## Dynamics of intergroup competition in two neighboring chimpanzee communities

### A DISSERTATION SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL OF THE UNIVERSITY OF MINNESOTA BY

Deus Cyprian Mjungu

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Anne E. Pusey, Adviser

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i

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ii

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# **DEDICATION**

To Monica and Asimwe

### THESIS INTRODUCTION

The large and rapidly increasing global human population poses severe threats to the survival of many species. Around the world, humans are clearing and degrading many forests and other natural habitat types at alarming rates and removing important resources critical for the survival of many wild animals. For species in which individuals defend a group territory, habitat destruction may increase intergroup aggression, intensify intergroup competition and threaten further the survival of individuals. Thus, for group territorial species, understanding the interplay between anthropogenic habitat destruction and intergroup competition is of paramount for their proper conservation.

In many group-territorial species where individuals defend or exclude neighbors in some parts of their area (Burt 1943), several studies have shown importance of group size during territorial encounters. In vervet monkeys, *Cercopithecus aethiops*, for example, larger groups were more likely to make incursions into the territories of smaller groups and displace smaller groups from resources (Isbell et al. 1990; Isbell 1991). A similar finding was also made in spotted hyenas, *Crocuta crocuta* (Henschel and Skinner 1991) and lions, *Panthera leo* (Mosser and Packer 2009), whereby larger groups were more likely to make incursions into the territory of neighbors. In Isbell and colleagues (1991) and in Mosser and Packer (2009) larger groups also occupied larger and better quality areas compared to those of smaller groups. Anthropogenic habitat destruction however may have unequal effects on neighboring groups (Pintea 2007). Groups that occupy habitat close to humans for example, are more likely to suffer more the negative effects of anthropogenic habitat destruction than those that occupy ranges further away from humans. Such groups, which occupy edge habitat, may lose part of its range due to the habitat destruction or some of its members may fall victims of human persecutions while ranging in human dominated matrices. Thus, unlike groups that occupy habitats further away from humans, groups that occupy edge habitats may have to face simultaneous pressure both from humans and from other groups for their survival and therefore, such groups are likely to fare poorly in intergroup competition.

Although group size has been found to predict the outcome of intergroup encounters in several species, in some cases, smaller groups with presumed lower fighting ability have been seen to emerge victorious (Cords 2002; Crofoot et al. 2008; Harris 2010). While factors such as asymmetries in valuing resources or possession of better fighters (Harris 2010) may assist a smaller group to win an intergroup contest against a larger group, how and when smaller groups are able to overcome numerical disadvantage is not precisely understood.

Intergroup competitions are costly and sometimes can lead to serious injuries or death to participants (Adams 1990; Wrangham 1999; Kitchen 2004). Because of the potential costs of intergroup encounters, selection should favor the ability of individuals to assess their odds of winning an encounter and refrain from costly contests that they are more likely to lose. In dyadic contests, game theoretical models predict that two factors, fighting ability and asymmetries in payoffs (consequences of losing or winning) should guide the decision of individuals whether to engage in a contest in the first place (Parker 1974; Maynard Smith 1976; Maynard Smith 1982) and whether to escalate once in the contest (Enquist and Leimar 1990).

Intergroup contests are more complex compared to dyadic contests due to the multiple interests of individuals. Nonetheless, studies of intergroup contests have shown that the underlying principles of dyadic contests also apply to intergroup contests. In several studies, individuals in groups have been shown to engage in contests according to their group fighting ability (Adams 1990; Grinnell et al. 1995; Wilson *et al.* 2001; Kitchen 2004) and asymmetries in payoffs (e.g. Crofoot et al. 2008). Thus, as in dyadic contests, the outcomes of intergroup contests appear to be context dependent and may vary from encounter to encounter depending both on the fighting ability and on asymmetries in the payoffs for groups.

Although intergroup interactions have attracted the attention of many researchers, in most studies observers have focused on understanding the function of intergroup encounters (Robinson 1988), the motivation of each sex in engaging in intergroup encounters (Cant et al. 2002), or the influence of group size on the outcome of encounters (Cheney 1987). Only a few studies have examined the effect of asymmetries in payoffs on the outcome of intergroup contests (e.g. Wich et al. 2002). Rarely have researchers considered the effect of fighting ability and asymmetries in payoffs on the outcome of intergroup contests simultaneously (but see Wilson et al. 2001; Crofoot et al. 2008; Harris 2010). Simultaneous consideration of how fighting ability and asymmetries of payoffs influence the outcome of intergroup encounter requires a large sample size in order to control for alternative hypotheses. However, a large sample size is hard to collect in natural settings, both because of the logistic difficulties of studying multiple groups and due to the rarity of intergroup encounters, which necessitates a long study period. Here I use data from the long-term study of two neighboring chimpanzee groups in Gombe National Park, Tanzania, which provides a uniquely long and detailed dataset on demography, ranging patterns and intergroup encounters. I explore how fighting ability and asymmetries in pay offs influence dynamics of intergroup competition. However, first, I examine how anthropogenic habitat destruction and intergroup interactions influenced the range size and population of a group that occupied range closed to humans.

Chimpanzees live in social groups known as communities (Goodall 1965) or unitgroups (Nishida 1968). Prior to the 1970s, people considered chimpanzees as peaceful creatures (Goodall 1965). However, a notion of chimpanzees being peaceful creatures was challenged by observations of Goodall and her colleagues (Goodall et al. 1979). Between 1972 and 1978, Goodall and her colleagues observed series of killings of Kahama chimpanzees by males of the Kasekela community that eventually led to extermination of Kahama community. Such observations prompted some people to considered chimpanzee as "war making" creatures and others to draw some similarities between chimpanzee's intergroup interaction and warfare in humans (Goodall 1986; Manson and Wrangham 1991; van Dennen 1995; Wrangham and Peterson 1996; Boesch and Boesch-Achermann 2000). However, other people considered observed intergroup interactions as artifact of artificial feeding of chimpanzees (Power 1991; Sussman 1997).

As more and more chimpanzee populations with no the history of artificial feeding are studied, it is becoming apparent that intergroup aggression is one of chimpanzee behavior repertories (reviewed in Wilson and Wrangham 2003) and that more killing of individuals of neighboring group appears to occur in communities with many males (Goodall 1986; Watts et al. 2006).

Although numerical advantage likewise is believed to confer competitive advantage to individuals of larger groups against neighbors of smaller groups, testing for this assumption in chimpanzees has not been possible. In most cases, human observers only know one community and the size and composition of rival communities is unknown (e.g. Wilson et al. 2001; Watts et al. 2006). In few sites where multiple communities are habituated to human observers, neighboring communities are existing in a very small sizes (e.g. Tai Forest, Herbinger et al. 2001; Boesch et al. 2008). My study focuses on two neighboring habituated communities, the larger Kasekela community and the smaller Mitumba community. Observations in the Kasekela community started in the 1960s by Jane Goodall (Goodall 1963) and centered mostly around the feeding station until in the 1973 when a full day focal follow of chimpanzees in the forest began. For the Mitumba community, habituation process began in the 1985 and by 1994; observers could identified most of the Mitumba chimpanzees. However, observers in the Mitumba community did not follow chimpanzees regularly in the forest until in the 2002 when I started working in the Mitumba community. I spent 18 months in the Mitumba community before I joined the University of Minnesota in the fall of 2003 where most of the Gombe chimpanzees' data are stored. Between 2004 and 2008, I spent 25 months in the Mitumba chimpanzee data.

Unlike the centrally located Kasekela community, most of the Mitumba community data are in Swahili. Being a Swahili speaker, I made an extensive effort in extracting intergroup information of the Mitumba community from Swahili notes of between 1985 and 2008 for my dissertation. In addition, I also extracted similar information from the Kasekela community for some years in which data exists in Swahili notes. Mitumba field maps used in my dissertation are digitized for the period between 1994 and 2007. I played an important role in digitizing and training students and volunteers to digitize most of the Mitumba field maps.

Х

My dissertation is organized into three chapters. In chapter 1, I provide a history of the Mitumba community, which occupy edge habitat and investigate the factors that caused changes in range size, group size and composition of the community over the past 25 years. In chapter 2, I examine whether the decrease in fighting ability of the Mitumba community led to a decrease in the community's range size and a change in range use. In my last chapter, I examine in detail the relative importance of fighting ability and location in the range on the outcome of territorial encounters.

### SPECIFIC CONTRIBUTIONS OF CO-AUTHORS

## **CHAPTER 1**

Effects of anthropogenic habitat destruction and intergroup aggressions on the home range size and population dynamics of the Mitumba Community of chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe National Park

Dr. Michael L. Wilson	supervised extraction of intergroup interaction data of the Kasekela chimpanzee community, discussed hypotheses as the paper developed, and reviewed the manuscript
Dr. Anne E. Pusey	supervised the long-term data used in my study, discussed hypotheses as the paper developed, and reviewed the manuscript

### **CHAPTER 2**

The influence of numerical asymmetries on range use in two neighboring groups of chimpanzees, *Pan troglodytes schweinfurthii*, in Gombe National Park, Tanzania

Dr. Michael L. Wilson	designed the vegetation study, discussed hypotheses as the paper developed, and reviewed the manuscript
Dr. Anne E. Pusey	supervised the long-term data used in my study, discussed hypotheses as the paper developed, and reviewed the manuscript
Dr. Lilian Pintea	assisted in quantifying habitat quality by using satellite imagery

## CHAPTER 3

The relative influence of the male party size and location in the range on the outcome of the territorial contests in Gombe chimpanzees

Dr. Michael L. Wilson supervised extraction of intergroup interaction data of the Kasekela chimpanzee community, discussed hypotheses as the paper developed, and reviewed the manuscript

# **TABLE OF CONTENTS**

ACKNOWLEDGEMENTS	i
DEDICATION	iv
THESIS INTRODUCTION	v
SPECIFIC CONTRIBUTIONS OF CO-AUTHORS	xii
TABLE OF CONTENTS	xiv
LIST OF TABLES	XV
LIST OF FIGURES	xvi
CHAPTER 1 : Effects of Anthropogenic Habitat Destruction and Inter-group Ag	gression
on the Home Range Size and Population Dynamics of the Mitumba Community	of
Chimpanzees (Pan troglodytes) in Gombe National Park, Tanzania	1
ABSTRACT	2
INTRODUCTION	4
METHODS	9
RESULTS	17
DISCUSSION	
CONCLUSIONS	
FIGURE CAPTIONS	
groups of chimpanzees, <i>Pan troglodytes schweinfurthii</i> , in Gombe National Park	, ,
Tanzania	
ABSTRACT	
METHODS	
RESULTS	106
	109
	118
FIGURE CAPTIONS	120
CHADTED 2 · The Polative Influence of Male Party Size and Location in the Po	ngo on
Outcome of Territorial Contests in Gombe Chimpanzees	1/6
ABSTRACT	
INTRODUCTION	1/0
METHODS	
RESULTS	155
DISCUSSION	101
CONCLUSION	160
FIGURE CAPTIONS	
KEFEKENLES	ראו

## LIST OF TABLES

## **CHAPTER 1**

Table 1.1. Names of chimpanzees identified in the Mitumba community between 1985      and 2009
Table 1.2. Annual estimates of the Mitumba chimpanzee community between 1985 and 2009. b.= birth; D = dead; I = immigrant; E = Emigrant; V = Visitor; F = Female; M = Male; U = unknown sex; AF = adult female; AM = adult male; SAM = adolescent male; $? =$ suspected to be in a community. unk = unknown
Table 1.3. Causes of death of the known Mitumba chimpanzees between 1985 and 2009. F = female; M = male; U = unknown sex
CHAPTER 2

Table 2.1. Sample size for each year used in estimating the annual range size using the	e
minimum convex polygon and kernel utilization distribution methods.	123
Table 2.2. Correlation values of the Mitumba chimpanzee community	124
Table 2.3. Correlation values of the Kasekela chimpanzee community	125

# **CHAPTER 3**

Table 3. 2. Output from logistic regression model based on observations of approaching rival community by the Mitumba community (N=61). Influence of male party size and contested area on the readiness of the Mitumba community to approach its rivals ...... 172

# LIST OF FIGURES

# **CHAPTER 1**

Figure 1.1. Location of sightings of chimpanzees outside the Park in the north	36
Figure 1.2. 1. 1973	36
Figure 1.2. 2. 1974	36
Figure 1.2. 3. 1975	36
Figure 1.2. 4. 1976	36
Figure 1.2. 5. 1977	36
Figure 1.2. 6. 1978	36
Figure 1.2. 7. 1979	36
Figure 1.2. 8. 1980.	36
Figure 1.2. 9. 1981	36
Figure 1.2. 10. 1982.	36
Figure 1.2. 11. 1983	36
Figure 1.2. 12. 1984	36
Figure 1.2. 13. 1985	36
Figure 1.2. 14. 1986	36
Figure 1.2. 15. 1987	37
Figure 1.2. 16. 1988.	37
Figure 1.2. 17. 1989	37
Figure 1.2. 18. 1990.	37

Figure 1.2. 19. 1991.	
Figure 1.2. 20. 1992.	
Figure 1.2. 21. 1993	

### **CHAPTER 2**

Figure 2.3. Annual variation in home range size of the Mitumba chimpanzee community between 1994 and 2007. Annual home range was estimated by using all 15-min focal follow points. KDU = Kernel utilization distribution and MCP = Minimum convex polygon. The correlation between annual area estimated by MCP and KDU was r = 0.9.

**Figure 2.7.** Annual use of the contested area by the Mitumba and Kasekela communities between 1994 and 2007. For the Kasekela community, values for percentage of use of

<b>Figure 2. 9.</b> Relationship between percentage use of the contested area and the relative number of males in the Mitumba chimpanzee community
<b>Figure 2. 10.</b> Relationship between percentage use of the contested area and the total community size of the Mitumba chimpanzees
<b>Figure 2. 11.</b> Relationship between percentage use of the contested area and the number of females in the Mitumba chimpanzee community
<b>Figure 2. 12.</b> Relationship between percentage use of the contested area and the absolute number of males in the Kasekela chimpanzee community
<b>Figure 2. 13.</b> Relationship between percentage use of the contested area and the relative number of males in the Kasekela chimpanzee community
<b>Figure 2. 14.</b> Relationship between percentage use of the contested area and the number of females in the Kasekela chimpanzee community
<b>Figure 2. 15.</b> Relationship between percentage use of the contested area and the community size of the Kasekela chimpanzees
<b>Figure 2. 16.</b> Activity center of the Mitumba chimpanzee community between 1994 and 2007

**Figure 2. 17.** Relationship between the distance the Mitumba chimpanzee community shifted away from the Kasekela chimpanzee community (relative to activity center of 1994) and the relative number of males of the Mitumba chimpanzee community. ..... 122

 Figure 2. 18.
 Summed values of basal areas of evergreen forest and thicket woodland for

 the Kavusinde and MitumbaValleys.
 122

## **CHAPTER 3**

Figure 3. 1. Distribution of type of the intergroup encounters in the contested and non-      contested area.    170
<b>Figure 3. 2.</b> Probability of counter-calling by the Mitumba chimpanzee community when parties contained different numbers of males
<b>Figure 3. 3</b> . Histogram of the latency of counter-calling by the Mitumba chimpanzee community
<b>Figure 3. 4.</b> Number of loud calls by the Mitumba chimpanzee community when parties contained at least one female
<b>Figure 3. 5.</b> Duration of escalation in intercommunity contest by the Mitumba chimpanzee community when the parties contained at least one female
<b>Figure 3. 6.</b> Histogram of the latency of approaching the rival chimpanzee community by the Mitumba chimpanzee community
<b>Figure 3. 7.</b> Histogram of the latency of moving away from the rival chimpanzee community by the Mitumba chimpanzee community

Figure 3. 8. Comparison of movements of the Mitumba and Kasekela chimpanzee
communities after an intercommunity encounter ( $N = 47$ )
<b>Figure 3. 9.</b> Locations of the Kasekela chimpanzee community during intercommunity encounters. MCP = Minimum convex polygon
<b>Figure 3. 10.</b> Distribution of the number of males of the Mitumba community over that of Kasekela community during an intergroup interaction

CHAPTER 1 : Effects of Anthropogenic Habitat Destruction and Inter-group Aggression on the Home Range Size and Population Dynamics of the Mitumba Community of Chimpanzees (*Pan troglodytes*) in Gombe National Park, Tanzania

### ABSTRACT

The large and rapidly increasing global human population poses severe threats to the survival of many species. Around the world, humans are clearing and degrading many forests and other natural habitat types at alarming rates and removing important resources critical for the survival of many wild animals. The situation may be exacerbated for species that compete aggressively for resources because habitat destruction also may increase inter-group aggression and further threaten the survival of many individuals. Here I examined how the range size and population size of the Mitumba community were influenced by anthropogenic habitat destruction outside the park and by chimpanzee intergroup aggression from the larger Kasekela community. Male chimpanzees engage aggressively in intergroup competition for access to resources that sometimes can lead to serious injuries or death of individuals. I found both anthropogenic habitat destruction and intergroup competition to have played a role in shaping the range size and population dynamics of the Mitumba chimpanzee community. The Mitumba chimpanzee community lost parts of its range both outside the park in north and inside the park in the south. The population size of the Mitumba chimpanzee community declined mainly due to habitat destruction, disease and inter- and intra-group aggression and the group composition became biased towards females. My findings confirm the suggestion that anthropogenic habitat destruction and intergroup aggression may have powerful effects on the range size and group size of neighboring chimpanzee communities. My study suggests that conservation efforts should consider both anthropogenic activities and potential effects of aggressive intergroup aggression when designing protected areas.

**Keywords:** Anthropogenic habitat destruction, intergroup competition, *Pan troglodytes schweinfurthii*, home range, Mitumba community

### **INTRODUCTION**

The large and still rapidly increasing global human population poses severe threats to the survival of many species, leading to extinctions on a scale seen perhaps only 5 times previously in earth's history (Diamond et al. 1989; Gaston 2005). Around the world, humans are clearing and degrading many forests and other natural habitat types at alarming rates (Ehrlich 1988; DeFries et al. 2002; Marsh 2003) and removing important resources critical for the survival of many wild animals (Cowlishaw and Dunbar 2000; Chapman and Peres 2001). The situation may be exacerbated for species that compete aggressively for resources because habitat destruction also may increase inter-group aggression and threatens further the survival of many individuals (Walsh et al. 2003). In order to be able to make realistic management plans and to evaluate conservation strategies, understanding how habitat destruction and intergroup aggression reduce range and population size of species is paramount. Here, I studied how pressure from humans and other chimpanzees affected the home range and population dynamics of the Mitumba community of chimpanzees in the Gombe National Park, Tanzania.

Chimpanzees – which are, along with bonobos (*Pan paniscus*), our closest living relatives – are facing grave threats to their existence (Goodall 1986; Pusey et al. 2008; Torres et al. 2010). Throughout their range, anthropogenic habitat destruction is occurring rapidly (Teleki 1989; Kormos et al. 2008), and as a result their home ranges, defined as the areas in which they range for food gathering, resting or caring of young

(Burt 1943), are frequently modified (Chapman and Chapman 1999; Pusey et al. 2008). Currently it is estimated that less than 300,000 chimpanzees remain in wild from over an estimated 1-2 million in the early 1900s (Oates 2006). All four sub-species of chimpanzees are classified as endangered (Torres et al. 2010).

Explosive human population growth and the consequent demands of land for agriculture and expansion of settlements are the principal factors that fuel anthropogenic habitat destruction (Balcomb et al. 2000; Harcourt and Parks 2003; McKee et al. 2004). Because of these demands, many forests and woodlands that harbor chimpanzees are cleared and/or degraded, and as a result these habitats become unsuitable for sustaining chimpanzees, as well as many other species (Worman and Chapman 2006; Campbell et al. 2008). In addition, encroachment by human populations threatens the suitability of many habitat areas that remain in a natural state. Such encroachment by human is making areas that were not easily accessible to humans become accessible and facilitate poaching, increase human-wildlife interactions (Skorupa and Johns 1987; Chapman and Peres 2001) as well as transmission of disease between wildlife and humans (Leendertz et al. 2004; Köndgen et al. 2008; Tan et al. 2008).

Although chimpanzees are capable of living in diverse habitats, ranging from arid savannah habitats to equatorial rainforests (e.g. Goodall 1986; Boesch and Boesch-Achermann 2000; Reynolds 2005), chimpanzees are most abundant in closed forests. In fragmented forests, chimpanzees persist at lower densities (Teleki 1989; Torres et al. 2010.

Chimpanzees live in permanent social groups known as communities (Goodall 1965) or unit-groups (Nishida 1968) of up to 150 individuals, within which individuals frequently join and split to form subgroups ("parties") of various size (Nishida 1990; Goodall 1986; Boesch and Boesch-Archemann 2000; Watts et al. 2006). In a community, males are more social than females and spend more time together. Females are less social, spending more of their time alone or with their dependent ones (Goodall 1986; but see Boesch and Boesch-Archemann 2000 and Lehman and Boesch 2005 for a contrasting view. In contrast to many primates, males stay in their natal community whereas females leave, mostly during adolescence (Pusey 1979, Pusey et al. 1997).

Generally, chimpanzee communities maintain or expand their home ranges through aggressive territorial competition with neighboring chimpanzee communities. Adult males (Goodall 1986, Wilson and Wrangham 2003, Williams et al. 2004), sometimes accompanied by females (Boesch and Boesch-Achermann 2000), play an important role in territorial competition by conducting boundary patrols and/or aggressively exchanging calls with opponent neighbors (Goodall 1986; Nishida 1990; Watts and Mitani 2001; Mitani and Watts 2005). Success in territorial competition between neighboring chimpanzee communities appears to depend mainly on the relative numbers of males in the communities, in which the side with more males stands a greater chance of winning disputes (Manson and Wrangham 1991; Wilson et al. 2001; Herbinger et al. 2001; Williams et al. 2004; Chapters 2 and 3).

As habitat destruction progresses, individuals that live at habitat edges may have to face simultaneous threats both from anthropogenic habitat loss and from other chimpanzees (Walsh et al. 2003). Because habitat loss and other associated anthropogenic factors (e.g. poaching and disease) may decrease population size in communities that occupy edge habitats, habitat destruction may compromise the ability of such communities to defend their home ranges (Pusey et al. 2008). As a result, such communities may lose their parts of their range due both to the habitat loss and encroachments of other chimpanzees.

Decreases in home range size can have negative fitness consequences for chimpanzees. Chimpanzees derive several nutritional and social benefits when their home range is large. For example, in Gombe National Park, the Kasekela chimpanzees weighed more and looked healthier (Pusey et al. 2005) and females in the community reproduced more rapidly (Williams et al. 2004) when they had larger ranges, presumably due to increased access to food. Pusey et al. (1997) found that higher-ranking females reproduced faster than lower ranking females and proposed that higher-ranking females to have better access to food than lower ranking females. Murray and colleagues (2007) found higher-ranking females to occupy higher quality areas and have better access to food (Murray et al. 2006). Thus, understanding how habitat destruction and intergroup aggression reduce home range size – and affect the population dynamics – of chimpanzees is essential for effective management and conservation of our closest relatives.

Obtaining a full understanding of the influence of these factors requires long-term data on habitat destruction, intercommunity interactions, ranging patterns and demography. The long-term study of chimpanzees at Gombe National Park, Tanzania, provides a uniquely long and detailed dataset for all these factors. To gain more insight into life at the edge for chimpanzees, I focused on the Mitumba chimpanzee community, which is located near the northern edge of Gombe National Park. Studies of chimpanzees in Gombe have continued for 50 years now (Goodall 1965; Goodall et al. 1979, Goodall 1986; Goodall 2000; Pusey et al. 2008). During this time, Gombe researchers have accumulated unparalleled information on ranging patterns and demography of individuals. In addition, data obtained through remote sensing provides an unusually detailed record of habitat change outside and inside the park for the past three decades (Pintea 2007). This study also takes advantage of ongoing studies of intercommunity aggression at Gombe (e.g. Wilson et al. 2004) which provide a detailed dataset on intercommunity aggression for the period between 1972 and 2007.

Studies of the Mitumba chimpanzee community provide an unusually detailed vantage point for examining how habitat destruction and intergroup aggression influence the home ranges and population dynamics of chimpanzees. At its northern edge, which corresponds today to the northern limit of Gombe National Park, the Mitumba community has been devastated by anthropogenic habitat destruction (Pintea 2007; Pusey et al. 2008). At its southern edge, inside the park, the Mitumba community range is adjacent to the Kasekela community. Both communities have been studied simultaneously for over 20 years, meaning that Gombe provides one of the few sites with detailed, long-term information on intercommunity interactions between neighboring habituated chimpanzee communities (Nishida et al. 1985; Goodall 1986; Boesch and Boesch-Achermann 2000).

Taking advantage of this unique dataset, I sought to examine the impact of human and intra-specific competition on the Mitumba chimpanzees. I focused on three main objectives: (1) to document factors that have influenced change in home range size of the Mitumba chimpanzee community, (2) to document change in population size of the community, and (3) to examine relationships between change in home range size and population dynamics.

#### **METHODS**

#### **Study Site and Communities**

Gombe National Park, Tanzania, covers approximately 35 km<sup>2</sup> (Pusey et al. 2007). The park extends from the eastern shore of Lake Tanganyika up the escarpment of

the western arm of the Great Rift Valley. On the north, east and south, the park is bounded by villages and cultivated land. Moving upwards to the east from the lakeshore, the elevation in the park rises gradually from 770-m above sea level to 1300-1600-m at the top of the Rift Valley escarpment (Pusey et al. 2008), and the vegetation grades from riverine forest in the valleys to woodland and grassland on the ridges.

Gombe National Park currently contains three communities of chimpanzees. The unhabituated Kalande community is in the south, the Kasekela community is in the center and the Mitumba community occupies the north, sandwiched between the Kasekela community and Mwamgongo village and cultivated land. Goodall began studying the Kasekela community in the 1960 (Goodall 1986). Observations of that community during much of the 1960s focused on behavior in and around a banana feeding station, but by 1973, researchers started to conduct a all-day focal follows of chimpanzees in the forest. This study focuses on the Mitumba community.

Efforts to habituate chimpanzees of the Mitumba community began in 1985 for the purposes of introducing tourism and releasing the previously habituated Kasekela community for research activities. However, the Mitumba community eventually proved poorly suited for tourism, both because of its small (and declining) population size and because of the steep terrain and dense vine tangles and thickets in this part of the park. Currently, tourism remains focused on the Kasekela community. The latest Gombe General Management plan (TANAPA, 2005) stipulated that tourism should be conducted only in the Kasekela community.

To accelerate habituation of the Mitumba community, as had earlier been done with the Kasekela community (Goodall 1986); field assistants provisioned the Mitumba chimpanzees with bananas. Initially, field assistants and expatriate volunteers searched for chimpanzees, and either placed bananas on the ground or left bananas hanging in trees for chimpanzees to take. However, this random system of searching and feeding chimpanzees with bananas whenever they were encountered did not work well. To improve the habituation process, in mid-1992, a permanent feeding station was established within the Mitumba chimpanzees' home range. The feeding station accelerated the identification of individuals and by 1994, field assistants could identify most of the chimpanzees in the community and it was possible to follow them outside the feeding station. Artificial feeding of chimpanzees was halted in mid-2000 because of concerns that feeding might be interfering with chimpanzee behaviors such as ranging, foraging or grouping. In addition, artificial feeding was thought to increase the likelihood of disease transmission between human and chimpanzees (Wallis and Lee 1999; Pusey et al. 2008).

### **Data Collection**

Since early 1994 (when most of the individuals in the Mitumba community became individually known), field assistants have followed essentially the same protocol for behavioral observations and data recording for the Mitumba community as has been used for the Kasekela chimpanzee community since 1973. A pair of field assistants has followed a focal individual in the forest, from the time the focal individual left its nest in the morning to the time s/he built another nest in the evening. During each focal follow, the field assistants recorded all individuals seen in addition to the focal individual, the sexual status of observed females, feeding information and intercommunity events on a checksheet, and they recorded any other behaviors of interest in narrative notes. Field assistants also recorded the location of the focal individual every 15 minutes on a field map (Goodall 1986). The narrative notes for the Mitumba chimpanzee community for the period between 1985 and 2009 were written in Swahili and have not been translated into English. Being a native Swahili speaker, I have been able to make extensive use of the notes.

#### **Estimating the Community Size and Composition**

To estimate the minimum and maximum annual community size of the Mitumba community between 1985 and 2009 (n = 25 years), I used two different techniques in recognition of different levels of knowledge of the community before and after 1994. Between 1985 and 1993 (n = 9 years), field assistants could identify only a subset of the chimpanzees in the community. From1994 to 2009 (n = 16 years), on the other hand,

field assistants could individually recognize most or all of chimpanzees in the community.

In the first period (1985-1993), I used chimpanzee sightings, evidence of births, deaths, migrations and unique morphological descriptions of individuals to reconstruct the demographic changes of the community. For example, by using sightings I documented the maximum party size observed each year and used this number as a minimum total size of the community for that year. In most cases, field assistants were able to count and give descriptions of all individuals present in the largest sighted party, and they stated clearly if any of the already-identified members of the community were missing in this party. Thus, in most years I was able to estimate the maximum community size by adding known individuals who were missing in the largest sighted party.

In addition to sightings, I also used evidence of death (e.g. "carcass of one adult male") and unique morphological descriptions (e.g. "one old male" and "one left missing toe adult female") in estimating community size in each particular year for which such evidence was available.

Moreover, since male chimpanzees normally do not transfer to another community (but see Sugiyama 1999), I assumed that any adult males seen in later years were present in previous years, back to their estimated birth date. For example, I used the carcass of an adult male that was found deep inside the home range of the Mitumba community in 1987 in estimating the community size in the previous two years (i.e. 1985 and 1986). Similarly, I used a description of an old male who was last seen in 1988 to extrapolate back his residency in the community. For females observed in the Mitumba community that otherwise had unknown residency, I took a conservative approach by assuming that a female immigrated to Mitumba one year before she gave a birth (as females usually only conceive after settling in their new community (Goodall 1986, Constable et al. 2001; Kahlenberg et al. 2008). I also extrapolated backwards the membership of each individual (male or female) in the Mitumba community based on what was/is known about his/her age and, for females also based on her parity.

In the second period (1994-2009), when virtually all chimpanzee individuals were know to the field assistants, I calculated the annual community size and composition of the Mitumba community by counting the number of individuals present, and their age-sex class, at the beginning of each year (e.g. 01 January 1994). I used the same age-sex classes as Goodall (1986). That is, 0-5 years old represented infants of both sexes, and 5-8 years old represented juveniles of both sexes. Females were categorized as adolescent from eight to 13 years, and males from eight to15, after which both sexes were considered mature. In consultation with other researchers, I estimated the age of individuals of the Mitumba community who were born before 1994 by comparing their morphological and behavioral characteristics with those of known-aged individuals in the Kasekela community. Most of the current Kasekela chimpanzees were born after 1960 and therefore their ages are well known.
#### **Estimating Home Range Size**

For the first period (1985-1993), thorough information from 15-minute focal follows locations of the Mitumba community was not yet available. I estimated the total range size of the Mitumba community between 1985 – 1993 by using information on sightings of chimpanzees outside the park by local people and by using recorded information on ranging and territorial activities in the neighboring chimpanzee community to the south, the Kasekela community.

#### Sightings of chimpanzees outside the park

In the 2002 while I was working at the Gombe Stream Research Center as a research assistant, Gabo Paulo (Mitumba field assistant) and I collected GPS locations and years in which local people reported seeing chimpanzees while chimpanzees were outside the northern boundary of the park. In addition, we also collected the opinions of local people about where they thought any chimpanzees that they saw had come from.

#### Information from study of the Kasekela community

To obtain information on the southern boundary, I used data from M. L. Wilson's long-term study of the socioecology of territorial behavior in chimpanzees (1973-2007).

Specifically, I extrapolated from the recorded territorial activities and the ranging data of the Kasekela community to estimate the southern limit of the Mitumba community range.

The recorded territorial data from the Kasekela chimpanzee community included locations where the Kasekela chimpanzees saw or physically encountered the Mitumba chimpanzee(s). The recorded territorial data also included boundary patrol information. Chimpanzees normally conduct boundary patrols in the overlapping areas of two neighboring communities, and during these patrols, the chimpanzees tend to be wary while traveling (Goodall et al. 1979). Boundary patrols suggest that a neighboring community is also using the area. I estimated the possible southern limit of the Mitumba community range based on the locations where the Mitumba and Kasekela communities physically or visually encountered one another, and where the Kasekela community frequently patrolled.

For the second period (1994-2007), annual ranges could be calculated more exactly because by early 1994, formal data collection provided improved information on the Mitumba community's ranging patterns. I used the digitized 15-minute location points from daily focal follows to estimate the annual range size for the Mitumba community between 1994 and 2007. For the Kasekela community, the 15-minute location points of daily focal follows for 1973-2007 are digitized. I used all these available data to calculate the ranging patterns of the Kasekela community for the period between 1973 and 2007. I could not use the 15-minute location points from daily focal follows for 2008 and 2009 for corresponding existing demographic information because in both communities the ranging data are yet to be digitized for those years.

I used the minimum convex polygon (MCP) method for estimating the range size of each community. In calculating a minimum convex polygon (MCP), a line is drawn to join all outermost points to form a convex polygon containing a defined percentage of all points (Worton 1987). However, the MCP method has some limitations (Worton 1989), especially its inability to distinguish between areas of high and low use. Furthermore, the MCP method tends to be sensitive to extreme, outlier points. Nonetheless, the MCP method is useful in that it encloses limits of home range boundaries better than other methods (e.g. Kernel utilization method), an important feature of interest in this study.

#### RESULTS

#### **Home Range Size**

Indirect evidence suggests that the Mitumba chimpanzees occupied a larger home range in the 1970s and 1980s than in the 1990s and 2000s. In the 1970s and 1980s, sightings of chimpanzees outside the park were relatively common (Figure 1.1). People reported seeing chimpanzees while the animals were feeding and occasionally when chimpanzees were hunting for bushpigs and bushbucks. In addition, people reported that in the 1970s and 1980s, they heard sounds of chimpanzees more frequently outside the park than they did by 2002. Some of the local people believed that chimpanzees they saw outside the park were from the park and that chimpanzees managed to utilize scattered forest remnants outside the park by travelling high in the hills, where the human population was less dense and thickets connected the park with other forest patches. One person described seeing chimpanzees moving back and forth between the park and Rubona area (Figure 1.1) and thought the chimpanzees were coming from the park. Another person told us that he encountered chimpanzees entering the park from outside while he was descending towards the village center. Field assistant Eslom Mpongo reported his opinion that in 1979, about 12 - 13 chimpanzees were denied access back to the Mitumba community after forest patches were cleared by refugees in the Rubona area, leaving chimpanzees frustrated outside the park (Eslom Mpongo, personal comm.).

In the 1990s and 2000s, reports of sightings of chimpanzees outside the park decreased (Figure 1.1). The decrease of sightings of chimpanzees outside the park was associated with rapid clearing of forest patches outside the park, which many people attributed to the activities of refugees from Burundi. However, some people believed that habitat destruction was fueled by local people to discourage chimpanzees from using areas outside the park, thereby thwarting possible expansion of the park (Gabo Paulo, pers. comm.). Additionally, at least some deforestation may have occurred as a result of the ban on seine net fishing in 1999 (Eslom Mpongo, personal comm.). Mpongo reported that after this ban, many people cut down trees in the former Mganza forest preserve to build fishing boats and canoes so that they could fish the deep lake. Mganza forest reserve is located far north of the Mitumba community (Figure 1.1) and up to 1998, chimpanzee sightings in Mganza forest reserve were common (Eslom Mpongo, personal comm.).

Inside the park, examination of territorial activities and ranging patterns of the Kasekela community between 1973 and 1993 (Figures 1.2.1-1.2.21) suggested that the Mitumba community used to occupy the area as far south as Linda Valley in the 1970s (Figure 1.3). Goodall et al. (1979) reported that the Kasekela chimpanzee community rarely used the area north of Linda Valley in the early 1970s. By the late 1980s, the Kasekela community had expanded, gaining some parts of the Mitumba community's southern range, as evidenced by the fact that there was a clear shift to the north in the area where visual and/or physical encounters between two communities occurred (see Figures 1.2.1-1.2.21).

In the 1970s and 1980s, the possible range of the Mitumba community enclosing all locations of chimpanzee sightings outside the park covered 13 km<sup>2</sup>. At least seven km<sup>2</sup> of this is within the area likely to have been used by Mitumba chimpanzees, with an additional 10 km<sup>2</sup> being possible Mitumba home range – if these sightings were not in fact sightings of chimpanzees inhabiting the Mganza forest. The polygon enclosing the likely range of Mitumba community within the park covered 12 km<sup>2</sup>. Thus, Mitumba

chimpanzees ranged over a total area that may have covered  $19 \text{ km}^2$  to  $25 \text{ km}^2$ , of which  $12 \text{ km}^2$  were within the park (see Figure 1.3).

In the 1990s, the majority of territorial activities of the Kasekela community occurred close to the core area of the Mitumba community (Figure 1.3) and the range size of the Mitumba community declined further, reaching its smallest size of 3.2 Km<sup>2</sup> in 1996 (Figure 1.4). In the period from 1994 to 2007, based on detailed information from the 15-minute location records from focal follows, the Kasekela community commonly ranged up to Mitumba Valley (Figures 1.5.1- 1.5.14). Investigation of the ranging patterns of the Mitumba chimpanzee community (Figures 1.5.1-1.5-14) revealed the community to range as far as south of the Rutanga Valley in early 1990s when the number of adult males in the community was five. However, in late 1990s, the community range shrank after its number of adult males was reduced to two. After this time, chimpanzees from Mitumba were rarely seen to travel south of Rutanga Stream (refer to Chapter 2).

# Mitumba chimpanzees

Between 1985 and 2009, a total of 63 chimpanzees have been identified in the Mitumba community (Table 1.1).

#### **Community Size**

The Mitumba community numbered at least at 30 individuals up to the middle of the 1980s (Table 1.2). The community declined from 30 individuals in 1985 to 24 individuals in 1989 (Figure 1.6). Between 1994 and 2009, the community size ranged between 21 and 25 individuals (Table 1.2).

# **Community composition**

The Mitumba community seems to have contained approximately six to eight adult males during the 1970s and 1980s. For example, on one occasion of a visual encounter between the Kasekela and Mitumba chimpanzees, Goodall et al. (1979) reported that the Mitumba party included six adult males. On another occasion, a party of five adult Kasekela males avoided a physical encounter with a Mitumba male. The Kasekela chimpanzees fled south, something that would be surprising unless the Kasekela males were outnumbered – a view supported by the observation that "Panthoots and waa's broke out from the Mitumba party, indicating that more males were present than the one who had been visible to the field assistants" (Goodall 1986). Field assistant Gabo Paulo (pers. comm.) likewise suggested that at least eight males lived in Mitumba around 1982. Paulo, who worked in Mitumba (1985-2007), was working in Kasekela at the time. Paulo and his colleague accidentally played back recorded sounds of the Kasekela chimpanzees while they were at upper Mitumba areas. Shortly afterwards, eight adult Mitumba males emerged charging towards them. The number of females in the Mitumba community during the 1970s and 1980s is hard to determine. One early source of evidence is from Paulo. On 26 October of 1988, Paulo gave a detailed description of individuals in a party he saw while chimpanzees were at the top of a tree branch. On that occasion, Paulo counted four adult females who had infants and five adult females without babies. Paulo reported that adult females that he recognized were not among the counted females. The community thus must have contained at least 11 adult females at the time, and may have contained more than 11 females in the 1970s when the community occupied a larger area.

By 1994, field assistants could identify most individuals in the community. Comparison of community composition between 1994 and 2009 shows that the number of males decreased from five in 1994 to two in 2009 (Figure 1.7). In contrast, the number of adult females has increased from seven in 1994 to eleven individuals in 2009 (Figure 1.7).

# **Causes of Decline in Community Size**

# Habitat Loss outside the Park

In the late 1960s and early 1970s, the Tanzanian government adopted a policy of Ujamaa ("Familyhood") in which the central government forcibly relocated people from scattered settlements into villages to engage collectively in agricultural activities (Kjekshus 1977; Ergas 1980). Because of this policy, the Mwamgongo village saw

influxes of people and the village expanded rapidly (Chepstow-Lusty et al. 1996). In addition, there were influxes of refugees to the Kigoma region during the early 1970s and 1990s from Burundi and the Democratic Republic of Congo, and some of these refugees settled around the park (Malkki 1992). Because of mass influxes of people, the Mitumba chimpanzee community possibly lost as much as 13 km<sup>2</sup> of its range outside the park by late 1990s. This loss was about half of the total area which the community may have occupied in the 1970s and 1980s. However, area outside the park might have contained scattered shrub-land (Pintea 2007) and thus may have been of only marginal use to chimpanzees at this time.

# Poaching

Two to three males may have been the victims of poaching by local people outside the park (Table 1.3). After adult male Sefa and adolescent male Tolkien disappeared from the park in 1998, villagers reported seeing two habituated chimpanzees roaming in the village land and asked the field assistants to go and take "their chimpanzees". However, while the field assistants were trying to decide how they could entice the chimpanzees back in the park, all reports of sightings ceased (Gabo Paulo, pers. comm.). It is possible – though of course, unconfirmed -- that local people killed them because they considered chimpanzees to pose a threat to their lives (Gabo Paulo, pers. comm.). A third male (Vidole Vitatu) disappeared from the park in 2001 and is suspected to have met the same fate as that of Sefa and Tolkien. Inside the park, indirect evidence suggests that some of the chimpanzees might have fallen victims to poaching (Pusey et al. 2008). For example, Greengrass (2000) found a male of the Kalande community dead and without hand and genital. In the Mitumba community, in 1996, Loretta was caught in a snare, after which a veterinarian amputated her hand. Furthermore, there have been several cases in which field assistants encountered local people with spears and dogs inside the park. Although chimpanzees are not the main target of poaching, sometimes clashes emerge between chimpanzees and dogs, and poachers avoid intervening on the side of dogs only after seeing researchers (pers. observation). In 2006, Edgar sustained serious injuries while fighting with three dogs. While Edgar's wounds recovered after about a month, this incident highlighted the dangers posed by poachers to chimpanzees.

#### Disease

At least eight individuals, including two adult males (Cusano and Gorbachev), three adult females (Baharia, Moeza and Rafiki) and three immature individuals (Merri, Roots and Shoots) died from an outbreak of respiratory disease that occurred in the Mitumba community in 1996 (Table 1.3). Disease may also have claimed additional individuals before the community was fully habituated. In 1987, there was an epidemic of respiratory disease in the Kasekela community, which killed eight individuals (Wallis and Lee 1999; Williams et al. 2008). At the same time, field assistants in the Mitumba community reported seeing one individual in the Mitumba community who was suffering similar symptoms to those of the Kasekela chimpanzees (Pusey et al. 2008), and around the same time of the epidemic disease in the Kasekela community, Mitumba field assistants recovered a carcass of an adult male. However, because most individuals of the Mitumba community were unknown in the late 1980s, we do not know whether additional individuals of the Mitumba community died in that epidemic.

#### Intercommunity aggression

In at least three cases, chimpanzees have been killed by intercommunity aggression (Table 1.3). In the first case, the Kasekela chimpanzees surprised an adult female Rafiki with her juvenile male (Rudi) and an infant (Rejea) while they were feeding at the top of a tree and killed Rejea after unsuccessful attempts by her mother to protect her (Wilson et al. 2004). In the second case an adolescent male (Rusambo) was apparently a victim (for details see Wilson et al. 2004). In the third case, Andromeda, the nine-month-old infant of Aphro was a casualty (Wrangham et al. 2006).

#### Intra-community aggression

Intra-community aggression has claimed lives of two and possibly three individuals (Table 1.3). In 1994, Rafiki's one-week old baby seems to have been killed by females from Mitumba (Pusey et al. 2008). A second case of intra-community aggression happened when two adult males teamed up against an injured alpha male Vincent and brutally killed him (Wilson et al. in prep.). After Vincent fell down from top of a tree and was injured, Vincent lost his alpha status and hid from other males. However, after months of hiding, one evening he was attracted by calls of successful hunting and joined the group. Unfortunately for Vincent, Rudi stopped feeding and started attacking him. After a few attempts by Edgar trying to protect Vincent failed, Edgar joined Rudi and they attacked Vincent viciously.

The last case of intra-community aggression involved Ebony, who was found dead with a broken neck and other wounds (Wilson et al. in prep.). Field assistants suspected Rudi to be the perpetrator of Ebony's death. Ebony was the young brother of Edgar, and field assistants proposed that Rudi killed Ebony out of fear that Ebony would eventually assist his brother Edgar when Edgar come to challenge Rudi for alpha position.

# **Other factors**

Nine known chimpanzees including Aqua, Kayoga, Lolita2, LORbaby1, Pom, PMbaby1, Trusha, TTbaby, Evababy1, have disappeared for unknown reasons (Table 1.3). While in some cases adolescent females are known to have emigrated (e.g. Trezia, Bahati and Vannila and more recently, Rumumba), in other cases death is known or suspected to be the cause of disappearance. In three cases, the individual's dead body was found, but the cause of death was unknown. In the first case, Aphro was seen carrying a carcass of her baby for about three weeks. In the second case Bima's baby died few days after it was born. In the third case, the carcass of adult female Rexona was found well decomposed (Table 1.3).

The death of Moeza's first baby also is worth mentioning. Moeza emigrated from Kasekela to Mitumba in 1983. In 1986, approximately one week after her infant was born, Moeza was seen with some wounds on her face and without the baby, but it remained unclear whether intercommunity aggression or intra-community aggression was the cause of the disappearance of her baby. Moeza's general behavior towards people did not change and left field assistants speculating that aggression from other chimpanzees (intra- or inter group aggression) might have been the cause of Moeza's wounds and death of her baby. This observation suggested that other Mitumba chimpanzees also might have fallen victims of inter- or intra-community aggression.

#### DISCUSSION

The data presented here indicate that the range of the Mitumba community has become considerably smaller in the last two decades. Based on observations of chimpanzees seen entering the park from outside in the 1980s and recent sightings of Sefa and Tolkien (1998) and Edgar and Konyagi (2006) in some of the northern areas, where sightings of chimpanzees often occurred in the 1970s and 1980s, the Mitumba chimpanzees possibly used an area of up to 13 Km<sup>2</sup> outside the park in the north in the 1970s and 1980s. However, in the last two decades they have largely ceased to range in these areas. The decrease in the home range size outside the park to the north was presumably mostly due to habitat loss outside the park while the decrease in home range size to the south within the park was due to the encroachment of the Kasekela community. Furthermore, the demographic records reveal that the Mitumba community contained at least 30 individuals through the 1980s, and it was probably as big or bigger in the 1970s, but in the 2000s it has numbered less than 25. Here, I discuss the causes of decrease in the home range and population size and give some recommendations for the conservation of the Mitumba chimpanzees and other chimpanzees in general.

#### **Decrease in Home Range Size**

The increase in human population size around the park has exerted enormous pressure on the habitat outside the park. As in many other places (e.g. in Balcomb et al. 2000; Chapman et al. 2005), forest patches outside the park slowly started to disappear as human population size increased, largely because of more demands on the land for agriculture and expansion of settlements. As a result, a long-standing stretch of a forest patches that connected the Mitumba community and the Mganza Forest Reserve was almost completely degraded by the late 1990s (Pintea 2007).

Although some agricultural activities such as tea or coffee plantations may be compatible with conservation of chimpanzees (Naughton-Treves et al. 1998), the rapid increase in human population around Gombe, fueled by natural fertility, Ujamaa policy and refugees, has caused cultivated land to expand at the expense of chimpanzee habitat. Expansion of cultivated land has removed important food items for chimpanzees such as *Uapaca kirkania* and *Aframomum* spp. and also has increased human-chimpanzee conflict (personal observation).

In addition to habitat loss outside the park, the size of the Mitumba community's range within the park also contracted substantially as the Kasekela community increased its range. This contraction of home range coincided with a decrease in the relative number of Mitumba community males. The number of adult males in a community has been shown to be important in territorial defense in several chimpanzee communities (Goodall et al. 1979; Nishida et al. 1985; Goodall 1986; Wilson et al. 2001; Wilson and Wrangham 2003; Watts et al. 2006; Chapter 2& 3). In the late 1980s, the Mitumba community lost at least two and possibly several males, and it was apparent that the range size of the Kasekela community expanded further north during that period. Similarly, detailed observations of ranging patterns and demography of the Mitumba community in late 1990s and 2000s showed a clear shift in range use by the Mitumba community when the number of males in the community was down to two adult males (Chapter 2).

These results show that intercommunity aggression can have a powerful effect on the range sizes of neighboring chimpanzee communities, especially for communities inhabiting edge habitats. In the case of the Mitumba community, it appears that once the habitat loss outside the park took a toll of some individuals, the resulting smaller community became ineffective in defending its range and in the end lost some parts of its home range inside the park to the larger Kasekela community.

A defended home range provides chimpanzees with several benefits, including supply of food, and there is likely to be a positive relationship between home range size and availability of food (Williams et al. 2004). Everything else being equal, as the home range size decreases, so does the amount of food. The amount of food is suggested to be one of the limiting factors of group size of chimpanzees (Goodall 1986; Boesch and Boesch-Achermann 2000); chimpanzees tend to form larger sub-groups when food availability is higher (Williams et al. 2004). With a decrease in home range size, forming of large sub-groups and spending more time together may be difficult because of likely increase in within-community feeding competition, making it hard for a smaller community to defend itself.

# **Community Composition**

In the period between 1994 and 2009, the composition of the Mitumba community has changed dramatically. The number of adult males has declined while the number of adult females has increased. The leading causes of dramatic change in the composition of the Mitumba community were disease, inter- and intra-specific aggression suspected poaching and habitat loss (see below). The decrease in the number of adult males in the Mitumba community compromised the ability of the community to defend itself from aggression from the much larger Kasekela community and contributed to the community's loss of its habitat.

# **Causes of Population Decline**

# Disease

Disease was the leading cause of known deaths in the Mitumba chimpanzees over the study period for this research. Along with poaching and habitat loss, disease is considered to be in general a major threat to the survival of chimpanzees (Boesch and Boesch-Achermann 2000; Nishida et al. 2003; Walsh et al. 2003; Leendertz et al. 2004; Pusey et al. 2007). Although the source of disease in most cases remains speculative, increasing human-chimpanzee interaction must be considered as a possible source for disease transmission to chimpanzees (Leendertz et al. 2004). The discovery that SIVcpz is pathogenic in chimpanzees (Keele *et al.* 2009) suggests that disease may have had, and may have in the future, more devastating effects than previously realized (Rudicell *et al.* in prep.).

# Poaching

Poaching is the suspected cause of death of three Mitumba chimpanzees during the time period of this research, although in none of these cases is the cause of death known for sure. Uncertainty should not suggest that Mitumba chimpanzees are completely safe from poaching (Pusey et al. 2008). Killing of chimpanzees by humans is known to occur at many other study sites (e.g. Boesch and Boesch-Acherman 2000; Williams et al. 2008; Wilson et al. 2007) and is considered to present a major threat to survival of chimpanzees (Oates 1996; Chapman et al. 1999; Chapman and Peres 2001; Pusey et al. 2008).

The killing of the two remaining adult males of the Mitumba community would signal the end of the community as a separate entity since adult females and their offspring would then likely die or be incorporated into the Kasekela community; young infants would possibly be killed (Nishada et al. 1985; Goodall 1986). However, if the two remaining adult males can survive and successfully defend the community over the years ahead, the maturation of two adolescent males and four juvenile males (Figure 1.7) can be expected eventually to restore the community's competitive ability, improving the community's chances of long-term survival.

# Habitat loss

Although chimpanzees are capable of utilizing fragmented forests (Naughton-Treves et al. 1998), they tend to occur in lower density in such habitats. Ranging in human-dominated landscape matrices has been shown to pose serious threats for the long-term survival of chimpanzees. For example, because of their predatory behavior, chimpanzees sometimes prey on human children (Wrangham et al. 2000; Hockings et al. 2009), leading sometimes to retaliation from people to prevent such attacks. Chimpanzees may also be killed by people for other reasons, including prevention of or retaliation for crop-raiding, or to obtain body parts (e.g., heart, penis, skull) traditionally attributed to have magical powers (Wilson et al. 2007; Goodall 1986; Williams et al. 2008). Habitat outside the Gombe National Park contains a mosaic of farmlands, abandoned farms and settlements. While the Mitumba chimpanzees sometimes exploited these areas in the past, the portion of the land suitable for chimpanzee habitat outside the park has decreased substantially, posing several risks to chimpanzees (see above).

# CONCLUSIONS

The home range and population size of the Mitumba chimpanzee community decreased between the 1970s and 2009, largely due to effects of anthropogenic habitat destruction and competition from other chimpanzees. Anthropogenic habitat destruction degraded habitat within the original range of the Mitumba community in the north. Simultaneously, the larger Kasekela chimpanzee community annexed some parts of south of the Mitumba range.

It is obvious that the Kasekela community has gained the upper hand in resource competition with the Mitumba community, and it seems very unlikely that the Mitumba community will regain its power soon. One factor that may help the Mitumba community in the future is the interconnected network of village forest reserves envisioned in recent village land-use plans (Greater Gombe Ecosystem 2007 report), if the network of forest reserves is implemented.

Areas outside the park in the north are currently a mosaic of farmlands, abandoned farms and scattered settlements, with few forest patches. This landscape poses a serious challenge for conserving the Mitumba chimpanzees in view of the fact that the Mitumba community currently has only a relatively small holding inside the park and exists at the park edge. However, with goodwill and all stakeholders working together for a common goal (local people, park management and researchers), it should be possible to help conserve the Mitumba chimpanzees by restoring and conserving the areas outside the park that are adjacent to area currently utilized by the Mitumba community and that the community once used. However, to achieve a proper conservation of the Mitumba chimpanzees, this will also depend on how local people are willing to cooperate on matters pertaining chimpanzees' conservation.

Local people can be good monitors of the chimpanzees once they are outside the park. However, for the local people to be willing to participate fully, the benefits of conservation for those people should extend down to individuals. This may be difficult to implement because of individual's perception of collective goods, whereby each one will want to over exploit resources held in common to his/her own benefits (Hardin 1968). However, if there are some incentives (Uphoff and Langhozl 1998), such as hiring temporary casual laborers by both Gombe National Park and Gombe Stream Research Center, local people may at least see the importance of chimpanzees indirectly and be willing to commit themselves for the betterment of everybody.

As is true in many chimpanzee populations (e.g., Bossou chimpanzees, Sugiyama 2003), Gombe chimpanzees are living in an island of suitable habitat. With settlements and farms to the north, east and south of the Gombe park boundaries, and the world's longest and second deepest lake to the west, the Gombe chimpanzee population is relatively isolated from other chimpanzee populations. The nearest remaining chimpanzee populations, in the hills of Zashe (5-6 km to the north of Gombe) and Kwitanga (15-20 km to the southeast of Gombe) have little formal protection on the ground. With the current pace of habitat destruction, it is only a matter of time before the Gombe population will be completely cut off from the chance of interacting with other populations. The resulting total genetic isolation of the Gombe population may eventually result in a concentration of deleterious alleles and increased inbreeding. Nonetheless, now that the risks posed by transmission of SIV (and other diseases) between populations are understood, thorough study of the SIV status of populations is called for before promoting connectivity among populations for allowing gene flow.

# **FIGURE CAPTIONS**

Figure 1.1. Location of sightings of chimpanzees outside the Park in the north.

Figure 1.2. 1. 1973.

Figure 1.2. 2. 1974.

Figure 1.2. 3. 1975.

Figure 1.2. 4. 1976.

Figure 1.2. 5. 1977.

Figure 1.2. 6. 1978.

Figure 1.2. 7. 1979.

Figure 1.2. 8. 1980.

Figure 1.2. 9. 1981.

Figure 1.2. 10. 1982.

Figure 1.2. 11. 1983.

Figure 1.2. 12. 1984.

Figure 1.2. 13. 1985.

Figure 1.2. 14. 1986.

Figure 1.2. 15. 1987.

Figure 1.2. 16. 1988.

Figure 1.2. 17. 1989.

Figure 1.2. 18. 1990.

Figure 1.2. 19. 1991.

Figure 1.2. 20. 1992.

Figure 1.2. 21. 1993.

**Figure 1.3.** The likely home range size of the Mitumba chimpanzee community inside and outside the park in the 1970s, 1980s and 1990s.

**Figure 1.4.** Annual home range size of the Mitumba chimpanzee community between 1994 and 2007 from 15-minute focal follow locations. The home range size was estimated by using 99% minimum convex polygon method.

Figure 1.5. 1. 1994.

Figure 1.5. 2. 1995.

Figure 1.5. 3. 1996.

Figure 1.5. 4. 1997.

Figure 1.5. 5. 1998.

Figure 1.5. 6. 1999.

Figure 1.5. 7. 2000.

Figure 1.5. 8. 2001.

Figure 1.5. 9. 2002.

Figure 1.5. 10. 2003.

Figure 1.5. 11. 2004.

Figure 1.5. 12. 2005.

Figure 1.5. 13. 2006.

Figure 1.5. 14. 2007.

**Figure 1.6.** Community size of the Mitumba chimpanzees between 1985 and 2009 estimated from known individuals and suspected ones.

**Figure 1.7.** Comparison of the composition of the Mitumba community between 1994 and 2009.

Name	ID	Gender	Date of birth
ANDROMEDA	AND	F	18-Nov-04
APBABY1	APB1	U	1-Jun-90
APHRO	AP	F	22-Jun-73
APPLE	APL	М	28-Mar-98
AQUA	AQ	F	4-Apr-92
ARIS	ARI	М	3-Aug-06
BAHARIA	BAR	F	2-Jul-61
BAHATI	BAH	F	2-Jul-88
BIMA	BIM	F	2-Jul-92
BIMBABY1	BIMB1	U	15-May-07
CALIFORNIA	CF	F	11-Aug-84
CUSANO	CUS	М	2-Jul-56
DARBEE	DB	F	28-Feb-84
EBONY	EBO	М	9-Nov-96
EDEN	EDE	F	13-Jun-04
EDGAR	EDG	М	2-Jul-89
EVA	EVA	F	2-Jul-65
EVABABY2	EVAB2	U	15-Jan-95
FANSI	FAN	М	2-Nov-01
FLOSSI	FS	F	8-Feb-85
FALIDI	FAL	F	5-Jul-09
FLOWER	FLW	F	7-May-05
FOREST	FOR	М	23-Jul-97
GORBACHEV	GOR	М	2-Jul-68
HILLARY	HY	F	2-Jul-81
KAYOGA	KAY	М	20-Jan-99
KOCHA	KOC	М	30-Apr-01
KOMOA	KOM	М	15-Jul-07
KONYAGI	KON	F	2-Jul-84
LAMBA	LAM	М	15-Dec-01
LOLITA2	LOL	F	9-Mar-96
LONDO	LON	М	30-Dec-00
LORBABY1	LORB1	F	5-Jan-95
LORETTA	LOR	F	2-Jul-80
LOSA	LOS	F	8-Jan-06
LUCY	LUC	F	2-Jul-86
LUTATA	LTT	М	28-Jan-07
MAYBEE	MAY	F	31-Mar-06
MERRI	MER	F	1-May-88
MGANI	MGA	F	2-Jul-91
MOEZA	MZ	F	20-Jan-69
MZBABY1	MZB1	U	5-Jun-86

**Table 1.1.** Names of chimpanzees identified in the Mitumba community between 1985 and 2009.

Name	ID	Gender	Date of birth
PMBABY1	PMB1	U	15-May-86
РОМ	PM	F	13-Jul-65
RAFBABY2	RAFB2	U	3-Jan-94
RAFIKI	RAF	F	2-Jul-71
REJEA	RJ	F	9-Nov-92
REXONA	REX	F	2-Jul-75
ROOTS	ROO	М	26-Mar-95
RUDI	RUD	М	2-Jul-86
RUGONGO	RUG	М	2-Jul-45
RUMUMBA	RUM	F	2-Jul-97
RUSAMBO	RUS	М	2-Jul-90
SEFA	SEF	М	2-Jul-60
SHOOTS	SHO	F	26-Mar-95
TITA	TT	F	12-Jan-84
TOLKIEN	TOL	М	2-Jul-85
TREZIA	TZ	F	2-Jul-78
TRUSHA	TRU	F	2-Jul-63
TTBABY1	TTB1	U	31-Mar-95
VANILLA	VAN	F	2-Jul-88
VIDOLE VITATU	VID	М	2-Jul-71
VINCENT	VIN	М	2-Jul-76

ID	Sex	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
AND	F																				b	Х	D			
AP	F				Ι	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
APB1	U						b	D																		
APL	М														b	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
AQ	F								b	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D					
ARI	М																						b	Х	Х	Х
BAH	F				b	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Е								
BAR	F	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D												
BIM	F								Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
BIMB1	U																							b	D	
CF	F										V															
CUS	М	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D												
DB	F														Ι	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
EBO	М												b	Х	Х	Х	Х	Х	Х	Х	Х	Х	D			
EDE	F																				b	Х	Х	Х	Х	Х
EDG	М					b	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
EVA	F	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
EVAB2	U											b	D													
FAN	М																	b	Х	Х	Х	Х	Х	Х	Х	Х
FLW	F																					b	Х	Х	Х	Х
FOR	М													b	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
FS	F												Ι	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
FAL	F																									b
GOR	М	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D												
HY	F												V													
KAY	М															b	Х	D								

Table 1.2. Annual estimates of the Mitumba chimpanzee community between 1985 and 2009. b.= birth; D = dead; I = immigrant; E = Emigrant; V = Visitor; F = Female; M = Male; U = unknown sex; AF = adult female; AM = adult male; SAM = adolescent male; ? = suspected to be in a community. unk = unknown

ID	Sex	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
KOC	М																	b	Х	Х	Х	Х	Х	Х	Х	Х
KOM	М																							b	Х	Х
KON	F										Ι	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
LAM	М																	b	Х	Х	Х	Х	Х	Х	Х	Х
LOL	F												b	Х	Х	Х	Х	D								
LON	М																b	Х	Х	Х	Х	Х	Х	Х	Х	Х
LOR	F								X?	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
LORS	F	Х	Х	Х	Х	Х	Х	Х	Х	Х	D															
LORB1	F											b	D													
LOS	F																						b	Х	Х	Х
LTT	М																							b	Х	Х
LUC	F																X?	Х	Х	Х	Х	Х	Х	Х	Х	Х
MAY	F																						b	Х	Х	Х
MER	F				b	Х	Х	Х	Х	Х	Х	Х	Х	D												
MGA	F																				Ι	Х	Х	Х	Х	Х
MZ	F	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D												
MZB1	U		b	D																						
PM	F	Х	Х	D																						
PMB1	U		b	D																						
RAF	F	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D												
RAFB2	U										b	D														
REX	F					X?	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D					
RJ	F								b	Х	D															
ROO	М											b	Х	D												
RUD	М		b	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х
RUG	М	Х	Х	Х	Х	D																				
RUM	F													b	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Е
RUS	М						b	Χ	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D						
SEF	М	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D										
SHO	F											b	Х	D												

ID	Sex	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
TOL	М	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D										
TRU	F	Х	Х	Х	Х	Х	Х	D																		
TT	F										Ι	Х	Х	Х	Е											
TTB1	U											b	D													
ΤZ	F	Х	Х	Х	Х	Х	Х	Е																		
VAN	F				Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Е				
VANM	F	Х	Х	Х	Х	Х	Х	Х	Х	D																
VID	М	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D							
VIN	М	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	D				
AF1	F	Х																								
AF1B1	U	Х																								
AF2	F	X?	X?	X?																						
AF3	F	X?	X?	X?	X?																					
AF4	F	X?	X?	X?	X?																					
AM1	М	Х	Х	Х	Х	D																				
AM2	М	Х	Х	Х	D																					
AM3	М	X?																								
SAM1	М	X?																								
SAM2	М	X?																								
SAM3	М	X?	X?	X?	X?	X?	X?																			
SAM4	М	X?	X?	X?	X?																					
SAM5	М	X?	X?	X?	X?																					
SAM6	М	X?	X?	X?	X?																					
SAM7	М	X?	X?	X?	X?																					
Minimun	n	20	18	18	18	19	21	21	21	23	21	23	25	20	22	21	22	22	23	22	20	22	20	23	25	25
Maximur	n	31	29	29	28	24	25	24	24	24	21	23	25	20	22	21	23	22	23	22	20	22	20	23	25	25

NameChimpIDSexAge status at deathCause of deathdeathMZbaby1MZB1UInfantAggression?1986AquaAQUFAdolescentDisappeared2003KayogaKAYMInfantDisappeared2000LoltaLOLFInfantDisappeared1995TrushaTRUFAdultDisappeared1995TrushaTRUFAdultDisappeared1995Evababy1EVAB1UInfantDisappeared1995BahariaBARFAdultDisease1996CusanoCUSMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFAdultDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantDisease1996RejeaRJFAdultDisease1996RejeaRJFInfantDisease1996RejeaRJFInfantAggression2002RejeaRJFInfantAggression2002RejeaRJFInfantAggression2006RejeaRAF2UInfantAggression2002RejeaRAF2UInfantAggression2004						Year of
MZbaby1     MZB1     U     Infant     Aggression?     1986       Aqua     AQU     F     Adolescent     Disappeared     2003       Kayoga     KAY     M     Infant     Disappeared     2000       Lolita     LOL     F     Infant     Disappeared     2000       LORB 1     LOR1     F     Infant     Disappeared     1995       Trusha     TRU     F     Adult     Disappeared     1995       Evababy1     EVAB1     U     Infant     Disappeared     1995       Evababy1     EVAB1     U     Infant     Disappeared     1995       Baharia     BAR     F     Adult     Disease     1996       Cusano     CUS     M     Adult     Disease     1996       Gorbachev     GOR     M     Adult     Disease     1996       Merri     MER     F     Adult     Disease     1996       Roots     ROO     M     Infant     Disease     1996       Shoots     SHO     F     Infant     Disease     1996       Rusambo     RUS     M     Adolescent     Aggression     2002       RAFB2     RAF2     U     Infant     Aggression	Name ChimpID		Sex	Age status at death	Cause of death	death
AquaAQUFAdolescentDisappeared2003KayogaKAYMInfantDisappeared2000LoltaLOLFInfantDisappeared1995TrushaTRUFAdultDisappeared1995TrushaTRUFAdultDisappeared1995Evababy1TTB1UInfantDisappeared1995Evababy1EVAB1UInfantDisappeared1996GorbachevGORMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MoezaMZFAdultDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantDisease1996RejeaRJFInfantDisease1996AndromedaANDFInfantAggression2002RejeaRJFInfantAggression2002RejeaRJFInfantAggression2005RAFB2RAF2UInfantAggression2005Killed by localMAdultpeople1994VincentVINMAdultpeople1998VidoleMAdultpeople?2001VitatuVID <td>MZbaby1</td> <td>MZB1</td> <td>U</td> <td>Infant</td> <td>Aggression?</td> <td>1986</td>	MZbaby1	MZB1	U	Infant	Aggression?	1986
KayogaKAYMInfantDisappeared2000LolitaLOLFInfantDisappeared2000LORB 1LOR1FInfantDisappeared1995TrushaTRUFAdultDisappeared1995Evababy1TTB1UInfantDisappeared1995BahariaBARFAdultDisease1996CusanoCUSMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MoezaMZFAdultDisease1996RootsROOMInfantDisease1996RootsROOMInfantDisease1996RootsROOMInfantDisease1996AndromedaANDFInfantDisease1996RejeaRJFInfantDisease1996RejeaRJFInfantAggression2002RAFB2RAF2UInfantAggression2002RAFB2RAF2UInfantAggression2004VincentVINMAdultaggression2004ViatuVIDMAdultpeople2001VideleMAdultpeople2001VideleFAdultDisease1998VideleFAdultpeople	Aqua	AQU	F	Adolescent	Disappeared	2003
LolitaLOLFInfantDisappeared2000LOR 1LOR1FInfantDisappeared1995TrushaTRUFAdultDisappeared1995Trbaby1TTB1UInfantDisappeared1995Evababy1EVAB1UInfantDisappeared1995BahariaBARFAdultDisease1996CusanoCUSMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MeezaMZFAdultDisease1996RootsROOMInfantDisease1996ShotsSHOFInfantDisease1996ShotsSHOFInfantDisease1996RejeaRJFInfantDisease1996RejeaRJFInfantAggression2002RejeaRJFInfantAggression2002RejeaRJFInfantAggression2002RAFB2RAF2UInfantAggression2002RAFB2RAF2UInfantAggression2004VincentVINMAdultaggression2004VitatuVIDMAdultpeople2001VitatuVIDMAdultpeople2001VitatuVID	Kayoga	KAY	М	Infant	Disappeared	2000
LORB 1LOR1FInfantDisappeared1995TrushaTRUFAdultDisappeared1995Trushy1TTB1UInfantDisappeared1995Evababy1EVAB1UInfantDisappeared1995Evababy1EVAB1UInfantDisappeared1995BahariaBARFAdultDisease1996CusanoCUSMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MoezaMZFAdultDisease1996RafikiRAFFAdultDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantAggression2006RejeaRJFInfantAggression2002RusamboRUSMAdolescentAggression2002RAFB2RAF2UInfantAggression2004VincentVINMAdultaggression2004ViatuVIDMAdultpeople2001VidoleViatuVIDMAdultpeople2001RugongoRUGMAdultOld age1988Bimbaby1BIMB1UInfantUnknown2007 </td <td>Lolita</td> <td>LOL</td> <td>F</td> <td>Infant</td> <td>Disappeared</td> <td>2000</td>	Lolita	LOL	F	Infant	Disappeared	2000
TrushaTRUFAdultDisappeared1990TTbaby1TTB1UInfantDisappeared1995Evababy1EVAB1UInfantDisappeared1995BahariaBARFAdultDisease1996GusanoCUSMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MezaMZFAdultDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996ShootsSHOFInfantDisease1996RejeaRJFInfantAggression2006RusamboRUSMAdolescentAggression2002RAFB2RAF2UInfantAggression2005RAFB2RAF2UInfantaggression2005RAFB2RAF2UInfantaggression2004VincentVINMAdultaggression2004ViatuVIDMAdultpeople1998VidoleKilled by local2001TokienTOLMAdultpeople2001RugongoRUGMAdultOld age1988Bimbaby1BIMB1UInfantUnknown2007RexonaREX	LORB 1	LOR1	F	Infant	Disappeared	1995
TTbaby1TTB1UInfantDisappeared1995Evababy1EVAB1UInfantDisappeared1995BahariaBARFAdultDisease1996CusanoCUSMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MoezaMZFAdultDisease1996RootsROOMInfantDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantDisease1996RejeaRJFInfantAggression2006RejeaRJFInfantAggression2002EbonyEBOMAdolescentAggression2002RAFB2RAF2UInfantAggression2005VincentVINMAdultaggression2004VidoleVIDMAdultpeople1998VidoleVIDMAdultpeople2001TolkienTOLMAdultDicauTolkiedTolkienTOLMAdultOld age1988Bimbaby1BiMB1UInfantUnknown2007RexonaREXFAdultUnknown2007	Trusha	TRU	F	Adult	Disappeared	1990
Evababy1EVAB1UInfantDisappeared1995BahariaBARFAdultDisease1996CusanoCUSMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MoezaMZFAdultDisease1996RotsROOMInfantDisease1996RotsROOMInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantDisease1996AndromedaANDFInfantAggression2006RejeaRJFInfantAggression2002EbonyEBOMJuvenileAggression2005RAFB2RAF2UInfantAggression2004VincentVINMAdultaggression2004ViatuVIDMAdultpeople2001VidoleKilled by local2001VitatuVIDMAdultDieage1988Bimbaby1BIMB1UInfantUnknown2007RexonaREXFAdultUnknown2007RexonaREXFAdultUnknown2007	TTbaby1	TTB1	U	Infant	Disappeared	1995
BahariaBARFAdultDisease1996CusanoCUSMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MoezaMZFAdultDisease1996RafikiRAFFAdultDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantAggression2006RejeaRJFInfantAggression1993RusamboRUSMAdolescentAggression2002EbonyEBOMJuvenileAggression2005RAFB2RAF2UInfantAggression2004VincentVINMAdultpeople1998VidoleKilled by local2004VitatuVIDMAdultpeople2001RugongoRUGKilled by local2001RugongoRUGMAdultOld age1988Bimbaby1BIMB1UInfantUnknown2007RexonaREXFAdultUnknown2007RexonaREXFAdultUnknown2007	Evababy1	EVAB1	U	Infant	Disappeared	1995
CusanoCUSMAdultDisease1996GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MoezaMZFAdultDisease1996RafikiRAFFAdultDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantDisease1996AndromedaANDFInfantAggression2006RejeaRJFInfantAggression2002RusamboRUSMAdolescentAggression2002BonyEBOMJuvenileAggression2005RAFB2RAF2UInfantAggression1994VincentVINMAdultaggression2004VidoleKilled by localKilled by local1998VidoleMAdultpeople2001RugongoRUGMAdultOld age1988Bimbaby1BIMB1UInfantUnknown2007RexonaREXFAdultUnknown2007RexonaREXFAdultUnknown2007	Baharia	BAR	F	Adult	Disease	1996
GorbachevGORMAdultDisease1996MerriMERFJuvenileDisease1996MoezaMZFAdultDisease1996RafikiRAFFAdultDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantDisease1996AndromedaANDFInfantAggression2006RejeaRJFInfantAggression2002RusamboRUSMAdolescentAggression2002BonyEBOMJuvenileAggression2005RAFB2RAF2UInfantAggression1994VincentVINMAdultpeople1998VidoleKilled by localKilled by local2004VidoleMAdultpeople2001TolkienTOLMAdultOld age1988Bimbaby1BIMB1UInfantUnknown2007RexonaREXFAdultUnknown2007RexonaREXFAdultUnknown2007	Cusano	CUS	М	Adult	Disease	1996
MerriMERFJuvenileDisease1996MoezaMZFAdultDisease1996RafikiRAFFAdultDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantDisease1996AndromedaANDFInfantAggression2006RejeaRJFInfantAggression2002RusamboRUSMAdolescentAggression2002EbonyEBOMJuvenileAggression2005RAFB2RAF2UInfantAggression2005VincentVINMAdultaggression2004VincentVINMAdultpeople1998VidoleKilled by localKilled by local2001VitatuVIDMAdultOld age1988Bimbaby1BIMB1UInfantUnknown2007RexonaREXFAdultUnknown2002	Gorbachev	GOR	М	Adult	Disease	1996
MoezaMZFAdultDisease1996RafikiRAFFAdultDisease1996RootsROOMInfantDisease1996ShootsSHOFInfantDisease1996ShootsSHOFInfantDisease1996AndromedaANDFInfantAggression2006RejeaRJFInfantAggression1993RusamboRUSMAdolescentAggression2002EbonyEBOMJuvenileAggression2005RAFB2RAF2UInfantAggression2005VincentVINMAdultaggression2004VincentVINMAdultpeople1998VidoleVidoleKilled by localF1998VidoleMAdultpeople2001TolkienTOLMAdolescentpeople?2001RugongoRUGMAdultOld age1988Bimbaby1BIMB1UInfantUnknown2002RexonaREXFAdultUnknown2002	Merri	MER	F	Juvenile	Disease	1996
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Table 1.3. Causes of death of the known Mitumba chimpanzees between 1985 and 2009. F = female; M = male; U = unknown sex.



Figure 1.1. Location of sightings of chimpanzees outside the Park in the north.

The annual range size of the Kasekela chimpanzee community between 1973 and 1993 (Figure 1.2.1-1.2.21) as estimated by using the minimum convex polygon method. Polygons from the smallest to the largest indicate the limit of 75%, 99% and 100% respectively.



Figure 1.2. 1. 1973



Figure 1.2. 2. 1974.



Figure 1.2. 3. 1975.



Figure 1.2. 4. 1976.



Figure 1.2. 5. 1977.


Figure 1.2. 6. 1978.



Figure 1.2. 7. 1979.



Figure 1.2. 8. 1980.



Figure 1.2. 9. 1981.



Figure 1.2. 10. 1982.



Figure 1.2. 11. 1983.



Figure 1.2. 12. 1984.



Figure 1.2. 13. 1985.



Figure 1.2. 14. 1986.



Figure 1.2. 15. 1987.



Figure 1.2. 16. 1988.



Figure 1.2. 17. 1989.



Figure 1.2. 18. 1990.



Figure 1.2. 19. 1991.



Figure 1.2. 20. 1992.



Figure 1.2. 21. 1993.



**Figure 1.3.** The likely home range size of the Mitumba chimpanzee community inside and outside the park in the 1970s, 1980s and 1990s.



**Figure 1.4.** Annual home range size of the Mitumba chimpanzee community between 1994 and 2007 from 15-minute focal follow locations. The home range size was estimated by using 99% minimum convex polygon method.

The annual range size of the Mitumba chimpanzee community in the north and the Kasekela chimpanzee community in the south for the period between 1994 and 2007 (Figure 1.5.1 - 14) as estimated by using the minimum convex polygon method. Polygons from the smallest to the largest indicate the limit of 75%, 99% and 100% respectively.



Figure 1.5. 1. 1994.



Figure 1.5. 2. 1995.



Figure 1.5. 3. 1996.





Figure 1.5.5. 1998.



Figure 1.5. 6. 1999.



Figure 1.5. 7. 2000.



Figure 1.5. 8. 2001.



Figure 1.5. 9. 2002.



Figure 1.5. 10. 2003.



Figure 1.5. 11. 2004.



Figure 1.5. 12. 2005.



Figure 1.5. 13. 2006.



Figure 1.5. 14. 2007.



**Figure 1.6.** Community size of the Mitumba chimpanzees between 1985 and 2009 estimated from known individuals and suspected ones.



**Figure 1.7.** Comparison of the composition of the Mitumba community between 1994 and 2009.

CHAPTER 2 : The influence of numerical asymmetries on range use in two neighboring groups of chimpanzees, *Pan troglodytes schweinfurthii*, in Gombe National Park, Tanzania

## ABSTRACT

In many group living species, groups compete for access to limited resources such as food or mates. In several studies, a larger group size has been seen to offer a competitive advantage and improve access for individuals of larger groups to resources by displacing individuals of smaller groups from the contested resources or by occupying bigger and higher quality range than that of smaller groups. In chimpanzees, larger groups with many males are likewise assumed to occupy bigger ranges and have better access to resources over neighboring groups with fewer males. However, until recently testing of this assumption has not been possible because in most studies observers have focused on only one group. Here I focused on two neighboring chimpanzees groups and examined whether numerical asymmetries influenced their range use. I found that the range size of the smaller group did not decrease as the numerical asymmetry between groups increased. This was contrary to what is expected from the relationship between range size and competitive ability. However, detailed analysis of patterns of range use showed numerical advantage to be an important factor in influencing how each group used the area of range overlap (defined here as the "contested area"). As the competitive ability of the smaller group got weaker, the smaller group decreased its use of the area contested by the two groups, and it shifted its center of activity away from the larger group. Thus, this study confirmed the importance of numerical advantage in intergroup competition in chimpanzees. The study also points out the need for detailed investigation of patterns of range use, rather than simply measuring overall change in range size, in efforts to understand the influence of numerical asymmetries in relations between groups.
Keywords: chimpanzee, numerical asymmetries, intergroup competition, Pan

troglodytes schweinfurthii, contested area

### **INTRODUCTION**

In many group-living animals, groups compete for access to resources. For individuals of these groups, access to resources will therefore depend on how effective a group is at competing for resources with other groups. In several studies, group size has shown to be an important factor in influencing access to resources between groups whereby, larger groups have frequently been observed to dominate and displace smaller groups from contested resources (Waser 1976; Bygott et al. 1979; Adams 1990; Cheney 1992; Isbell et al. 1991; Tanner 2006; Radford 2008). In chimpanzee studies, such group size effects likewise is believed to play an important role in range use and access to resources between neighboring groups (e.g. Goodall 1986; Boesch and Boesch-Achermann 2000). However, unlike in many other animals, it is unclear whether larger chimpanzee groups have a competitive advantage and occupy larger ranges and/or have better access to resources over smaller groups. This discrepancy is largely because in most studies observers knew the group size and composition of only one group. In this study, I examine the influence of numerical asymmetries on range use in two simultaneously studied neighboring chimpanzee groups in Gombe National Park, Tanzania. Such understanding is important both for increasing our knowledge of the influence of numerical asymmetries on group competition and for enhancing our understanding of the origin and evolution of aggressive behavior, including warfare, in humans (Wrangham 1999).

Intergroup competition in chimpanzees tends to be very hostile and sometimes can result in serious injury or death of participants (Goodall et al. 1979; Goodall 1986; Wilson et al. 2001; Wilson and Wrangham 2003; Wilson et al. 2004; Watts *et al.* 2006). This high level of intergroup aggression has only been observed in a few species such as lions, *Panthera leo* (Bygott et al. 1979), spotted hyenas, *Crocuta crocuta* (Boydston et al. 2001), social ants, *Azteca trigona* (Adams 1990) and humans (Manson and Wrangham 1991; Wrangham and Peterson 1997). Because of the high level of hostility, intergroup competition in chimpanzees exerts strong pressure on neighbors and may have strong influence on how neighbors use their ranges, especially when two groups differ in competitive ability.

Based largely on observations of single groups, several studies on chimpanzees have suggested that larger groups control larger ranges and limit smaller groups to smaller ranges (e.g. Goodall 1986; Boesch and Boesch-Achermann 2000; Herbinger et al. 2001; Lehman and Boesch 2003). However, tests of this prediction have not yet been possible because in most studies observers only knew one group (e.g. Wrangham et al. 2007). In a few cases in which observers knew multiple groups, studies were of too short duration to draw a strong conclusion regarding the relationship between relative number of males and range size (e.g. Herbinger et al. 2001) or were not quantitatively robust (Nishida et al. 1985). As a result, our understanding of the influence of group size on range use is still based largely on speculations. Inter-group encounters in chimpanzees occur mostly in the overlapping area of the ranges of two or more groups (Boesch and Boesch-Achermann 2000; Wilson and Wrangham 2003; Watts et al. 2006). As such, ranging in the overlapping area appears to pose more risks to the survival and fitness of individuals compared to other parts of the range. Probably, the risks associated with intergroup encounters in overlapping areas explain why individuals normally range infrequently in those areas (Goodall 1986; Boesch and Boesch-Achermann 2000), despite the fact that overlapping areas appear to contain the same amount (Anderson et al. 2002) or even more resources than other parts of the range (Stanford 1998). As a result, overlapping areas tend to be an underutilized part of animals' ranges (Wilson et al. 2007; Wrangham et al. 2007).

Underutilization of overlapping area is particularly expected to occur when neighbors have about same competitive abilities and thus exert equal threats to each other. When differences in competitive ability exist, individuals of larger groups may face less risk compared to those of smaller groups and may increase their ranging in overlapping areas while foraging or searching for mates. In contrast, smaller groups may avoid visiting the same areas. Such change in the use of overlapping areas with change in competitive ability has been observed in spotted hyenas (Henschel and Skinner 1991) and in experimentally weakened groups of social ants (Adams 1990).

Although differences in competitive ability between chimpanzee groups is expected to have a strong influence on the range use of neighbors, detailed understanding of this effect until recently has not been possible because in most studies observers focused only on one group (reviewed in Wilson and Wrangham 2003; Watts et al. 2006). Here I use exceptionally detailed demographical and ranging information from 14 years of simultaneous observation of two neighboring chimpanzee groups to examine the relationship between competitive ability and range use.

Chimpanzees live in multi-male, multi-female groups called communities (Goodall 1968) or unit groups (Nishida 1968) of up to 150 individuals (Watts et al. 2006). These are fission-fusion societies (Nishida 1968; Goodall 1986) in which individuals associate in temporary parties whose size and composition may change throughout a day (Boesch and Boesch-Achermann 2000; Wrangham 2000; Anderson et al. 2002; Williams et al. 2004). In a community, males generally spend most time together while females spend most of their time alone or with their offspring, except when they are in sexually receptive condition (Goodall 1986). Unlike in most primates (Pusey and Packer 1987), male chimpanzees are philopatric and participate in territorial defense by conducting boundary patrols, exchanging vocalizations or physically attacking members of other communities (Goodall et al. 1979; Goodall 1986; Wilson and Wrangham 2003; Wilson et al. 2004; Watts et al. 2006). In contrast, females normally leave their natal community when they reach adolescence (Pusey 1979; Pusey et al. 1997), and their level of participation in territorial-defense activity appears to vary across study sites. For example, in East African chimpanzees, females appear to play little role in territorial defense (Goodall 1986; Mitani et al. 2002; Williams et al. 2004), while in

western African chimpanzees, females are reported to participate more in territorial encounters (Boesch and Boesch-Achermann 2000; Boesch et al. 2008).

Two adjacent chimpanzee communities in Gombe National Park, Tanzania, the Kasekela and Mitumba communities, were studied for the present research. During the study period (N = 14 years), the number of grown males (males 12 years old or above) in the larger Kasekela community remained relatively high (11 –13) while that in the smaller Mitumba community decreased from five to two. To test for a relationship between numerical advantage and range use, I considered four predictions.

My first prediction concerned how measures of competitive ability (i.e. absolute and relative number of males) influenced the range size of the Mitumba community. Since males play an important role in maintaining and expanding territory size (Goodall 1986; Wilson and Wrangham 2003) and because the number of males in the Mitumba community decreased, I predicted a decrease in the range size of the Mitumba community with the decrease in the absolute number of males. However, since success in intergroup competition appears to depend not only on the absolute number of males in a given group but also on that in neighboring groups (Williams et al. 2004), I also predicted a decrease in the range size of the Mitumba community with the decrease in the number of males relative to that of the Kasekela community.

In my second prediction, I examined how the two neighboring groups were using their ranges. The minimum convex polygon method for estimating range size used to test my first prediction while it defines the range boundaries well, it is likely to inflate the range size depending on the sample size and on influential outlier points and thus confound relationship between range size and competitive ability. To overcome this methodological weakness of estimating range size, I examined also patterns of range use by focusing on how two neighboring groups used the contested area. I define the contested area as the region enclosed by the minimum convex polygons of the Kasekela and Mitumba communities during the study period (1994 - 2007). I introduce this new way of studying the relationship between the competitive ability and range use by investigating the use of the contested area because the contested area poses more risks of intercommunity encounters than other parts of the range and therefore the use of this area by neighbors will depend on their competitive abilities. Thus, in my second prediction, I predicted that as the numbers of males in the two groups became more different, the Mitumba community (fewer males) decreased its use of the contested area while the Kasekela community (many males) increased its use of the same area. Furthermore, since females and total community size in other studies have been suggested to influence ranging activities, I also examined whether the number of females in each community influenced the community's use of the contested area.

My third and fourth predictions examined whether the larger Kasekela community compressed the Mitumba community and forced the Mitumba community to shift the location of its center of activity and increase its ranging in poor habitat patches. In some studies, larger groups have been reported to depose smaller groups and/or force them to change their ranging patterns (Isbell 1991). My third prediction was that the Kasekela community would cause the Mitumba community to shift its center of activity as the imbalance in number of males increased, as we would expect if territories behave as elastic discs (Huxley 1934). Since in the north, east and west the Mitumba community is not bordered by chimpanzees groups, I predicted that a decrease in competitive ability would compel the Mitumba community to shift its ranging activities towards those compass directions – the directions where the likelihood of encounters with other chimpanzee groups were minimal.

In my fourth prediction, I predicted that the center of activity of the Mitumba community would shift towards poorer habitat quality. This prediction was based on evidence that animals generally choose higher quality habitats before moving to a lower quality habitat (Brown 1964; Fretwell and Lucas 1970) and competitive fighting ability of a group appears to correlate positively with habitat quality (Robinson 1988; Mosser and Packer 2009).

# **METHODS**

#### **Study Site and Communities**

Gombe National Park, Tanzania measures about 35 km<sup>2</sup> (Pusey et al. 2007). The park extends from the eastern shore of Lake Tanganyika up the escarpment of the western arm of the Great Rift Valley. On the north and south, the park is bounded by villages and cultivated land. Moving upwards to the east from the lakeshore, the elevation in the park rises gradually from 770m above sea level to 1300-1600m at the top of the Rift valley escarpment (Pusey et al. 2008), and the vegetation grades from riverine forest in the valleys to woodland and grassland on the ridges.

Gombe National Park contains three communities of chimpanzees. The unhabituated Kalande community is in the south, the Kasekela community is in the center and the Mitumba community is in the north. The Kasekela and Mitumba communities have been observed since 1960 and 1985, respectively, and are the subjects of this study. Between 1994 and 2007, the Kasekela community consisted 11 - 13 grown males, 11 - 23 grown females and 18 - 29 immatures while the Mitumba community consisted of two to five grown males, four to nine grown females and 8 - 13 immatures (Chapter 1).

## **Data Collection**

Since 1973, a pair of field assistants in the Kasekela community has followed a focal chimpanzee daily, normally from the time when the focal individual left its nest in the morning to the time when it built another nest in the evening (Goodall 1986). These

field assistants recorded all individuals seen during the focal follow, the sexual status of females observed and feeding information on a checksheet. They also recorded intercommunity events and other behaviors of interest in narrative notes. Field assistants also recorded the location of the focal individual every 15-minute on a field map and checksheet (Goodall 1986). For the Mitumba community, similar information started to be collected in 1994 by using the same protocol as that of the Kasekela community.

#### **Calculating the Absolute and Relative Number of Males**

I assumed that the fighting ability of a community of chimpanzees depends mainly on the number of grown males in that community. Because I did not have any *a priori* means to determine how the chimpanzees themselves perceived group fighting ability, I tested two measures of male fighting power: absolute number of males and relative number of males. I established annual absolute and relative numbers of males as I describe below.

#### Annual absolute number of males

First, I estimated the number of grown males present in each community by taking the total number of all males known to be alive in a given year weighted by the number of months for which each individual was known to be alive. I only used males who were 12 years old and/or older to estimate fighting ability of a community. I chose

12 years because at 12 years old, males start gradually to integrate with adult males (adult male  $\geq$  15yrs; Goodall 1986) and become more independent from their mother (Goodall 1986; Pusey 1990). Furthermore, at 12 years old, a male potentially can sire offspring (Wroblewski et al. 2008) and therefore may assume more responsibilities of territorial defense.

I calculated each male's contribution by taking the number of months in which that male was alive in a year and dividing by total number of months in a year (i.e. 12 months). For example, if a given male was present throughout the year, his contribution to the territory defense was one (i.e. 12 months present divided by 12 months of the year). However, in a case where individual was present only in part of the year or attained 12 years old during that year, I calculated his contribution to territorial defense by taking number of months in which he was alive (or number of months after he turned 12 years old) over 12. Then, I summed all individual males' contributions to get absolute number of males in a group. By weighting each male's contribution in territorial defense by the number of months in which he was at least 12 years old and alive in a given year, I minimized the chances of inflating the competitive ability of the community by counting individuals who were too young to be involved in intergroup competition or who died later in a year.

Annual relative number of males

I calculated the annual relative number of males in each community by dividing the annual absolute number of grown males in that community by the annual absolute number of males in the rival community. I defined a resident community as the community of interest for a particular test and a rival community as a community that was competing with the resident community.

# Number of Females

I estimated number of all grown females by counting individuals who were alive at the beginning of the year (e.g. 01- January-1994). I considered a female as grown when she was 12 years old or above (Goodall 1986).

# **Community Size**

I estimated the community size of each community by counting the number of all individuals present at the beginning of each year (e.g. 01- January-1994).

### Estimating the Range Size of the Mitumba Community

As part of the long-term project, a team of data entry research assistants digitized the 15 minutes location points of all focal follows of the Kasekela (1974 - 2007) and the Mitumba (1994 - 2007) communities by using digitizing tablets in Arc View and Arc GIS software. I used all available data (n = 14 yrs) to estimate annual range sizes for the Mitumba community. I focused only on the range size of the Mitumba community because the range size of the Kasekela community depended not only on its interactions with the Mitumba community (which I studied) but also on interactions with the unhabituated Kalande community (which I did not study).

Several methods have been employed to estimate the range sizes of animals (Anderson 1982; Worton 1987; Harris et al. 1990; Seaman et al. 1998; Borger et al. 2006; Boyle et al. 2009), and there is little agreement on which method is the best (Anderson 1982; Seaman and Powell 1996; Borger et al. 2006). I used two methods, the minimum convex polygon (MCP) method and the kernel utilization distribution (KDU) method, to estimate the annual range sizes of the Mitumba community for the period between 1994 and 2007.

Because the KDU method is a statistical method, it requires independent points (Worton 1989). However, statistical realism is not also the same as biological realism. Thus, I used two approaches to establish range size. In the first approach, I took a conservative approach and used all the digitized 15-minute daily location points of focal follows in both the MCP and KDU methods to estimate range size of each year. In the second approach, to control for autocorrelation, I used only one point (Herbinger et al. 2001) picked randomly from the daily 15-minute focal follow points. This sub-sampling resulted in reduction of points in each year (Table 1).

In calculating a minimum convex polygon (MCP), a line is drawn to join all outermost points of a range to form a convex polygon containing a defined percentage of all points. However, the MCP method has some limitations (Worton 1987), especially its inability to distinguish between areas of high and low use. Furthermore, the MCP method tends to be sensitive to extreme points. Nonetheless, the MCP method defines better limits of home range boundaries than the kernel utilization method.

To minimize the influence of extreme points in the MCP method, a common approach is to calculate a MCP that includes fewer than 100% of all location records. Various researchers have adopted different percentages of all location records to be included in the calculated range (e.g. Wrangham 1979; Chapman and Wrangham 1993; Newton-Fisher 2003; Basabose 2005). I chose to include 99 % of all location records in the MCP in estimating the annual range size because this approach removed most of the influential outlier points.

I used the fixed kernel method as my second method for estimating the home range size. The kernel utilization distribution (KDU) method has currently gained popularity over other methods, including MCP (Seaman and Powell 1996; Börger et al. 2006). Unlike the MCP method, the KDU method incorporates a measure of varying intensity of use within a range, by estimating a probability of finding an individual at a certain location of its range over time. In the KDU method, fine grids are superimposed over the range, and the intensity of use in a given grid square is calculated, based on the number of animal-location points recorded in that grid square. However, the KDU method is sensitive to the choice of the grid-square size, termed bandwidth (Worton 1989). For example, when using a small bandwidth, the method may give too much detailed information that may reduce the ability to see the general trend of intensity of range use. In contrast, a large bandwidth may excessively obscure detail because it increases extent of the region on which each observation point is assessed.

Several approaches have been suggested to overcome the weakness of bandwidth choices in the KDU method (Worton 1987; Katajisto and Moilanen 2006). I used least-squares cross-validation in a fixed kernel that provides a fixed bandwidth for the whole data set. This approach is currently assumed to be the best approach in estimating the range size comparing with other kernel approaches (Katajisto and Moilanen 2006).

# Establishing and Calculating Communities' Uses of the Contested Area

Rather than focusing on annual overlapping areas, I established the long-term overlapping area by using all 15-minute location records of daily focal follows for the period between 1994 and 2007 to calculate the 100% MCPs of the Kasekela and Mitumba communities between 1994 and 2007. I termed this long-term overlapping area the contested area (Figure. 2.1).

After I established the contested area, I overlaid all of each year's 15-minute location records from daily focal follows of the Mitumba community on its habitat range by using ArcView 3.2 software. Then I calculated the percentage of location records that were in the contested area by taking the number of records that were in the contested area over total annual number of records for that particular year. I performed a similar procedure for each year (n=14 years). This yielded the annual measure of use of the contested area by the Mitumba community over time. I followed the same procedure for the Kasekela community.

#### **Estimating Center of Activity**

I followed Herbinger et al. (2001) and assumed the annual average of Xcoordinates and Y-coordinates for the 15-minute location records to be a good measure of annual center of activity of the Mitumba community. Therefore, for each year, I estimated the center of activity of that year by calculating the average value of Xcoordinates and Y-coordinates from all the annual 15-minute records of that year. I used ArcView 3.2 software for the visual display of these centers and for calculating the distances between centers. Because no systematic ranging data were collected for the Mitumba community before 1994, to estimate the overall shift in center of activity, I used 1994 as the reference center of activity and measured the extent to which the center of activity of subsequent years shifted away from this reference year.

## **Estimating Habitat Quality**

In 2007 and 2008, I randomly established 30 vegetation plots, each 20 m  $\times$  20 m, in the home range of the Mitumba chimpanzee community. In each plot I identified and measured the diameter of all trees that were greater than 10 cm diameter at breast height and categorized my plots based on five categories: Evergreen forest, Thicket woodland, Open woodland, Vine tangle, Beach/Bare ground (Rudicell et al. in review).

Within each 20m x 20m vegetation plot, I established a 5m x 5m sub-plots and identified all vines and shrubs that were present in it. I used the 20 m  $\times$  20 m vegetation plots to calculate the basal area of chimpanzee food trees, and with the 5 m  $\times$  5 m sub-plots, I calculated the availability of vines and shrubs by counting the stems used by chimpanzees as food following Rudicell and colleagues (in review). I calculated the basal area of the stems of trees in each vegetation type (i.e. Evergreen forest, Thicket woodland, Open woodland, Vine tangle, Beach/Bare ground). I summed the basal areas of evergreen forest and thicket woodland to create a single value of basal area for the major valleys of Mitumba and Kavusindi within the Mitumba community range (Figure 2.1).

In addition, I used satellite imagery to quantify habitat quality each year by estimating amount of coverage of evergreen forest, dense woodland, open woodland and grassland/ beach in the 99% minimum convex polygon of each year. I assessed the quality of habitat in the 99% minimum convex polygon of each year based on normalized

difference vegetation index (NDVI) data derived from Landsat ETM+ imagery of 1999 (Pintea 2007).

#### **Statistical Methods**

I used linear regression analysis to examine the relationships between range size and numbers of males (absolute and relative), with the absolute and relative numbers of males being my independent variables. To evaluate whether the percentage use of the contested area depended on the absolute and relative numbers of males, I did similar linear-regression analyses for both the Mitumba and Kasekela communities but using the percentage use of the contested area as the dependent variable. I also used linear regression analysis to assess whether the percentage use of the contested area depended on the number of females and community size of each community.

To determine which of my variables accounted most for relationships between my dependent variables (range size or percentage use of the contested area) and independent variables (absolute and relative numbers of males, number of females and total community size), I performed multiple linear regressions. However, I tested first for correlation between my four independent variables. I chose for further analysis only variables that showed weak correlation. When two or more independent variables are highly correlated ( $r \ge 0.6$ ), multicollinearity can adversely affect the significant relationship between dependent and independent variables, making it advisable to use

only one of the independent variables. For the Mitumba community, number of females, absolute number of males and relative number of males were highly correlated (Table 2.2). Therefore, I chose relative number of males and total community size for the multiple regression analysis. In contrast, in the Kasekela community, it was the absolute and relative number of males that showed weak correlation (Table 2.3). Therefore, for the Kasekela community, I used the absolute and relative number of males for the multiple regression analysis. I considered all tests significant with P-values  $\leq 0.05$  (two-tailed). I performed all statistical tests with R software (R Development Core Team 2009).

### RESULTS

## **Range Size**

The annual range sizes of the Mitumba community varied from year to year and depended on the sample size (Figure 2.2) and on which method I used (Figure. 2.3). Subsampling overall resulted in smaller annual range sizes (Figure. 2.4). The MCP method in most cases produced larger range size compared with the fixed kernel (KDU) method (Figure. 2.3 and 2.4). However, there was a strong correlation between the areas produced by MCP and KDU. For *all 15-minute daily focal follow annual points, the correlation between MCP and KDU was* 0.9 and for *one randomly selected point per day, correlation between MCP and KDU was* 0.74. For examining relationships between annual range size and measures of competitive ability (absolute and relative number of males), I chose to use MCP methods and used only range sizes estimated by using all 15minute daily focal follow points. While there was a relationship between range size and sample size (Figure 2.2), I found non-significant relationships between range size and absolute and relative number of males when I used simple linear regressions (absolute number of males,  $r^2$ = 0.13, p= 0.21, Figure. 2.5; relative number of males,  $r^2$ = 0.13, p= 0.21, Figure. 2.6). Similarly, both measures of fighting ability (absolute and relative number of males) were not statistically significant when I used the multiple regression analysis (Table 2.4).

## Use of the Contested Area

The percentage use of contested area by the Mitumba and Kasekela chimpanzee communities varied from year to year (Figure. 2.7). In the Mitumba community, analysis of linear regressions showed both the absolute and relative number of males to account for the use of contested area (Absolute number of males,  $r^2 = 0.69$ , p< 0.001; Figure. 2.8; Relative number of males,  $r^2=0.60$ , p= 0.001, Figure. 2.9). However, the total community size did not account for the use of the contested area ( $r^2=0.03$ , p= 0.54, Figure 2.10). The percentage use of the contested area was inversely related to the number of females ( $r^2=0.82$ , p< 0.001, Figure 2.11). In the analysis by multiple regression, it was only the relative number of males that accounted for the percentage use of the contested area by the Mitumba group; the total community size had no effect (adjusted  $r^2=0.53$ ; F<sub>2,11</sub> = 8.13, p= 0.006; relative number of males p= 0.002; total community size p= 0.76).

For the Kasekela community, in the linear regressions analysis, the absolute number of males had no statistically significant effect on the community's use of the contested area ( $r^2 = 0.23$ , p = 0.08; Figure. 2.12). However, the linear regressions analysis showed the use of contested area to be statistically significant for the relative number of males ( $r^2 = 0.53$ , p = 0.003; Figure. 2.13), number of females ( $r^2 = 0.43$ , p = 0.011; Figure. 2.14) and total community size ( $r^2 = 0.013$ , p = 0.41; Figure. 2.15).

In the analysis of multiple regressions, both absolute and relative number of males of the Kasekela community had statistically significant influence on the use of the contested area (Adjusted R Square = 0.66; F<sub>2,11</sub> = 13.6, p= 0.001; Relative number of males p= 0.001; Absolute number of males p= 0.002). However, the value of coefficient of regression in the absolute number of males was negative.

# Shift in Center of Activity of the Mitumba Community

Between 1994 and 2007, there was an overall shift in the center of activity of the Mitumba community away from the Kasekela community. Using the 1994 center of activity as the reference point (0 meter), the overall shift of center of activity for the Mitumba community was approximately 430 meters towards the north (Figure. 2.16) and this shift correlated with decrease in the relative number of males (Figure. 2.17).

### Habitat Quality of the Mitumba Community Range

Based on basal area of chimpanzee food trees and count of stems of important food vines and shrubs, there was no great difference in habitat quality between the Mitumba and Kavusindi valleys when basal areas of important vegetation categories (i.e. evergreen forest and thicket woodland) were summed together (mean basal area; Kavusindi =  $1.33 \text{ m}^2$ , Mitumba = $1.63 \text{ m}^2$ , Figure. 2.18). Similarly, according to analysis of vegetation coverage of evergreen forest and dense woodland based on satellite imagery in annual ranges of the Mitumba community of 1994 – 2007 showed non-significant change in vegetation coverage as indexed by NDVI between years ( $r^2 = 0.2023$ , p = 0.11; Figure. 2.19).

#### DISCUSSION

# **Change in Community Range Size**

Although relationships between range size and numbers of males in the Mitumba community were not statistically significant, the general trends are worthy of note. The overall range size of the Mitumba community between 1994 and 2007 increased from 3.2 Km<sup>2</sup> in 1996 to 5.9 Km<sup>2</sup> in 2006 despite a decrease in both absolute and relative number of males. Generally, it is expected that the range size should decrease as the competitive ability of the community decreases (Nishida et al. 1985; Goodall 1986, Boesch and Boesch-Achermann 2000). However, this expectation was not borne in this study. At

least four explanations may account for a lack of a strong relationship between community range size and number of males in a community and for the general trend that seems opposite to what would be expected.

First, several studies have suggested that chimpanzee population size inside the park is declining (Goodall 1986; Greengrass 2000; Chapter 1). A decline in population size might possibly have relaxed the pressure of intercommunity competition between the Kasekela and Mitumba communities and allowed the Mitumba community to enlarge its range despite its numerical disadvantage, as has been observed in other studies (e.g. Kruuk and MacDonald 1984; Janson and Goldsmith 1995). This line of argument, however, seems unlikely to explain the trend in increase of the range size of the Mitumba community. During the study period (1994 - 2007), the number of chimpanzees in the Kasekela community has been increasing (Pusey et al. 2007), and the number of chimpanzees in the Mitumba community has remained around 23 – 25 individuals (Chapter 1). Furthermore, the Kasekela community has encroached on the range of the Mitumba community, and the Mitumba community has appeared to shift away from Kasekela (see below). Thus, rather than being at a reduced pressure, the Mitumba community might have been facing ever increasing pressure of intercommunity competition from the Kasekela community. Based on these observations, I conclude that the observed trend in increase in the range size probably is not a consequence of a decrease in population density.

Second, decrease in habitat quality can force individuals to increase their foraging efforts in order to meet their daily nutritional requirements and this in turn may lead to range expansion (e.g. Pulliam and Caraco 1984; Wrangham et al. 1996; Isbell et al. 1991). Factors such as trees falling due to the loosening of soil or uncontrolled fire may cause a change in forest vegetation structure and lower habitat quality (O'Brien et al. 2003; Barlow et al. 2006). While trees falling in the park, especially during the wet season, and fires in the dry season are common (personal observation), the vegetation study by Pintea (2007) showed that, vegetation coverage inside the park has increased over time, and Rudicell et al. (in review) found a close correlation between vegetation coverage and availability of food. These observations refute the idea that poor habitat quality in the Mitumba community range might have been a reason for increased community range size.

Third possibility is that, change in range size of the Mitumba community might have been a result of increase in amount of following of chimpanzees. While there was evidence that more follows led to an increase in the range size of the Mitumba community, increase in chimpanzee follows accounted only for half of the change in range size (p =0.002,  $r^2$ = 0.51). This suggests that, other factors also must have played a role in the observed increase in range size.

The fourth possible explanation for the increase in range size of the Mitumba community is that, because the Mitumba community is bordered by villages and

cultivated farms in north and northeast, the Mitumba community has faced little risk of intercommunity encounters in those directions and therefore, it has expanded its range size towards those areas. While the community has expanded its range outside the park, the overall change in range size cannot be attributed solely to this enlargement. Despite its numerical disadvantage, the Mitumba community has not totally abandoned some parts of its southern range. Thus, complete understanding of the factor(s) that led to observed increase in range size of the Mitumba community despite decrease in its numerical strength still require more investigation.

# Use of the Contested Area

Analysis of linear regressions showed that the percentage use of the contested area by the Mitumba community depended on both the absolute and relative number of males in the community. The percentage use of the contested area decreased as the absolute and relative number of males in the community decreased. The total community size had no effect, while the number of females pointed in the opposite direction. However, when only weakly correlated variables were used in the multiple regressions analysis, it was only the relative number of males that appeared to account for the variation in annual use of the contested area. Total community size had no significant effect.

Regarding the Kasekela community, linear regression analysis showed that the relative number of males, the number of females and the total community size helped to

explain the annual variation in the percentage use of contested area, while the absolute number of males had no significant effect. In the multiple regression analysis, performed by using only weakly correlated variables, however, both absolute and relative number of males helped to account for the annual variation of percentage use of the contested area. Nevertheless, unlike the relative number of males that had a positive regression coefficient value, absolute number of males had a negative regression coefficient value.

My findings concur with the expectations based on how chimpanzees should compete in intercommunity interactions (Goodall et al. 1979; Nishida et al. 1985; Goodall 1986; Wrangham 1999; Wilson et al. 2001; Wilson and Wrangham 2003; Wilson et al. 2004; Watts et al. 2006). Each community used the contested area more often when numerical advantage was on its favor. However, as the discrepancy in the numerical strength increased individuals of smaller community used the contested area less and less.

These observations suggest that individuals in a larger group of males might face a lower risk from intercommunity interactions compared to those of a community with relative fewer males. This may be the case in two ways. First, males of the larger community possibly form larger groups and use their numerical advantage in increasing their ranging in the contested area. Second, simply because of the sheer number of males in the larger community relative to their neighbors, males of larger community are more likely to be in larger group of males. Although I did not test which grouping strategy prevailed, in either case, an increase in relative number of males relative to other community appears to lower the risks of intercommunity interactions, as has been experimentally shown by Wilson et al. (2001). Thus, the Kasekela community could afford to range in the contested area more while searching for mates or foods and consequently restricted the Mitumba community's use of the same area because of huge discrepancy in relative number of males.

I did not find the total community size of the Mitumba to influence the use of the contested area. At least two explanations could account for this insignificant relationship. First, the overall community size did not change much during the study (Chapter 1). This suggested that the level of intra-community feeding competition possibly did not change sufficiently to force individuals to range into the contested area where risks of intergroup aggressions were high. A second possibility is that females who were the larger source of overall change in community composition played little role in territorial defense (Chapter 3). In addition, although I did not test for sex differences in range use because it is beyond the scope of this study, most studies have shown females to avoid boundary areas or to drop out of the group while males proceed to boundary areas (e.g Goodall 1986; Wilson and Wrangham 2003; Wilson et al. 2007). In this study, the contested area included also boundary areas.

Lack of females' interest in territorial defense is surprising given that females – like males – face risks of intercommunity attacks, infanticide or range encroachment from intruding males of neighboring communities (Williams et al. 2002; Murray *et al.* 2007; Sherrow and Amsler 2007). Because of such factors, females may be expected to help males of their communities in repelling intruding males, in particular when the relative number of males in the community is small as it was in the Mitumba community. However, unlike males, females can be incorporated into a rival community, if their community ceases to exist as a social entity (Nishida et al. 1985; Pusey et al. 2007). Possibly, the cost of engaging in territorial defense for females is greater than the cost of changing residence.

For the larger Kasekela community, while the relationship between the absolute number of males and the use of contested area was significant, the direction of the relationship was negative. The negative relationship implied that, as the absolute number of males increased, the community decreased its use of the contested area. This would have been a case, if some males in the community elected not to aid in community defense and consequently disrupted the defensive ability of the community or if only fewer males in the community use more the contested area. Data on the use of the contested area do not support either hypothesis because over time most of the Kasekela males have been seen in the contested area (Chapter 3) and the community has increased its use of the contested area (This chapter). Furthermore, a study by Wroblewski et al. (2009) showed while reproductive skew is important, males of varying ranks and ages nonetheless have chances of siring offspring. Therefore, many males are expected to be involved in territorial defense. Thus, although the absolute number of males appeared to be significant in the use of the contested area, the negative direction of the coefficient value suggests that the absolute number of males had little role in intercommunity competition for resources, especially when compared to relative number of males as has been suggested by Williams et al. (2004).

Mechanisms by which neighbors assess their relative numerical strength are slowly starting to emerge. Chimpanzees usually use loud pant-hoots for various purposes including advertizing their whereabouts to their fellows and to rivals (Nishida et al. 1985; Goodall 1986; Notman and Rendall 2004; Crockford et al. 2004). Wilson and colleagues (2001) by using playback experiments found individuals of small parties to be unwilling to approach the playback when numerical odds were not favoring them. However, individuals approached faster when they had numerical advantage. These results suggest that by using vocal cues, chimpanzees like other animals (Grinnell et al. 1994; Kitchen 2004) can assess their own numerical advantage relative to that of their neighbor community and avoid any encounter with a likely unfavorable outcome. In this way, chimpanzees may avoid entering potentially costly encounters (Parker 1974). My finding support the general understanding of how animals should contest for resources, by showing the tendency of chimpanzees to use the contested area only when numerical advantage was in their favor.

Natural selection should favor individuals' ability to take advantage of their numerical advantage and modify their ranging behavior accordingly when the situation

116

allows, because the ability to do so appears to improve individuals' access to resources (Williams et al. 2004). As in many species, chimpanzees reproduce faster when food availability is higher (Pusey et al. 1997; Murray et al. 2006; Emery Thompson and Wrangham 2008). Furthermore, as has been suggested from research in Taï National Park (Herbinger et al. 2001), higher availability of resources may increase territorial activities of individuals and in turn may help chimpanzees to acquire more food or females (Nishida et al. 1985).

#### Shift in Center of Activity

The overall center of activity of the Mitumba community shifted towards the northwest. Using 1994 as the baseline center of activity, the highest distance the community moved was 430 meters. This shift in activity center correlated with the change in competitive ability of two communities. However, I did not detect a significant difference in habitat quality between valleys that spanned this distance.

Nevertheless, given the heterogeneity of habitat and spatial and temporal availability of food resources in the park (Goodall 1986), detailed study of phenology is still needed to understand patterns of fruiting and assess whether this shift in center of activity had any effect on individuals' access to important food types. In fact, anecdotal evidence suggests this to be the case. In 2005, the Mitumba chimpanzees' ability to feed on *Parinari curatellifolia* was restricted by the Kasekela community that literally "camped" in the range of the Mitumba community where this important food species occurs.

## CONCLUSION

This study showed that the range size of the Mitumba community did not decrease as would be expected from the relationship between the competitive ability and range size. Rather, there was a trend in increase in range size with the decrease in the competitive ability of the community. However, observations of how the two communities used the contested area revealed the importance of relative number of males in the range use and showed that the larger community influenced how the smaller community accessed the competed resources.

My study thus suggests that, for clearer understanding of the effect of competitive ability between neighboring groups, one should also consider examining how neighbors use the contested area rather than just measuring the overall change in the range size. The contested area poses several risks of intercommunity encounters with neighbors and therefore, understanding patterns of neighbors' use of this area can help in drawing strong conclusions about the effect of numerical asymmetries on range use.

Understanding the factors that influence range use and hence access to resources has implications both for behavioral ecology (Wrangham 1980) and for people interested in understanding the origin and evolution of aggressive behavior, including warfare in humans (Wrangham and Peterson 1996). Chimpanzees – our closest living relatives – are suggested to have changed little since we last diverged from common ancestor. Like in humans, intergroup interaction in chimpanzees is predominantly male activity. Furthermore, in both humans and chimpanzees, males' coalitions attack lone or small parts of neighboring groups (Wilson and Wrangham 2003). Thus, because of similarities in patterns of intergroup interactions between humans and chimpanzees, understanding factors that govern aggressive intercommunity interactions in chimpanzees may help us to understand evolution of aggressive behavior in humans including warfare.

Studies of intergroup competition in animals have played an important role in increasing our understanding of the evolution and maintenance of sociality in animals (Wrangham 1980; Hoogland 1981; Cheney and Seyfarth 1991). My study adds to this understanding by showing the importance of numerical advantage in competition for resources. However, because group size in chimpanzees constantly changes throughout the day, this study emphasizes the need for more understanding of how individuals assess numerical asymmetries and how this assessment affects their short-term and long-term behavioral strategies.

### **FIGURE CAPTIONS**

**Figure 2.1.** The contested area between the Mitumba and Kasekela communities between 1994 and 2007. The contested area was established by calculating 100% MCPs for all 15-minute daily focal follow location records in the designated period.

**Figure 2.2.** Relationship between home range size and sample size (amount of chimpanzee follows in each year) in the Mitumba chimpanzee community between 1994 and 2007.

**Figure 2.3.** Annual variation in home range size of the Mitumba chimpanzee community between 1994 and 2007. Annual home range was estimated by using all 15-min focal follow points. KDU = Kernel utilization distribution and MCP = Minimum convex polygon. The correlation between annual area estimated by MCP and KDU was r = 0.9.

**Figure 2. 4.** Annual variation in home range size of the Mitumba chimpanzee community between 1994 and 2007. For each year, annual home range was estimated by using annual points formed from one randomly selected point per day. KDU = Kernel utilization distribution and MCP = Minimum convex polygon. The correlation between annual area estimated by MCP and KDU was r = 0.74.

**Figure 2. 5.** Relationship between annual range size and absolute number of males in the Mitumba chimpanzee community. Range size was estimated by using all 15-minute daily focal follow points of each year.

**Figure 2.6**. Relationship between annual range size and relative number of males in the Mitumba chimpanzee community. Range size was estimated by using all 15-minute daily focal follow points of each year.

**Figure 2.7.** Annual use of the contested area by the Mitumba and Kasekela communities between 1994 and 2007. For the Kasekela community, values for percentage of use of the contested area between 2000 and 2004 are underestimated because field assistants

stopped following chimpanzees over the Public Footpath fearing that following further Kasekela community in the Mitumba range encouraged the Kasekela chimpanzees. In 2000, number of days field assistants stopped at Public Footpath were = 23 days, 2001 = 27 days, 2002 = 17 days, 2003 = 9 days and 2004 = 4 days.

**Figure 2. 8.** Relationship between percentage use of the contested area and the absolute number of males in the Mitumba chimpanzee community.

**Figure 2. 9.** Relationship between percentage use of the contested area and the relative number of males in the Mitumba chimpanzee community.

**Figure 2. 10.** Relationship between percentage use of the contested area and the total community size of the Mitumba chimpanzees.

**Figure 2. 11.** Relationship between percentage use of the contested area and the number of females in the Mitumba chimpanzee community.

**Figure 2. 12.** Relationship between percentage use of the contested area and the absolute number of males in the Kasekela chimpanzee community.

**Figure 2. 13.** Relationship between percentage use of the contested area and the relative number of males in the Kasekela chimpanzee community.

**Figure 2. 14.** Relationship between percentage use of the contested area and the number of females in the Kasekela chimpanzee community.

**Figure 2. 15.** Relationship between percentage use of the contested area and the community size of the Kasekela chimpanzees.

**Figure 2. 16.** Activity center of the Mitumba chimpanzee community between 1994 and 2007.

**Figure 2. 17.** Relationship between the distance the Mitumba chimpanzee community shifted away from the Kasekela chimpanzee community (relative to activity center of 1994) and the relative number of males of the Mitumba chimpanzee community.

**Figure 2. 18.** Summed values of basal areas of evergreen forest and thicket woodland for the Kavusinde and MitumbaValleys.

**Figure 2. 19.** The relationship between the sum of vegetation coverage of important chimpanzee food types and year in the Mitumba chimpanzee community.

**Table 2.1.** Sample size for each year used in estimating the annual range size using the minimum convex polygon and kernel utilization distribution methods.

Year	Annual number of points based on all daily focal follow 15-minute points	Annual number of points from one randomly selected point per day			
1994	5643	210			
1995	3663	135			
1996	2899	92			
1997	6391	201			
1998	6991	224			
1999	3699	124			
2000	4270	141			
2001	4090	160			
2002	7363	189			
2003	9610	255			
2004	10549	279			
2005	12396	322			
2006	11532	313			
2007	11487	323			
	Contested	Absolute number of	Relative number of	Number of	Community
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Variables	area	males	males	females	size
Contested area	1				
Absolute number of males	0.83	1			
Relative number of males	0.77	0.98	1		
Number of females	-0.9	-0.68	-0.61	1	
Community size	0.16	0.21	0.13	-0.7	1

**Table 2.2.** Correlation values of the Mitumba chimpanzee community

		Absolute number of	Relative number of	Number of	Community
Variable	Contested area	males	males	females	size
Contested area	1				
Absolute number of males	-0.48	1			
Relative number of males	0.73	-0.07	1		
Number of females	0.65	-0.42	0.84	1	
Community size	0.64	-0.3	0.9	0.92	1

<b>Fable 2.3.</b> Correlation values of the Kasekela chimpanzee community
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**Table 2.4.** Output from multiple regression analysis. The influence of sample size and measures of community's competitive ability (absolute and relative number of males) of the Mitumba community on the range size.

Variable	Coefficients	SE	t Stat	P-value
Intercept	1.8282	1.2477	1.4653	0.1736
Absolute number of males	0.2252	0.8583	0.2624	0.7984
Relative number of males	0.6230	10.9210	0.0570	0.9556
Sample size	0.0002	0.0001	3.4655	0.0061



**Figure 2.1** The contested area between the Mitumba and Kasekela communities between 1994 and 2007. The contested area was established by calculating 100% MCPs for all 15-minute daily focal follow location records in the designated period.



**Figure 2.2.** Relationship between home range size and sample size (amount of chimpanzee follows in each year) in the Mitumba chimpanzee community between 1994 and 2007.



Annual Range Size Estimated by Using All 15min Daily Focal Follow Points

**Figure 2.3.** Annual variation in home range size of the Mitumba chimpanzee community between 1994 and 2007. Annual home range was estimated by using all 15-min focal follow points. KDU = Kernel utilization distribution and MCP = Minimum convex polygon. The correlation between annual area estimated by MCP and KDU was r = 0.9.



Annual Range Size Estimated From One Randomly Selected Points Per Day

**Figure 2. 4.** Annual variation in home range size of the Mitumba chimpanzee community between 1994 and 2007. For each year, annual home range was estimated by using annual points formed from one randomly selected point per day. KDU = Kernel utilization distribution and MCP = Minimum convex polygon. The correlation between annual area estimated by MCP and KDU was r = 0.74.



**Figure 2. 5.** Relationship between annual range size and absolute number of males in the Mitumba chimpanzee community. Range size was estimated by using all 15-minute daily focal follow points of each year.



**Figure 2.6.** Relationship between annual range size and relative number of males in the Mitumba chimpanzee community. Range size was estimated by using all 15-minute daily focal follow points of each year.



**Figure 2.7.** Annual use of the contested area by the Mitumba and Kasekela communities between 1994 and 2007. For the Kasekela community, values for percentage of use of the contested area between 2000 and 2004 are underestimated because field assistants stopped following chimpanzees over the Public Footpath fearing that following further Kasekela community in the Mitumba range encouraged the Kasekela chimpanzees. In 2000, number of days field assistants stopped at Public Footpath were = 23 days, 2001 = 27 days, 2002 = 17 days, 2003 = 9 days and 2004 = 4 days.



**Figure 2. 8.** Relationship between percentage use of the contested area and the absolute number of males in the Mitumba chimpanzee community.



**Figure 2. 9.** Relationship between percentage use of the contested area and the relative number of males in the Mitumba chimpanzee community.



**Figure 2. 10.** Relationship between percentage use of the contested area and the total community size of the Mitumba chimpanzees.



**Figure 2. 11.** Relationship between percentage use of the contested area and the number of females in the Mitumba chimpanzee community.



**Figure 2. 12.** Relationship between percentage use of the contested area and the absolute number of males in the Kasekela chimpanzee community.



**Figure 2. 13.** Relationship between percentage use of the contested area and the relative number of males in the Kasekela chimpanzee community.



**Figure 2. 14.** Relationship between percentage use of the contested area and the number of females in the Kasekela chimpanzee community.



**Figure 2. 15.** Relationship between percentage use of the contested area and the community size of the Kasekela chimpanzees.



**Figure 2. 16.** Activity center of the Mitumba chimpanzee community between 1994 and 2007.



**Figure 2. 17.** Relationship between the distance the Mitumba chimpanzee community shifted away from the Kasekela chimpanzee community (relative to activity center of 1994) and the relative number of males of the Mitumba chimpanzee community.



**Figure 2. 18.** Summed values of basal areas of evergreen forest and thicket woodland for the Kavusinde and MitumbaValleys.



**Figure 2. 19.** The relationship between the sum of vegetation coverage of important chimpanzee food types and year in the Mitumba chimpanzee community.

# CHAPTER 3 : The Relative Influence of Male Party Size and Location in the Range on Outcome of Territorial Contests in Gombe Chimpanzees.

## ABSTRACT

Many species compete for resources by defending a group territory. In most of these species, the outcome of territorial contests often depends on group size whereby members of larger groups tend to dominate and displace members of smaller groups from resources. However, smaller groups with presumed lower fighting ability sometimes have emerged victorious. Nonetheless, when and how smaller groups are able to overcome the numerical advantage of larger groups is poorly known. Here I examined the relative importance of fighting ability and location in the range on the outcome of territorial encounters between two neighboring chimpanzee groups of different sizes by focusing my analysis in the smaller Mitumba community. I predicted the community to respond aggressively to calls of their neighbors by counter-calling and approaching their rivals more quickly when they were in the heart of their range. I found a significant increase in number of loud calls after the Mitumba community heard calls of its neighbors. However, location of intercommunity encounters and the distance between communities did not influence the probability of the community to counter-call. Rather, the probability of counter-calling increased when the number of males in the party increased from zero or one to three and more. These results partially supported my hypothesis. The community increased effort in defending its range by calling more after hearing rivals. However, the lack of influence of location in the range on the outcome of territorial contests was a surprise. My findings suggest that, despite a huge difference in fighting ability, male chimpanzees in this population did not shift defensive efforts towards center of their range.

147

Keywords: chimpanzee, numerical asymmetries, intergroup competition, Pan

troglodytes schweinfurthii, contested area

## **INTRODUCTION**

Many group-living species compete for resources such as food or mates by defending a group territory. For these species, invasion by intruders in a territory normally evokes an aggressive response (e.g. Banded mongoose, Mungos mungo, Cant et al. 2002; Spider monkeys, Ateles geoffroyi yucatanensis, Aureli et al. 2006). Aggressive responses include vocal exchanges, chases or physical attacks, and often the larger group is more likely to dominate and displace the smaller group in such contests (e.g. vervet monkey, Cercopithecus eathiopis, Cheney 1987; lions, Panthera leo, Packer et al. 1990; Spong 2002; social ants, Formica xerophila, Tanner 2008). However, although a larger group size often confers a competitive advantage over a smaller one, numerical strength does not guarantee success all the time. Smaller groups with presumed lower competitive advantage sometimes have emerged victorious over larger groups (Cords 2002; Pride et al. 2006; Crofoot et al. 2008). Nonetheless, how and when smaller groups are able to stand up to larger groups is still not well understood. Here I use long-term data from simultaneous observations of two neighboring chimpanzee communities in Gombe National Park, Tanzania to examine how the number of males and location in the range influenced the outcome of territorial contests.

Game theoretical models of animals' contests suggest that two major factors, fighting ability and the value of resources to the contestants, guide animals' decisions on whether to enter into a contest in the first place and on whether to escalate after entering such a contest (Parker 1974; Maynard Smith 1982). In dyadic interactions, experimental and observational studies show that individuals usually use cues such as body weight (e.g. red deer stags, *Cervus elaphus*, Brock and Albon 1979), body size (e.g. toad. *Bufo bufo*, Davies and Halliday 1978) or weaponry (e.g. red deer stags, Brock and Albon 1979) in assessing their relative fighting ability. When assessment reveals one individual to be on the losing side, such an individual normally refrains from entering the contest or escalating further in aggression (reviewed in Adams 2001).

In group-living animals, group size appears to provide reliable cues of fighting ability. Evidence gathered from experimental studies shows that when members of one group are confronted with members of another group, the members of smaller groups are less likely to approach their rivals or to counter-call (e.g. lions, McComb et al. 1994; Grinnell et al. 1995; Chimpanzees, *Pan troglodytes*, Wilson et al. 2001; Black howler monkeys, *Alouatta pigra*, Kitchen 2004). However, when members of the smaller groups decide to approach those of the larger groups, the out-numbered members tend to approach slowly and with great cautious. This is in contrast to members of larger groups who normally approach their rivals with high speed (McComb 1994; Wilson et al. 2001).

Similarly, observational studies have also documented cases of intergroup dominance (e.g. vervet monkey, Cheney 1992; spotted hyenas, *Crocuta crocuta*, Boydston et al. 2003). In wedged capuchin monkeys, *Cebus olivaceus* (Robinson 1988), larger groups were more likely to displace smaller groups when two groups of unequal size encountered each other and in lions, larger groups appear to occupy higher quality habitat (Mosser and Packer 2009).

Although it is widely accepted that larger group size confers competitive advantages over smaller groups, encounters between larger groups and smaller groups do not always result in the predicted outcome. For example, in experimental studies conducted on female lions of two different populations, Heinsohn (1997) found that, despite being out-numbered, female lions of one population living at high densities always approached simulated roars of their rivals. In ring-tailed lemurs, *Lemur catta*, Pride and colleagues (2006) showed group size to play little role in determining the outcome of intergroup competition and in blue monkeys, *Cercopithecus mitis*; (Cords 2002) and wedged capuchin monkeys (Crofoot et al. 2008), smaller groups were sometimes successful in chasing larger groups in their range.

The above observations suggest that, apart from fighting ability, other factors may also play important roles in determining the outcomes of intergroup competition. Maynard Smith (1982) argued that, as an individual(s) moves away from the center of its home range, the value of resources may diminish and create asymmetries in pay offs (consequences of winning or losing). Because, intergroup contests are costly, individuals should react to a given intergroup contest in a context specific manner and be prepared to fight harder in contests that occur closer to their range center than those that occur at the periphery (Maynard Smith 1982). Although a clearer understanding of how the location of inter-group interactions modifies the competitive advantage of groups may improve our understanding of the dynamics of intergroup interactions and resource acquisition between groups, only a few studies have attempted to examine the role of location on the outcome of inter-group interactions (but see Wilson et al. 2001; Crofoot et al. 2008). This is mostly, because intergroup interactions are rare events and thus a relatively long time is required to collect reasonable sample size for testing alternative hypotheses.

Using fourteen years of observational data from two neighboring chimpanzee communities in Gombe National Park, I examine the relative importance of number of males and location in the range on the outcome of territorial contests. Chimpanzees live in multi-male, multi-female groups called communities that range in size from fewer than 20 to nearly150 individuals (Goodall 1986; Watts et al. 2006). Unlike in most groupliving species where individuals live in cohesive groups (Cheney and Seyfarth 1987), chimpanzees in a community associate in temporary parties whose size and composition change constantly throughout a day (Nishida 1968; Goodall 1986; Boesch and Boesch-Achermann 2000; Wrangham 2000; Williams et al. 2004). Males in a community generally spend more time together while females spend most of their time alone or with their offspring, except when they are in a sexually receptive condition (Goodall 1986). Male chimpanzees are philopatric and participate most in territorial defense, by conducting boundary patrols, exchanging vocalizations or physical attacking of members of other communities (Goodall et al. 1979; Goodall 1986; Wilson and Wrangham 2003; Wilson et al. 2004; Watts et al. 2006). In contrast to males, females normally leave their natal community when they reach adolescence (Pusey 1979; Pusey et al. 1997) and their level of participation in territorial activity is lower, although it appears to vary across study sites (Goodall 1986; Boesch and Boesch-Achermann 2000; Williams et al. 2004; Mitani et al. 2002).

Because males generally play the key role in territorial defense, the fighting ability of a community depends on the number of adult males in the community relative to that of its opponents (Williams et al. 2004; Chapter 2). Intercommunity encounters are sometimes lethal (Manson and Wrangham 1991; Wrangham 1999, Kutsukake and Matsusaka 2002; Mitani et al. 2002; Wilson et al. 2004, Watts et al. 2006). Encounters typically occur in the periphery (Watts and Mitani 2001; Mitani and Watts 2005; Boesch et al. 2008; Mitani and Studies 2009), but sometimes occur when males make deep incursions into the neighboring territory (Wilson *et al.* 2004).

Most intercommunity interactions involve only vocal exchanges (Goodall 1986; Wilson et al. 2001; Boesch et al. 2008). Nonetheless, vocal exchanges, like physical encounters, normally tend to modify the behavior of neighbors. For example, following a call from neighbors, chimpanzees may counter-call, approach, retreat or continue with the course of their activity (Nishida 1979; Goodall 1986; Boesch and Boesch 2000; Wilson and Wrangham 2003; Watts et al. 2006). In an experimental study, Wilson et al. (2001) found the number of males in a group to be the decisive factor regarding whether individuals will counter-call or approach their rivals. However, Wilson and colleagues did not find the location of an encounter to influence the decision of individuals to counter-calling or approach their rivals possibly because relatively few of playbacks were conducted in the far periphery.

Faced with ever-increasing pressure from larger neighbors, individuals of smaller groups should somehow try to counteract the forces of larger groups. However, both because of the simple geometric argument of Maynard Smith (1982), and because habitat is heterogeneous, some parts of home range may be more valuable than other parts. Thus, individuals should spend more efforts in trying to resist incursions of larger groups in areas where benefits of doing so are likely to be higher.

During the study period (N = 14 years), the number of grown males (males 12 years old or above) in the larger community has remained relatively high (11 –13) while that of the smaller community has been between five and two (Chapter 2). Because of this persistent imbalance of power, I predicted that the probability of individuals of the smaller group to counter-call or approach their rivals to be higher towards the center of home range compared to the periphery. Furthermore, because failure to defend the center may precipitate losing the whole home range, I also predicted individuals of the smaller community to respond and approach more quickly to the calls of their rivals when in the center of their range than when they were in the periphery. Lastly, because in the center

the community faces less competition from neighbors, individuals may prepare to escalate in the contest when at the center of their range. Thus, I predicted that the average duration of intercommunity interaction should be higher for intercommunity interactions that occurred nearer the center of the range compared to that in the overlap zone.

## METHODS

#### **Study Site and Communities**

Gombe National Park, Tanzania measures about 35 km<sup>2</sup> (Pusey *et al.* 2007). The park extends from the eastern shore of Lake Tanganyika up the escarpment of the western arm of the Great Rift Valley. On the north and south, the park is bounded by villages and cultivated land. Moving upwards to the east from the lakeshore, the elevation in the park rises gradually from 770m above sea level to 1300-1600m at the top of the Rift valley escarpment (Pusey et al. 2008), and the vegetation grades from riverine forest in the valleys to woodland and grassland on the ridges.

Gombe National Park contains three communities of chimpanzees. The unhabituated Kalande community is in the south, the Kasekela community is in the center and the Mitumba community is in the north. The Kasekela and Mitumba communities have been observed since 1960 and 1985 respectively and are the subjects of this study. Between 1994 and 2007, the Kasekela community consisted 11 – 13 grown males, 11 – 23 grown females and 18 - 29 immatures while the Mitumba community consisted two to five grown males, four to nine grown females and 8 - 13 immatures (Chapter 1).

## **Data Collection**

Since 1973, pair of field assistants in the Kasekela community has followed a focal chimpanzee daily, usually starting from the time when the focal individual leaves its nest in the morning to the time when it builds another nest in the evening. During the focal follow, field assistants record all individuals seen during the focal follow, feeding information and the location of the focal individual every 15min on a field map and checksheet. Field assistants also recorded opportunistically intercommunity events and any other behavior of interest in narrative notes (Goodall 1986). For the Mitumba community, similar information started to be collected in 1994 by using the same protocol as that of the Kasekela community. Thus, I am restricting my analysis for the period between 1994 and 2007.

### **Location of Intercommunity Encounters**

I divided the range of the Mitumba community into two parts, the contested area in which the range of the Mitumba community overlapped with that of the Kasekela community and the non-contested area (the area of exclusive use, which including the center of the range) (Chapter 2). I considered non-contested area as the center of range center. I used Arc View software to assign location of each intercommunity encounter between 1994 and 2007 to its respective area in the Mitumba community range.

## **Vocal Activity**

To determine whether the Mitumba community increased their production of loud calls after hearing calls of their neighbors, I counted number of loud calls (Pant-hoots) (Goodall 1986) that occurred within one hour before an intercommunity encounter and those that occurred within one after an intercommunity encounter.

## **Coding the Outcome of Intercommunity Encounters**

I extracted all cases of intercommunity encounters (vocal exchanges, visual encounters and physical encounters) from the Swahili narrative notes of both the Kasekela and Mitumba communities for the period between 1994 and 2007. I defined an intercommunity encounter following previous studies (see Goodall 1986; Boesch and Boesch-Achermann 2000; Wilson and Wrangham 2003). I considered an event to be an intercommunity encounter if (1) my target party heard calls of members of the neighboring community, (2) individuals of opposing parties saw each other at a distance, or (3) two parties of opposing communities encountered each other and one party physically attacked or otherwise harassed members of the opponent party. On a given day, multiple intercommunity encounters were scored if the start of one event occurred more than an hour since the end of the previous event.

Because information on individual participation in intercommunity interactions was not collected systematically, I assumed all members to participate equally in the intercommunity interactions. Thus, I used all grown males, grown females or the total number of grown males and females in establishing the party size. Intercommunity interaction events were recorded opportunistically, therefore, the location of the intercommunity interaction did not necessarily correspond with the location of the 15 minutes focal follow sampling. In such cases, I recorded the location of intercommunity interaction as that of the closest sampling location of 15-minute focal follow (e.g. if the intercommunity interaction occurred between 9:00 and 9:07am, I assumed the location of the interaction to be at the party's location at 9:00am. Otherwise, I assumed the location of interaction to be at the 9:15am location if the interaction occurred between 9:08 and 9:15).

## **Duration of Intercommunity Encounters**

I assumed the duration of an intercommunity interaction to be the total time during which two opponent parties exchanged vocalizations, stared at each other or were engaged in physical fighting.

## **Estimating Latency of Vocal Response and Movement**

I measured the latency of vocal response as the time (in minutes) that a focal party took to respond to a call of its opponents (limited to calls that occurred within one hour after hearing their rivals). I scored "yes" if the party responded to call(s) of its opponents. Otherwise, a party scored a "no" if it did not respond to its rival within one hour after hearing them.

For the latency of movement, I used the narrative notes and map data to estimate the time a party took to move towards or away from its opponents (considering only movements within one hour of the start of the interaction). However, in some cases the time of the movement was not obvious. In such cases, I averaged the time between two location points if there was evidence that a party moved at least 100 meters at the end of the next 15 minutes of the focal follow point. For example, if at the subsequent 15-minute interval a party seemed to have moved at least 100 meters, I assumed the total time of the movement to be 7.5 minutes (i.e. the average of time at the start of intergroup interaction (0-minute) and time after it has moved at least 100 meters (15-minute)).

## **Matched Intercommunity Interactions**

I identified all intercommunity interactions in the Mitumba and Kasekela community in which the time of the intercommunity encounter reported by field assistants of both communities matched and data on the location of each community were
available. I used the location at the start of the intercommunity encounter and after one hour in assessing the tendency of movement of each community. I focused my analysis on the factors that influenced the probability of counter-calling and approaching only on the Mitumba community.

## **Statistical Analysis**

To examine the factors influencing vocal response I used logistic regression models with male's size categories (zero or one, two and three or more), number of females, party size and contested area (yes/no) as my explanatory variables and vocal response (yes/no) as my response variable. I ran three models and retained only statistically significant variables. I used the likelihood ratio test in selecting the best-fit model. For testing the readiness of the community to approach or avoid its rival community, I did a similar analysis but using male category sizes and contested area only as my explanatory variable. However, I first created two categories (quick/not quick) of response by the Mitumba community to approach or avoid its rival community after hearing them based on the distribution of the time the community used in responding its rival community (see below). I used two sample t-tests to assess difference in number of loud calls produced before and after the intercommunity vocal encounters and for testing difference in the number of calls produced in the contested area and in non-contested area. I performed all statistical tests with R software (R Development Core Team 2009) and considered significant with P-values  $\leq 0.05$ .

### RESULTS

During observations made on the Mitumba community between 1994 and 2007, 225 intercommunity encounters were recorded in which five were physical encounters, 10 were visual encounters and 210 were vocal encounters. Of these 225 intercommunity encounters, 57% of the encounters occurred when the Mitumba community was in the contested area and 43% occurred when the community was in the non-contested area. All of the physical encounters and most of the visual encounters occurred when the Mitumba community was in the contested area (Figure 3.1). However, for auditory encounters, 55% of the auditory encounters occurred when the Mitumba community was in the contested area and 45% occurred when the community was in non-contested area (Figure 3.1).

# **Vocal Response**

The Mitumba community increased significantly number of loud calls (Panthoots) after they heard calls of neighboring community (t (165) = 1.974, p<0.001). However, being in the contested area, did not predict whether the community would counter-call (Table 3.1). The time over which the community escalated in vocal exchanges ranged from 1 minute to 60 minutes with the mean duration of 22 minutes. There was no significant difference in duration of counter-calling by the community between the contested area and non-contested area (t (221) = 1.971, p= 0.08). The community was less likely to call when in male party zero or one (Table 3.1). However, probability of counter-calling increased when number of males in the party increased from zero or one to three and more (Figure 3.2).

## Latency of Counter-calling and Movement

After hearing calls of the neighboring community, the majority of vocal responses of the Mitumba community occurred within the first ten minutes of the intercommunity encounter (Figure 3.3). The number of females in the party did not account for the increase in number of calls (Adjusted R Square = 0.01; F<sub>1,173</sub> = 0.13, p= 0.7; Figure. 3.4) or duration (Adjusted R Square = 0.02; F<sub>1,173</sub> = 2.8, p= 0.1; Figure. 3.5) in which the community escalated in vocal exchanges.

Similarly, the Mitumba community moved towards it rival community (Figure 3.6) or away (Figure 3.7) from its rival mostly within the first ten minutes after the vocal encounter. However, neither male party size nor being in or out of the contested area influenced the probability of the community to approach (Table 3.2) or avoid its rival community (Table 3.3).

### **Matched Intercommunity Interactions**

There were 47 cases of intercommunity interactions in which intercommunity encounter time reported by field assistants of both Mitumba and Kasekela communities matched and other variables such as number of males in each community and location of intercommunity encounter were available. Of these 47 cases, 39 were vocal encounters, four were visual encounters and four were physical encounters. The average distance at the start of the intercommunity encounter was 1299 meters and after one hour of intercommunity encounter, the average distance increased to 1399 meters. Both the Mitumba and Kasekela communities showed a similar tendency to approach or avoid each other (Figure 3.8). However, the majority of intercommunity encounters occurred when the Kasekela community was in the range of the Mitumba community (Figure 3.9).

For the Mitumba community, most of the matched intercommunity encounters occurred when the Mitumba party contained two males. While there was a variation in the number of males of the Kasekela community, there was no much variation in male ratio (Mitumba males over Kasekela males, Figure 3.10). Thus, I could not test for the effect of number of males or male ratio on the outcome of territorial contests. Tests of the influence of the range location and initial distance of intercommunity encounter on vocal response of the community showed non-significant relationship (Table 3. 4).

## DISCUSSION

My data showed an increase in production of calls by the Mitumba community after they heard calls of their rival community. However, being in the contested area did not account for this increase. The male category size was the most important factor in improving chances of the community to counter-call. I discuss the findings and their implications for the smaller community of chimpanzees.

## **Vocal Response**

The Mitumba community increased their number of loud calls after they heard calls of their rivals. However, the community increased loud calls only when in number of males in a party was large. The location of the range during the intercommunity encounter did not appear to influence the probability of counter-calling by the Mitumba community. My results support the idea that chimpanzee loud calls evoke vocal responses from neighbors and that vocal encounters may function in regulating space between communities and serve as a component of territorial defense (e.g. Goodall 1986; Wilson *et al.* 2001; Wilson and Wrangham 2003; Watts et al. 2006). Furthermore, my results also illustrate the importance of male party size in intercommunity competition in chimpanzees.

Increase in production of loud calls by the Mitumba community can be an energetically expensive activity and risky to undertake. Loud calls require more energy to produce (Ghiglieri 1984; Riede et al. 2006) and can reveal location and identity of individuals (Wilson et al. 2001). In the short term, production of loud calls may also interfere with other social activities such as feeding, grooming or resting (Goodall et al. 1979; pers. observation). Thus, by engaging in energetically costly and risky activity, the Mitumba chimpanzees may be conveying information of their intent to defend their territory.

Chimpanzees in general seem to attend more to the costs of intercommunity encounters than to the benefits they might gain (Wilson et al. 2001; Wilson and Wrangham 2003; Watts et al. 2006). Therefore, the Mitumba community by advertising their presence especially when in a large party of males and revealing the potential cost of such an encounter, they may discourage the neighboring community from approaching them. This strategy may help the Mitumba chimpanzees to keep away the large Kasekela community and partly, may explain why the Mitumba community has been able to persist alongside the Kasekela community.

However, following hearing their neighbors, individuals of both communities did not always avoid contact with their neighbors (see below). This implies that vocal advertising may possibly also be serving another function. For example, by engaging in vocal exchanges even when the odds are against them, males may try to impress females and discourage them from leaving the community (e.g. Nishida et al. 1985, Pusey et al. 2008). In addition, males may use vocal encounters to show their quality and win the trust of a female when it comes to the time of taking her on a consortship. The number of females in the Mitumba community has increased over time despite the community possessing only two adult males for over eight years (Chapter 1) and consortships have been observed on the Mitumba community (pers. observation). However, whether these are proximate causes of the increased in number of calls by the community still needs further investigation, to tease apart calls made only by males and that made by females.

Location in the range at the time of the intercommunity encounter did not appear to influence the probability that the Mitumba community would counter-call. This was a surprising result given the expectation that an increase in discrepancy in fighting ability should have compelled the Mitumba community to prioritize its defensive effort and defend more high valuable areas. However, the average distance between parties during intercommunity encounters was quite high (about 1.3-km). Probably the high average distance between parties exerted lower threats to the use of available food. Nonetheless, like males of many other species (e.g. Trivers 1972; Emlen and Oring 1977), reproductive success of male chimpanzees may be limited by the access of males to females rather than to food. Therefore, Mitumba males may be more concerned about defending females rather than a physical location of their range and they may prepare to engage in vocal exchange with a rival community wherever females are located.

Study of females' distribution in the Mitumba community range has not been done. However, anecdotal evidence does not seem to support the hypothesis that the distribution of females may have some influence on the outcome of intercommunity encounters. Apart from one case that occurred on 10-June-2006, where alpha male Rudi rescued two Mitumba females from the Kasekela chimpanzees after he returned to the scene-displaying, males as well as females often run away from Kasekela chimpanzees (See below). Furthermore, the presence of females in the party during vocal exchange did not appear to influence the duration of an encounter nor the likelihood of counter-calling by the community.

### Latency of Counter-calling and Movement

The Mitumba community responded to calls of their rivals and moved towards or away from them mostly within the first ten minutes. This observation suggests that the first ten minutes following a vocal intercommunity encounter may be critical for the Mitumba community in assessing their competitive ability and on deciding on whether to escalate in a contest on not. Factors such as the location of the contest, the distance between the two communities or the number of males could aid individuals in deciding whether to approach or to avoid its rival community. However, I did not find that any of these factors (the location of the contest, distance between two communities or male party size) influenced the readiness of the community to approach or avoid its rival community.

### **Matched Intercommunity Interactions**

The average distance at the start of an intercommunity encounter was about 1.3km and after one hour, communities were apart by about 1.4-km. Neither community showed a tendency to approach or avoid more its rival community. Furthermore, neither the initial distance between the two communities at the start of intercommunity encounter nor the location of the Mitumba community appeared to influence vocal responses of the Mitumba community.

Both communities approached or avoided each other at about the same time. This was in contrast to what I expected given the higher fighting ability of the Kasekela community. At least two explanations can account for why the Kasekela community did not more often approach the Mitumba community. First, possibly because the majority of the encounters occurred in the range of the Mitumba community, the Kasekela community had less to lose in avoiding potentially costly encounters. In at least one case, the Mitumba chimpanzees were able to launch serious attacks that severely wounded and caused the death of one the Kasekela females who was in consortship with a Kasekela male (Wilson et al in prep; Wrangham et al. 2006 and Williams et al. 2007). This incident highlights the potential threat that the Mitumba community poses to the Kasekela community despite its lower fighting ability.

Second, individuals' participation in- and expectation from territorial contests also may have influenced the observed outcome. Chimpanzees live in a fission-fusion society (Nishida 1968; Goodall 1986). Therefore, any given encounter is likely to contain different individuals with different expectations and level of participation in territorial encounters. High-ranking males, for example, may expect more from territorial encounters and thus participate more significantly than lower- ranking males (Mitani and Watts 2001, but see Wilson et al. 2001). Therefore, difference in levels of expectations from success in territorial interactions among individuals possibly influenced how the Kasekela males engaged in territorial contest against the smaller Mitumba community despite its numerical superiority.

### CONCLUSION

My study showed the importance of male party size in territorial contests. The Mitumba community escalated in vocal exchanges only when the number of males in the party was large. Location in the range and distance between communities did not influence the probability of the community to counter-call. This study suggests that, despite huge imbalance in fighting ability, male chimpanzees in this population continue to engage in territorial encounters. While my studies did not find the location of the range to influence male chimpanzees in this population to engage in territorial encounters, the smaller range size, which remained after the community lost more than half of its original size (Chapter 1&2) possibly made each piece of land worth finding for. Thus, individuals in the smaller community in this population may be fighting for their life in each piece of their land.

# **FIGURE CAPTIONS**

**Figure 3. 10.** Distribution of type of the intergroup encounters in the contested and noncontested area

**Figure 3. 11.** Probability of counter-calling by the Mitumba chimpanzee community when parties contained different numbers of males.

**Figure 3. 12**. Histogram of the latency of counter-calling by the Mitumba chimpanzee community.

**Figure 3. 13.** Number of loud calls by the Mitumba chimpanzee community when parties contained at least one female.

**Figure 3. 14.** Duration of escalation in intercommunity contest by the Mitumba chimpanzee community when the parties contained at least one female.

**Figure 3. 15.** Histogram of the latency of approaching the rival chimpanzee community by the Mitumba chimpanzee community.

**Figure 3. 16.** Histogram of the latency of moving away from the rival chimpanzee community by the Mitumba chimpanzee community.

**Figure 3. 17.** Comparison of movements of the Mitumba and Kasekela chimpanzee communities after an intercommunity encounter (N = 47).

**Figure 3. 18.** Locations of the Kasekela chimpanzee community during intercommunity encounters. MCP = Minimum convex polygon.

**Figure 3. 10.** Distribution of the number of males of the Mitumba community over that of Kasekela community during an intergroup interaction.

**Table 3. 1.** Output from logistic regression model based on observations of countercalling by the Mitumba community (N= 225). Influence of male party size and contested area on the probability of counter-calling by the Mitumba community

Variable	Estimate	Std. Error	Ζ	Р
Intercept	1.253	0.802	1.562	0.828
Male group size two	-0.469	0.844	-0.555	0.579
Male group size zero or one	-2.639	0.977	-2.7	0.007
Contested area	0.134	0.923	0.145	0.885
Male group size two: Contested area	0.017	0.992	0.017	0.987
Male group size zero or one: Contested area	0.966	1.165	0.828	0.408

**Table 3. 2.** Output from logistic regression model based on observations of approaching rival community by the Mitumba community (N=61). Influence of male party size and contested area on the readiness of the Mitumba community to approach its rivals

Variable	Estimate	Std. Error	Ζ	Р
Intercept	-0.200	0.748	-0.267	0.789
Male group size two	0.330	0.714	0.462	0.644
Male group size zero or one	0.059	0.969	0.061	0.952
Contested area	0.571	0.603	0.947	0.343

**Table 3. 3.** Output from logistic regression model based on observations of avoiding rival community by the Mitumba community (N=91). Influence of male party size and contested area on the readiness of the Mitumba community to avoid its rivals

Variable	Estimate	Std. Error	Ζ	Р
Intercept	0.2067	0.6049	0.342	0.733
Male group size two	-0.4548	0.5584	-0.814	0.415
Male group size zero or one	-0.3526	0.6810	-0.518	0.605
Contested area	-0.1161	0.4700	-0.247	0.805

**Table 3. 4.** Output from logistic regression model based on observations of vocal encounters of both the Mitumba and Kasekela communities (N=43). Influence of the contested area and initial distance of intercommunity encounter on the probability of counter-calling by the Mitumba community

Variable	Estimate	Std. Error	Z	Р
Intercept	2.177	1.428	1.524	0.128
Contested area (Yes)	0.504	1.010	-0.499	0.618
Initial distance of encounter	-0.0002	0.001	-0.254	0.799



Figure 3.1. Distribution of type of encounters in the contested and non-contested area



**Figure 3. 2.** Probability of counter-calling by the Mitumba community when parties contained different numbers of males.



**Figure 3. 3**. Histogram of the latency of counter-calling by the Mitumba chimpanzee community.



**Figure 3.4.** Number of loud calls by the Mitumba chimpanzee community when parties contained at least one female.



**Figure 3. 5.** Duration of escalation in intercommunity contest by the Mitumba chimpanzee community when parties contained at least one female.



**Figure 3.6.** Histogram of the latency of approaching the rival chimpanzee community by the Mitumba chimpanzee community.



**Figure 3. 7.** Histogram of the latency of moving away from the rival chimpanzee community by the Mitumba chimpanzee community.



**Figure 3. 8.** Comparison of movements of the Mitumba and Kasekela chimpanzee communities after an intercommunity encounter (N = 47).



**Figure 3. 9.** Locations of the Kasekela community during intercommunity encounters. MCP = Minimum convex polygon.



**Figure 3.10.** Distribution of the number of males of the Mitumba community over that of Kasekela community during an intergroup interaction.

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