1992) and females remain sexually receptive throughout their menstrual cycle (Thompson-Handler et al. 1984). Consequently, the bonds between female and male bonobos involve frequent sexual behavior and result in fewer agonistic interactions than those seen with chimpanzees (White 1996). Once thought of as a uniquely human trait, the majority of bonobo mating includes relatively high frequencies of ventro-ventral mating (Badrian and Badrian 1984) although most male-female sex is dorso-ventral unless the male is smaller than the female (Thompson-Handler 1990). Additionally, the high levels of female bonding (White 1996) include a mutual homosexual behavior referred to as genito-genital (GG) rubbing (Badrian and Badrian 1984) also thought to reduce tensions and strengthen alliances (Kano 1992). Male bonobos are far less affiliative with each other (Kano 1992, White 1996, Hohmann and Fruth 2003) and may benefit from bonding with females by increased reproductive success via rank acquisition (Hohmann et al. 1999).

Ecologically, bonobos inhabit a diverse mixture of forest types with the majority of research sites found in mature polyspecific evergreen forests with intermittent use of swamp and secondary forests (Badrian and Malenky 1984, White 1989, Reinartz et al. 2008). The forest-savannah mosaic found at the site of Lukuru in the southern portion of their range may be an exception (Thompson 2002). In general, however, the forests in which bonobos live are dense and moist and do not experience drastic seasonal changes due to their proximity to the equator (White 1998). Consequently, food sources in the form of ripe fruit and terrestrial herbaceous vegetation are generally considered to be more abundant spatially and temporally when compared with chimpanzee sites (Malenky and Wrangham 1994, White 1998).

The ecological conditions which define bonobo habitat are largely believed to shape their unique social behaviors. Female bonobos do not have to compete over food to the same degree as female chimpanzees and can therefore forage in semi-stable groups (White and Burgman 1990) perhaps in order to cooperatively defend food patches (White 1986) or ally against infanticidal males (Wrangham 1986). Males, in turn are more likely to be found traveling independently, at times attempting, not always successfully, to lead groups of females to preferred food patches in hopes of gaining favor and perhaps mating opportunities (White and Waller, in prep.)

Still, little is quantitatively known about the ranging behavior of bonobos. Studies at Wamba have been the most illuminating in this regard. There have been six communities that ranged at least in part within the study area with the E group being the primary focus of research (Hashimoto et al. 1998). According to Kano (1992), as much of 60% of the E group home range is shared by other groups resulting in a core range and an overlap range. Since that time, the E group has split into two independent groups named E1 and E2 (Hashimoto et al. 1998). When researchers returned to the site after political instability in the DRC interrupted research, they found that three of the six Wamba communities had been wiped out through hunting (Furuichi personal communication) and males had transferred into the E1 group from neighboring areas. This occurrence suggests that, unlike chimpanzees, there is tolerance among males from differing communities. These findings combined with reportedly peaceful inter-group interactions (Idani 1991) hint at a reduced level of territoriality and an absence of lethal raiding in bonobos.

Although informative, the results from Wamba can be critiqued on two fronts. First, the majority of data on the ranging behavior at the site was collected when the animals were artificially provisioned with sugar cane and other foods at an artificial feeding site (Hashimoto et al. 1998).. This provisioning undoubtedly affected the location and composition of the social groups as well as the type and number of inter-group interactions. Furthermore, the site is located in close proximity to a plantation with several roads and other human disturbance affecting the landscape (Hashimoto et al. 2008). The effect of these disturbances may not be known. The purpose of this paper is to better understand the ranging behavior of bonobos with regard to territoriality in an unprovisioned population.

Methods

The data presented here was collected at the Ndeli field site (0.7994° N, 21.143° E) in the Lomako Forest Reserve, Equateur Province, Democratic Republic of the Congo (DRC). The 40 km² study area consists of several forest types, but is principally climax evergreen and polyspecific primary rain forest (75.2% of study site) with smaller areas of second-growth, slope, and swamp forest (White, 1992). While bonobos use all forest types, swamp and secondary areas are utilized less often (Hashimoto et al. 1998, Waller and White in prep). In an effort to determine the extent to which bonobos behave territorially, two predictions based on the Imbalance of Power hypothesis were conceived. First, if lethal raiding and territoriality play an important role in bonobo behavior, females (especially those with infants) and smaller parties should avoid border areas. Secondly, groups found in closer proximity to border areas should contain a higher percentage of males. Additionally, the ranging data presented here will be applied to two indices formulated to predict territoriality: the Mitani-Rodman defendability index (1979) and the Lowen- Dunbar fractional monitor rate index (1994). See Chapters II and III for complete descriptions of ranging methods.

Observations

Field studies of bonobo behavior began at Lomako in the 1970s and have focused primarily on two groups: the Bakumba and the Eyengo communities (Chapter III, Badrian and Malenky 1984, White 1998, Hohmann and Fruth 2002). Data presented here are from 112 bonobo sightings including 428 hours of focal animal observations recorded by White (1998) during field seasons conducted in October 1984 - July 1985, June - August 1991, and June - August 1995. For each sighting, data was recorded on total party size, as well as the number of males, females, sub-adults and infants within each party (Tables 5.1 and 5.2). Additionally, the location and movement of each sighting was described in relation to the well established transects.

Table 5.1. Party composition for the Eyengo and Bakumba groups during the project period.

Group	**Sightings**	**Males**	**Females**	**Sub-adults**	**Infants**
Bakumba	36	4	11	8	5
Eyengo	76	11	10	4	5
Combined	112	15	21	12	10

Table 5.2. Mean values of bonobo parties for the Eyengo and Bakumba communities at N'deli in Lomako. Note the Splinter group contained no sub-adults or infants.

Group	Party Size	Males	Females	Sub-adults	Infants
Bakumba	8.26	1.79	3.76	1.53	1.35
Eyengo	7.86	2.16	3.03	1.04	1.71

GIS Mapping and Analysis

During the summers of 2007 and 2009, a map of the trails and transects at Lomako was created using a Garmin handheld GPS (global positioning system). The map was then imported into ArcGIS, a geographic information system software program that has become instrumental in spatial analysis. Next, the sightings and their movements were plotted onto the map. Once the sightings were placed on the map, a 100% minimum convex polygon (White and Garrott 1990) was generated to estimate the home range and boundary of each group. Once the boundary was established, the parties' distance from the edge was measured and a series of regressions was calculated based on overall party size, number and percentage of males, number of females, number of sub-adults, and the number of infants.

Defendability Indices

While the relationships between social behavior, territoriality and ranging behaviors allows for specific predictions and can illuminate more clearly the socio-ecologic conditions that affect the degrees to which an animal may behave territorially, there have been few efforts to quantify territoriality based on the evolutionary economics of defendability first proposed by Brown (1964). The conspicuous and gregarious nature of most primates makes monkeys and apes particularly attractive for quantitative studies of this kind. Consequently, two indices have been created to predict whether a primate species will be territorial or not. The Mitani-Rodman defendability index, expressed as:

$$\mathrm{D} = d/(4A/\pi)$$

where D equals the ratio of the daily path length (d) to an area equal to the diameter of a circle which is equal to the area of the home range ($4A/\pi$), was created in an effort to predict whether or not an individual or group could maintain a territory based on recorded ranging data. Primate species that score > 1.0 could cross the diameter of their range at least once in a day theoretically rendering them more capable of defending their range while those that score < 1.0 had a daily path length that was shorter than the diameter of their home range were unable to defend their area. When tested using a two-way classification analysis of 33 species, a highly dependent relationship between territoriality and the Mitani-Rodman defendability index was observed (Mitani and Rodman 1979).

Criticized as oversimplified, the Mitani-Rodman index was more fully developed by Lowen and Dunbar (1994). Their new index, known as the Fractional Monitor Rate, is based on the kinetic theory of gasses and takes into account boundary length as well as detection distance while allowing the results to be extended to species that practice fission-fusion foraging behavior. It is expressed as:

$$M = N(sv/d^2)$$

where M equals defendability, N equals the number of independently moving parties, s equals the mean detection distance, v equals velocity (km/day) and d equals the diameter of a circle that is equal in area to home range. Species that score > .08 are considered territorial while those that score < .08 are not. This index has been more successful at predicting territoriality based on ranging behavior and factors relating to detection distance and number of independent foraging groups (Lowen and Dunbar 1994).

Results

Each clique’s range is relatively small in area (Table 5.3) when compared with those of chimpanzees. The Eyengo group had a home range of 2.94 km^2 and an average daily path length (DPL) of 2192.94 meters. There were no significant relationships between the number and percentage of males, females, sub-adults, or infants and the distance from their border. The Bakumba group had a home range of 2.80 km^2 and an average DPL of 1088.34 meters. The DPL of the Bakumba group may be low due to several long sightings at one particular fig tree which required little movement. There was no significant relationship between the number and percentage of males, females, or sub-adults and distance from the border of their range. There was a significant relationship between the number of infants and the border but it is the opposite of what one would expect according to the Imbalance of Power Hypothesis. In the Bakumba range, the number of infants, a proxy measurement for the number of females with infants, increased significantly closer to the border range (Table 5.4).

Table 5.3. Home Range and Daily Path Length estimates at Ndeli, Lomako

Clique	MCP Annual Home Range (km²)	Avg DPL (m)
Bakumba	2.80	1088.34
Eyengo	2.94	2192.44

Table 5.4. Results from the regressions of males, females, sub-adults, and infants on distance from the edge of home range. *significant

Clique	Males	Females	Sub-adults	Infants
Bakumba	p = .67 F = .19	p = .24 F =1.42	p = .29 F = 1.11	* p = .004 F = 9.66
Eyengo	p = .10 F = 2.75	p = .08 F = 3.23	p = .14 F = 2.24	p = .07 F = 3.63

When applying the ranging behavior and the daily path length to the two indices of territoriality, there are contrasting results (Table 5.5). Using the Mitani-Rodman defendability index, both the Splinter (1.18) and Eyengo (1.06) cliques are theoretically capable of territoriality while the Bakumba (0.60) group is not. When taking into consideration a 500 meter detection distance based on the distance in which vocalizations can be heard (Hohmann and Fruth 2002), all three groups were considered non-territorial according to the Lowen-Dunbar index.

Table 5.5. Results from the Mitani-Rodman and Lowen-Dunbar indices for territoriality (t = territorial, n.t. = non-territorial).

Group	MR	LD
Bakumba	.60 – n.t.	.022 – n.t.
Eyengo	1.06 - t	.013 – n.t.

Discussion

Competition is a central tenet of Darwin's theory of evolution and plays a major role in the manner in which animals move and place themselves within their environment. Chimpanzees appear to employ a despotic free distribution spatial arrangement both within and between communities resulting in differential access to resources, unequal reproductive success, and inter and intra-group aggression at times resulting in what can only be called inter-community warfare. The study of chimpanzees has and will continue to offer unique insight into our own warring behavior.

The bonobos at Ndeli in Lomako, however, do not show any of the components involved in lethal raiding. This is not to say that they are not territorial as there is evidence that suggests that groups may avoid overlap areas (Waller and White in prep.) but they certainly do not take territoriality to the same level as chimpanzees. In this regard one might say that the spatial arrangement of bonobos more closely resembles that of an ideal free distribution. There is little evidence of inter or intra-group dominance hierarchies and interactions are typically amicable (although see Kano 1992). In fact, the integration of the Splinter group into the Bakumba group, male transfer into a new group at Wamba (Hashimoto et al. 2008), and observations of peaceful inter-group encounters at Lomako (Badrian and Badrian 1984) and Wamba (Kano 1992) suggest that bonobos do not behave in the same way when it comes to territoriality. This is most likely due to the relatively more abundant distribution of food and the corresponding differences in social structure of bonobos.

Bonobos are not thought to live in “communities” as the term refers to chimpanzees. Rather, the results of this and other studies suggest that a new term may be warranted. The term “clique” may best apply as females make up the core of bonobo social groups, the groups are temporary both in space and time, and both males and immigrating females attempt to get closer to the core females. Regardless of what we call these groups, it is clear that there is a fundamental difference between the species that should not be forgotten when modeling the potential behavior of our hominin ancestors.

CHAPTER VI

MODELING EARLY HOMININ BEHAVIOR

Introduction

The dramatic increase in the number of fossil hominins recovered since the discovery of the Feldhofer Cave Neanderthal in the mid-nineteenth century has shed much light on the evolutionary past of humans (Tattersall 2000). Species such as *Sahelanthropus tchadensis* (Brunet et al. 2001), *Orrorin tugenensis* (Senut et al. 2001), *Ardipithecus kadabba* (Haile-Selassie 2001), and a growing number of australopiths (Johanson et al. 1978, White et al. 1994, Asfaw et al. 1999, Leakey et al. 2001, Berger et al. 2010) have helped construct an image of the first humans as essentially ape-like with the exception of cranial and post-cranial adaptations to bipedal locomotion. But how did these creatures behave? How was their society organized? Were they aggressive? Cooperative? This final chapter investigates the use of apes as models useful for elucidating the potential spectrum of behavior employed by our earliest ancestors. More specifically, I summarize the research presented in earlier chapters in an attempt to expand the spectrum of potential behavior. Before this can be done, however, it is important to understand the ecological conditions our early ancestors may have faced.

Early Hominins

Studies of anatomical structures to ascertain the functions of extinct species have been relatively successful. For example, tooth (Tobias 1998) and pelvic morphology (Ruff 2010) have been reliably associated with specific diets and locomotion, respectively. Yet any predictable relationship between a trait and behavior necessitates that the two are tightly linked. While there are broad and important relationships that can be seen at the higher taxonomic levels between morphology and behavior, such as the association of sexual dimorphism and male-male competition, when attempting to apply details of socioecological traits to bones, those links are far less cohesive (Clutton-Brock & Harvey 1977). Still, to more fully understand the factors affecting the evolution of hominins, some insight into the socioecological behavior of our ancestors is desirable. Much as morphological characteristics have been used to infer the functional adaptations of specific traits, the comparative approach to reconstructing the socioecology of past species extrapolates detailed social and ecological information from living taxa to make inferences on the behavior of extinct species (Dunbar 1992, Nunn and van Schaik 2001). As these extinct species did not exist solely in phylogenetic trees but rather, evolved in complex and dynamic ecosystems (Kingston 2007), a solid understanding of the environments in which they inhabited is necessary.

Despite distinct limitations, the ability of paleoanthropologists to better understand ancient ecosystems has been greatly expanded. Deep-sea oxygen and carbon isotope records have shown that, in general, Earth has generally been getting colder (-10°C) since the mid Miocene (Zachos et al. 2001). According to Potts (1998), faunal analysis pertaining to the relative abundance of different animal species as well as particular morphological characteristics (especially teeth) allows a general glimpse into the local habitats in which they are found. For example, fossils of the Hippopotamidae suggest the presence of water while an abundance of ungulate grazers suggests ample grasses.

Similarly, palynology, the study of ancient pollen, has been a useful component in reconstructing paleoenvironments (Thomas 2000). The emergence of C4 grasses (named for the photosynthetic pathway employed) in the late Miocene has been associated with the large-scale habitat changes that drove major faunal shifts in Africa (Segalen et al.

2006). In the tropics, the proportions of C3 and C4 plants are indicative of the structural characteristics of paleo-ecosystems with C4 dominated habitats reflecting savanna-type grasslands, C3 dominated ecosystems reflective of bushland, woodland, or forested conditions, and equal C3–C4 signals representing open woodland or heterogeneous forest-grassland environments (Kingston et al. 2002). Mammal fossils, including hominins, are excellent indicators of C4 as the dietary preferences of a particular animal are often "caught" within the enamel and can tell us much about the environments in which the animals were found (Cerling and Ehleringer 1998). This type of isotopic analysis has seen an overall shift from C3 to C4 on a global as well as local scale. Not coincidentally, C4 from grasses, sedges, or the animals that utilized these plants have been found in *Australopithecine* enamel and are thought to account for as much as 35% of their diets (Sponheimer et al. 2006).

The uses of these techniques have been applied to several sites where extinct hominins have been found. At Toros-Menalla in Chad where *Sahelanthropus tchadensis* was found, faunal fossils found include catfish (Otero et al. 2007), foxes (de Bonis et al. 2007), hippos and suids (Boisserie et al. 2006), aardvarks (Lehmann et al. 2006), giraffes (Likius et al. 2007), a variety of carnivores (Peigne et al. 2005) and primates, rodents and elephants Vignaud et al. 2002). The diversity of fossil animals suggests a variable habitat. Additionally, sedimentological evidence suggests that the area was near a lake, with pockets of gallery forest and savannah, but not far from a desert (Vignaud et al. 2002). Similar studies have been conducted at Laetoli (Leakey and Hay 1979, Reed 1997, Kingston and Harrison 2005), Olduvai (Cerling and Hay 1986, Bonnefille 1984, Bamford 2004, Liutkus et al. 2005), Turkana (Sept 1998, Schoeninger et al. 2003, Grine 2006), and the Middle Awash (WoldeGabriel et al. 2001, Haile-Selassie and

WoldeGabriel 2009, White et al. 2009, WoldeGabriel et al. 2009) within the East African Rift Valley, all showing a general trend towards drier, more variable habitats consisting of mixed open and closed ecosystems. The limitations to understanding past environments are formidable, however, especially after one considers the limitations involved in measuring existing ecosystems. Furthermore, to better understand their behavior, one needs to choose an extant model and record the detailed information about their external variables (rainfall, temperature, and habitat), morphology (body size, locomotion), and behavior (social system, diet, ranging). For a variety of reasons, chimpanzees have been considered the best model for reconstructing early human behavior (McGrew et al.1981, Zihlman 1996).

Apes as Models

According to Wrangham (1987), extant apes can be used to reconstruct hominin social behavior by (1) providing models for specific behavior, (2) comparing traits with humans to identify phylogenetically conservative traits, and (3) testing theories of social behavior in relationship to ecological conditions. Knowledge of the socioecological behaviors such as feeding strategies, ranging patterns, territoriality, group size, and social organization of extant species are vital for understanding all three of these methods (Nunn and van Schaik 2001). No primate species has been as well studied in the wild as chimpanzees.

Chimpanzees

Even before Linnaeus (1735) created his taxonomic classification system and lumped humans with monkeys and apes, the close relationship between humans and the other primates of the world was apparent to many. Socrates, Plato, Aristotle and Galen were all thought to comment to varying degrees on the similarities of monkeys to humans

(Corbey 2005) while the Roman poet Ennius (in Jocelyn 1972, pp. 990) wrote around 200 BC " How similar the monkey, the ugliest of beasts, is to ourselves." More recently, Charles Darwin wrote in the margins of a notebook that "He who understands baboons would do more toward metaphysics than Locke" meaning that a clear understanding of non-human primate behavior could be a powerful tool for better apprehending the forces that have crafted human behavior (in Cheney and Seyfarth 2007, pp. 1). Today fossil and genetic analysis has confirmed the relationship between human and non-human primates (i.e. Sarich and Wilson 1967a, 1967b, Chen and Li 2001) and the challenge issued by Darwin over 170 years ago has been taken up by modern day primatologists as researchers look to reconcile primate behavior observed in the field with the environmental and social drivers of those behaviors and apply the results of such inquiries to scenarios of hominin evolution and concepts of human nature.

Due to their genetic relatedness, tool-use abilities, social intelligence, behavioral diversity, adaptability, and wide geographic and ecologic range, chimpanzees have become the standard referential and analogous model for the behavior of the earliest hominin species (Wrangham 1987). Using mitochondrial DNA analysis, Ruvolo et al. (1994) showed that chimpanzees and humans shared a common ancestor as recently as 5-6 million years ago while other studies have shown that chimpanzees and humans differ genetically by approximately 1.24% while chimpanzees and gorillas differ by 1.63% (Chen and Li 2001). They are the most accomplished non-human tool users (McGrew 1992), form abstract representations of the behavior of others (Povinelli and Vonk, 2003), and display a range of diverse behaviors that are taught socially and have been construed as a chimpanzee culture (McGrew 1992). Although they are primarily frugivorous, their diet includes substantial amounts of flowers, terrestrial herbaceous vegetation (THV), termites and other insects, as well as vertebrate prey that is often hunted collectively (Goodall 1986, Stanford 1998, Pruetz 2006). Furthermore, chimpanzees are the most wide-ranging of the great apes inhabiting much of equatorial Africa from Tanzania in the east to in Senegal in the west.

Chimpanzees living in the Sahel region of southeastern Senegal may be particularly useful in developing our understanding of human evolution (McGrew et al., 1981). Tutin and colleagues (1983) describe the habitat used by chimpanzees at Mt. Assirik in Niokola-Koba National Park as hot, dry and open with less woody vegetation than any other site at which chimpanzees had been studied. Faunal analysis in southeastern Senegal is incomplete but it is believed that chimpanzees at Mt Assirik are sympatric with more potential predators than any other population studied (Hunt and McGrew 2002). Animals seen at Mt Assirik include lions, leopards, spotted hyenas, African hunting dogs, elephants, elands, antelope, hartebeest, buffalo, bushbucks, duiker, jackals, oribi (Hunt and McGrew 2002), genets, civets, mongeese, Guinea baboons, patas monkeys, vervets, and bushbabies. Mean daily high temperatures never fall below 30°C and mean daily low temperatures never fall below 20°C (Pruetz 2006). Humidity varies from near 100% in the rainy season to 50% during the dry season (Tutin et al. 1983). Rainfall data for the area comes primarily from Mt Assirik (Hunt and McGrew 2002). The year is divided into two distinct seasons, a wet one (May-October) and a dry one (November-April). During the wet season, the monthly mean rainfall is 155.6mm while during the dry season it is 3.5mm. Mean annual rainfall is 954mm even including an atypically wet year (1224mm). The area consists primarily of plateaus, valleys and hills (Pruetz 2006) with water runoff from the open plateaus creating narrow gallery forests (Hunt and McGrew 2002) that supply chimpanzees with essential food and shelter including caves and nesting trees (Pruetz 2007). Although C4 plants are locally abundant, chimpanzees consume fruit and other C3 resources (Sponheimer et al. 2006). Common woody tree species include *Zizyphus Mauritania* and *Combretum glutinosum* of the Sudanian zone and *Pterocarpus erinaceus* and *Piliostigma thonningii* of the Sudo-Guinean zone (Ba et al. 1997). Specific Mt Assirik habitats listed by Hunt and McGrew (2002) include grassland (27%), woodland (37%), plateau (28%), bamboo thickets (5%), and gallery forests (3%). Conditions at the Fongoli site 45km southeast of Mt Assirik may be even drier and hotter (Pruetz 2006) with a similar mosaic of ecosystems: grassland (45%), woodland (24%), plateau (16%), disturbed (8%), ecotone (5%), and gallery forest (2%) make up the habitat (Waller 2005). According to Van Couvering (1980), the earliest hominin most likely emerged from a similar mosaic of habitats that included open plains, woodland, and gallery forests. Chimpanzees at Fongoli have also been found to use caves in times of extreme heat (Pruetz 2007), hunt vertebrates with modified “spears” (Pruetz and Bertolani 2007), nest closer to the ground than other populations (Pruetz et al. 2008), and fish for termites (Bogart and Pruetz 2011).

All of these variables make the chimpanzees living there attractive models for reconstructing hominin behavior. Yet there are several limitations to this approach. First, the diversity with which chimpanzees behave between sites appears to be the result of ecological and cultural diversity making the identification of “typical” chimpanzee behavior difficult (Boesch 2002). For example, all chimpanzee communities consist of intense male hierarchies (de Waal 1982, Newton-Fisher 2002, Muller and Wrangham 2004), appear territorial (Goodall et al. 1979, Manson and Wrangham 1991, Mitani and Watts 2005), and cooperatively hunt (Stanford 1998b, Mitani and Watts 2001). Factors such as female gregariousness (Newton-Fisher 2006, Wakefield 2008, Reidel et al. 2011), tool use (McGrew 1992, Whiten et al. 2005), and grooming (Arnold and Whiten 2003), however, vary in substantial ways among populations. It remains to be seen whether the lethal raiding of neighbors is a species-wide characteristic. As studies continue to explore the ecological and cultural diversity within chimpanzees, I expect the known ways in which chimpanzees behave to further diversify. In general, we can assume that our earliest ancestors behaved in similarly diverse ways further stressing the importance of accurate paleoecological research in order to establish distinct links.

Secondly, there are several human behaviors that chimpanzee studies can not fully address. Trade, inter-group peace, tolerance, and cooperation are terms that are equally descriptive of our species as are war, territoriality, and aggression. As such, their evolutionary importance requires us to look elsewhere. Fortunately, there is a closely related primate species that may offer insight into peace and cooperation. The socioecological behavior of bonobos allows us to expand the spectrum of potential conditions that may have affected our evolutionary path.

Bonobos

While not as well known as chimpanzees, bonobos have been studied in the wild since the 1970s. Since that time, a wide variety of behaviors that differ significantly from chimpanzees have been identified. Most notable, bonobo females are more gregarious, forming alliances and maintaining bonds via a homosexual behavior known as genito-genital (G-G) rubbing. Furthermore, heterosexual sex is used as a tool for defusing tension (Woods 2010). Consequently, they have been called the “Hippy” or “Make Love not War” ape. But while the sexual behavior of bonobos makes for popular reading, it is really the availability of food that is most important in determining their socio-ecological behavior and adaptations.

Situated in the remote regions of the Congolese rainforest, the forests in which bonobos inhabit are rich in fruits, often occurring in large patches, and protein rich terrestrial herbaceous vegetation (THV). It is largely this environment that is thought responsible for the social organization of bonobos and is clearly implicated in ranging behavior.

As mentioned in Chapter I, the ranging behavior of a species can tell us much about their behavior. It is also a behavior that can be applied in a limited manner to extinct hominins. Using the proportion of early human fossils compared with other species measured in the Shungura Formation, Omo Ethiopia, Boaz (1979) estimated early hominin population density at between .0001 and 2.48 individuals per square kilometer, hinting at the potential for population pressures. Others have used the estimated weights of extinct species and applied the Hartestad and Bunnell (1979) equation. In an attempt to combine some of the factors affecting home range, this equation:

$$H = RP^{-1}$$

where H is home range, R is the metabolic energy requirements of an individual, and P is the productivity of the environment relative to trophic level, has revealed strong relationships between home range size and body weight for mammalian herbivores, omnivores, and carnivores (Martin 1981, McHenry 1994). Leonard and Robertson (1992, 1994) used the Hartestad and Bunnell equation to show that primates (including humans) with larger brains required more high-quality, nutrient dense diets which in turn should affect their ranging behavior. This suggests that changes in hominid brain sizes were likely accompanied by changes in movement and foraging patterns (Leonard and Robertson 2000). It has also been suggested that bipedalism evolved in just such a manner, granting upright walkers higher energy efficiency (Rodman and McHenry 1980) and greater heat dissipation (Wheeler 1991) as humans moved into more open environments. Yet as instructive as these studies have been, none of them have factored bonobo movements into their models.

The results of this dissertation confirm that the bonobos of Lomako live in one of the most food rich environments for any population of the genus *Pan*. Unlike the chimpanzees at places like Fongoli or Ngogo, bonobos do not have to go very far to get food. In fact, they may have the smallest annual home range of any *Pan* study site. They also show a negative correlation between party size and daily path length (Chapter III). While more research is needed, this may be because food patches are large enough so that even large groups can utilize them spending long periods of time in the same patch.

In Chapter IV, I showed that females are not as competitive over areas and can cooperatively defend food patches or coordinate defenses against strange males. For this reason, I introduced the term “cliques” to describe these associations of bonobos, in contrast to the term “community” applied to chimpanzee groups. The cohesive manner in which the females, especially those with infants, spend time and the various means by which males attempt to establish relationships with those cohesive females make the term “clique” seem appropriate. Regardless of what it is called, the social organization of bonobos at Lomako is structurally and functionally different from chimpanzees and needs to be considered when thinking about early hominin female behavior in food rich environments. The fact that bonobo females are responsible for the majority of hunting bouts at Lui Katol (Surbeck and Hohmann 2008) is further evidence in favor of reconsidering the role females played in our evolutionary past.

Finally, in Chapter V I reveal how bonobos do not appear to engage in territorial or lethal aggressive behavior in relationship to neighboring groups. It should probably not be too much of a surprise that groups and individuals that do not have to worry about finding food are not as aggressive as those that do. Furthermore, at some point in our evolution, non-related males began to tolerate one another. The lesson from Lomako suggests that this may have been accomplished at a time when local food conditions reduced the need for competition. Here, bonobo behavior can be insightful. As small ranging apes, it is possible that a high rate of repeated encounters increased the need for reciprocal cooperation. This may help explain how females form cliques in the absence of kin bonds and why there has not been a reported case of infanticide.

Summary

It is easy to think about bonobos and chimpanzees as representative of some good and evil side of humanity. The idea of patrolling chimpanzees attacking neighboring individuals elicits images of human violence. Likewise, the life of a female chimpanzee can be brutal due to male sexual coercion, especially infanticide. Bonobos live in very different environments. Their food rich environs conjure images of paradise, Eden. The mainstream reports of bonobo behavior would have one think that males and females lounge about all day copulating. Males are voluntarily helpless deferring to females in all cases because it simply is not worth the hassle. The truth, for both of these species, lies somewhere in between. Two observations, one from my masters thesis research at Fongoli, another from Lomako, highlight the problems with our perceptions.

On my last field day as a research assistant with the Fongoli Chimpanzee Project in southeastern Senegal, my research assistant and I heard the low calls of a couple of chimpanzees. It was dusk, a time of calm transition into darkness. By the time my research assistant and I arrived in the wooded thicket, two chimpanzees, a male and a female, were quietly termite fishing from the same mound. I watched transfixed as they took turns inserting their twigs into the termite home and extracted their dinner. It was hard not to think of a couple out on a date. They were calm and gentle. After about an hour, the sun had fully set. The chimpanzees slipped away into the dark, likely to have built their night nests next to each other.

Over five years later, I had traded the open, arid environment of the Sahel for the dense, dark, and humid rainforests of the DRC. Again, as I collected nest data, my research assistant and I heard the familiar calls of nearby apes. Rather than chimpanzees, however, this time the focus of my study was bonobos. After the tracking the calls, we came across another male and female party. Perched over 25 meters high in the tree, the female did not pay us much attention. The male on the other hand, was quick to act. He quickly descended, territorially "waa-ing" as he moved to a branch a mere 5 meters over our heads. As we slowly and steadily retreated, the male perhaps emboldened by our movements, began to follow us all the while throwing and shaking branches in a display of strength and stamina that would make a chimpanzee proud.

The anecdotes above outline the difficulty in using any one species as the model for our earliest ancestors. While debates are held over the importance of bonobos (Stanford 1998, Parish and deWaal 2000) or whether differences are a matter of degree or kind (Newton-Fisher 2006), the behavior of both species are instrumental to filling in the puzzle pieces of our evolutionary past.

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