IMBALANCES OF POWER:

HOW CHIMPANZEES RESPOND TO THE THREAT OF INTERGROUP AGGRESSION

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ABSTRACT

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Imbalances of Power:
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Male chimpanzees (Pan troglodytes) defend group territories and sometimes kill members of other groups. Most hypotheses attempting to explain such attacks focus on the benefits gained from resource competition. In contrast, the imbalance-of-power hypothesis focuses on the costs of aggression, arguing that lethal attacks occur when the costs to attackers are low. To increase our understanding of lethal intergroup aggression, I tested predictions of the imbalance-of-power hypothesis for wild chimpanzees.

Lethal intergroup aggression can have profound fitness consequences for chimpanzees, but occurs infrequently and is difficult to observe when it does occur. Instead of waiting for such rare events to occur, I used systematic observations, playback experiments, and mathematical models to examine behavior during two types of elevated intergroup threat. First, I tested whether ranging, grouping and vocal behavior changed near the boundaries of other communities. Second, I conducted playback experiments to test factors underlying response to a simulated intruder.

I tested seven main predictions, and found clear support for five: chimpanzees (1) avoided borders; (2) traveled in large parties when visiting borders; (3) called and approached a simulated intruder whenever they had sufficient numerical advantage; (4) called and approached a simulated intruder regardless of range location; and (5) approached faster when predicted net benefits were greater. I found qualified support for the two remaining predictions. First, males were predicted to visit borders more often than females. Males did range more widely than females, but “peripheral” females spent more time near borders than males. Second, chimpanzees were predicted to suppress loud call production during border patrols and other contexts of increased threat. Chimpanzees did stay quiet when raiding crops. During border visits, chimpanzees tended to give fewer loud-calls; this decrease bordered on statistical significance. More work is needed to distinguish patrols (when silence is predicted) from other types of border visit, in which vocal advertising might be expected.

Overall, these results support the imbalance-of-power hypothesis, and suggest that coalitionary killing should be ubiquitous in species with hostile intergroup relations and opportunities for low-cost attacks. Most human societies, including small-scale foraging societies, appear to satisfy these conditions.

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To Becky

Who quit her job, sold her house, and left her dog

to walk a ways with me.

CHAPTER ONE

INTRODUCTION

1.1 OVERVIEW

Each year, millions of people are killed, injured, or dispossessed by warfare, genocide, ‘ethnic cleansing,’ and other forms of lethal intergroup aggression. That humans should be so willing and able to kill their neighbors not only causes untold suffering, but also presents an intriguing problem for behavioral biology. Lethal intergroup aggression appears to be quite rare in nature (Huntingford & Turner 1987; van der Dennen 1995; Wrangham 1999). Until the observation of brutal intergroup attacks by chimpanzees (Pan troglodytes), many argued that such behavior was unique to humans and our immediate ancestors (Lorenz 1966). Field studies have shown that in addition to chimpanzees, lethal intergroup aggression occurs in a number of other species, including many ants (Hölldobler & Wilson 1990) and several social carnivores (Gittleman 1989; Wrangham 1999). Attempts to understand human warfare, however, continue to emphasize the many parallels between humans and our chimpanzee cousins (Trudeau et al. 1981; Otterbein 1985; Goodall 1986; Alexander 1987; Ghiglieri 1987; 1988; Alexander 1989; van Hoof 1990; Hamburg 1991; Manson & Wrangham 1991; Boehm 1992; van der Dennen 1995; Wrangham & Peterson 1996; Otterbein 1997; Ghiglieri 1999; Boesch & Boesch-Achermann 2000). Nevertheless, nearly three decades after the first observations of intergroup killing in chimpanzees, the mechanisms underlying such attacks remain disputed. In this study, I seek to add to our understanding by testing theoretical predictions of how chimpanzees should respond to the threat of intergroup aggression.

Understanding the behavioral biology of lethal intergroup aggression has great practical and theoretical importance. In practical terms, a better understanding of the relevant mechanisms may help us reduce the frequency and severity of warfare and other violent conflicts. In theoretical terms, lethal intergroup aggression appears to be a remarkably cooperative endeavor, and raises many questions about the evolution of such cooperation. Moreover, various authors have argued that lethal intergroup aggression has been a powerful selection force in human evolution, resulting in such hallmark human traits as dramatically advanced cognitive and communicative powers (Darwin 1871), extreme levels of cooperation including state formation, and even a moral sense (Alexander 1987). Understanding lethal intergroup aggression in chimpanzees seems a crucial step towards understanding ourselves.

Several striking parallels exist between intergroup aggression in humans and chimpanzees. In both species, intergroup aggression is largely the business of males, who tend to be philopatric (Manson & Wrangham 1991; Rodseth et al. 1991) and hence more closely related to one another than females (Morin et al. 1994). Both species prefer to attack their rivals during surprise ambushes (“raids” or “gang attacks”) in which attackers kill at low risk to themselves (Manson & Wrangham 1991). Over a 20-year period at Gombe, intergroup aggression accounted for 30% of adult male mortality (Goodall 1986), a rate similar to human groups with endemic warfare such as the Yanomamö

(Chagnon 1988). Human warfare regularly leads to group extinctions (Soltis et al. 1995). Repeated lethal attacks caused the extinction of one and probably two chimpanzee communities in Tanzania; in both cases, the surviving community recruited at least some of the remaining adult females and expanded territory (Goodall et al. 1979; Nishida et al. 1985).

Many attempts have been made to explain the observed patterns of lethal intergroup aggression in chimpanzees and humans, but hypothesis testing has been limited by the scarcity of the relevant data. Intergroup interactions occur infrequently, and when they do, they are difficult to observe. Good observations require that neighboring communities be habituated; otherwise, the neighboring chimpanzees simply run away on seeing researchers. Chimpanzees take many years to habituate, and most study sites focus on a single habituated group. In the 1970s, neighboring groups were habituated at Gombe and Mahale, but at both sites the larger community apparently destroyed the smaller community. A promising development is that neighboring communities are being habituated at several sites today (Gombe: Stanford (1998); Taï: Herbinger et al. (2001); Ngogo: Watts & Mitani (in press)). Nevertheless, the only direct observations of intergroup killing remain the five attacks observed at Gombe. The only group exterminations reported are the certain case of Kahama at Gombe and the likely case of K-Group at Mahale.

Four of the most prominent explanations of lethal intergroup aggression in chimpanzees are: “Cultural Bias”, “Human Influence”, “Male Philopatry,” and “Imbalance-of-Power.” I discuss each of these below.

Cultural Bias

Some critics argue that the evidence for lethal intergroup aggression in chimpanzees is weak, and that cultural biases lead to inappropriate comparisons with human warfare. For example, Sussman (1997) argues that while chimpanzees do behave aggressively, lethal attacks are rare and presumably of little consequence for chimpanzee social evolution. Chimpanzee violence receives undue attention because it fits certain cultural expectations, such as a belief that human beings are inherently sinful (Sussman 1997). Sussman (1997) makes no testable predictions regarding the frequency or intensity of chimpanzee aggression, so it is difficult to falsify his claims. Nevertheless, at least four reasons suggest that intergroup aggression is a real and pervasive force in chimpanzee lives, not simply an imposition of the cultural expectations of scientists. First, in a long-lived, slowly reproducing species such as chimpanzees, fatal attacks are necessarily rare. As mentioned above, the handful of attacks observed at Gombe added up to 30% of the adult males in the population dying from intergroup aggression (Goodall 1986). If chimpanzees killed their neighbors at a much higher rate, they would rapidly run out of neighbors to kill. Second, rather than fulfilling cultural expectations of researchers, the brutal attacks came as a disquieting surprise to researchers (Goodall 1986; Wrangham & Peterson 1996), who had been describing chimpanzees as peaceful creatures whose aggressive displays had more bluff than bite (Goodall 1968). Third, accumulating evidence at long-term study sites across Africa indicates that aggressive territoriality, coalitionary killing, and cannibalistic infanticide are typical of chimpanzees (Nishida 1996; Wrangham 1999; Boesch & Boesch-Achermann 2000; Fawcett & Muhumuza 2000; Watts & Mitani 2000). Fourth, as indicated by the sources just cited, people who have observed chimpanzees in the wild generally agree about the role of aggression in chimpanzee lives, whether their cultural background is Japanese, European, American, or African.

Human Influence

Some authors have taken the scarcity of data as evidence that such attacks are not in fact “natural” for chimpanzees, but instead are the result of human disturbance. In particular, Power (1991) argues that the lethal attacks observed at Gombe were the result of the history of banana provisioning at Gombe. Power suggests that the reduction of provisioning in the 1970s led to frustration, which led to increased levels of aggression. In the absence of provisioning, chimpanzees should live in peaceful, egalitarian societies.

In contrast to such claims, the previously cited evidence from long-term studies in which provisioning has never taken place suggests that hostile intergroup relations are typical of chimpanzees. In addition, the frustration hypothesis cannot explain why provisioning led to intergroup killing in chimpanzees but not baboons, despite the many bananas taken by baboons at the provisioning station (Wrangham 1999).

Male Philopatry

Of the various explanations proposed for coalitionary killing in humans and chimpanzees, perhaps the most prominent is the “male philopatry” hypothesis (Ghiglieri 1987; Alexander 1989; Nishida 1991; Boehm 1992), which emphasizes the importance of competition for food, females and territory among groups of related males. Nishida (1991) summarizes this model succinctly: “Males affiliated genetically by philopatry may form a strong cooperative task force that enables them to raid neighboring groups. Sexual selection working through competition among individuals may originally have favored various masculine physical and behavioral characteristics in fighting and subsequently favored the evolution of the tendency toward ‘imperialistic’ expansionism among males, who can maximize reproductive success by gaining more resources and hence more females.”

Many features of this hypothesis seem plausible. Winners of intergroup fights likely do gain improved access to such resources (Williams 2000), and as discussed above, most human societies share with chimpanzees a tendency towards male philopatry. Nevertheless, this hypothesis fares poorly in explaining the distribution of lethal intergroup aggression among other species. Competition for resources seems a necessary but not sufficient condition for lethal intergroup aggression. Groups in many species compete over resources, yet such competition is rarely lethal (Cheney 1987). Likewise, male philopatry is neither necessary nor sufficient for coalitionary killing. Wolves (Canis lupus) in Minnesota and Alaska experience higher levels of mortality from intraspecific attack than most human or chimpanzee populations (Mech et al. 1998). Philopatry is not sex-biased in wolves, and both sexes are killed at high rates (Mech et al. 1998). Both spotted hyenas (Crocuta crocuta) and lions (Panthera leo) are female-philopatric, and females in both species participate in coalitionary killing (Kruuk 1972; Packer et al. 1988). Many species with male philopatry show no evidence of coalitionary killing, including bonobos, Pan paniscus (Kano 1990); hamadryas baboons, Papio hamadryas, (Kummer 1995); red howler monkeys, Alouatta seniculus (Sekulic 1982); and most populations of red colobus, Colobus badius (Struhsaker 1975). In the one red colobus population with evidence of coalitionary killing, females joined with resident male(s) to attack potentially infanticidal extragroup males (Starin 1994).

Imbalance-of-Power

A more promising theoretical perspective is the ‘imbalance-of-power’ hypothesis (Manson & Wrangham 1991; Wrangham & Peterson 1996; Wrangham 1999). This model is especially attractive in that it is the only one to focus on the costs of aggression as well as the benefits. According to this hypothesis, coalitionary killing should occur for any species satisfying two conditions: intergroup hostility and sufficient variation in party size. Variation in party size creates opportunities to reduce the coalitionary strength of rival groups at little risk to the aggressors. Other species with lethal intergroup aggression, such as wolves, lions, and spotted hyenas, appear to satisfy both conditions (reviewed in Wrangham 1999).

In this study, I tested several predictions of the imbalance of power hypothesis. Although existing data generally support this hypothesis (Wrangham 1999), the present study is the first attempt to collect data specifically designed to test the model's predictions. Instead of relying on direct observations of intergroup attacks, I used two indirect methods. First, using border zones as a proxy of intergroup threat, I examined how grouping and vocal behavior were effected by range location. Second, I used playback experiments to simulate intrusions by foreign males. Playback experiments have been widely used in studies of birds and other primates, but this study marks the first successful use of playbacks with chimpanzees.

1.2 ORGANIZATION OF THIS STUDY

Chapters Two through Five are written as self-contained units, with each chapter giving details of the hypotheses tested and methods used. Chapter Four is currently in press (Wilson et al. 2001) and chapter Five is currently in review (Wilson et al. in review).

In Chapter Two, I analyze the ranging behavior of the study community. Lethal intergroup attacks occur infrequently, but the risk of such attacks should influence ranging behavior profoundly. I tested three main predictions. First, to reduce the risk of being attacked by neighbors, both males and females should avoid borders (Wrangham 1999; Herbinger et al. 2001). Second, males, who are more involved in territory defense, should visit borders more often than females (Chapman & Wrangham 1993). Third, when visiting borders, males should travel in larger parties to increase the chances of winning intergroup encounters (Manson & Wrangham 1991).

In Chapter Three, I examine the effects of range location on vocal communication. Specifically, I test whether chimpanzees suppress the production of their loudest and most conspicuous call, the 'pant-hoot,' when visiting border areas and when crop-raiding. Many observers have reported that chimpanzees suppress pant-hoots when patrolling borders (Goodall et al. 1979; Boesch & Boesch-Achermann 2000; Watts & Mitani in press), but this claim has not been supported by quantitative data. Moreover, contrasting predictions can be made for the production of pant-hoots in border areas. First, chimpanzees should suppress pant-hoots to increase the chances of making surprise attacks on vulnerable neighbors (Manson & Wrangham 1991). Second, chimpanzees should maintain or increase their rate of pant-hoot production to advertise ownership or claim possession of disputed territory (Clark 1991). A thorough test of this issue proved beyond the scope of this study. Instead, I focused on the suppression of calls when crop-raiding, an activity which may be functionally similar to raiding food resources of neighboring communities.

In Chapter Four I describe a series of playback experiments, in which I tested whether the response to a single male intruder depended on numerical assessment, range location, or the dominance rank of the defender(s). These experiments permitted a test of two of the key predictions of Manson & Wrangham (1991). First, attacks should take place only in cases of overwhelming numerical superiority. I tested this by playing the call of a single intruder to parties of varying size and composition. Second, attacks should occur whenever opportunities arise. I tested this by conducted playbacks at the center and edge of the study group's territory. Studies of several other territorial species have found that individuals respond more aggressively towards intruders at the center than the edge of their range (Falls 1982; Mitani 1985). In contrast, if the goal of attacking is not primarily to defend territory, but rather to reduce the coalitionary strength of the neighboring group, individuals should be willing to attack whenever they have a numerical advantage, regardless of range location.

The playback experiments also provided an opportunity to examine the mechanisms underlying cooperative intergroup aggression in chimpanzees. Defense against intruders is a classic collective action problem (Nunn 2000). If benefits are shared among a group of actors, it will pay some actors to become "free-riders", benefiting from the fruits of others' labors. One solution to a collective action problem is to reduce the number of actors (in essence, taking the "collective" out of the action). For instance, if mating success is strongly correlated with rank, high-ranking males will stand to benefit more from excluding extragroup males, and should therefore be expected to participate more in excluding intruders. If participation in excluding extragroup males does not depend on rank, the collective action problem must be solved through some other means, such as kin selection or mutualism.

Chapter Five represents an attempt to broaden the perspective on lethal aggression by incorporating predictions based on Lanchester's theory of combat (Lanchester 1916).

Wrangham and colleagues have focused attention on "gang-attacks," in which many individuals attack a single victim (Manson & Wrangham 1991; Wrangham & Peterson 1996; Wrangham 1999). Despite the clear importance of gang-attacks in chimpanzee and human societies, other patterns of lethal aggression are theoretically possible and do in fact occur in humans and other species. In addition to gang-attacks, lethal fights may involve duels (one competitor on each side) or battles (multiple competitors on each side). Lethal duels, once thought to be rare, have been observed in a variety of species (e.g. fig wasps (West et al. 2001), mountain goat Oreamnos americanus and bighorn sheep Ovis canadensis (Geist 1975), pronghorn antelope Antilocapra americana (Byers 1997), musk oxen Ovibos moschatus (Wilkinson & Shank 1976)) and may account for a substantial portion of adult mortality. Lethal battles are more rare, but occur in several species of ant (e.g. Adams (1990)), are common among human societies, and have been observed in lions (Grinnell et al. 1995). Moreover, battles include a variety of strategies. Battles may be fought either as a series of duels, as in slave-making ant (Franks & Partridge 1993), Homeric heroes (Homer 1951 (c. 850 BCE)) and medieval knights (Keegan 1976), or they may be fought in concentrated attack, as in army ants (Franks & Partridge 1993), and many human battles since the advent of archery and other missile technology (Keegan 1976). A general theory seeking to explain lethal aggression should encompass these different strategies.

Models based on Lanchester's theory seem a promising step towards a general theory of lethal aggression. Like the imbalance of power theory, Lanchester's models emphasize the importance of assessment in the decision to enter a contest. All else being equal, individuals should only attack if they expect to win. Lanchester focuses not only on numerical assessment, but also on assessment of individual fighting value. The decision to attack should be based on a prediction of attrition, in which the loser suffers greater losses. Lanchester proposed two models of attrition, the “square law” and the “linear law”, which focus on different battle strategies. The linear law describes attrition when battles are fought mainly as a series of duels. In linear law battles, individual fighting value can matter as much or even more than relative numbers. The square law describes attrition when battles are fought in concentrated attack. In this case, the relative number of fighters on each side matters much more than individual fighting value. Gang-attacks in chimpanzees, humans, wolves and other species can be considered a special case of the square law, in which many individuals concentrate attack on a single victim. In collaboration with mathematician Nicholas Britton and entomologist Nigel Franks, I tested whether the response to playback experiments followed the predictions of the square law, and speculated on possible applications of this theory to other species.

In Chapter Six I discuss the results of this study and suggest directions for future research.

1.3 OVERVIEW OF METHODS

This section serves as a general methodological overview. More detailed methods will be given for each of the following chapters.

Study site and subjects

I studied the Kanyawara community of chimpanzees (Pan troglodytes) living in Kibale National Park, Uganda. The study site, described in detail elsewhere (Struhsaker 1997), is located at 0° 34' north latitude and 30° 21' east longitude. The rolling terrain varies in elevation from 1500 to 1700 m. Vegetation within the park includes a mosaic of moist evergreen forest, colonizing forest, papyrus swamp, and exotic softwood plantations. Outside the park, relict forest patches and swamps exist in a patchwork dominated by smallholder farms and tea plantations. Makerere Biological Field Station maintains a trail system within the park covering approximately 12 km^2 (Chapman & Wrangham 1993). New trails cut during the study period increased the accessible area considerably, especially in the north, west, and southwest of the Kanyawara community's home range. Chimpanzees spent most of their time within the park but sometimes traveled outside the park to visit forest patches and raid the crops of villagers.

Table 1.1 List of study subjects, giving name, two-letter identity code, sex, age-sex class (Adult, Subadult, Juvenile, or Infant), year of birth, death, immigration and emigration, and mother for adults and subadults (a) and infants and juveniles (b). Age estimates from Wrangham (unpublished data).

(a) Adults and subadults.

Name	ID	Sex	Age-Class	Birth	Death	Immig.	Emig.	Mother
Badfoot	BF	M	A	1966	1998			
Big Brown	BB	M	A	1966				
Imoso	MS	M	A	1975				
Johny	AJ	M	A	1975				
Lamy	LM	M	A	1950	1996			
Light Brown	LB	M	A	1968				
Makoku	LK	M	A	1982				Lope
Slim	SL	M	A	1971				
Stocky	SY	M	A	1964				
Stout	ST	M	A	1955				
Tofu	TU	M	A	1960				
Yogi	YB	M	A	1973				
Kakama	KK	M	S	1985				Kabarole
Auntie Rose	AR	F	A	1943				
Bubbles	BL	F	A	1960				
Ekisigi	EK	F	A	1974				
Finger	FG	F	A	1955	1998			
Gombe	GO	F	A	1957				
Josta	JO	F	A	1960				
Kabarole	KL	F	A	1970				
Lia	AL	F	A	1982		1994		
Lope	LP	F	A	1955				
Muguru	MG	F	A	1945	1997			
Mususu	MU	F	A	1970				
Ngonya	NG	F	A	1965	1997			
Outamba	OU	F	A	1979		1992		
Pepsi	PE	F	A	1970				
Stump	PU	F	A	1955				
Tongo	TG	F	A	1980				
Umbrella	UM	F	A	1981		1995		
Bwindi	BW	F	S	1985		1996	1996	
Nile	NL	F	S	1983		1997		
Nyenka	NE	F	S	1983			1998	Auntie Rose?
Wire	WR	F	S	1982			1996	

Table 1.1(continued)

(b.) Juveniles and infants

Name	ID	Sex	Age-Class	Birth	Death	Immig.	Emig.	Mother
Cola	PC	M	J	1992				Pepsi
Edward	ED	M	J	1988				Ekisigi
Ngonzi	JZ	M	J	1986	1996			Josta
Twig	PG	M	J	1988				Stump
Barbara	BR	F	J	1989				Bubbles
Goodall	GA	F	J	1991				Gombe
Kaana	JK	F	J	1992				Josta
Nectar	FN	F	J	1989	1998			Finger
Rosa	LR	F	J	1989				Lope
Sanyu	AS	F	J	1990				Auntie Rose
Bud	PB	M	I	1995				Stump
Eslom	ES	M	I	1994				Ekisigi
Kabila	AK	M	I	1997	1998			Lia
Kaboyo	KB	M	I	1998				Kabarole
Lanjo	TJ	M	I	1995				Tongo
Mandela	AM	M	I	1998				Auntie Rose
Pollen	FP	M	I	1996	1998			Finger
Temba	MB	M	I	1994	1996			Mususu
Uganda	UG	M	I	1996				Umbrella
Beatle	BE	F	I	1995				Bubbles
Budongo	BU	F	I	1997				Bubbles
Ipassa	LS	F	I	1996				Lope
Kilimi	OK	F	I	1994				Outamba
Omuga	KO	F	I	1993	1996			Kabarole
Tenkere	OT	F	I	1998				Outamba

The Kanyawara community contained 49 - 53 individuals during the study period (June 1996 - December 1998), including 11 adult males and 15 - 16 adult females, all of whom were individually recognized (Table 1.1). Ghiglieri conducted occasional observations of this community in 1976-78, during a study focusing on the nearby Ngogo community (Ghiglieri 1984; Ghiglieri 1988). Isabirye-Basuta initiated systematic study in 1983 (Isabirye-Basuta 1989), and the community has been studied continuously since 1987 (Hauser 1990; Wrangham et al. 1992; Wrangham et al. 1996). At the time of the present study, habituation was good for all of the commonly seen individuals, consistently allowing observations from 10 m or less. Some rarely seen individuals remained skittish, and several adult females were shy and difficult to follow when traveling alone. As is typical of chimpanzees studied elsewhere, males in this population breed in their natal communities, whereas females typically disperse before breeding.

Time frame

I conducted research in three field seasons: a pilot season (June — August 1996) and two longer field seasons (April —December 1997 and March – December 1998) for a total of approximately 21 months in the field. During the pilot season I conducted six playback experiments, began learning to identify the chimpanzees, recorded calls, conducted pilot focal follows, and trained a field assistant, John Barwogeza. During the 1997 field season I conducted 18 complete playback experiments and recorded calls. I trained a second field assistant, Donor Muhangyi, who together with J. Barwogeza conducted the bulk of the focal and party follows. During the 1998 field season I conducted the final six intergroup playback experiments and two pilot experiments using within-group calls. I continued with recording and observational data collection. I served as Field Manager of Kibale Chimpanzee Project (KCP) during the 1997 and 1998 field seasons.

Data collection

This study depends on three sets of data. First, KCP field assistants collected party composition data as described in Chapter Two. Second, D. Muhangyi, J. Barwogeza and I collected focal and party follows as described in Chapter Three. Third, I conducted playback experiments with the help of field assistants, as described in Chapter Four. I devoted much of my time in the field to collecting a fourth set of data, recordings of chimpanzee calls. These recordings served two main purposes. First, I obtained stimuli for within-community playback experiments. Second, I collected a sufficiently large set of calls (over 340) to enable a test of which acoustic cues correlate best with body size in chimpanzees. This body of calls served as the basis for R. Gupta's senior honors thesis (Gupta 2001) which I supervised in collaboration with T. Fitch.

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CHAPTER TWO

EFFECTS OF BORDER ZONES ON GROUPING AND RANGING

2.1 SUMMARY

I examined ranging and grouping patterns to test whether chimpanzees modify their behavior in response to the threat posed by borders with neighboring communities. I focused on three predictions of the imbalance-of-power hypothesis: (1) chimpanzees should avoid borders; (2) males should range more widely and visit borders more often than females; and (3) chimpanzees should be more likely to visit borders when traveling in parties with more males. The results support these three predictions, with some qualifications. Chimpanzees generally avoided border areas, with 90% of observations occurring in the central 40% of their Total Range. Males ranged more widely, using larger individual home ranges than females. Females appeared to adopt one of two ranging strategies: "central" or "peripheral." Central females used home ranges located towards the center of the Total Range, whereas peripheral females used ranges located closer to borders. Males spent more time near borders than central but not peripheral females. Parties visiting borders contained more males than parties that remained in the central Core.

2.2 INTRODUCTION

Defense of territories can lead to the creation of areas between adjacent territories that are dangerous for residents of either territory to enter. These areas have been described as “buffer zones” (Hickerson 1965; Mech 1977; Deboer 1981), “no-mans-lands” (Myers 1976), and “war zones” (Martin & Szuter 1999). Entering a buffer zone probably entails costs for many territorial species, given the increased risk of encountering neighbors and being forced to display, fight, flee or otherwise expend energy. The costs for entering a buffer zone should be particularly high, however, for species with lethal intergroup aggression. Not surprisingly, then, the best descriptions of buffer zones are for species with a high rate of intergroup killing, such as many species of ants (Hölldobler 1979; Mabelis 1979; Adams 1990; Pezzolesi & Hager 1994), wolves (Mech 1977; 1994), and humans (Hickerson 1965; Myers 1976; Deboer 1981). Chimpanzees (<u>Pan</u> <u>troglodytes</u>) defend territories and sometimes injure and kill members of neighboring groups (Goodall et al. 1979; Nishida 1979; Goodall 1986; Watts & Mitani 2000; in press). Chimpanzee territories generally include extensive areas of overlap with neighboring communities (Goodall 1986; Herbinger et al. 2001). Evidence reviewed below suggests that these overlap areas function as buffer zones. In this chapter, I test whether chimpanzees modify their grouping and ranging behavior in potential buffer zones, as predicted by the imbalance-of-power hypothesis (Manson & Wrangham 1991; Wrangham 1999).

I focus on three predictions. First, if border zones are dangerous, individuals should visit borders less often than expected. Second, members of the sex that invests most in territorial defense should range more widely, visiting borders more often. Third, since success in intergroup fights likely depends on relative numbers, individuals should be more likely to visit borders when traveling in large subgroups (“parties”). Existing data for chimpanzees provide some support each of these predictions (chimpanzees avoid borders: (Herbinger et al. 2001); males visit borders more than females: (Chapman & Wrangham 1993); subgroups have more males border areas: (Bauer 1976)). This study builds on previous work by (1) using quantitative methods to examine all three questions for a single study community; (2) taking advantage of increased habituation and improved understanding of ranging behavior of the study community; (3) using three years of data to gain a more complete picture of ranging behavior than is possible in shorter studies (such as the ten months examined by Herbinger and colleagues (2000)); and (4) examining feeding behavior as a possible influence on grouping patterns. In the following sections, I discuss each of the three predictions in more detail, with reference to available data from chimpanzees and other species with lethal intergroup aggression and territorial defense.

Border avoidance

Buffer zones clearly represent a region of increased mortality risk for several species with territorial defense and lethal intergroup aggression. In particular, humans, wolves, and various species of ants appear to avoid borders. Among humans, buffer zones commonly form between warring groups in both small- and large-scale societies (Hickerson 1965; Myers 1976; Deboer 1981; Martin & Szuter 1999). Borders between large, mutually hostile states often include small, weak nations explicitly created or treated as buffer states, such as the Eastern Bloc nations between NATO and the Soviet Union (Chaliand & Rageau 1985). Having worked in western Uganda during a time of chronic rebel activity, I can personally attest to the strong inclination of humans to avoid regions of intergroup conflict.

Apart from humans, the most detailed mammalian data are available for wolves (Canis lupus). In northeastern Minnesota, most wolves killed by conspecifics were found near territory borders, with 41% of wolf-killed wolves found within 1 km of the estimated border of their territory (Mech 1994). Wolves generally avoid buffer zones and select dens that are relatively far from borders (Ciucci & Mech 1992). Ants of several species appear to avoid the edges of their territories, producing a “no-ants-land” (Hölldobler 1979; Mabelis 1979; Adams 1990; Pezzolesi & Hager 1994).

The border avoidance resulting from intergroup strife can lead to increased prey densities in buffer zones. White-tailed deer (Odocoileus virginianus) are more abundant in the buffer zones between wolf territories (Mech 1977), and analyses of historical records indicate that white-tailed deer were also more abundant in the buffer zones between warring Native American nations (Hickerson 1965; Martin & Szuter 1999). Hickerson documents that in Minnesota in the 18th and 19th century, both Sioux and Chippewa Indians relied on hunting deer, which were more populous in the buffer zone between these warring tribes. A truce between the tribes led to rapid depletion of the deer population, which in turn led to famine and a resumption of hostilities (Hickerson 1965). In some areas today, the disruptions caused by armed conflict contribute to the conservation of wildlife (Kim 1997; Davalos 2001). Chimpanzees at Gombe prey primarily on red colobus monkeys (Colobus badius), which live in larger groups in the buffer zones between chimpanzee territories (Stanford 1998).

Quantitative and anecdotal studies at several sites suggest that chimpanzees avoid borders, spending most of their time in small core areas (reviewed in Herbinger et al. 2001). For example, chimpanzees in three communities in Taï Forest, Côte d'Ivoire, spent 75% of their time in core areas accounting for 19 to 29% of their total range (Herbinger et al. 2001). In contrast, Chapman & Wrangham (1993) found that at Kanyawara, chimpanzees did not spend significantly more time in the core than the periphery, as measured by the index of dispersion. Analysis of more recent data from Kanyawara (Wilson et al. 2001) suggests that Chapman & Wrangham's (1993) result may have been biased by incomplete knowledge of the extent of the community's range. Wilson and colleagues (in press) found that from 1996 to 1998, the Kanyawara community used a range of 37.8 km^2, 2.5 times larger than the 14.9 km^2 estimated by Chapman & Wrangham (1993). This increased estimate probably results from improvements in habituation and tracking of chimpanzees, rather than an expansion by the study community (see Methods). I therefore examine recent data to test whether Kanyawara chimpanzees use their territory in a clumped manner, avoiding edges, as reported for other populations.

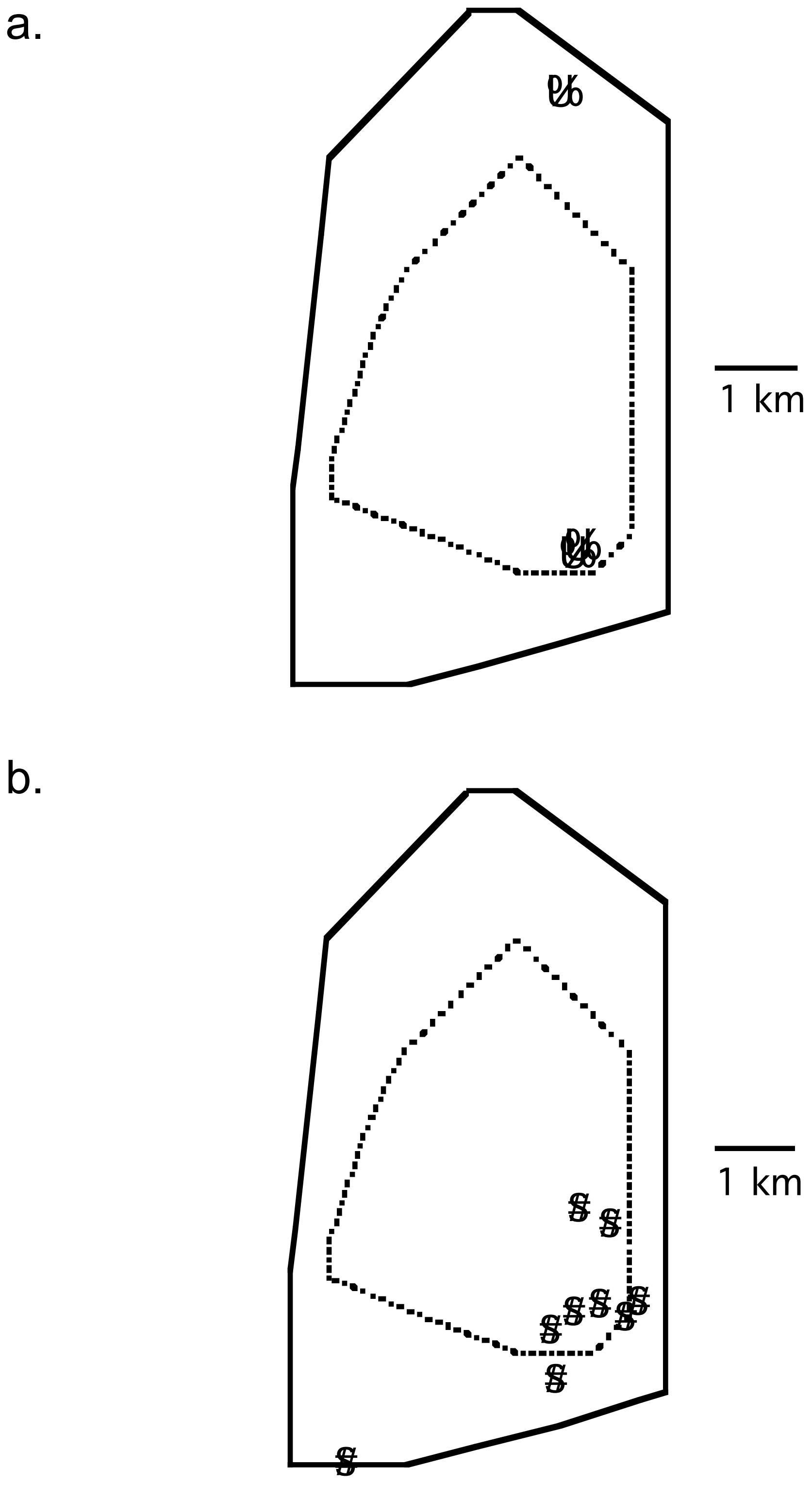
That borders represent an increased mortality risk for chimpanzees is supported by the locations of various intergroup interactions, including vocal exchanges, encounters within visual range, and lethal attacks (Wrangham, unpublished data; Fig. 2.1). The known and suspected lethal attacks documented at Kanyawara all occurred in border areas. In 1988, the body of an adult was found 350 m inside the current Nesting Range. Cause of death was uncertain, but evidence including the location and an apparently full stomach at time of death suggests it may have been killed by chimpanzees. In 1992, foreign chimpanzees killed a subadult male from Kanyawara in the same region, 290 m inside the Nesting Range. In 1998, Kanyawara males killed a male from the Sebitole community 1080 m north of the Nesting Range.

Sex differences in ranging

Few studies have reported sex differences in ranging patterns for territorial species with lethal intergroup aggression. In ants, all workers and soldiers are female, so that territorial defense is exclusively the business of females. In wolves, both sexes defend territories and appear to face similar mortality risks from intergroup aggression (Mech 1994). For a variety of primates with fission-fusion social organization, including both humans and chimpanzees, the sex with the longer day range participates more actively in territory defense (Wrangham & Wilson in review).

Figure 2.1 Locations of intergroup interactions. These data cover varying time periods based on available records and are intended to give an overall sense of the geography of intergroup relations at Kanyawara. The bold outer line encloses the Total Range, while the dotted inner line encloses the Nesting Range. Symbols indicate the locations of (a) chimpanzees known (two cases) or suspected (one case) to have been killed during intergroup encounters, 1988-1998; (b) vocal exchanges between Kanyawara and foreign chimpanzees, 1996-1998; (c) direct encounters in which Kanyawara chimpanzees saw foreign chimpanzees, 1992-1999; and (d) sightings of foreign chimpanzees by human observers when Kanyawara chimpanzees were absent, 1993-1998. The only identified individuals from neighboring communities belong to “Gusaziire’s Community,” shown in the cluster of sightings starting to the west of the park and progressing towards the center of the Nesting Range. Gusaziire’s community made their deepest observed incursion, 500 m from the park boundary and 980 m within the Nesting Range, in January 1996.

Figure 2.1 (continued)



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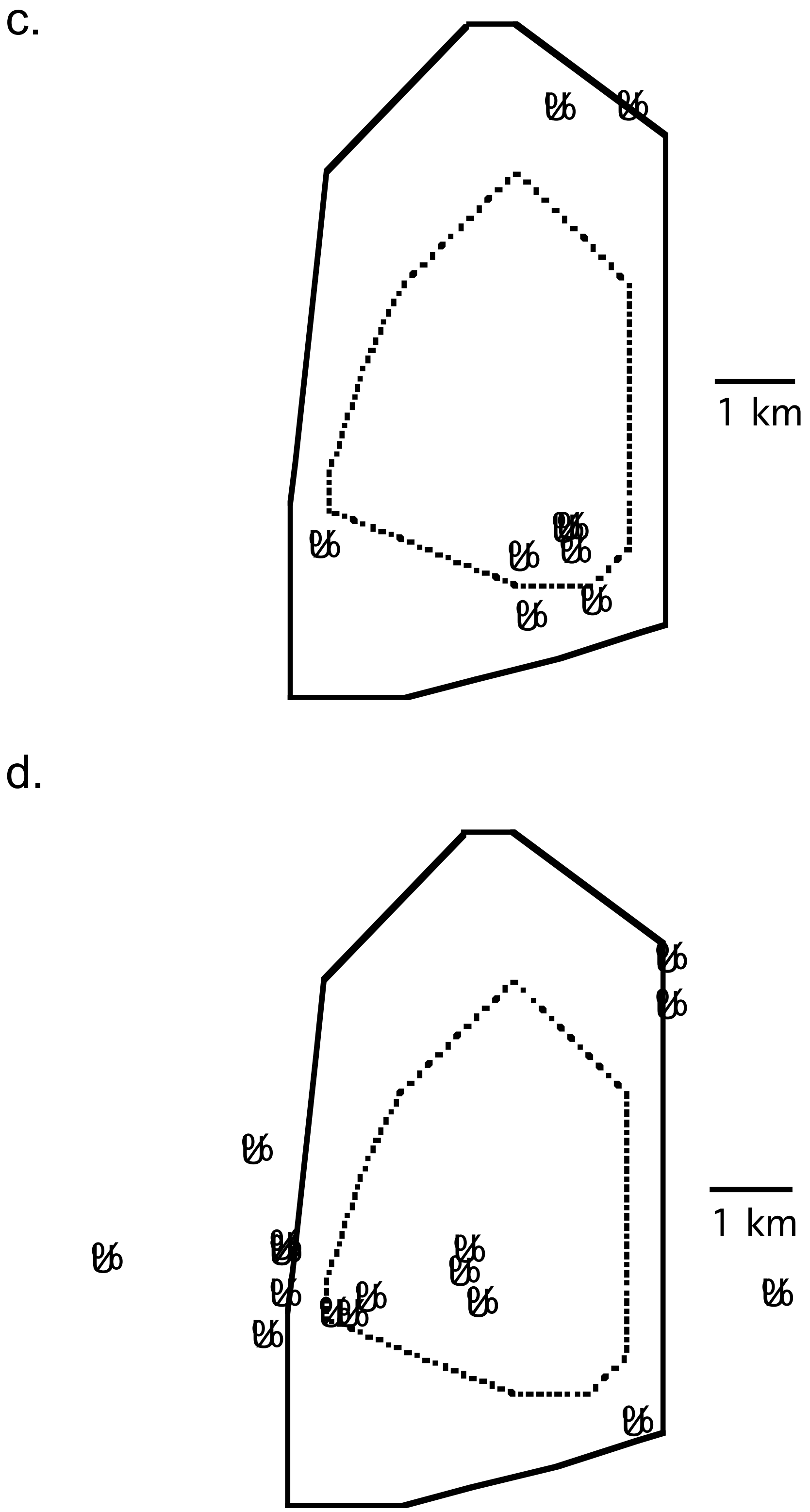


Chapman & Wrangham (1993) found that at Kanyawara, males used an area 1.5 to 2 times larger than the area used by females, and that males were more likely to be seen in border areas than females. As discussed above, the total home range is now known to be much larger, suggesting the possibility that the reported sex difference is an artifact of sample bias. Moreover, it is now clear that females in this community differ in their ranging patterns (Wrangham et al. 1996), in a pattern similar to that observed in Gombe (Goodall 1986; Williams 2000). Although some females are seen most commonly in the central part of the community's range, and generally avoid borders, other females appear to have home ranges centered towards the northern or southern boundaries, and hence may visit borders more often than males. In this paper, I test whether border avoidance by females represents a general sex difference or depends instead on the location of female home ranges within the total range.

I also test whether differences in the size of male home ranges depend on male dominance rank. The benefits gained by territoriality may be shared unequally by males, with high-ranking males benefiting more (e.g. Nunn 2000, Watts in press). High-ranking males might therefore be more willing to patrol borders, resulting in larger estimated home ranges.

Grouping near borders

For many species, the outcome of intergroup contests depends on the relative number of opponents on each side, with larger groups defeating smaller groups (Adams 1990;

McComb et al. 1994; Wilson et al. 2001). The importance of relative numbers in winning intergroup contests suggests that for species with fission-fusion social organization and territory defense, range location should have a profound effect on ranging and grouping patterns.

Few data are available on grouping patterns near borders for species other than chimpanzees. During times of prey scarcity, female lions sometimes leave their territories in search of food. When doing so, they travel as a unit, apparently as a defense against intergroup aggression (Packer et al. 1990). Likewise, females in small prides appear to be unusually gregarious, another apparent response to risks of intergroup aggression (Packer et al. 1990). Hickerson (1965) reports that in the war zone between the Chippewa and Sioux tribes, visits to war zones were limited to groups hunting groups of 10-15 men. Women and children stayed in the distant villages, and men avoided the war zone when trapping fur-bearing animals (an activity conducted alone or in pairs).

For chimpanzees, the best evidence for increased party sizes near boundaries is presented in an unpublished Ph.D. thesis (Bauer 1976); also cited in (Bauer 1980). Bauer found that at Gombe, both males and anestrous females traveled in larger parties towards the edge of the range. Bauer’s finding is intriguing but problematic. The division of the home range into center and edge was based on subjective ratings of use rather than quantitative data. Statistical tests treated all half-hour observations as independent points, which may have artificially inflated the significance of statistical tests. Data from all individuals were pooled, obscuring any differences among individuals. Bauer also cites preliminary analyses by Riss and Busse of a 50-day observation of one male, in which the focal male traveled in parties with more males at the edge of the range. Riss & Busse (Riss & Busse 1977), however, did not include this result.

Other data support the prediction that chimpanzees should travel in larger parties in border zones but do not provide definitive tests. Chapman and Wrangham (Chapman & Wrangham 1993) found that males were more likely to visit boundary areas than females, but did not test whether males traveled in larger parties in border areas. Watts and Mitani (in press) found that parties conducting boundary patrols contained a large number of males (mean = 9.4 ± 3.8 adult males per party). They did not, however, provide data on average party size for this community needed to test whether these parties were in fact unusually large. Moreover, they provided no explicit criteria for distinguishing core from border areas.

At least two alternative explanations exist for an observed increase in party size in peripheral areas. First, larger parties may be easier to find and follow in peripheral areas, leading to sampling bias. Second, chimpanzees may visit peripheral areas more often when those areas contain abundant food sources, which in turn would attract unusually large parties. In the present study, I attempt to test whether these alternative hypotheses can account for any observed increases in party size near borders.

2.3 METHODS

Study Site and Population

I observed the Kanyawara community of chimpanzees living in Kibale National Park, Uganda. The study site is described in detail elsewhere (Struhsaker 1997). Vegetation within the park includes a mosaic of moist evergreen forest, colonizing forest, papyrus swamp, and exotic softwood plantations. Outside the park, relict forest patches and swamps exist in a patchwork dominated by smallholder farms and tea plantations. Makerere University Biological Field Station maintains a trail system within the park covering approximately 12 km^2 (Chapman & Wrangham 1993). New trails cut during the study period increased the accessible area considerably, especially in the north, west, and southwest of the Kanyawara community's home range. Chimpanzees spent most of their time within the park but sometimes traveled outside the park to visit forest patches and raid the crops of villagers.

The Kanyawara community contained 49-53 individuals during the study period (1996 - 1998), including 10-11 adult males, 1-2 subadult males, 15-16 adult females, and 2-5 subadult females, all of whom were individually recognized. Isabirye-Basuta initiated systematic study of this community in 1983 (Isabirye-Basuta 1988) and the community has been studied continuously since 1987 (Hauser 1990; Wrangham et al. 1992; Wrangham et al. 1996). At the time of this study, habituation was good for all of the commonly seen individuals, consistently allowing observations from 10 m or less. Some rarely seen individuals remained skittish, and several adult females were shy and difficult to follow when traveling alone. As is typical of chimpanzees studied elsewhere, males in this population breed in their natal communities, whereas females typically disperse before breeding.

Data collection

Together with a team of field assistants, I conducted party composition scan samples (Altmann 1974) during 7385 hours of observation over a three-year period (1996-98). At 15-min intervals, observers recorded the identity of all individuals known to be feeding, resting, or traveling together (within roughly 50 m). If chimpanzees were feeding, observers noted the species and part being eaten. Observers recorded the location with reference to the trail grid or other nearby landmarks, and later drew the path traveled onto a gridded map of the study area.

Range analysis

Party composition data were entered into FileMaker Pro database software for analysis. Locations were transcribed onto a 500 by 500 m grid. The center of each grid cell was plotted based on comparison of the trail grid maps with a topographic map (1:50,000 Y732 Series map, 1960, Department of Overseas Surveys). To test the accuracy of the grid cell method, I also estimated the home range using the locations of 30 extreme range points measured by a Garmin 12 Global Positioning System (GPS; position accuracy to 15 m RMS).

Biotas ecological software (Ecological Software Solutions 2000) was used to calculate the minimum convex polygon (MCP) based on the list of grid cells occupied at any time (Total Range) or used for nesting (Nesting Range). Following Chapman & Wrangham (1993), I considered each unique grid cell occupied during each day to be an independent observation. For the Total Range, I determined the unique grid cell occupied by any chimpanzee on that day. For individual home ranges, I determined the unique grid cells used by that individual each day. During the study period, several adolescent individuals matured or approached maturity. I recognize the possibility that ranging patterns change with maturational events, such as the birth of a female's first infant. Nevertheless, preliminary analyses showed that adults and subadults had similar ranging patterns. I therefore included all individuals who regularly traveled independently, so that "males" included 11 adult males and one subadult male and "females" included 17 parous and 2 nulliparous females.

Although the MCP method has shortcomings, such as sensitivity to outliers and to sample size, it has the advantage of making no assumptions regarding independence of observations, and is statistically stable (Jennrich & Turner 1969). Moreover, it is widely used among researchers studying chimpanzees, facilitating comparisons with other studies (Chapman & Wrangham 1993; Boesch & Boesch-Achermann 2000; Williams 2000; Herbinger et al. 2001).

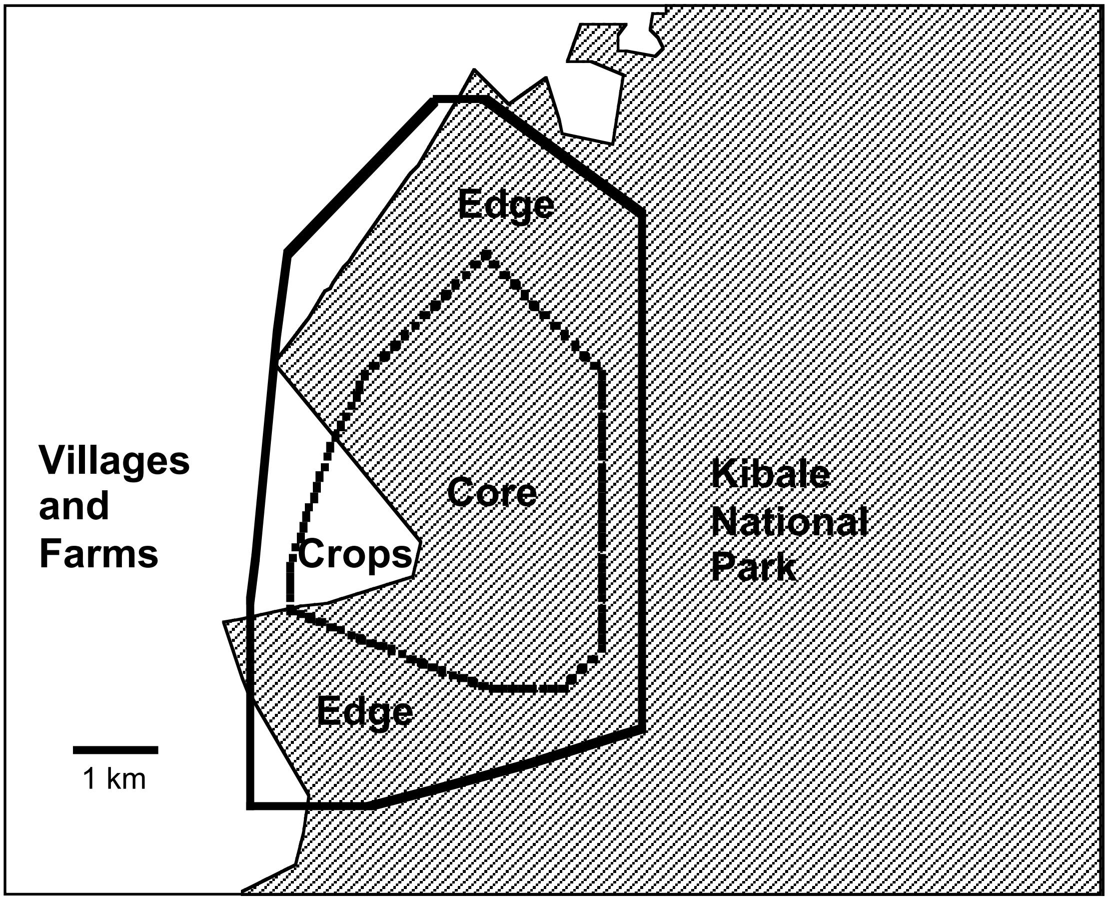


Figure 2.2 Range areas of Kanyawara chimpanzees, 1996-1998. Diagonal hatching indicates land within Kibale National Park. As with Fig. 2.1, the solid line encloses the Total Range of the Kanyawara community, and the dotted line encloses the Nesting Range.

I use the following definitions: “Total Area” is the MCP enclosing 100% of observations. “Nesting Range” is the MCP enclosing 98% of nesting points (to eliminate overly influential outliers). “Core” is that part of the Nesting Range located with the park. “Edge” consists of all points within the park but outside the Core. “Crops” included all land outside the park (Fig. 2.2). The percentage of observations chosen to calculate the size of individual home range is somewhat arbitrary. To facilitate comparison with other chimpanzee studies (Wrangham 1979; Wrangham & Smuts 1980) I calculated home ranges using 80% of observations. To test whether the percentage of observations used affected the results, I also calculated home ranges using 50, 75, 99 and 100% of observations.

Grouping near borders

An increase in the number of males observed in border areas could result from strategies for success in intergroup contests, but at least two alternative explanations exist. First, finding and following small parties may be inherently more difficult in border areas than in central areas. Second, large parties could result from unusually abundant food in border areas. Below I describe in detail our attempts to control for these factors.

Sample bias

At least three factors could result in a bias towards finding larger parties in peripheral areas. First, central areas are more intensively searched than peripheral areas, as they are closer to the research camp and more thoroughly covered by trails. Second, smaller parties may be quieter and hence harder to find. Third, smaller parties may be more difficult to follow in peripheral areas. Large parties are noisier (see Chapter Three) and generally easier to follow, particularly in regions with few trails (pers. obs.).

Controlling for all these biases presents many difficulties and is beyond the scope of the present study. Nevertheless, I attempted to control for some sources of bias in the following ways. First, I examined data from all observations, but limited statistical analysis to parties that were followed for at least 10 hours in a day ("all-day follows"). By using all-day follows I hoped to reduce the detection bias inherent in finding parties by chance later in the day. I treated each party as an independent data point to avoid the inflation of statistical significance that results from treating all scans as independent observations (e.g. Bauer (1976)). I compared each party to itself in the different range locations used during the day. To test whether larger parties were more likely to visit outlying areas, I compared to the composition of three categories of party: (1) those that visited only Core; (2) those that visited Core and Crops; and (3) those that visited Core and Edge. To facilitate comparison among these three categories, I limited this comparison to observations taken in the Core.

Distribution of food

I examined feeding data to compare whether location affected either the total percentage of time spent feeding or the quality of food eaten. As a proxy for food quality, I considered all ripe fruits (including figs and non-fig fruits) to be high quality and herbs (THV) to be low quality.

Table 2.1 Total Range estimated using different percentages of all observations. The first column indicates the percent of observations used to calculate each minimum convex polygon (MCP). The second column indicates the estimated range size based on each MCP. The third column shows the percentage of the Total Range covered by each MCP.

% MCP	Range Size (km^2)	% Total Range
100	37.8	100.0
90	15.3	40.4
80	10.3	27.2
70	7.8	20.5
60	5.3	13.9
50	3.4	8.9

2.4 RESULTS

Range size and border avoidance

The Total Range covered 37.8 km^2 (Table 2.1). The Nesting Range, based on 445 nest locations, covered 15.8 km^2, which closely corresponded in both size and location with the polygon enclosing 90% of all observations (15.3 km^2). Of the Total Range, the Core covered 13.9 km^2, the Edge 16.7 km^2, and Crops 7.2 km^2 (Fig. 2.2). Although the Core accounted for only 37% of the total range, 85% of observations were recorded there. The larger Edge area (44% of total range) accounted for 11% of observations, and crops (19% of total range) accounted for only 4% of observations. Chimpanzees traveled up to 2.5 km beyond the Core, but during most observations outside the Core remained closer (mean distance to the nearest edge of the Core ± s.d. = 240 ± 350 m). When travelling outside the park, chimpanzees were never observed more than 710 m from the park boundary, and usually stayed closer (mean distance from park boundary when outside park = 200 ± 170 m).

Sex differences in home range size

To examine sex differences in home range size, I first determined how many observations were required to obtain a relatively unbiased estimate of range size. In general, estimates of home range increased with increasing sample size. Using 99% MCPs as an example of a pattern consistent for all %MCPs, the estimated home range area increased significantly with months observed for both males ($r^2 = 0.51$, $F_{1,11} = 11.7$, $p < 0.01$) and females ($r^2 = 0.52$, $F_{1,17} = 18.4$, $p < 0.001$). For individuals with observations spanning at least 20

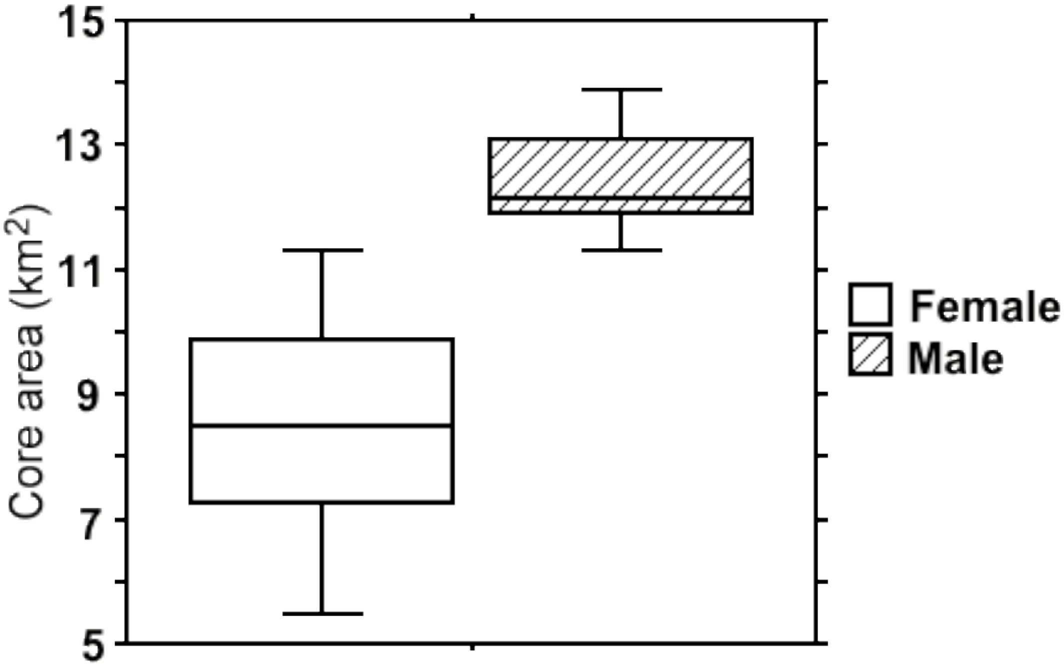


Figure 2.3 Box plots of male and female home ranges (80% minimum convex polygons). Horizontal lines indicate the 10th, 25th, 50th, 75th, and 90th percentiles. The home ranges of 12 adult and subadult males are compared to the home ranges of the nine adult and subadult females who were observed for a minimum of 20 months each.

Table 2.2 Size of male and female home ranges for minimum convex polygons using different percentages of observations, restricted to individuals with at least 20 months (and 400 days) of observations. Values for U and significance levels for Mann-Whitney U tests are also presented.

% MCP	Median Male Range (km^2)	Median Female Range (km^2)	Male Range / Female Range	U	P
50	4.4	3	1.5	12.5	<0.005
75	9.6	7.4	1.3	10	<0.005
80	12.1	8.5	1.4	2	<0.0005
99	31.8	19	1.7	4	<0.0005
100	35.4	21.6	1.6	4	<0.0005

months, however, estimated home range did not increase with increasing months of observation (males: $r^2 = 0.09$, $F_{1,10} = 1.0$, NS; females: $r^2 = 0.05$, $F_{1,7} = 0.36$, NS). I therefore limited analyses to individuals who were observed during a minimum of 20 months. Males consistently had larger home ranges than females (Fig. 2.3). Depending on the percent of observations used to calculate the MCP, male home ranges were 1.3 to 1.7 times larger than female home ranges (Table 2.2).

Sex differences in frequency of border visits

Individual male ranges showed almost complete overlap, with several males being observed throughout the total range (Fig. 2.4a). In contrast, individual females used smaller ranges with less overlap among female ranges (Fig. 2.4b). Analysis of the percentage of observations obtained for each individual in Core, Edge and Crops revealed differences both within females (Fig. 2.5) and between males and females (Fig. 2.6). Figure 2.4 shows the contrasting patterns of range use for males and females. Males shared large, overlapping home ranges, whereas females used smaller home ranges with less overlap among individuals.

Analysis of both observation time and ranging patterns suggests that females can be divided into two groups, "central" and "peripheral." The nine females who were seen during at least 20 months all appeared to have home ranges centered in the Core, and are hence labeled central females. As shown in Fig. 2.5a, these central females showed considerable overlap in their home ranges. The ten females who were observed less frequently had more distinct home ranges. Observers follow the central females

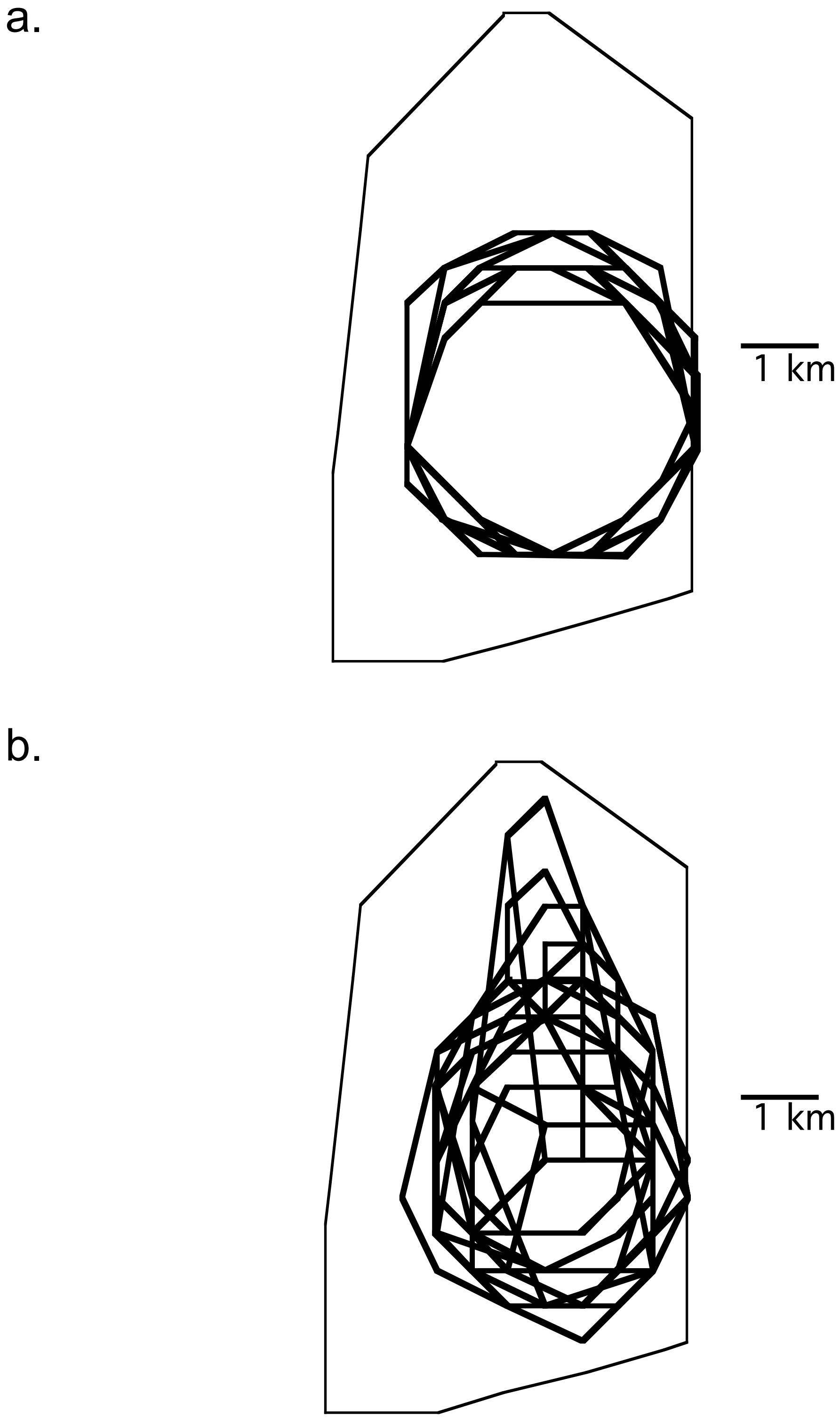


Figure 2.4 Comparison of male and female home ranges. The outer polygon encloses the Total Range. The 80% MCP home ranges are shown for 12 males (a) and 19 females (b).

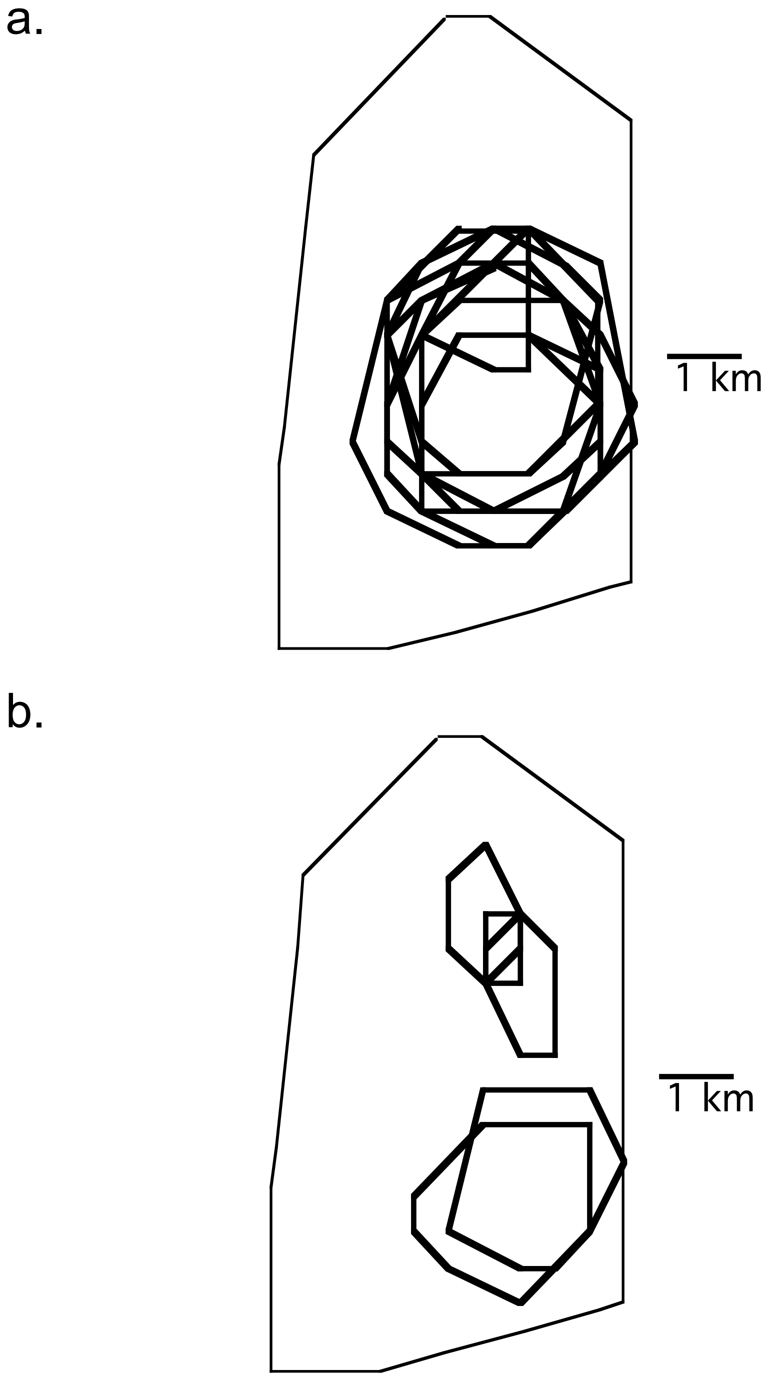


Figure 2.5 Comparison of central and selected peripheral females. The 80% MCP home ranges are shown for all nine central females (a) and for five of ten peripheral females (b).

frequently and these females are therefore well habituated. Observers encounter the peripheral females less often, and consequently these females are more difficult to follow. The small sample sizes for these peripheral females preclude definitive descriptions of their ranging patterns, but as Wrangham and colleagues (1996) suggest, they can be divided into "northern" and "southern" females. Figure 2.5b shows the home ranges of three northern females and two southern females.

Central females spent a median 13% of observations in the Edge, in contrast to peripheral females, who spent 31% of observations in Edge. These observations probably underestimate the percentage of time spent in the Edge by peripheral females, as these females were infrequently observed. Males spent a median 17% of observations in the Edge. The percent time spent in the Edge differed significantly for these three groups (Kruskal-Wallis: $H_2 = 23.3$, $p<0.001$; Fig. 2.6). Central females were less likely to visit borders than males, but peripheral females appeared to have home ranges centered near border areas.

Rank differences in male home range size

High-ranking males had larger home ranges than low-ranking males (Fig. 2.7). This effect was consistent for MCPs using various percentages of observations, and was statistically significant for all but 75% and 80% (Table 2.3).

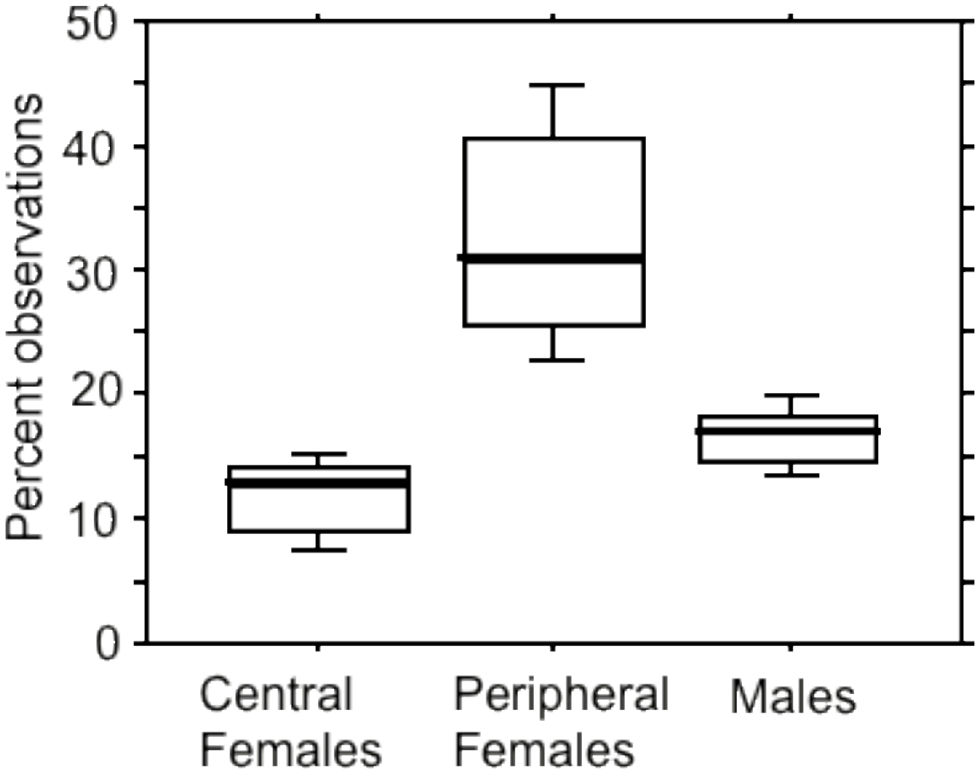


Figure 2.6 Box plots showing the percent of all observations at the Edge by the nine central females, ten peripheral females, and twelve males.

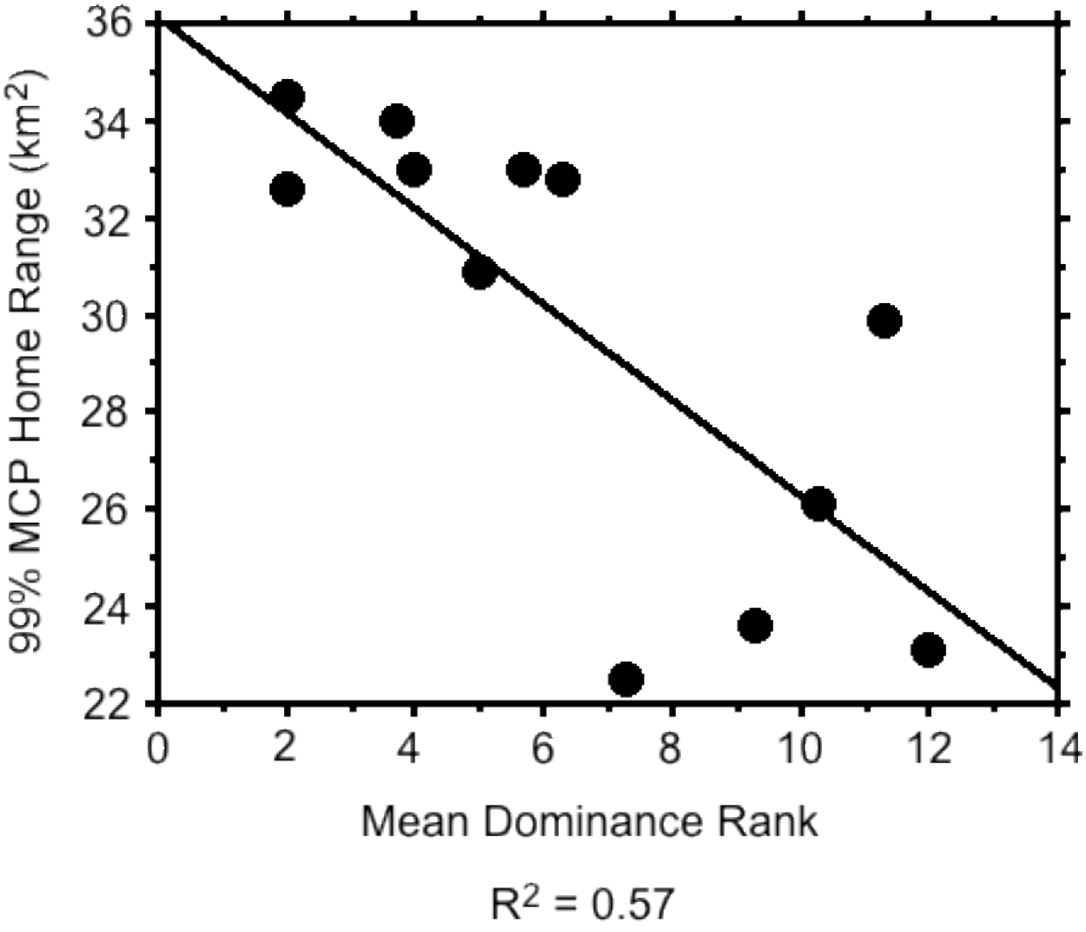


Figure 2.7 Home range size and mean dominance rank for males.

Table 2.3 Results of linear regression of male home range size versus dominance rank.

% MCP	R^2	$F_{1,10}$	P
50	0.347	5.3	<0.05
75	0.212	2.7	>0.1
80	0.174	2.1	>0.1
99	0.569	13.2	<0.005
100	0.475	9	<0.05

Grouping near borders

Party size and composition varied considerably across different locations. Pooling all observations, the total number of individuals per party was larger at the Edge (mean ± s.d. = 12.0±6.5) than either Core (8.6±5.8) or Crops (8.6±4.4). The mean number of adult males was higher at the Edge (5.5±3.2) and in Crops (5.3±2.7) than the Core (3.0±3.1). The mean number of adult females was least in Crops (1.4±1.4) and somewhat higher in both Core (2.4±1.8) and Edge (2.7±1.9).

All-day follows:

In parallel with the analyses of pooled data, analyses of all-day follows revealed a strong effect of location on party composition (Fig. 2.8). The 97 parties that remained in the Core had a median 2.7 males (range = 0 to 9.4). The 44 parties that visited both Core and Edge had a median 6.4 males when in Core (range = 0 to 9.8) and significantly more males when in Edge (median = 7.0, range = 0 to 10.0;Wilcoxon signed rank test: $N = 44$, $z = -3.2$, $p < 0.005$). The 19 parties that visited both Core and Crops had a median 6.4 males when in Core (range = 0.6 to 9.5) and a median 6.0 males when in Crops (range = 0 to 10; this difference was not statistically significant). Considering just the number of males when each party was in the Core, parties that also visited the Edge or Crops had significantly more males (Fig. 2.8; Kruskal-Wallis test: $H_2 = 35.7$, $P < 0.005$).

Parties that remained in the Core had a median 2.5 adult females (range = 0.6 to 6.6). Parties that visited both Core and Edge had a median 2.8 females when in the Core (range

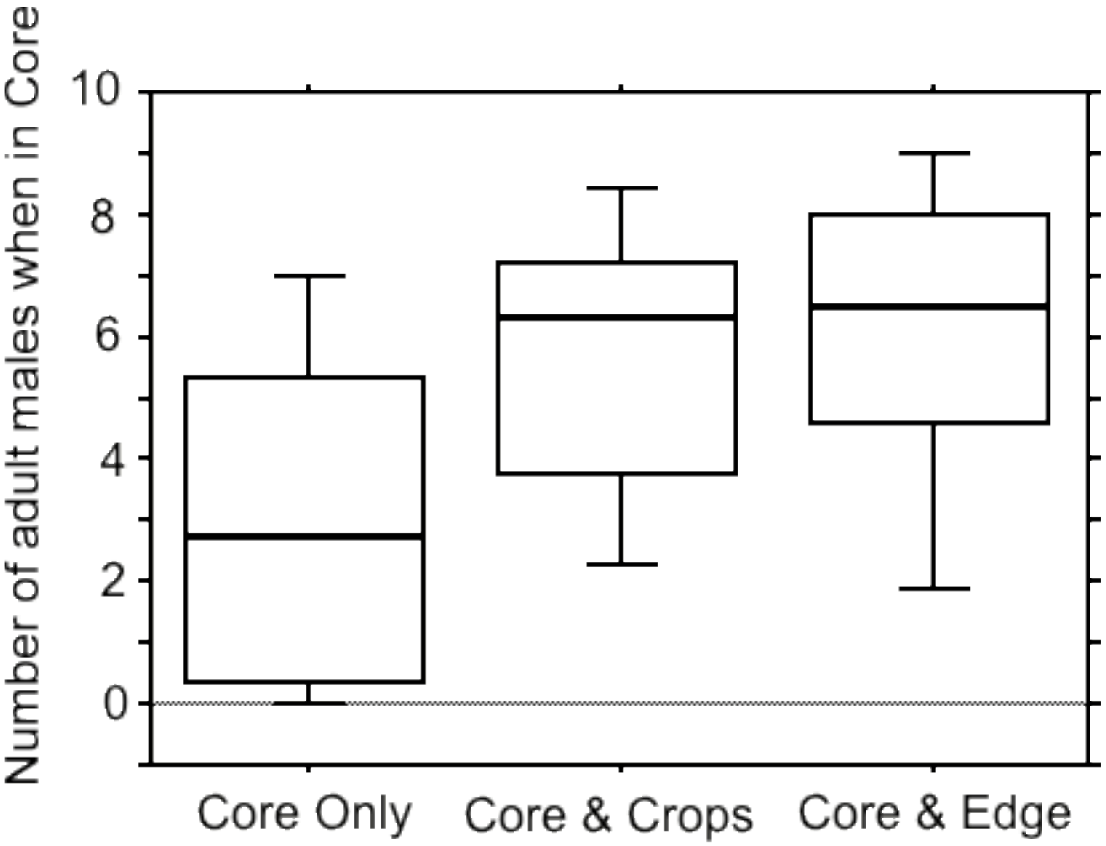


Figure 2.8 Box plots showing the mean number of males when in the Core for parties that stayed in the Core for the entire day, parties that visited Core and Crops, and parties that visited Core and Edge.

= 0 to 7.8) and a median 3.6 females when in Edge (range = 0 to 8.0; Wilcoxon signed rank test: N = 44, z = -2.4, P<0.05). Parties that visited both Core and Crops had a median 1.6 females when in Core (range = 0.3 to 3.8) and a median 1.8 females when in Crops (range = 0 to 3.5; Wilcoxon signed rank test: N = 19, NS). Comparing the number of females in the Core for parties that remained in the Core with parties that also visited either Edge or Crops reveals a significant difference (Kruskal-Wallis Test, $H_2 = 9.3$, P <0.01).

Feeding

Independent of whether parties were at the Core, Edge, or Crops, the percent of observations with feeding remained similar. Parties that visited only Core fed during a median 59% of observations (range = 11.5 to 94.3; Fig. 2.9). Parties that visited both Core and Edge spent a similar percent of their time feeding in both locations. When in Core, these parties spent a median 58% of observations feeding (range = 5.9 to 100%; Fig. 2.10) compared to 62% at Edge: 62% (range = 0 to 100%; Wilcoxon Signed Rank Test: NS). Parties that visited Core and Crops also spent a similar amount of time feeding in both locations, with a median of 66% of observations spent feeding when in Core (range = 8.7 to 90) and 76% when in Crops (range = 0 to 100; Wilcoxon Signed Rank Test: NS).

In contrast to the time spent feeding, the type of food eaten did vary across locations. Parties that visited only Core fed on fruit for a median 59% of feeding observations (range = 0 to 100; Fig. 2.9). Parties that visited both Core and Edge fed on fruit for a

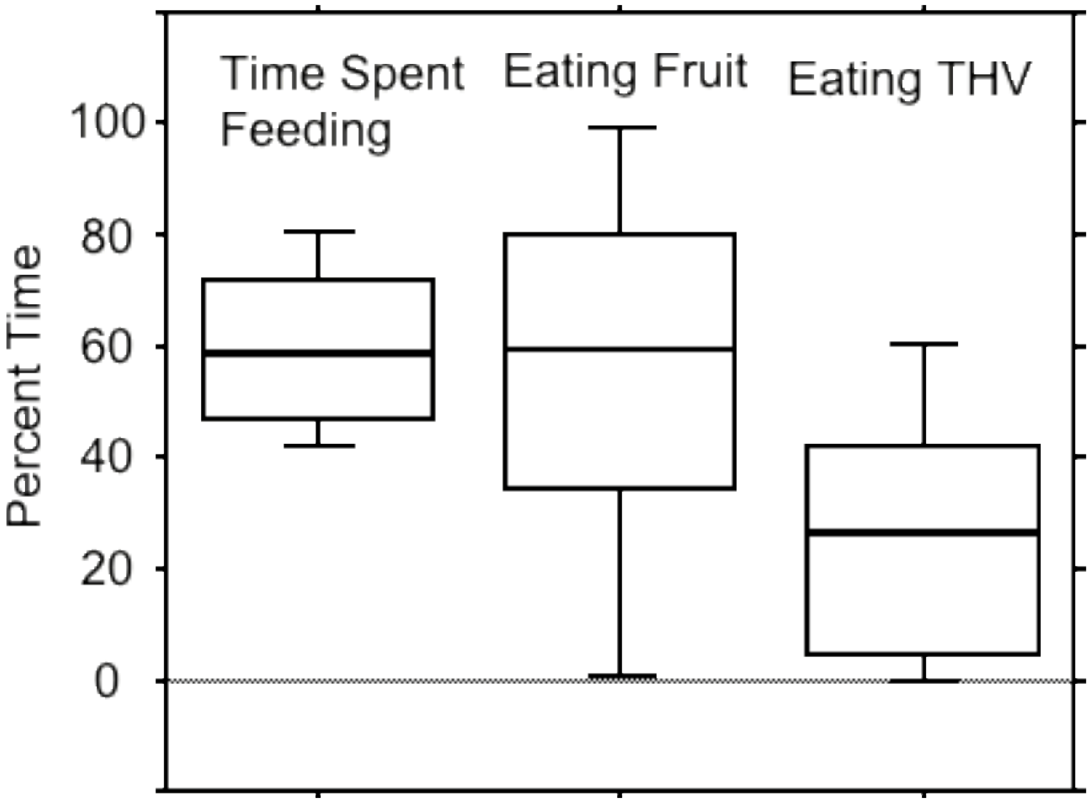


Figure 2.9 Feeding data box plots for parties that stayed in Core all day. Plots show the percent time spent feeding, and of that time, the percent time spent eating forest fruits and the percent time spent eating terrestrial herbaceous vegetation (THV).

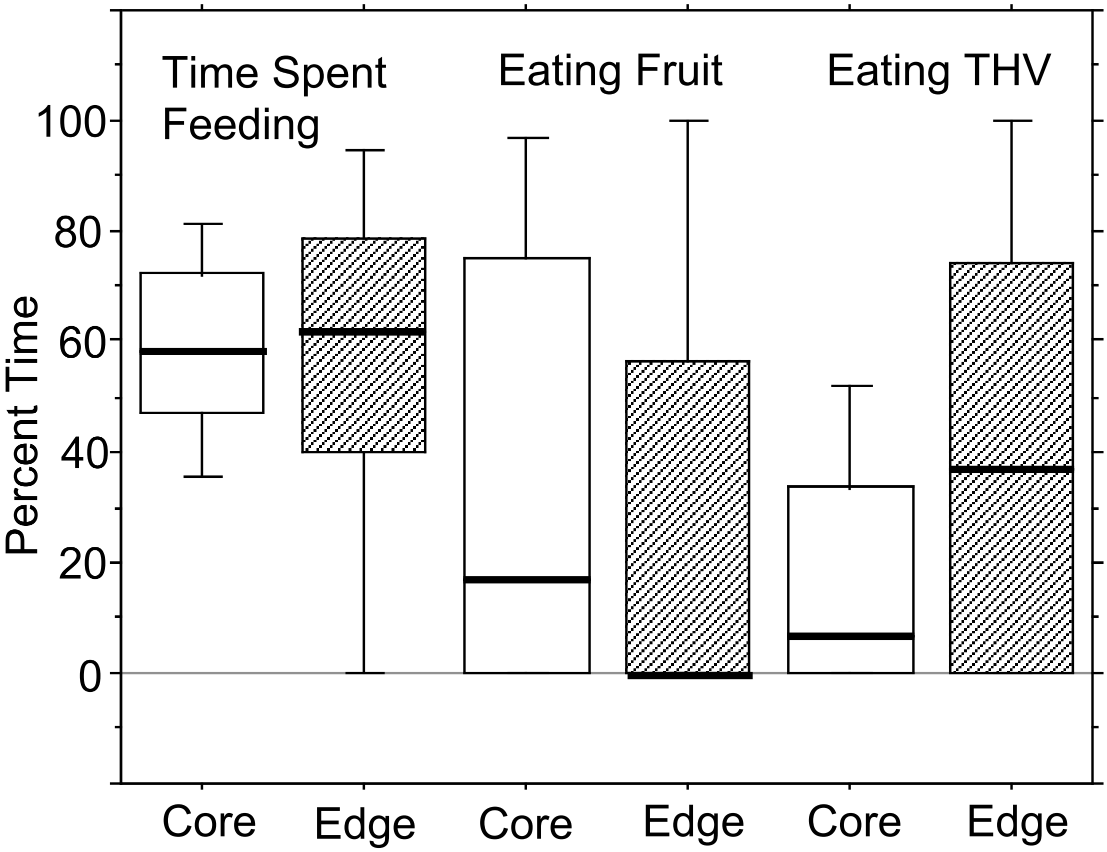


Figure 2.10 Feeding data box plots for parties that visited both Core and Edge. Plots show the percent time spent feeding, and of that time, the percent time spent eating forest fruits and the percent time spent eating terrestrial herbaceous vegetation (THV).

median 17% of observations in Core and a median 0 observations in Edge (range = 0 to 100; Wilcoxon signed rank test: N = 36, z = -0.9, NS; Fig 2.10). Parties that visited both Core and Crops fed on fruit for a median 47% in Core and 0% in Crops (range = 0 to 100; Wilcoxon signed rank test: N = 14, z = -2.5, P > 0.05).

Parties that visited only Core fed on THV for a median 27% of feeding observations (range = 0 to 85; Fig. 2.9). Parties that visited both Core and Edge fed on THV for a median 7% of observations in Core (range = 0 to 85) and a median 37% of observations in Edge (range = 0 to 100; Wilcoxon signed rank test: N = 36, z = -2.5, P<0.05; Fig. 2.10). Parties that visited both Core and Crops fed on THV for a median 22% in Core (range = 0 to 100) and 0% in Crops (range = 0 to 100; Wilcoxon signed rank test: N = 14, z = -2.3, P > 0.05).

When visiting Crops, chimpanzees fed on bananas (mainly the stems) for a median 96% of observations (range = 0 to 100).

2.5 DISCUSSION

I found general support for the three main predictions tested. First, chimpanzees concentrated their range use within a central area of a much larger Total Range, visiting borders infrequently. Second, pronounced sex differences existed, with males using most or all of the Total Range and females using smaller home ranges. Males visited borders more often than the 11 central females, but in contrast to the general prediction, eight peripheral females ranged in border areas more often than males, and appeared to have home ranges centered near borders. High-ranking males had larger home ranges, suggesting they were more active in range defense. Third, parties observed in border areas had more males, and parties with more males were more likely to visit border areas. I discuss each of these results in more detail below.

Border avoidance

Although the study community ranged more widely than previously reported (Chapman & Wrangham 1993), they continued to concentrate their range use within an area of approximately 15 km^2. The size and location of the Core range of the Kanyawara community appears to have remained stable.

Sex differences in ranging

Consistent with previous studies of Kanyawara (Chapman & Wrangham 1993) and other communities (Wrangham & Smuts 1980; Goodall 1986; Herbinger et al. 2001), females had smaller home ranges than males. Males ranged over the entire territory, whereas females ranged over smaller areas within the territory. Males visited borders more often than central but not peripheral females. Peripheral females may suffer increased risk of infanticide from males (Arcadi & Wrangham 1999), but may also benefit by greater food abundance in border areas.

High-ranking males had a larger home range than low-ranking males. This relationship was most pronounced for analysis of polygons that enclosed the more peripheral points. The increase in home range with rank could in principle result from higher-ranking males participating more actively in boundary patrols. The possibility exists, however, that the effects of sex and rank on ranging patterns result from searching for mates rather than searching for rival males. Males in many species range over an area large enough to include the home ranges of multiple females (e.g. Saharan gerbils: Psammomys obesus (Daly & Daly 1974); meadow voles: Microtus pennsylvanicus (Madison 1978); galagos, Galago demidovii (Charles-Dominique 1977); orangutans: Pongo pygmaeus (Rodman & Mitani 1987)). Distinguishing between these explanations is likely to prove difficult, however, since searching for females in peripheral areas and checking borders for male intruders can be conducted simultaneously.

Grouping near borders

It is difficult to eliminate the possibility of sample bias. For instance, I undoubtedly undersampled the home ranges of peripheral females, and our understanding of ranging in peripheral areas remains incomplete. Nevertheless, the increase in number of males per party appears consistent across a variety of analyses. Parties that visited both Core and Edge contained more males than parties that remained in Core.

If party size in Edge increased due to food abundance, chimpanzees would presumably spend a greater percent of their time feeding at the Edge, or a greater percentage of feeding observations should be on relatively high quality food such as fruit. Instead, chimpanzees spent a similar percent of their time feeding in all range locations. In sharp contrast to the prediction that large party size resulted from abundant high-quality food, parties that visited both Core and Edge showed an increase in feeding on THV.

In conclusion, I found that chimpanzees in this population responded as predicted to the increased risks posed by intercommunity boundaries. Chimpanzees in general avoided border areas, except for the peripheral females. Males used the entire range, whereas females traveled in smaller home ranges. Males visited the Edge more often than central females, but less than peripheral females. Females therefore demonstrated a diversity of behavioral strategies, similar to observations from Gombe. Parties visiting the Edge contained more males than parties that visited only the Core. I predict that similar patterns will be observed in other species that defend territories and incur high costs from intergroup aggression.

CHAPTER THREE

STEALTHY RAIDERS: VOCAL SUPPRESSION IN WILD CHIMPANZEES

3.1 SUMMARY

The degree to which animals are able to voluntarily control their vocalizations remains controversial. Numerous anecdotes have been reported, describing cases in which chimpanzees (Pan troglodytes) appear to suppress their vocalizations. Nevertheless, few quantitative data are available to test such claims or to assess the frequency of call suppression in the wild. Here I provide evidence that unprovisioned, free-ranging chimpanzees living in Kibale National Park, Uganda, decrease the rate of production of their loudest call, the pant-hoot, when crop-raiding. Chimpanzees often produce pant-hoots when feeding on abundant food sources, but giving such loud calls when crop-raiding risks discovery by farmers, who typically chase crop-raiding animals from their fields. A total of 1419 hours of all-occurrences sampling of pant-hoot production by 252 different parties revealed that parties produced fewer pant-hoots when in crops than in either the core or edge of their range. Focal follows of individuals revealed a similar trend, in that adult and subadult males produced fewer pant-hoots when eating cultivated foods than when eating wild fruits or herbaceous vegetation. During a total of 6.9 hours of focal observation distributed over an 18 month period, individuals eating cultivated foods pant-hooted on only one occasion. These results support the claim that wild

chimpanzees are able to suppress their vocalizations, especially under circumstances when the costs associated with call production are high.

3.2 INTRODUCTION

The extent to which animals have voluntary control over their vocal production remains controversial. A traditional and persistent view is that animals respond automatically to a specific set of stimuli, and are incapable of varying the rate of signal production (reviewed in Cheney & Seyfarth (1990); Hauser (1996; 2000)). In contrast, recent studies have shown that for a variety of animals, production of calls depends not only on physical stimuli, such as food or predators, but also on more cognitively sophisticated factors. Much of the discussion on voluntary signaling has focused on the 'audience effect,' in which animals base their decision to call upon whether individuals such as mates, kin, or allies are present (Cheney & Seyfarth 1985; Marler et al. 1986; Hauser & Nelson 1991; Marler et al. 1991; Mitani & Nishida 1993; Hauser 1996). For example, various ground squirrels and vervet monkeys (Cercopithecus aethiops) are more likely to give alarm calls to predators when kin or potential mates are nearby (Dunford 1977; Sherman 1977; Hoogland 1983; Cheney & Seyfarth 1985). Likewise, rhesus macaques (Macaca mulatta) and chickens (Gallus domesticus) are more likely to call upon discovering high-quality food items when kin or potential mates are in view (Marler et al. 1986; Hauser & Marler 1993). In this chapter, I examine whether chimpanzees (Pan troglodytes) modify their rate of loud-call production when facing two potentially dangerous audiences:

chimpanzees from other communities and human farmers. In doing so, I use quantitative data to test claims that up until now have been based largely on anecdotal evidence.

A growing number of anecdotes suggest that when chimpanzees face costs to calling, they are able to suppress calls. Calling can be costly when individuals attempt to monopolize high-quality food or mate surreptitiously, or during travel near the ranges of other communities. Goodall (1986) describes how a young male learned to suppress calls: "On one occasion when Figan was an adolescent, he waited in camp until the senior males had left and we were able to give him some bananas (he had had none before). His excited food calls quickly brought the big males racing back and Figan lost his fruit. A few days later he waited behind again, and once more received his bananas. He made no loud sounds, but the calls could be heard deep in his throat, almost causing him to gag." During the same time period, another adolescent male, Evered, failed to learn to suppress his food-associated calls and continued to suffer the depredations of adult males at the banana feeding station. De Waal (1982) describes a female who learned to suppress copulation calls during surreptitious matings with low-ranking males.

Goodall and others report that chimpanzees stay unusually silent when patrolling their territory boundaries (Goodall 1986; Boesch & Boesch-Achermann 2000; Watts & Mitani in press). Goodall notes that "they avoid treading on dry leaves and rustling the vegetation . . . A male may perform a charging display during which he drums on a treetrunk, but he does not utter pant-hoots" (Goodall 1986). Goodall describes adults punishing juveniles who called on patrols, and that adults even threatened human observers who made too much noise (Goodall 1986). During consortships in peripheral areas, females appear to suppress copulation calls (Goodall 1986).

Such anecdotes give vivid pictures of rare events and can provide key insights that might otherwise be lost in statistical number crunching. Nevertheless, anecdotes are prone to observer bias and cannot be used to estimate rates of behavior (Altmann 1974). For instance, Figan learned to suppress his calls, while Evered didn't. Was Figan unusually clever? Or was Evered unusually slow-witted? How widespread is the ability to suppress calls among wild chimpanzees? Claims about vocal suppression during border visits suffer similar problems. Chimpanzees are quiet much of the time. It is possible that ordinary stretches of silence may be interpreted as extraordinary if the observer suspects the subjects are conducting a patrol. Systematic data collection is crucial to test the hunches of observers.

Little quantitative work has focused on vocal suppression, but several systematic observational and experimental studies indicate that chimpanzees do have some degree of voluntary control over their rate of production. Field observations have shown that the production of pant-hoot calls does not simply depend on social excitement or the presence of stimuli such as abundant fruit (Clark 1993; Mitani & Nishida 1993). Instead, pant-hoot production is closely linked with social status; high ranking adult males produce pant-hoots more frequently than other males (Wrangham 1977; Mitani & Nishida 1993; Clark & Wrangham 1994). The highest ranking (alpha) male generally calls more than any other male, and if an alpha is deposed, his call rate decreases and his rival's call rate increases (Uhlenbroek 1996). Whether the relation between rank and vocal production necessarily implies voluntary vocal control is unclear, however, because rank also relates to hormonal factors such as testosterone levels. It may be that high ranking males call more frequently not because they "know" they are high ranking, but because they have higher circulating testosterone levels. In a more clear-cut case for voluntary vocal control, Mitani & Nishida (1993) showed that chimpanzees are more likely to produce pant-hoot calls when their allies and associates were nearby (with "nearby" defined as seen that day but not currently with the focal subject). Chimpanzees appear to pant-hoot to maintain contact with specific individuals.

Two sets of experimental evidence suggest some degree of voluntary vocal control: food discovery experiments and playbacks of intruder calls. In the food discovery experiments, Hauser and colleagues (Hauser & Wrangham 1987; Hauser et al. 1993) presented varying quantities of highly preferred food to captive chimpanzees. Chimpanzees were more likely to call on discovery of larger food piles (Hauser & Wrangham 1987). When the amount of food was held constant, chimpanzees were more likely to call if the food was divisible (Hauser et al. 1993). These observations suggest that chimpanzees attend not only to the presence and size of a food stimulus, but also to whether the divisibility of the food is likely to reduce the cost of sharing with others.

In the playback experiments, Wilson and colleagues (Wilson et al. 2001) played a single pant-hoot from a foreign male to parties of varying size and composition. The vocal response to the playback depended strongly on the listener's sex and party composition.

Females remained silent when unaccompanied by males, and males generally remained silent if in parties of one to two males. In parties with three or more males, however, males and sometimes females as well joined in a loud chorus of screams, waas and pant-hoots immediately after the playback. Both high- and low-ranking males showed a similar pattern of response. These results show that pant-hooting to foreign calls is not a reflexive response to a given stimulus, or a function of high testosterone levels, but instead appears to depend on an assessment of the number of males (and hence fighting strength) in the listener's party.

In an effort to test claims based on anecdotal evidence and to build on previous work on factors affecting call production in chimpanzees, I conducted systematic observations focusing on two contexts in which production of loud calls is expected to be costly: border visits and crop-raiding. As discussed previously, visits to border areas increase the likelihood that chimpanzees will encounter members of neighboring communities. Intercommunity interactions are generally hostile in chimpanzees, with all ages and sexes being vulnerable to attack, with the partial exception of nulliparous females displaying full sexual swellings (Goodall 1986; Wrangham 1999; Watts & Mitani 2000).

At least two contrasting predictions exist for the behavior of chimpanzees near borders. First, if chimpanzees seek to avoid being detected by neighbors, either to reduce the risk of being attacked or to increase the chances for conducting a surprise attack (Manson & Wrangham 1991), they should be silent at borders. Second, if chimpanzees seek to advertise the presence of large parties, either to claim territory or to advertise coalitionary strength, chimpanzees should maintain or increase their rate of pant-hoot production (Clark 1993). Chimpanzees may employ both strategies, with silence being favored during border patrols and loudness being favored during what Goodall (1986) describes as “excursions,” visits to rich food patches in peripheral areas. Distinguishing patrols from excursions proved to be beyond the scope of this study, so I considered all border visits together, acknowledging the potential loss of information from lumping together distinct types of visit.

Crop-raiding provides a more clear-cut case. When visiting crops outside the forest, chimpanzees encounter bountiful supplies of food that would normally elicit food-associated calls. Due to the risks of being detected by the crop owners, however, chimpanzees should always remain quiet when crop-raiding. Farmers who detect chimpanzees raiding their crops routinely chase them away. Although chimpanzees and other wildlife are legally protected in Uganda, villagers sometimes injure or kill crop-raiding animals. In 1997, a villager killed an adult female from the study community when she raided bananas. Necropsy revealed that the female’s stomach was full of banana fruit (pers. obs.). Opportunities for crop-raiding arose relatively recently in the evolutionary history of chimpanzees, and may therefore seem a rather artificial context to test. Nevertheless, the clear-cut cost of calling when crop-raiding provides an opportunity to test whether chimpanzees possess the ability to suppress calls during more “natural” but more difficult to study contexts, such as border patrols and consortships in peripheral areas (Goodall 1986).

In addition to chimpanzees, other animals also may suppress calls when raiding crops, including elephants (Lisa Naughton, pers. comm.), baboons (Frank Marlowe, pers. comm.), and vervet monkeys (Kavanagh 1980). To my knowledge, however, the present study is the first attempt to systematically test whether habituated, known individuals suppress calls when crop-raiding.

3.3 METHODS

Subjects and Study Site

I studied the Kanyawara community of chimpanzees living in Kibale National Park, Uganda. This community contained 49 - 51 individuals during the study period (June 1997- November 1998), including 11 adult males and 15 - 16 adult females, all of whom were individually recognized. Isabirye-Basuta initiated systematic study of this community in 1983 (Isabirye-Basuta 1988), and the community has been studied continuously since 1987 (Hauser 1990; Wrangham et al. 1992; Wrangham et al. 1996). The study site, described in detail elsewhere (Struhsaker 1997), is located at 0° 34' north latitude and 30° 21' east longitude. The undulating terrain varies in elevation from 1500 to 1700 m. The vegetation at Kanyawara includes a mosaic of moist evergreen forest, colonizing forest, swamp, and exotic softwood plantations within the park as well as forest patches, tea plantations and smallholder farms outside the park. During 1996-98, the Kanyawara community ranged over an area covering 37.8 km^2 and spent the night in nests located within a 15.8 km^2 subset of the total range (Wilson et al. 2001). Land outside the park covered 6.9 km^2 (18%) of the total range and 2.2 km^2 (14%) of the nesting range (Chapter Two).

Study design

Chimpanzees live in fission-fusion communities, traveling in subgroups ("parties") of varying size and composition. Observers followed parties throughout their range, staying with them all day when possible. I estimated rates of pant-hoot production from data collected during follows of parties ("party follows") and individuals ("focal follows"). Data collection was designed to address the variety of factors that may influence the probability of pant-hoot production, as well as various potential sampling biases. Such factors include: (1) sampling bias caused by difficulty of observation in dense vegetation such as thickets of elephant grass (Pennisetum purpureum) and gardens of bananas (Musa spp.); (2) range location (Goodall 1986); (3) time of day (Wrangham 1975); (4) party composition (Clark 1993); (5) individual age-sex class and rank (Clark 1993; Mitani & Nishida 1993); and (6) the abundance, quality, and divisibility of the food source (Wrangham 1977; Hauser & Wrangham 1987; Hauser et al. 1993). I attempted to control for each of these factors as follows:

1. Difficulty of observation. Unbiased estimates of behavior rates generally require focal follows of individuals (Altmann 1974). However, focal follows are difficult to conduct when subjects are feeding in dense vegetation, resulting in undersampling for those conditions. I therefore collected party follows, in which I sampled all occurrences of

pant-hooting, in addition to individual focal follows. Although rates calculated from party follows obscure individual differences, pant-hoots are loud enough to be heard even when individuals are temporarily out of view, so that all occurrences of pant-hoots can be recorded even when focal follows are impractical. Together, the two sets of data may be used to complement their respective biases.

2. Range location. Given the frequent assertion that chimpanzees suppress vocalizations when visiting border areas (e.g. Goodall 1986, Watts & Mitani in press), I distinguished three locations: Core, Edge, and Crops (see Chapter Two, Fig. 2.1). Core consisted of all locations within both the park boundary and the minimum convex polygon enclosing all points used for night nests. Edge consisted of all points within the park, but outside the Core. Crops consisted of all locations outside the park boundary. Although the land labeled "Crops" includes other habitat such as villages, tea plantations, swamps and forest patches, chimpanzees rarely left the park except to raid crops. Methods for range analysis are described in detail below.

3. Time of day. I examined the party follow data to determine the temporal patterning of pant-hoots in each location (Core, Crops and Edge). I used analysis of variance to test for any interaction between time of day and location, which would indicate a bias due to uneven time distribution of samples from different locations.

4. Party composition. I limited analysis of party follow data to comparisons of parties that visited two locations during the day, either Core and Crops or Core and Edge. Each party

therefore served as its own control. I also used nonparametric statistics to test whether parties changed in composition between the two locations.

5. Sex and rank of caller. I used focal follow data to estimate rates of calling for individuals. I limited these samples to the age-sex classes most likely to produce pant-hoots: adult and subadult males. Analyzing individual rates permitted the detection of any effect of agonistic rank on call production.

6. Abundance, quality, and divisibility of the food source. I assumed that crops are an abundant, high-quality, and divisible food source. During observations, chimpanzees fed mainly on the pith of banana stems, but also on ripe banana fruits and sugar cane. Compared to wild sources of pith such as Pennisetum, banana stems and particularly sugar cane are relatively high in free simple sugars (Table 3.1). Nevertheless, to control for the possibility that chimpanzees consider banana pith to be a low-quality food, I compared observations from three feeding contexts: banana stems, wild ripe fruits (including figs Ficus spp., Mimusops, Uvariopsis, Pseudospondias, and others, all presumed to be high-quality foods), and terrestrial herbaceous vegetation (“THV”; species not identified, but principally Pennisetum and Aframomum, all presumed to be low-quality foods). Given the limited sample size, I made no attempt to distinguish among the abundance and quality of wild ripe fruits.

Chimpanzees often pant-hoot on arriving in trees with abundant fruit (Wrangham 1977). In contrast, chimpanzees did not call on arrival in Crops (pers. obs.). Due to the thick vegetation within and surrounding banana fields, however, it was rarely possible to conduct focal follows at the moment of arrival in Crops. To avoid bias introduced by comparing arrivals in fruit trees with non-arrivals in Crops, I limited analysis to samples collected while feeding, rather than immediately after arriving at the food, for all three food contexts. Food arrival samples will be analyzed separately in a future study.

Data Collection

As described above, observers collected two complementary sets of data on vocal behavior: party follows and focal follows.

Party follows

Observers followed chimpanzees throughout their range, all day when possible, noting the time to the nearest minute for all occurrences of pant-hoots. For each pant-hoot, observers recorded whether the pant-hoot was made by the focal party or by a distant party, and whether one or more than one individual appeared to be calling. At 15 minute intervals, observers recorded the identity of all individuals known to be traveling with the party and the location, with reference to intersections on the trail system or other landmarks, such as the name of the nearest village when crop-raiding.

Table 3.1 Nutritional chemistry of piths (from Conklin-Brittain et al., unpublished data)

	Sugar Cane	Musa spp. (banana stem)	Pennisetum purpureum (elephant grass)
Lipid	0.7	0.7	0.1
Free simple sugar	45.5	29.5	21.8
Crude protein	4.1	3.0	4.4
Neutral detergent fiber	44.2	24.5	63.3
Ash	4.7	3.0	10.4
Total insoluble fiber	0.8	39.3	0.0
Total	100	100	100

Focal follows

Observers conducted focal follows of individuals throughout the day. Each focal follow consisted of a series of 5 point-samples at two-minute intervals, noting the behavior state of the subject (feed, groom, being-groomed, rest, move, other), concurrent with continuous sampling of vocalizations and other selected behaviors. The five point-samples enclosed four two-minute intervals, yielding eight minutes of continuous observation per sample. Observers recorded the call-type of all vocalizations made by the focal subject following Clark's categories (Clark 1993). If the subject was recorded feeding, the species and part eaten were recorded. A variety of herbs including Pennisetum, Aframomum and Marantachloa were simply designated THV. Given the unpredictability of party composition, choice of subject was opportunistic. A minimum of 30 minutes separated the start time of samples on the same individual.

Three observers contributed to the collection of vocal behavior data, obtaining 334 hours of focal samples and approximately 3000 hours of party follow data during an 18 month period (June 1997 through November 1998). For this study, I analyzed a subset of this data, following the criteria listed below.

Data analysis

Party follows

Party follow data were entered into the FileMaker Pro database program (FileMaker 1999) which was used to calculate the number of pant-hoots produced by the focal party each hour as well as the mean number of adult males and females present during that hour. To standardize the sampling regime, only hours in which observations were taken for the entire hour were used (for instance, if an all-day follow began at 6:15 and ended at 19:30, I limited analysis to the period 7:00 to 19:00). Females rarely pant-hoot, so I limited analysis to parties with at least one male present.

Range location

ArcView GIS software (Environmental Systems Research Institute 1997) was used to analyze the ranging behavior of this community (Chapter Two). Locations noted in the party follows were plotted onto a 500 x 500 m grid cell map of the study site. ArcView was used to measure the distance from the center of each grid cell to the park boundary and to the line enclosing the Core. For each hour of observation, I calculated the mean distance to the nearest boundaries of the park and Core. Hours in which the average location was outside the park were designated Crops; hours in which the average location was within the park but outside the Core were designated Edge. The land outside the park includes forest patches and other vegetation besides crops, but all such locations are close to human habitation. Taking the average location for each hour seems appropriate given the rather coarse-grained measures available from 500 x 500 m grid cells, as well as the likelihood that chimpanzees do not perceive these boundaries to be abrupt.

Focal follows

Focal follow data were also analyzed using FileMaker Pro. The number of pant-hoots recorded in each sample was multiplied by (60 min per hour)/(8 min continuous observation per sample) = 7.5 to give an estimate of hourly rate.

Statistical tests were conducted using StatView (Caldarola et al. 1998).

3.4 RESULTS

Party Follow Data

I obtained a total of 1419 hours of party follow data for a total of 252 parties (Table 3.2). Chimpanzees spent 6.5% of observation time in Crops (92 hours) and 14.0 % in Edge (199 hours). The majority of parties (165) stayed within Core for the duration of the follow. A total of 25 parties visited both Core and Crops, and 34 parties visited both Core and Edge. No parties were observed visiting all three locations, and only three parties visited both Crops and Edge. I limited analyses to paired comparisons of parties that visited two locations, so that each party served as its own control.

Table 3.2 Number of parties observed per location

Locations visited	# Parties	Hours in Core	Hours in Crops	Hours in Edge	Total Hours
Core & Crops	25	139	69	0	208
Core & Edge	34	158	0	114	272
Crops & Edge	3	0	9	7	16
Core only	165	831	0	0	831
Crops only	6	0	14	0	14
Edge only	19	0	0	78	78
Total	252	1128	92	199	1419

Parties visiting both Core and Crops were observed for a median of 10 hours, during which they spent a median 5 hours in Core (range = 1 to 11) and 2 hours in Crops (range = 1 to 8). These parties pant-hooted more often in Core (median = 1.6 pant hoots per hour, range = 0 to 5.7) than in Crops (median = 0, range = 0 to 5; Wilcoxon signed rank test; n = 25, z = -2.8, P < 0.01; Fig. 3.1a).

Parties visiting both Core and Edge were observed for a median 9.5 hours (range = 3 to 14), during which they spent a median 4 hours in Core (range = 1 to 13) and a median 3 hours in Edge (range = 1 to 8). These parties pant-hooted more often in Core (median = 3.0, range = 0 to 10) than Edge (median = 1.0, range = 0 to 10.7), though this difference fails to reach statistical significance (Wilcoxon signed rank test; n = 34, z = -1.8, p = 0.07; Fig. 3.1b).

Parties that visited both Core and Crops did not change in party composition, whereas parties that visited both Core and Edge had more males and fewer females when visiting Edge (Table 3.3). Parties that visited Core and either Crops or Edge contained more males than parties that visited only Core (Core: median = 2.6 adult males, range = 0.3 to 10) and parties that visited Edge contained more estrous females (Core: median = 0.0, range = 0 to 3.3 estrous females).

Parties visiting only Edge were observed for a median 3 hours (range = 1 to 13) and produced pant-hoots at a median rate of 1.9 per hour (range = 0 to 6.7). These parties contained a median 5.2 males (range = 0 to 8.6, n = 19) and a median 0 adult females (in all 5 cases with females present, only estrous females were present).

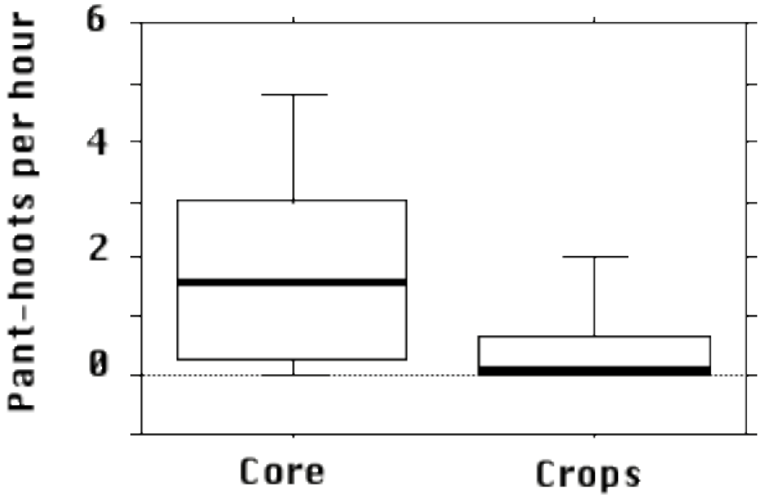
Temporal patterning

The rate of pant-hoot production peaked early in the morning (0700 - 0800) and decreased thereafter until rising to a minor peak in the early evening, just before nesting (1800 – 1900; Fig. 3.2a). This pattern held for parties in both Core and Edge, whereas the rate of pant-hoot production for parties in Crops remained low throughout the day (Fig. 3.2.b). Analysis of variance revealed that pant-hoot rate depended on both time of day ($F_{13,\ 1376} = 3.17$, $p = 0.0001$) and location ($F_{2,1376} = 7.35$, $p < 0.001$), with no significant interaction between these two factors ($F_{26,1376} = 0.80$, NS).

Focal follow data

I obtained a total of 432 focal follows in which the adult or subadult male subject fed on bananas (n = 52), fruit (n = 303), or THV (n = 77). I compared the rate of pant-hoot production in two pairs of conditions: fruit vs. bananas, and fruit vs. THV. I conducted these tests separately because only six individuals had a sufficient number (minimum = 4) of samples in all three conditions. The median rate of pant-hoot production was 0 in all conditions for all males. I therefore report rates in terms of means, though I recognize that these data are not normally distributed.

a. Core vs. Crops



b. Core vs. Edge

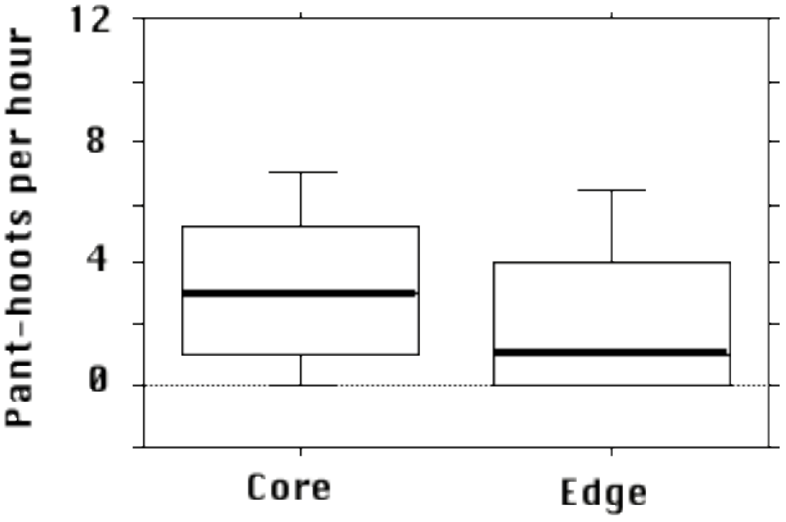


Figure 3.1 Box plots comparing pant-hoot rate in different locations for parties that visited (a) both Core and Crops and (b) both Core and Edge.

<u>Table 3.3</u> Results of Wilcoxon signed rank tests comparing party composition in different locations. In each case, parties that visited two locations during the day are compared with themselves in those locations. AM = Adult Male, AF = Adult Female, and EF = Estrus Female.

		Median	Min	Max	n	z	p
Core	AM	5.0	0.0	8.6			
Crops	AM	5.0	0.0	9.0	25	-0.21	NS
Core	AM	5.7	0.0	10.0			
Edge	AM	6.0	0.0	10.0	34	2.44	0.02
Core	AF	2.0	0	4.8			
Crops	AF	2.0	0	5.2	25	-0.81	NS
Core	AF	2.0	0	5.1			
Edge	AF	1.0	0	3.0	34	-5.78	<0.0001
Core	EF	0.0	0.0	1.0			
Crops	EF	0.0	0.0	1.0	25	-1.34	NS
Core	EF	1.0	0	2.8			
Edge	EF	1.0	0	3.0	34	-0.31	NS

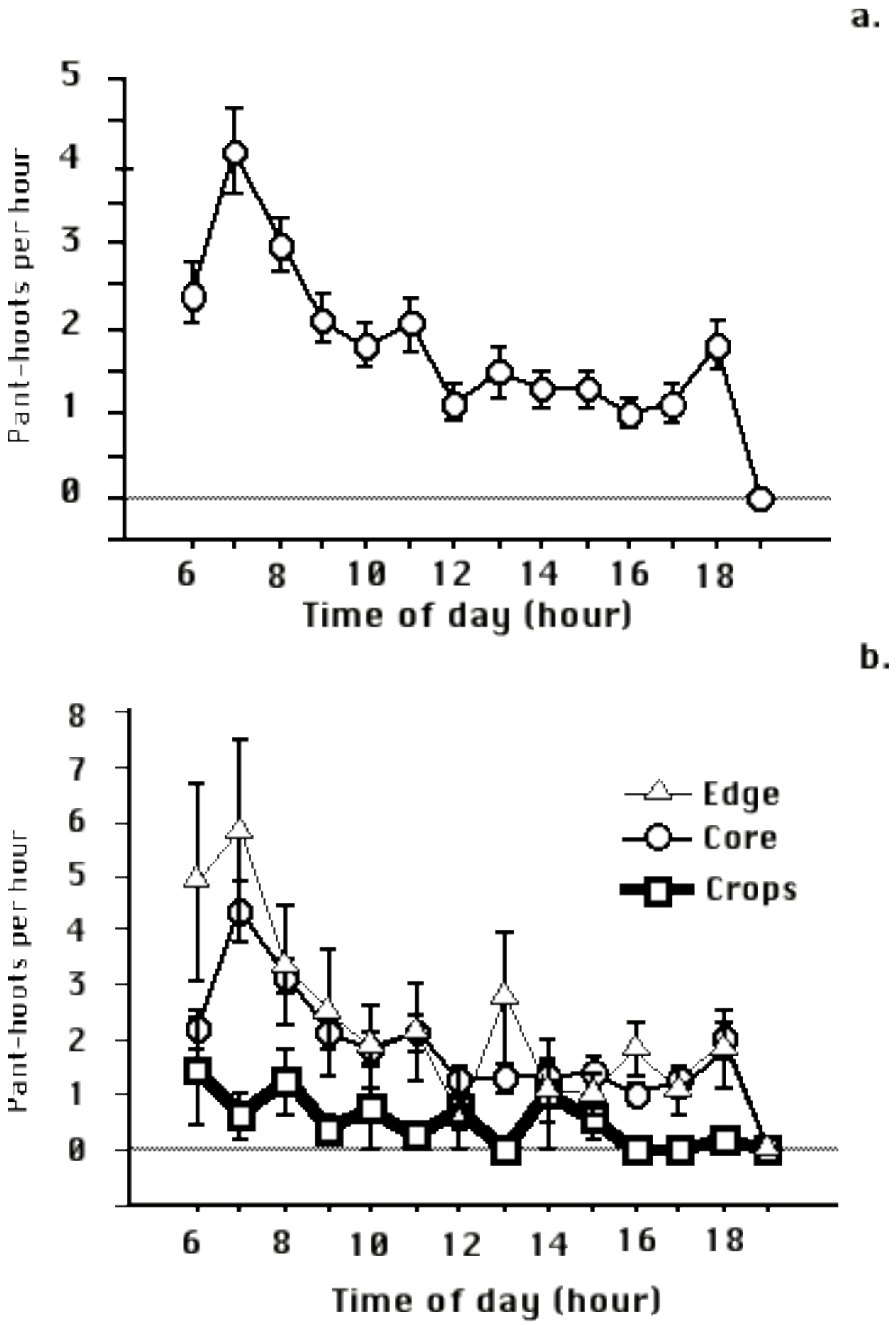


Figure 3.2 Temporal pattern of pant-hoot production. The mean number of pant-hoots produced each hour is shown (a) for all parties and (b) split by location.

Six of seven individuals pant-hooted at a higher rate when feeding on fruit (mean ± s.d. = 1.1 ± 0.9 pant-hoots per hour) than bananas (0.5 ± 1.4; n = 7 individuals; see Fig. 3.3). The median number of samples per individual was 6 for bananas (range = 4 to 13) and 31 for fruit (range = 20 to 41)). In only one of 52 samples did a focal subject pant-hoot in bananas, and this was the highest ranking male MS, who pant-hooted twice. Nevertheless, the difference in pant-hoot rates between fruit and bananas approaches statistical significance only if the one exceptional sample is excluded (ANOVA: $F_{1,6} = 3.88$, $p = 0.05$; otherwise, $p > 0.1$). The eight individuals sampled in both fruit and THV showed no consistent difference in pant-hoot rate between the two conditions (fruit: 1.0 ± 0.9 pant-hoots per hour; THV: 0.9±1.0 pant-hoots per hour; ANOVA: NS; see Fig. 3.3b). Median

samples per individual were 29.5 in fruit (range = 20 to 41) and 7.5 in THV (range = 5 to 17).

3.5 DISCUSSION

Despite the many factors likely to affect pant-hoot production, chimpanzees called less often when crop-raiding than when feeding in other areas of their home range. The two methods of data collection employed, party follows and focal follows, yielded comparable results. Because of the small sample size, the results from focal follows are suggestive rather than definitive. Nevertheless, it is striking that in 6.9 hours of focal observation in crops, distributed over a period of 18 months, pant-hoots were recorded on

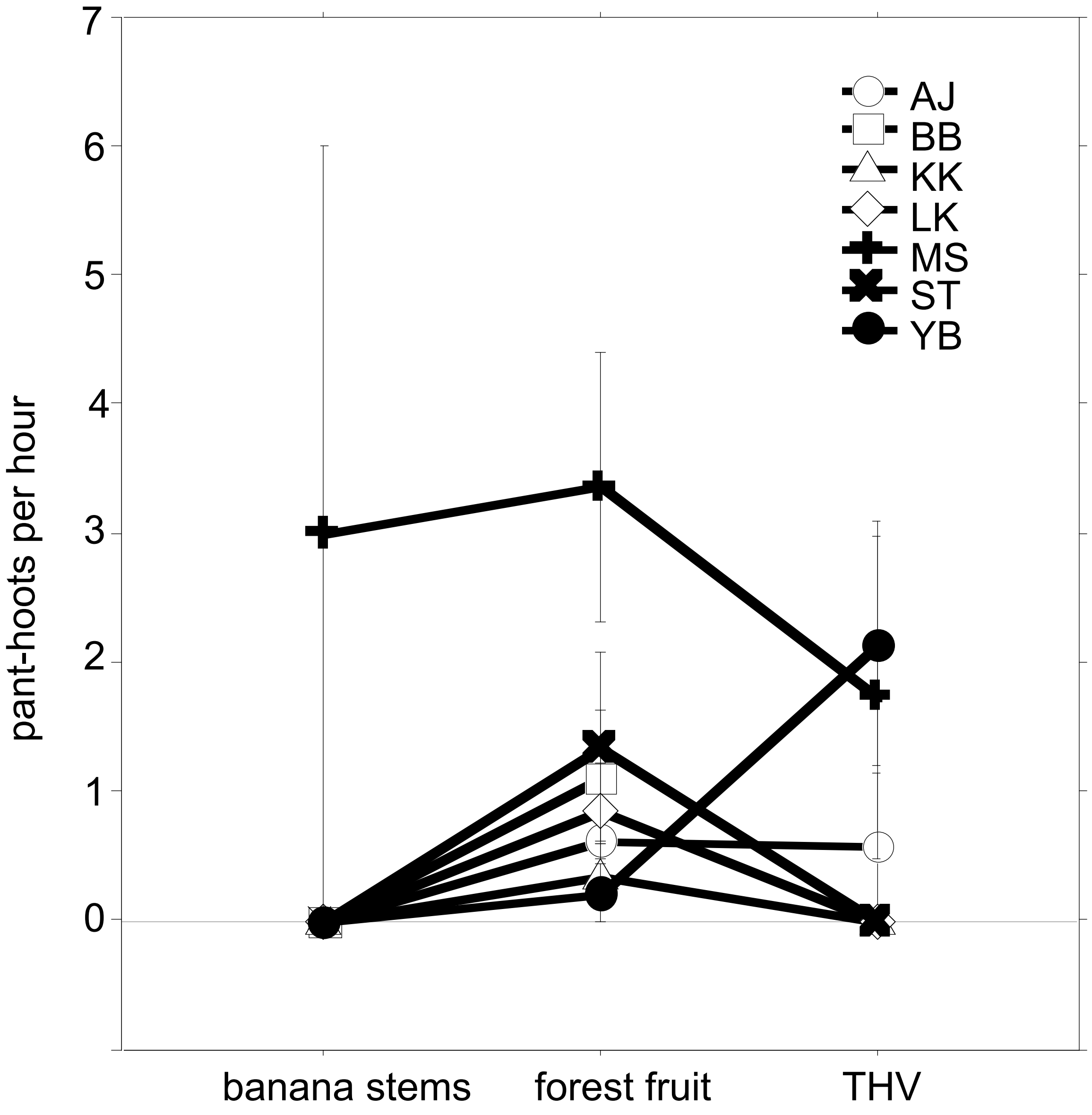


Figure 3.3 Mean number of pant-hoots per hour (plus or minus one standard error) for each of seven males in three feeding contexts: banana stems, forest fruits, and terrestrial herbaceous vegetation (THV).

only one occasion.

In contrast to previous assertions that chimpanzees suppress calls when visiting peripheral areas, I found only a slight and statistically non-significant reduction in pant-hoot rate in Edge areas. A more detailed examination of behavior in peripheral areas is necessary to distinguish patrols, in which chimpanzees are expected to be silent, from excursions, in which chimpanzees might be expected to advertise their presence to claim territorial ownership.

Time of day strongly affected pant-hoot production, in a temporal pattern similar to that reported by Wrangham (Wrangham 1975), with a sharp peak in the early morning and a lesser peak in the evening. In contrast to the pattern observed in the forest, crop-raiding chimpanzees remained relatively quiet throughout the day.

By using each party as its own control, I controlled for any effects of party composition. Parties that visited Core and Crops showed little change in party composition, so the reduction in call rate when in Crops cannot be attributed to a reduction in the number of males. Indeed, parties that visited Crops had more males than parties that remained in Core all day, making the reduced rate of pant-hooting even more striking. Parties that visited Edge also contained more males. This is consistent with the predictions of the lethal raiding hypothesis in which males visiting border areas should travel in larger subgroups when possible to reduce risks of lethal attack by neighboring groups (Manson & Wrangham (1991); Chapter Two). Why chimpanzees should travel in larger parties when visiting Crops is unclear. At least four explanations are possible. First, given the difficulty of following small parties in Crops, a sampling bias may exist. Second, the abundant food of Crops may reduce the costs of traveling in large parties during times of fruit scarcity. Third, most or all of the Crops area is used to some extent by a neighboring community. Though this community appears to be small (perhaps two adult males, one subadult male, and two to four females), the risk of encountering neighbors may increase the incentive for traveling in larger parties. Fourth, traveling in larger groups could reduce the costs of vigilance. To test between these hypotheses, additional observations will be required, perhaps accompanied by experiments that simulate detection by farmers in crop areas.

The abundance, quality, and divisibility of cultivated foods suggest that these resources would normally elicit pant-hoots if humans did not defend them. Even if chimpanzees classify banana stems as relatively low-quality food, they would surely be expected to pant-hoot upon discovery of sugar cane and ripe banana fruits. On several occasions I observed chimpanzees eating sugar cane and banana fruits without pant-hooting, or found recently eaten banana peels when tracking silent chimpanzees through crops. It might be possible to test whether chimpanzees pant-hoot on arriving in chronically undefended fields by observing chimpanzees in the southern part of Kibale National Park, where encroachers have been evicted and their fields left to grow wild. Such a test was not possible during my study period, both because no chimpanzees were habituated in that region, and because the area was thought to be unsafe for researchers due to rebel activity.

Physiological factors

It is likely that physiological factors affect vocal production in chimpanzees, as in other animals. For instance, Bercovitch and colleagues (Bercovitch et al. 1995) showed that rhesus monkeys with experimentally suppressed cortisol levels showed a decreased likelihood of giving alarm calls. Given that crop-raiding is likely to be a stressful situation for chimpanzees, it seems likely that chimpanzees experience elevated cortisol levels in this situation. Whether elevated cortisol levels affect the probability of pant-hooting is currently unknown.

Another relation between physiological state and pant-hoot production is suggested by the temporal pattern, which closely corresponds with the patterns found in this population for testosterone levels and associated behaviors (Muller & Wrangham 2001). Muller found that testosterone levels, aggression rates and copulation rates all peaked early in the morning and decreased thereafter, with a slight peak in the evening (Muller, in prep.). Moreover, afternoon testosterone levels correlated with rank, much like the pattern of pant-hoot production (Muller, in prep.). As in other studies (Clark 1993; Mitani & Nishida 1993; Uhlenbroek 1996) the highest-ranking male produced pant-hoots most often, and was indeed the only individual observed pant-hooting in Crops during a focal follow. Nevertheless, the fact that chimpanzees generally remained quiet throughout the day when crop-raiding suggests that whatever physiological factors relate to call production may either be over-ridden, by cognitive factors, physiological factors, or both.

Cognitive questions: Do chimpanzees know what farmers know?

Despite the robust evidence presented here for reduced pant-hoot production when crop-raiding, the mechanisms underlying this reduction in call rate remain unclear.
Vocal suppression could in principle result from very simple associational learning: chimpanzees who call get chased away and remember not to call next time. More sophisticated mechanisms are also possible. Based on experiments conducted in captivity, Hare and colleagues argue that "chimpanzees know what conspecifics can and cannot see, and, furthermore, that they used this knowledge to devise effective social-cognitive strategies in naturally occurring food competition situations" (Hare et al. 2000). If chimpanzees know what conspecifics can and cannot see, it seems possible that chimpanzees have theories about what farmers can and cannot hear, and modify their behavior accordingly.

In support of a richer interpretation, anecdotal descriptions suggest that chimpanzees have some awareness that parts of their bodies produce signals, and that chimpanzees take steps to intercept the signal from being seen or heard by others. De Waal (1982) reports that a female covered the mouth of her infant when screams seemed likely to bring male retribution. During a time of intense status competition, an adult male covered up his mouth, apparently to prevent squeaking in fear, when his rival began to pant-hoot (de Waal 1982). In a non-vocal example of signal interception, a young male covered his erect penis when a senior male caught him courting (de Waal 1982).

It is also possible, however, that chimpanzee vocal suppression does not require cognitive sophistication and is based on mechanisms common to many mammals. Distinguishing between these hypotheses is likely to prove difficult. It would be helpful to determine the developmental trajectory of vocal suppression. Do chimpanzees learn to suppress calls as they mature? If so, do chimpanzees learn mainly from being chased out of fields after calling? Do adults punish juveniles for calling? The difficult observation conditions prevalent during crop-raiding limited my ability to observe juveniles, but it may prove possible to address such questions in the future.

Selection for vocal suppression

As discussed in the introduction, crop-raiding is an admittedly artificial context, an opportunity unavailable to chimpanzees before the spread of agriculture to tropical Africa in the past few thousand years. The ability to suppress calls during an evolutionarily novel context raises the question of what features of chimpanzee ecology might have selected for the ability to suppress calls. In many ways, crop-raiding is analogous to entering the territory of a community of hostile conspecifics to feed. If in fact chimpanzees do suppress calls during border patrols, a history of lethal raiding may have pre-adapted chimpanzees for crop-raiding.

As mentioned in the introduction, however, anecdotal accounts suggest that several species without lethal raiding (elephants, baboons, and vervet monkeys) also stay unusually quiet when crop-raiding. A more widespread selection pressure for vocal suppression, affecting chimpanzees and many other animals, may be predation. Tutin and colleagues (Tutin et al. 1981) found that chimpanzees in Senegal frequently called upon detecting predators if the predators were within about 100 m. These calls apparently functioned to warn the predator that it had been spotted. Chimpanzees remained silent, however, if they were in a small party, or if they unexpectedly encountered a predator at very close range. Some evidence exists that other primates modify their vocal response to primates according to the risk of being attacked. For example, Bshary and Noë (1997) found that red colobus monkeys varied their vocal response according to the pursuit strategy of two potential predators: leopards and chimpanzees. Leopards specialize in surprise attacks, and may abort a hunting attempt if detected. In contrast, chimpanzees hunt cooperatively and do not rely on surprise for success. In response to playback of leopard calls, red colobus alarm called extensively. In contrast, red colobus called immediately after hearing chimpanzee call but then stayed relatively quiet and moved away from the speaker (Bshary & Noë 1997). Whether chimpanzees perceive crop-raiding to be more analogous to invading the territory of neighboring conspecifics or entering an area of high predation risk is uncertain.

Conservation implications

At this point, it seems important to emphasize that crop-raiding not only provides an interesting context for understanding chimpanzee vocal production, but also presents real dangers to chimpanzees. Approximately 15% of farmers illegally set traps for wild animals in their fields (Naughton-Treves et al. 1998). Snares are set in the forest as well, but it seems likely that the density of snares is highest near human habitation. Many of the chimpanzees in this population have lost fingers, toes, hands, and even their lives from wire snares set for duikers and other animals. Chimpanzees appear to understand the danger of wire snares, avoiding any snares they detect (pers. obs.). On one occasion during my study, however, an adult male was caught in such a snare while raiding a banana field.

Crop-raiding also inflicts real costs on farmers living near the forest edge. Although chimpanzees in this population destroy fewer crops than baboons or bush pigs, crop-raiding by chimpanzees fuels local resentment towards the park (Naughton-Treves et al. 1998). Chimpanzees who exploit crops pose other dangers in that they sometimes attack human children (Wrangham et al. 2000), although no members of the study community have been implicated in such attacks. Given that chimpanzees in this population, as in most or all populations across Africa, depend on the good will of their human neighbors for survival, it is important that we understand the frequency and impact of crop raiding by chimpanzees. Despite living on the forest edge, with 18% of their total range under cultivation, chimpanzees in this population spent only 6.5% of observed time outside the park. Chimpanzees are stealthy raiders, but they also appear to understand the dangers inherent in crop-raiding and do so relatively infrequently.

In conclusion, chimpanzees reduced their production of loud calls during at least one context in which calling would be costly: crop-raiding. Chimpanzees showed a tendency to produce fewer loud calls when visiting borders, but more detailed analysis is necessary to determine whether they reduce call rate when patrolling borders compared to when they visit borders to feed. Pant-hoot production depended on sex, rank, and time of day in a pattern strikingly similar to testosterone levels, suggesting that pant-hoot production is correlated with high testosterone levels. Nonetheless, high ranking adult males generally stayed quiet when crop-raiding, even during the early morning, despite their presumably high testosterone levels. These findings support the claims from anecdotal literature that chimpanzees are, at least under some circumstances, able to control their rate of vocal production.

CHAPTER FOUR

DOES PARTICIPATION IN INTERGROUP CONFLICT DEPEND ON NUMERICAL ASSESSMENT, RANGE LOCATION, OR RANK FOR WILD CHIMPANZEES?

4.1 SUMMARY

Male chimpanzees, Pan troglodytes, engage in cooperative territorial defense and sometimes kill members of neighbouring communities. Observations of intergroup interactions suggest that escalation of aggression depends on numerical assessment, with lethal attacks occurring when numerical advantage reduces the costs of attacking. In order to gain a better understanding of the factors guiding participation in intergroup conflict, I conducted a series of playback experiments with the Kanyawara chimpanzee community of the Kibale National Park, Uganda. I tested whether the response to the playback of the 'pant-hoot' call of a single extragroup male depended on the number of adult males in the listening party, the location of the speaker relative to the territory edge, and each male's agonistic rank. These playbacks elicited cooperative responses, with the nature of the response depending on the number of adult males in the party. Parties with three or more males consistently joined in a chorus of loud vocalizations and approached the speaker together. Parties with fewer adult males usually stayed silent, approached the speaker less often, and traveled more slowly if they did approach. In contrast to many territorial species, the location of the simulated intruder did not affect the response.

Although high ranking males might be expected to benefit more from repelling outside males, both high and low ranking males showed a similar pattern of response. Each male responded as if he benefited from repelling intruders, but only if he had strength in numbers. This pattern of response is consistent with cooperation based on mutualism.

4.2 INTRODUCTION

Contests between social groups include striking examples of cooperation, in which individuals risk injury and death to acquire or defend shared resources. The mechanisms underlying cooperative intergroup aggression remain a central problem for behavioural biology. In general, animals should enter an intergroup contest when the benefits appear to outweigh the costs (Parker 1974), which may result from the perception of either high benefits or low costs. Benefits include the acquisition or defense of food, mates, and territory. Individuals may also benefit from killing infant or adult members of other groups. For instance, infanticide may increase future mating opportunities for males (Hausfater 1984; Packer et al. 1988; Breden & Hausfater 1990; Palombit 1999), and killing adults may reduce the competitive strength of rival groups (Wrangham 1999). Failure to defend against intruders may result in loss of territory, resources and lives of group members, and eventually result in group extinction (Nishida et al. 1985; Goodall 1986; Packer et al. 1988; Soltis et al. 1995; Mech et al. 1998). The costs of entering an intergroup contest may depend critically on the number of opponents on each side. In territorial species, the expected benefits may vary with location relative to the opponents' territorial boundaries (e.g. Maynard Smith (1982)). Additionally, individuals may vary in the expected benefits from an intergroup contest, and may modify their participation accordingly. In many primate species, for instance, higher-ranking males participate more actively in intergroup contests than lower-ranking males (Nunn 2000).

In the present study, I conducted a series of experiments on chimpanzees, Pan troglodytes, designed to test how willingness to participate in an intergroup contest varies with the number of defenders, experiment location, and individual agonistic rank. Chimpanzees live in fission-fusion communities of 20 to more than 120 individuals who travel in temporary parties of varying size, ranging from one to more than 20 individuals (Goodall 1986; Chapman et al. 1994; Watts 1998). Males breed in their natal communities and participate in a number of group-level activities, including hunting (Boesch 1994; Stanford et al. 1994), mate guarding (Watts 1998), and intergroup aggression (Goodall et al. 1979; Nishida 1979). Theoretical considerations suggest that chimpanzee home ranges are defendable (Mitani & Rodman 1979; Lowen & Dunbar 1994), at least in forest and woodland habitats, and in fact all long-term study sites with multiple social groups report territorial defense (reviewed in Wrangham 1999). Males form stable dominance hierarchies in which higher-ranking males appear to have greater mating success (e.g. Watts 1998). Females typically disperse before breeding. During intergroup conflict, females may participate by vocalizing or approaching, but females avoid direct physical attacks (Goodall 1986; Boesch & Boesch-Achermann 2000).

Contests between groups may have a profound effect on individual fitness and social organization. Over a 20 year period at Gombe, Tanzania, intergroup aggression accounted for 30% of adult male mortality (Goodall 1986). Although such high rates of mortality from intergroup aggression are unusual among mammals, similar rates have been reported for humans (Chagnon 1988; Soltis et al. 1995) and wolves, Canis lupus (Mech et al. 1998). Nevertheless, intergroup contests occur infrequently and are often difficult to observe. Playback experiments provide an opportunity to simulate intergroup interactions under controlled conditions, making it possible to test the relevant hypotheses.

Experimental Design and Rationale

I tested the response of chimpanzees to an intruder by playing back a recorded 'pant-hoot' call from a foreign male. Chimpanzees pant-hoot throughout the day, with a peak in frequency between 0700 and 1000 hours (Wrangham 1975). Pant-hoots can be heard over distances of 1-2 km (Reynolds & Reynolds 1965; Ghiglieri 1984), and are produced in a variety of circumstances, including arrival at fruiting trees and during reunions, hunts, and intergroup encounters (Marler 1976; Goodall 1986; Clark 1993; Mitani & Nishida 1993). Pant-hoots appear to play important roles within and between groups, as do the long-distance calls of other species with fission-fusion societies (e.g. lions, Panthera leo: (McComb et al. 1994); wolves: (Harrington 1979); spotted hyenas, Crocuta crocuta (East 1991)). Pant-hoots enable allies and associates to maintain contact across long distances (Mitani & Nishida 1993), and by advertising the presence of large parties, pant-hoots may deter approach by extragroup chimpanzees (Nishida et al. 1985; Clark 1991).

I tested whether willingness to enter an intergroup contest depended on the following three factors: 1) numerical assessment, 2) experiment location, and 3) individual agonistic rank. The following represents a brief synthesis of why I considered these three factors to be important for our experimental design.

1) Numerical Assessment

In many species, larger groups tend to defeat smaller groups (e.g. ants: Hölldobler (1981); Adams (1990); social carnivores: Kruuk & Macdonald (1985); primates: Cheney (1987); Isbell (1991); humans: Keeley (1996)). Individuals seeking to minimize costs should therefore be more willing to enter contests in which their side has a numerical advantage. A recent series of experiments has demonstrated that such numerical assessment guides the decision of female lions to enter intergroup contests (McComb et al. 1994) Specifically, experiments simulating the intrusion of unfamiliar females found that resident females were more likely to approach a single intruder's roar if they outnumbered the intruder, and were more likely to approach a single roar than a chorus of three strangers' roars.

While numerical assessment should be widespread among species with intergroup contests, such assessment should be particularly important for species with fission-fusion social organisation. Wrangham and colleagues (Manson & Wrangham 1991; Wrangham 1999) argue that in such species, intergroup encounters will sometimes involve extreme numerical imbalances, allowing members of one group to kill outnumbered opponents at relatively low cost. Members of such species should seek out opportunities to kill members of rival groups at low cost in order to reduce the coalitionary strength of rival groups, increasing likelihood of success in future territorial contests.

Observational data support the prediction that the outcome of intergroup contests in chimpanzees depends critically on numerical imbalances. Battles between parties of roughly equal size rarely lead to injury (Nishida 1979; Boesch & Boesch-Achermann 2000). In contrast, the five lethal attacks observed at Gombe involved parties with at least three adult males attacking lone or outnumbered individuals (Goodall 1986).

2) Experiment Location

The net benefits of entering an intergroup contest should depend not only on numerical assessment but also other factors, such as asymmetries in ownership (Davies 1978) and the value of the contested resource to each opponent (Austad 1983; Enquist & Leimar 1990). Lions, for instance, will approach intruders even if outnumbered, depending on such factors as the sex of the intruders and defenders (Grinnell et al. 1995), the presence of cubs (McComb et al. 1994), and population density (Heinsohn 1997).

It is possible that, under some circumstances, it would not pay for individuals to enter a contest even if they had a numerical advantage. For instance, arguments from evolutionary game theory predict that in territorial species, the benefits of range defense should be highest towards the center of the territory (Maynard Smith 1982). In many territorial species, residents are more likely to win than intruders (Davies 1978; Cheney 1981), and response to the call of an extragroup individual decreases with increasing distance from the center of the defenders' territory (many songbirds: Falls (1982); gibbons and siamangs Hylobates spp: (Chivers & MacKinnon 1977; Raemaekers & Raemaekers 1984; Mitani 1985).

Nevertheless, response to intruders does not necessarily vary with location in all species. For instance, Waser (1977a) found that groups of gray-cheeked mangabeys, Lophocebus albigena, in Kibale Forest maintained spacing by mutual avoidance rather than territory defense, and location did not affect the response to a simulated intruder. Although chimpanzees, in contrast to mangabeys, actively defend territories, at least two lines of argument suggest that the response of male chimpanzees to intruders should not depend on location. First, van Schaik and others (van Schaik et al. 1992; Nunn 2000) have argued that males may be more concerned with defending females than with defending a particular geographic boundary, since male reproductive success depends more on access to females than on the resources within a particular boundary. By this argument, males should always seek to repel outsiders, regardless of location. Second, the observations and theoretical considerations discussed above suggest that the principal benefit of intergroup aggression in chimpanzees is the opportunity to reduce the coalition strength of neighbouring groups by killing rival adult males (Manson & Wrangham 1991; Wrangham 1999). The payoff for intergroup aggression in chimpanzees and species with similar social organization should therefore be independent of location.

3) Individual Agonistic Rank

Benefits may also vary among individuals within a group. In species with male dominance hierarchies, high ranking males may gain greater benefits from excluding extragroup males, and may therefore be more willing to fight male intruders (Nunn 2000). For instance, in multimale groups of mangabeys, only one male in each group consistently approached the playback of a male intruder (Waser 1977a).

It is unclear from observational reports whether high ranking male chimpanzees participate more actively in intergroup encounters. High ranking males give pant-hoot calls at a higher rate than low ranking males (Clark 1993), suggesting they are more willing to advertise their presence. Nevertheless, no obvious effect of dominance rank has been reported for participation in border patrols or battles (Goodall 1986; Boesch & Boesch-Achermann 2000).

4.3 METHODS

Study Site and Population

I studied the Kanyawara community of chimpanzees living in Kibale National Park, Uganda. The study site, described in detail elsewhere (Struhsaker 1997) is located at 0° 34' north latitude and 30° 21' east longitude. The rolling terrain varies in elevation from 1500 to 1700 m. The vegetation at Kanyawara includes a mosaic of moist evergreen forest, colonizing forest, swamp, and exotic softwood plantations within the park as well as forest patches, tea plantations and subsistence farms outside the park. The Kanyawara community contained approximately 50 individuals during the study period (June 1996 - December 1998), including 10-11 adult males and 15-16 adult females, all of whom were individually recognized. Isabirye-Basuta initiated systematic study of this community in 1983 (Isabirye-Basuta 1989), and the community has been studied continuously since 1987 (Hauser 1990; Wrangham et al. 1992; Wrangham et al. 1996).

Playback Experiments

Overview

I played back a single foreign pant-hoot call to chimpanzees in parties of varying size and composition. The number of adult males in each party varied from zero to nine. The location of trials varied somewhat opportunistically, following seasonal changes in range use; I attempted, however, to balance the number of trials towards the edge and center of the territory (Fig. 4.1).

Test Stimuli

Test stimuli consisted of 12 different digitized recordings of pant-hoots collected by J. Mitani from five different individuals from the M-Group of chimpanzees in Mahale,

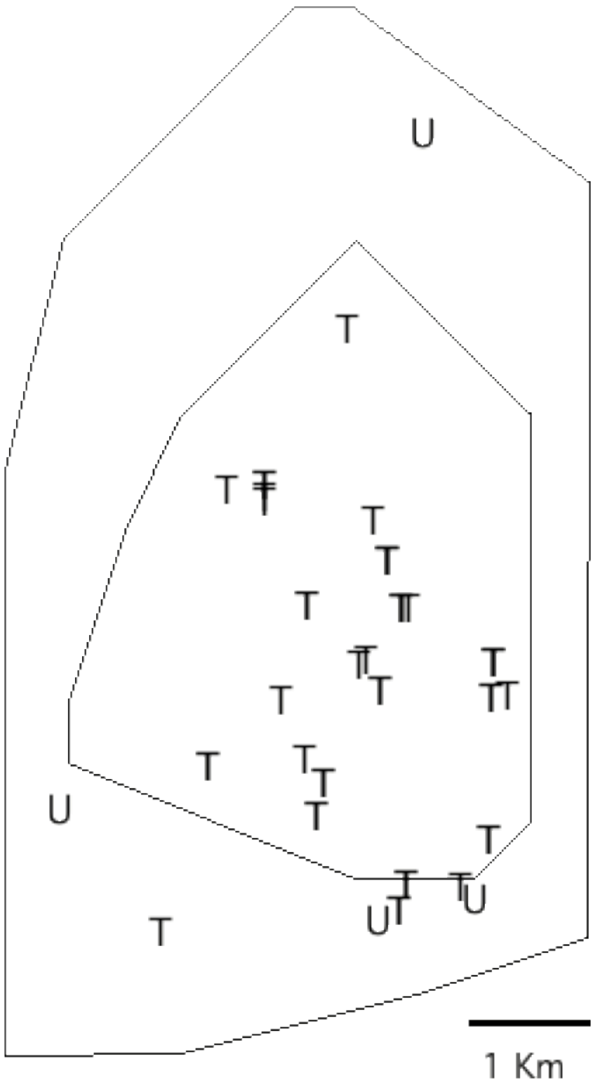


Figure 4.1 Kanyawara community range use (1996-1998) and playback locations. The outside polygon encloses the centers of all 500 by 500 m grid cells used by the community. The inside polygon encloses the centers of grid cells containing 98% of nest sites used during the study. Triangles indicate the speaker location for each playback, and squares indicate locations for all intergroup interactions in which members of outside groups were directly observed during the study period.

Tanzania, with one to four exemplars per individual. No two consecutive trials used the same call. Calls were stored on digital audio tapes and played from a Sony TCD-D8 DAT recorder linked to a Peavey Impulse 652 speaker (frequency range = 60 Hz - 18 kHz; 100 watts power). Calls lasted a median 6.9 sec (range: 5.7 - 14.6) and were played at a peak sound pressure level of X±SE=92.4±2.5 dB at 5 m.

Protocol

Two operators ran the playback equipment and maintained radio contact with observers. Up to six observers recorded the response. I selected situations in which the chimpanzees were likely to remain stationary for about 30 min (e.g., feeding, grooming or resting). Mornings offered the best such opportunities. The median playback time was 0932 hours (range: 0727 - 1215). Playbacks were conducted when subjects were calm and quiet.

Signal transmission varied considerably, depending on terrain and vegetation. The operators placed the speaker in a site suitable for transmission, a median 300 m from the nearest chimpanzee (range: 110 - 610 m). To confirm the audibility of the signal, and also to test whether subjects were responding to an odd noise rather than a species-specific call, the operators played a heterospecific control stimulus (the roar of a male black and white colobus, Colobus guereza, or the contact call of a juvenile crowned hawk eagle, Stephanoaetus coronatus). Chimpanzees pay little attention to these calls when they occur naturally. The operators repeated the control stimulus until it was clearly audible to the observers, resulting in a median of two control stimulus playbacks per trial (range: 1 - 7), a median 16 min before the pant-hoot playback (range: 1 - 120 min), with a median 11 min passing between repeated control stimuli (range: 1 - 84).

After playing the control stimulus, the operators played a pant-hoot. The operators removed the equipment immediately after playback so that chimpanzees never saw the equipment in operation. One operator remained concealed at the speaker site to observe the response of any approaching chimpanzees, who generally did not appear to see or react to the operator.

To prevent chimpanzees from habituating to the playbacks, I waited at least five days between trials in 1996, and in 1997 increased this minimum interval to 10 days. No more than three trials were conducted in any one month. A median of 12 days passed between trials (range: 5 - 301 days). Because party composition varied across trials, each individual heard only a subset of the trials. The median inter-playback interval experienced by each adult was 28 days for males (range: 11-119) and 30 days for females (range: 13-137).

I tested a total of 12 adult males and 15 adult females. Males heard a median 11 trials (range: 2 - 17) and females heard a median 4 trials (range: 1 - 13), including cases both directly observed and inferred (either because they approached the speaker within an hour of the playback, they were heard counter-calling to the playback and later identified, or they were found within a few hundred meters of the speaker within an hour of the playback).

Documenting Response to Playback

Observers recorded the response using focal behavioural samples of selected adult males and females, all-occurrences sampling of pant-hoots and other loud calls, and ad libitum observations (Altmann 1974). Observers recorded the party composition at the beginning of the trial and when subsequent changes occurred. One observer recorded the vocal behaviour of the group on audio tape for 5 min before and after the playback, and seven trials were also recorded using a video camera. Observers conducted systematic observations for a minimum of 20 min before and after each playback, though in some cases observers lost rapidly moving subjects. Male chimpanzees generally responded in a coordinated fashion (see Results), so that observers generally documented the approach behaviour of all males in the party. When chimpanzees moved towards the speaker, observers recorded the order of individuals in the progression.

Every two minutes, each observer recorded the location of the focal subject with respect to the trail grid system or other landmarks, and, starting in 1997, the identity of all individuals within 1, 5, and 10 m of the focal subject. Within the central trail system, trails were spaced 25 to 50 m apart. In areas with lower trail density, this method provided little resolution of travel distance. Starting in 1997, I improved the resolution by marking the location of one male in each focal party with flagging tape every two minutes. I measured the position of flagged locations, trail intersections, and the speaker site using a Garmin GPS 12 Global Positioning System (GPS; position accuracy to 15 m

RMS). In dense forest canopy, obtaining an accurate GPS reading can take 5-10 minutes, so all such readings were taken after the experiment. In order to verify the GPS readings, and also to obtain more accurate measurements of shorter distances such as closest approach to speaker, I used a 50 m measuring tape, Hip Chain measuring string, and compass bearings, with reference to trail maps and a 1:50,000 scale map of the study area. With these measurements, I determined the rate of travel between known points, and used a map of the approach path to estimate latency to 100 m, the time taken to move 100 m closer to the speaker, to the nearest minute.

Sample Size and Independence of Parties Within Trials

I conducted 26 playback trials from June 1996 through July 1998, with a total of 28 focal parties observed. In four trials, the focal party included only females and their dependent offspring. The remaining 22 trials included from one to nine males in the focal party. Because of strong expectations that males and females should respond differently to the call of a foreign male, I restricted analyses to parties with at least one male, discussing female-only parties separately, unless stated otherwise.

The definition of “party” varies from study to study (Chapman et al. 1994). Chimpanzee parties generally travel as discrete units but sometimes spread out over larger distances, and in dense forest it is seldom possible to determine the distance separating all individuals. Here I use “party” to mean all individuals traveling, feeding, resting, or socializing within about 50 m of one another (Wrangham et al. 1992; Clark 1993). In two borderline cases, in which individuals were separated from the rest of the party by 50-60 m but had been together with other party members in the previous 15 min, I considered them all to be members of the same party. In practice, a minimum of 90 m separated the parties I considered to be distinct.

When chimpanzees assess their numbers relative to an intruder, they might include individuals present in nearby parties. In eight trials, evidence indicated that at least two parties heard the playback. For two of these trials, I conducted focal follows on members of both parties present. I examine whether parties within trials responded independently below (Results). In order to avoid possible pseudoreplication, I took the conservative approach of limiting analysis to one party per trial. As it turned out, in the two trials with multiple focal parties, the focal parties were of similar composition and responded in a similar manner, so that in all but one case, neither the restriction of analysis to one party per trial nor the choice of which party to exclude affected the general pattern or statistical significance of the results. I discuss the one exception below (Results).

Within-community Playbacks

I conducted two within-community playbacks, using pant-hoots recorded from Kanyawara males in 1997. I restricted playback of resident male calls to parties with fewer than three males, using the call of a male who had not recently been seen. I chose to use parties with few males for two reasons. First, the presence of few males would increase the probability that males for whom I had playback stimuli would be absent. Second, I reasoned that parties with few males would be more likely to give a distinct response to resident males, based on the results of earlier trials. Specifically, males often call in response to the pant-hoots of resident males (Mitani & Nishida 1993), but males in small parties almost always remained silent when hearing the foreign male pant-hoot playback (see Results). Although this sample size is extremely limited, I report the results below, recognizing the need for more such trials in future experiments.

Determination of Range Boundaries

As in other populations, the Kanyawara community's range includes areas of extensive overlap with neighbouring communities, complicating any attempt to determine community boundaries. Different studies have used different criteria for determining the boundaries of animal territories (Maher 1995). For this study, I used the "nesting range": the minimum convex polygon containing 98% of locations used for night nests during the study period. The nesting range is thus similar to the "core" area of other studies (Goodall 1986; Williams 2000). Using the nesting range has the following advantages: nesting seems a good indicator of whether chimpanzees consider a given location to be safe, as chimpanzees are unlikely to nest deep inside neighbouring territory, and nesting provides independent data points for each party.

To determine the nesting range, I plotted a total of 494 nest locations from January 1996 through December 1998 on a 500 by 500 m grid map of the area. Limiting the polygon to 98% of the nest sites eliminated overly influential outliers. I used ArcView GIS (Environmental Systems Research Institute 1997) software to measure the distance from the GPS measurements of the initial subject location and speaker location for each playback trial to the nearest edge of the nesting range polygon.

Dominance Rank and Approach Rank

I determined the dominance rank of males from the direction of agonistic wins and losses, using a probabilistic model (Jameson et al. 1999) that permitted ranking of individuals with few observations. Because ranks changed from year to year, I calculated mean dominance rank, weighted by the number of trials in which each male was observed at a given rank. Approach rank was calculated following Heinsohn & Packer (1995). Each animal's order within the approaching party was standardized to a value between -1 (last) and 1 (first) to control for party size.

Statistical Analysis

For statistical analyses, I used Stata 6.0 (Stata Corporation 1999) with two-tailed hypothesis testing and significance set at $P < 0.05$. To facilitate comparison across studies, I followed methods described for similar studies with lions (McComb et al. 1994; Grinnell et al. 1995; Heinsohn 1995). I conducted analyses at two levels: parties and individuals. In party-level analyses, I used one value per trial, rather than the separate response of each chimpanzee, to avoid pseudoreplication (e.g. Grinnell et al. 1995). Analysis of individual behaviour, using repeated measures analysis of variance, enabled us to test both for differences among individuals and for the possibility that the observed patterns of response resulted from sampling bias. Though I describe the responses for parties with only females and dependents, due to the small sample size of such parties (N = 4), I limit all statistical analyses to parties with at least one male.

I determined the readiness of the defenders to engage in a contest with the foreign male by whether they answered the playback with counter-calls and whether they approached the speaker. Counter-calling was scored as a binary response of 'yes' or 'no,' describing whether any members of the focal party responded to the playback with loud calls (pant-hoots, waa-barks, screams (Goodall 1986)) within 5 min of the playback. In practice, all responses scored as 'yes' occurred within seconds of the playback, and all parties scored as 'no' stayed quiet for over 20 min, except for one case in which a male began pant-hooting 19 min after the playback. Approach was likewise scored 'yes' or 'no,' describing whether any members of the focal party responded to the playback by moving forward at least 50 m within 20 min of the playback. In practice, all parties scored as approaching moved forward at least 120 m and all parties scored as not approaching moved forward 20 m or less. To understand which factors influenced the probability of counter-calling and approaching, I ran backward stepwise logistic regressions with the following independent variables: number of adult males in the immediate party, number of adult males within acoustic range of the speaker, number of adult females in the immediate party, distance from speaker to the nearest edge of the nesting range, distance between speaker and subjects at the time of playback, and date; I used a P-level-to-retain of 0.10.

I examined two additional variables which should be related to willingness to enter an intergroup contest: distance traveled relative to the speaker in the 20 min following playback, and the speed of approach as measured by the latency to reach 100 m. I conducted stepwise regression with the following independent variables: number of males in the immediate party, number of males within acoustic range, number of females in the immediate party, distance from subjects to speaker at the time of playback, distance from speaker to nearest edge of the nesting range, and the date of the playback, with P-level-to-retain of 0.10.

I examined the grouping behaviour of males following playback, both to assess response to playback and also to verify that males tended to travel close enough together to justify our use of a single value for approaching parties. Sample size for this analysis was limited due to two factors: I did not begin systematic data collection on the number of individuals within 10 m until 1997, and in three subsequent cases I was unable to obtain sufficient data for paired comparisons because focal males were temporarily lost from view. Despite these limitations, I obtained grouping data both before and after playback for 18 focal males in 12 of the 18 parties that approached, giving one to three focal males per party. To avoid pseudoreplication, I calculated the median value for the focal males in each party, giving one measure per party.

The directness of approach to speaker clarifies whether movements following playback were in fact directed towards the simulated intruder, and also tests the minimum capabilities of chimpanzees to localize calls of conspecifics. In order to assess the directness of approach, I calculated the angular error of localization, following Waser (1977b). This method could only be used in cases where subjects moved past the speaker location, which restricted the sample size to 11 parties. The angle, θ, was calculated as follows: $\theta = \arctan(\underline{D}_p/\underline{D}_i)$, where $\underline{D}_p$ equals the distance from speaker to subject when the subject crossed the arc drawn through the speaker site and centered on the subject's initial location, and $\underline{D}_i$ equals initial distance between speaker and subject at the time of playback. Since approaching chimpanzees typically traveled in single file, with each individual passing the speaker at roughly the same distance from the speaker, I report this result for approaching parties rather than for individuals.

Ethical Note

The possibility exists that playing back calls of foreign males may increase stress levels and even lead to inter-community violence. Nevertheless, playback experiments have been used extensively to explore territorial responses in birds and mammals, including species in which lethal intergroup aggression occurs, such as lions. In no case that I am aware of have these experiments resulted in increased levels of aggression between experimental subjects and their neighbours. Lions in particular experience high rates of injury and mortality from intergroup aggression (Packer et al. 1988), yet playback experiments conducted at a rate similar to those in this study have not resulted in any apparent increase of intergroup conflict (e.g. McComb et al. 1994; Grinnell et al. 1995). Although systematic comparisons are difficult due to the low rate of intergroup encounters in this population, the rate of intergroup encounters did not appear to change following the initiation of playback experiments. One lethal intergroup attack did occur after the completion of the foreign male playback series (Wrangham et al. in prep), but such attacks also occurred before this study began. Moreover, the playback experiments did not appear to cause a long-term change in the community's home range area; only short-term changes in location occurred within a day or so following the playback.

4.4 RESULTS

During the study period, the Kanyawara community ranged over an area covering 38.6 km^2 and spent the night in nests built within a smaller area of 15.8 km^2. All intergroup encounters observed during the study period took place beyond the edge of the nesting range (Fig. 4.1). The speaker was located a median 740 m inside the nearest edge of the nesting range (range: -1050 to 1730, where negative values indicate distances beyond the nesting range).

In the 20 min prior to the pant-hoot playback, focal parties remained relatively quiet, producing a median of zero loud call bouts per party (range: 0 - 3 bouts). Apart from individual movements of a few meters, such as changing position within the crown of a feeding tree or within a resting party, focal parties showed no tendency to move relative to the speaker. In fact, only in one party did individuals move a measurable distance; in this exception the two males in the party left the feeding tree and moved a net 40 m away from the speaker before stopping to rest and groom.

The heterospecific control stimuli consistently elicited responses from monkeys in the area. Mangabeys and red colobus, Procolobus tephrosceles, both responded to the crowned hawk eagle call with alarm calls. Black and white colobus responded to the colobus roar with roars of their own, whereas the same stimulus (possibly an alarm call) elicited alarm calls from redtails, Cercopithecus ascanius, mangabeys, and red colobus. The various monkey species thus responded to these stimuli in a manner consistent with previous studies at this site (Waser 1977a; Hauser & Wrangham 1990). The chimpanzee subjects, however, never gave any overt responses to the eagle or colobus playbacks.

In marked contrast, chimpanzees gave dramatic responses to the pant-hoot playbacks, and these responses were consistent with response to a foreign male's call. On hearing the pant-hoot playback, males and females alike oriented towards the speaker, and in some cases joined in a chorus of calls. Adult females unaccompanied by adult males often showed signs of fear, including fear grimaces. Males showed signs of aggressive arousal, including piloerection, similar to those observed during actual intergroup encounters (Goodall 1986). Whether or not chimpanzees counter-called or approached the speaker varied according to the number of adult males in the focal party, as described in detail below. Chimpanzees who approached the speaker site followed a direct route, with the adult males leading the way, traveling single file. Upon nearing the speaker site they sometimes searched the area, sniffed the ground, and then continued traveling in the direction of the stranger's call. The pant-hoot playbacks consistently elicited similar responses over the two years of testing, suggesting that our efforts to avoid habituation to playbacks succeeded.

Vocal Response

Of all the factors tested, counter-calling depended only on the number of adult males in the party ((Fig. 4.2a; $\underline{N}= 22$, $\underline{\chi^2} = 16.8$, $\underline{\text{pseudo } r^2} = 0.58$, $\underline{P} < 0.0001$; $\underline{\text{pseudo } r^2}$ provides a description of the fit of logistic models but lacks the straight-forward explained-variance interpretation of true $\underline{r^2}$ for ordinary least squares regression (Hamilton 1998)). Parties with three or more adult males counter-called in 12 of 13 trials, with the one exception being a party with three males. Parties with one to two adult males counter-called in only one of nine trials; in the one exception, a male in a party with two males joined the calls of a male in a non-focal party 90 m away. In none of the four trials without adult males present did individuals counter-call.

Counter-calling usually involved a chorus of most or all of the males present, with females sometimes joining as well. Although determining the individual vocal response for all males in the party was usually not possible, especially for large parties, in cases of counter-calling observers were able to determine the vocal response for a median 55% of the males present (range: 0 to 100%). In 12 cases 100% of the males whose vocal response

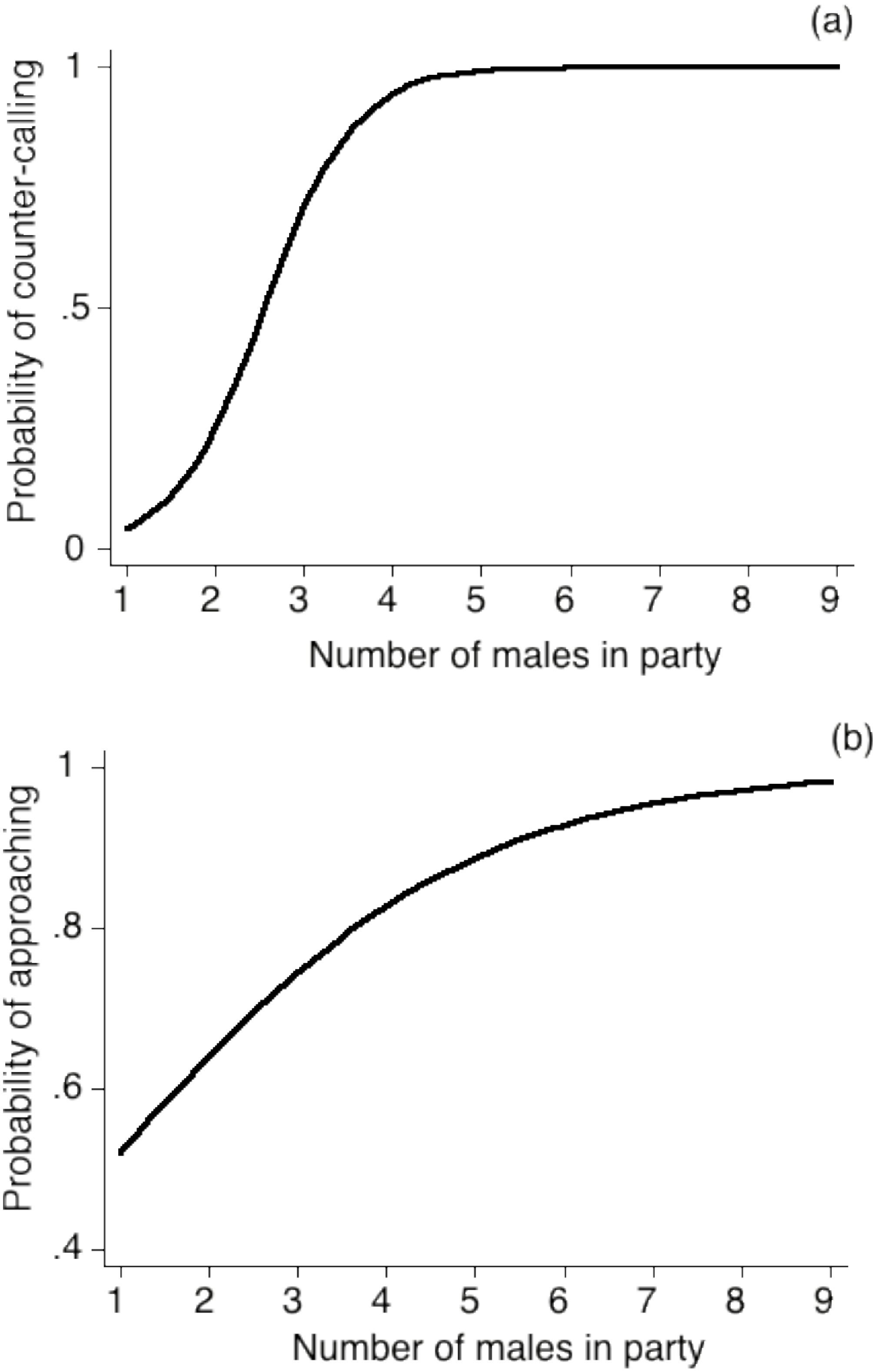


Figure 4.2 Logistic regressions fitted to the probability of (a) counter-calling and (b) approaching the speaker vs. the number of adult males in the party.

was determined joined the counter-calling chorus, in two cases a single male failed to join the chorus, and in one case the individuals present joined in a loud chorus but it was not possible to determine which of the males called. Overall, counter-calling appeared to be an unambiguous response to the playback, occurring immediately after the playback, with individuals orienting towards the speaker and calling together.

The number of adult males present affected not only whether counter-calling occurred, but also the number of loud call bouts produced. In the five min before playback, most parties remained silent, with no correlation between number of loud call bouts and number of adult males ($\underline{F}_{1,20} = 1.64$, NS). In the five min following playback, the number of loud call bouts produced increased with the number of males ($\underline{F}_{1,20} = 29.18$, $\underline{r}^2 = 0.59$, $\underline{P} < 0.0001$).

Travel Response

Following the pant-hoot playback, individuals in many parties oriented towards the speaker, descended to the ground if in a tree, and began moving. Females, if unaccompanied by males, either stayed stationary or moved up to 160 m away from the speaker. Adult males either remained stationary or approached the speaker (Fig. 4.3). Parties with three or more adult males approached the speaker in 12 of 13 trials; in the one exception, the distance traveled (20 m) fell short of the 50 m required for an approach. Parties with one to two adult males approached in five of nine trials.

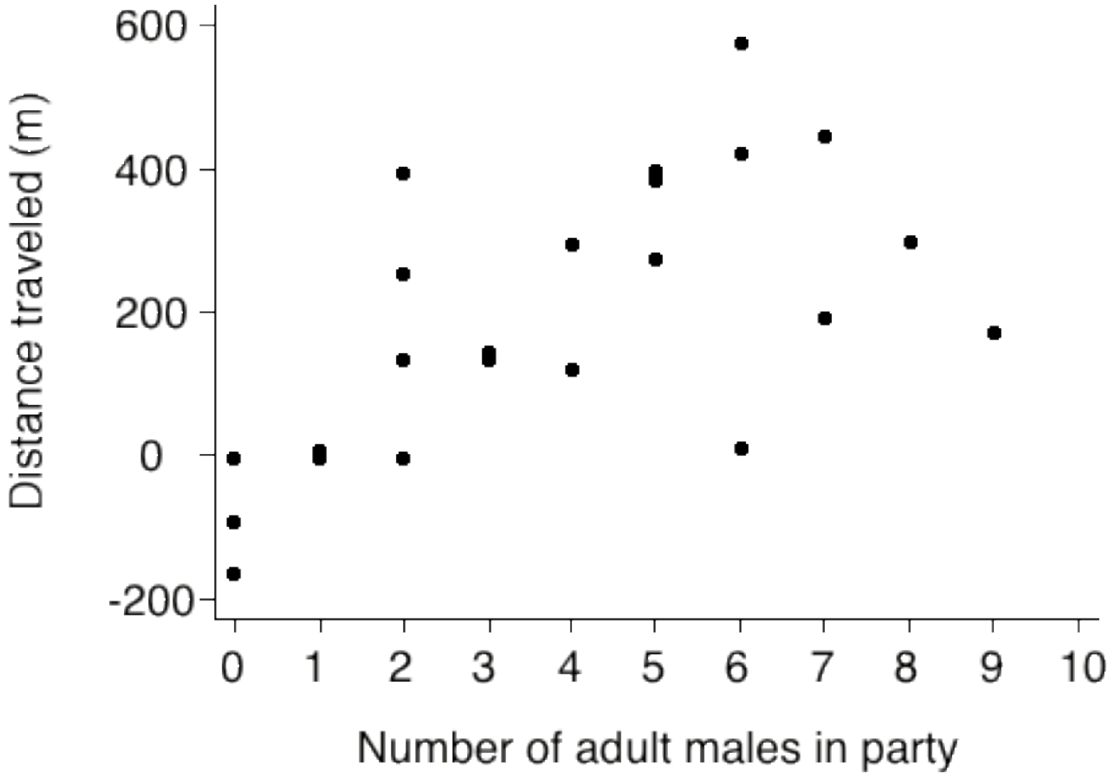


Figure 4.3 Distance traveled relative to the speaker in the 20 min after playback vs. the number of adult males in the party. In order to show the full range of responses, values are shown for all focal parties whose response could be determined, including parties excluded from statistical analysis (namely, parties with only females and their dependents (N = 4) and both parties for the two trials in which two focal parties were observed).

Approaching males generally grouped together and continued to stay close to one another as they approached the speaker. One minute before playback, a median 25% (range: 0 to 100) of each party's males were within 10 m of the focal males. By the time the approaching party had reached 100 m, a median 4 min after the playback (range: 1 to 13 min), the percentage of the party's males within 10 m of each focal had increased to 100% (range: 0 to 100; Wilcoxon matched pairs signed-rank test: $\underline{z} = -2.9$, $\underline{N} = 12$, $\underline{P} < 0.005$). The distance separating males within each party was thus generally smaller than the resolution of our distance measures (± 15 m for GPS). I therefore give travel measurements for parties rather than for individuals. In cases where not all individuals approached or some lagged significantly behind, the party measurement given is the distance traveled by the leading subgroup.

Approaching parties traveled a median 290 m towards the speaker in the 20 min following playback (range: 120 - 580 m), and reached their closest approach to the speaker site, a median 30 m (range: 0 - 330 m) in a median 12 min (range: 3 - 49 min). Two parties were temporarily lost from view following playback, so their location at 20 min post playback and distance traveled at that time could not be determined. In one case observers lost a focal party with one male and three females nine min after the playback. All members of this party initially moved away from the speaker, but after hearing pant-hoots from a distant party with four males, the male and a subadult female from the focal party began moving toward the speaker. I could not determine if the chimpanzees satisfied the approach criteria of moving 50 m toward the speaker within 20 m, but I did see them 35 min after playback, by which time they had joined the other party and moved

240 m toward the speaker. In the other case, two males moved at least 300 m towards the speaker; although they remained within acoustic range of the observers, they were temporarily lost from view several times.

Despite the uneven terrain and limited visibility in the forest, chimpanzees proved exceptionally accurate in finding the speaker location with a median angular error of 3 degrees ($\underline{N}$ = 10, range = 0 - 23 degrees). Although this represents group as opposed to individual approach data, the chimpanzees' capacity to localize the sound source from memory of a single pant-hoot lasting 6 - 15 seconds is at least as good, if not better than mangabeys presented with a comparable problem at the same study site (Waser 1977b).

The probability of approaching, as determined by logistic models, proved to be the one case in which the significance of the result depended on limiting analysis to one party per trial and on the choice of which parties to exclude. If all parties with at least one male are included, the response depends significantly on the number of adult males in the party (Fig. 4.2b; $\underline{N} = 24$, $\underline{\chi}^2 = 4.67$, $\underline{\text{pseudo } r^2} = 0.17$, $\underline{P} = 0.03$). If analysis is limited to one party per trial, however, the only factor to approach statistical significance is either the number of males in the party ($\underline{N} = 22$, $\underline{\chi}^2 = 3.43$, $\underline{\text{pseudo } r^2} = 0.15$, $\underline{P} = 0.06$) or the number of males in acoustic range ($\underline{N} = 22$, $\underline{\chi}^2 = 3.26$, $\underline{\text{pseudo } r^2} = 0.14$, $\underline{P} = 0.07$), depending on which parties are excluded. In both cases the P-value remains greater than 0.05.

Multiple linear regression found that only the number of adult males in the immediate party significantly affected the distance traveled in the 20 min following playback ($\underline{F}_{1,18}$ = 4.72, $\underline{r}^2$ = 0.21, $\underline{P}<0.05$). This effect results from including parties that did not approach. Restricting analysis to approaching parties reveals that if males decided to approach, the distance traveled did not depend on the number of males in their party ($\underline{F}_{1,13}$ = 0.88, NS).

Latency to 100 m depended on both the number of adult males within acoustic range and the number of adult females (Fig. 4.4; $\underline{F}_{2,12}$ = 8.45, $\underline{r}^2$ = 0.58, $\underline{P}$ = 0.005). For the trials in which I could estimate latency to 100 m, however, the number of males in the party and the number of males in acoustic range were largely identical, differing only for two trials.

Independence of Parties Within Trials

To test whether the presence of nearby parties affected response, I compared the response of both parties in all eight trials with multiple parties. For this analysis, I used trials in which both parties were directly observed ($\underline{N}$=2) and trials in which the response of the non-focal party could be inferred ($\underline{N}$=6), recognizing the limitations inherent in such data. Vocal response could be determined for both parties for all eight trials, because loud calls could be heard by distant observers. Travel response could be determined for both parties in six trials, excluding the two cases in which the non-focal parties were not

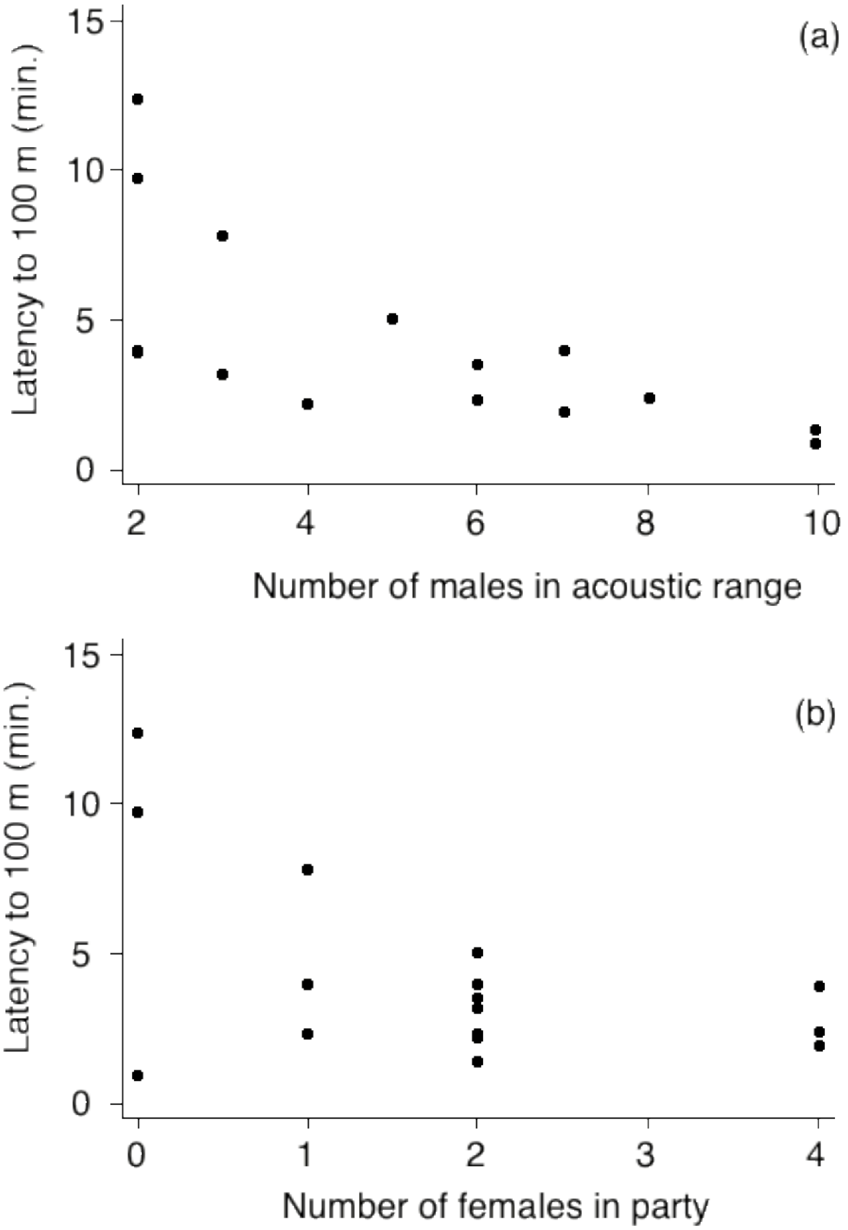


Figure 4.4 Latency to 100 m vs. (a) number of males within acoustic range of speaker and (b) number of females in the party. Values are shown for both parties observed in one trial with 10 males within acoustic range. One of these parties was excluded from statistical analysis to prevent pseudoreplication, but the particular party excluded did not affect the results.

directly observed approaching the speaker. The distance between parties at the time of playback could be determined for four trials, in which a median 125 m separated the parties (range: 90 - 190 m). Estimates for four other trials, based on loudness of calls, time of arrival to the speaker site, and location when first observed after the playback, ranged from 100 to 800 m.

The vocal response was independent of trial ($\underline{N} = 8$, $\underline{\chi^2_7} = 7.5$, NS) but depended significantly on party composition ($\underline{N} = 8$, $\underline{\chi^2_2} = 9.6$, $\underline{P} < 0.01$) with three levels of party composition (0 males, 1-2 males, and 3 or more males). Likewise, travel response did not depend on trial ($\underline{N} = 6$, $\underline{\chi^2_5} = 4.0$, NS) but did depend on party composition ($\underline{N} = 6$, $\underline{\chi^2_2} = 8.8$, $\underline{P} < 0.05$). Nevertheless, other evidence suggests that individuals did modify their behaviour according to the presence of nearby parties. For example, in the one case of counter-calling by an individual in a party with only two males, the caller in the focal party was joining the calls of a male 90 m away, who joined the focal party nine minutes after the playback. In six of the eight trials the two parties eventually joined together after the playback, taking from 9 to 90 min to do so. The influence of neighbouring parties on response may depend on the distance between parties.

Experiment Location

In none of the above analyses did experiment location affect the response. Our inability to detect an effect of location could in principle result from the limited statistical power of a small sample size as well as the small number of tests outside the nesting range. However, parties that did not approach were actually further (though not significantly further) towards the center of the range than parties which did approach (median distance from speaker to nearest edge of nesting range: 840 vs. 730 m; Kruskal-Wallis test: $\underline{\chi^2_1}$ = 0.018 , NS)

Within-community Playbacks

Because of time constraints and difficulty of finding parties with fewer than three males, I was only able to conduct two within-community playbacks before the end of the study. In both cases I played back the call of a male who had not been seen recently by observers (8 and 92 days, respectively). The party composition consisted of an adult female with her subadult male and infant male offspring for the first trial, and two adult males for the second trial. The subadult male in the first trial and both adult males in the second trial counter-called in response to the playback, and all members of both parties approached the speaker (latency to 100 m = 4 and 5 min respectively). While this small sample size prevents statistical comparison, this pattern of response contrasts strikingly with the response to foreign males, in which parties with fewer than three males almost always stayed silent and rarely approached. Moreover, in neither case did subjects show any fear response to the playback, a further indication that the call was not perceived as a threat.

Differences Among Individuals in Vocal and Travel Response

The previously described results show that parties with three or more males were more likely to counter-call and approach the speaker than parties with fewer males. To test whether this pattern of response was consistent across individuals, I compared the response of the seven males who were tested in two conditions of party composition: 1-2 males and 3 or more males. Trials with large parties were more likely to sample individuals repeatedly, with the result that each individual was tested less often in parties with 1-2 males (median number of times tested: 3; range: 1 - 4) than in parties with 3 or more males (median: 8; range: 4 - 9). I examined both vocal and travel response. Because of the difficulty of identifying all callers in a chorus lasting only a few seconds, the sample sizes for vocal response are somewhat smaller than for travel response.

For vocal response, I examined the number of loud-call bouts produced by each male in the 5 min following playback (Fig. 4.5a). All males called more frequently when in parties with 3 or more males. In fact, only one male (LK) ever called in the 5 min following playback when in a party with fewer than 3 males; he did so in the case described above in which he joined the calls of a male in a nearby party. When tested in parties with 3 or more males, four males always called in response to playback, and all seven males called in at least 50% of trials. Repeated measures analysis of variance, limited to the four males who were tested at least twice in both conditions of party size,

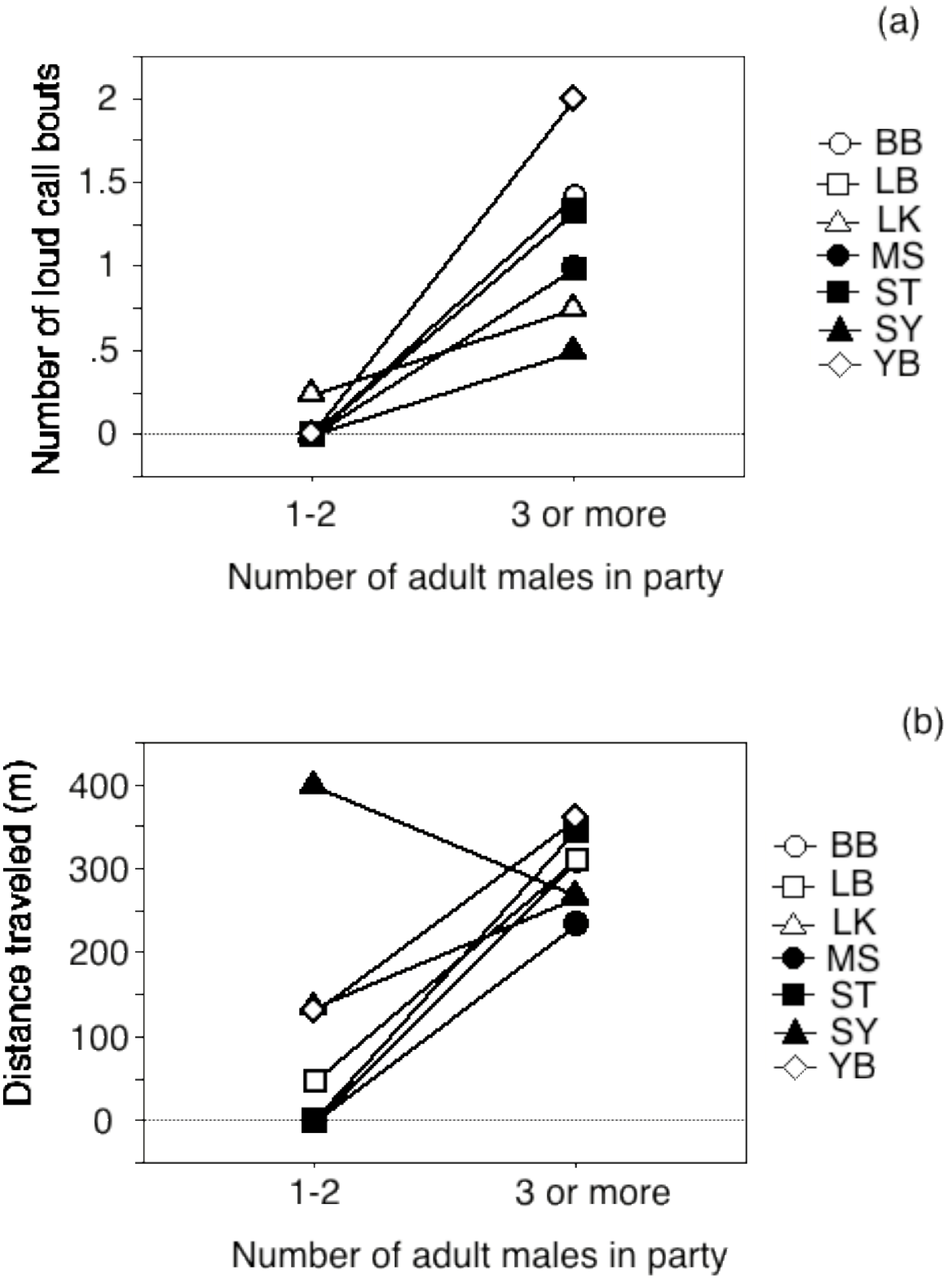


Figure 4.5 Individual variation in response, showing (a) mean number of loud call bouts produced by each individual in the 5 min. following playback and (b) the mean distance traveled relative to the speaker in the 20 min after playback, for each of seven males tested in both conditions, 1-2 males and 3 or more males.

found a significant effect of party composition (ANOVA: $\underline{F}_{1,3} = 56.16$, $\underline{P}<0.01$), and no significant difference among individuals ($\underline{F}_{3,3} = 2.24$, NS). Likewise, six of the seven males tested in both conditions traveled farther when in parties with 3 or males than in parties with 1-2 males (Fig. 4.5b). The one exception was a male whose travel response was determined for only one trial with 1-2 males. As with vocal response, the distance traveled in the 20 min following playback did not differ among individuals (ANOVA: $\underline{F}_{3,3} = 0.36$, NS), but instead consistently depended on party composition ($\underline{F}_{1,3} = 10.54$, $\underline{P} < 0.05$).

Individuals did differ in that some but not all defected, defined as cases in which one or more individuals stayed behind while others approached the speaker. Defection occurred in three cases. In the first case, the second-highest ranking male (MS) stayed behind with a female with a full sexual swelling (GO). Several other males made partial approaches before returning to the vicinity of MS and GO, while the highest ranking male (BB) and several others approached the speaker. In the second case, MS showed interest in hunting red colobus monkeys shortly before the playback. After the playback, he actually moved away from the speaker while the other males approached. The third case involved LK, who stayed behind while YB approached. LK was the youngest adult male, approximately 16 years old in 1998. All other adult males were at least 20 years old at the start of the study. All males who defected approached the speaker in earlier and later trials, suggesting that defection is a context-dependent behavior, rather than a characteristic of particular individuals.

Approach Rank and Agonistic Rank

Analysis of variance found that individuals differed significantly from one another in the order in which they approached the speaker ($\underline{F}_{11,39} = 3.39$, $P<0.005$). Three males had negative mean approach ranks, i.e. they tended to stay at the rear of the approaching party: LM, an old male who died in 1996 (mean rank = -0.5); LK, the youngest male (mean rank = -1.0); and AJ, a prime adult male (mean rank = -0.16). Five of the 12 males in this sample had serious injuries from snares or other causes (BB, LK, LM, SY, and YB). Three of these had positive mean ranks, including the two individuals with the highest mean ranks (BB and SY), suggesting that approach rank was not primarily affected by injuries. Mean approach rank decreases with decreasing mean agonistic rank, but this relationship fails to reach statistical significance ($\underline{F}_{1,10} = 3.34$, $\underline{r}^2 = 0.25$, $\underline{P} = 0.098$; Fig. 4.6).

4.5 DISCUSSION

An individual's decision to participate in cooperative intergroup conflict is likely to be influenced by a variety of social and ecological factors. Of the various factors measured in this study, including the number of defenders, the experiment location, and individual agonistic rank, only the number of defenders significantly affected the response. Male chimpanzees counter-called and approached when the costs of aggression appeared to be

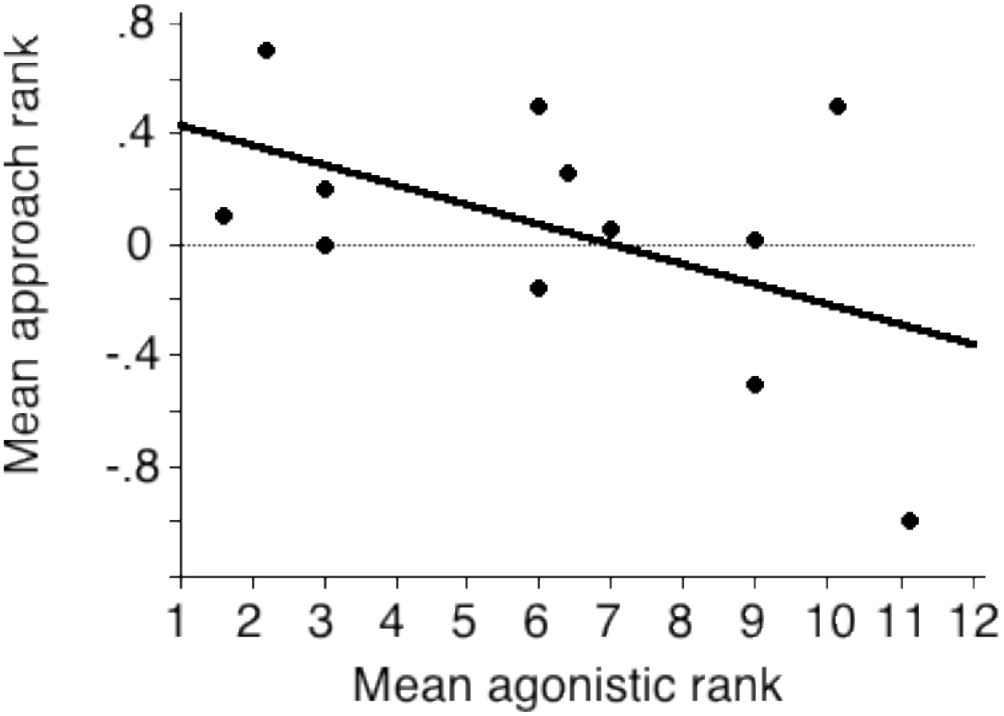


Figure 4.6 Mean approach rank vs. mean agonistic rank for each of 12 males tested.

low. Given the likely importance of avoiding unwinnable contests, as well as the demonstrated ability of lions to assess relative numbers (McComb et al. 1994), it is perhaps not surprising that chimpanzees should possess such an ability. Indeed, the capacity for numerical assessment may be widespread among animals (Hauser 2000).

For male chimpanzees, counter-calling depended more strongly on the number of defenders than did approaching. Parties with 1-2 males approached the speaker in 5 out of 9 trials, whereas they only counter-called in 1 of 9 trials. Males who failed to call in small parties did call in larger parties, showing that this pattern of response did not result from sampling bias. Counter-calling probably serves at least three functions. First, calls present a challenge to the intruder, advertising willingness to defend their territory. Second, since chorused calls are overlapping and probably cannot be faked, they provide an honest signal of the number and hence fighting power of the defenders (e.g. McComb et al. 1994). Finally, calls may recruit allies (Mitani & Nishida 1993). That male chimpanzees failed to counter-call except when in larger parties likely relates to the great potential costs of being caught outnumbered by one or more intruders. Although one or two males might risk little danger from a lone intruder, the call of a single intruder may represent an unknown number of silent intruders. Males in small parties appeared willing to silently investigate a single intruder's call, but they were unwilling to openly advertise their presence unless they appeared to outnumber the intruder.

Studies of lions present a useful context for interpreting the results of the present study. Lions have a complex social system with many interesting parallels to chimpanzees, including cooperative hunting, coalitionary aggression, fission-fusion ranging patterns, and lethal intergroup aggression. Male chimpanzees resembled female lions in their unwillingness to approach an intruder without a numerical advantage. In contrast, male lions continued to approach, albeit more slowly, even when outnumbered 3:1 (Grinnell et al. 1995). This difference in response makes sense in light of the respective life history trajectories of the two species. Male lions stay with a pride for an average of two years before being deposed, and are unlikely to attain residence in another pride (Packer et al. 1988). Any failure to defend their territory against rival males could result in eviction, with complete loss of lifetime reproductive success. In contrast, male chimpanzees in Kanyawara face a situation similar to female lions in the Serengeti: intergroup encounters bring the risk of injury or death, especially to outnumbered individuals, and defeat may result in loss of territory. In contrast, an individual's lifetime reproductive success rarely depends on any single contest.

Experiments with lions have also demonstrated the importance of ecological factors in guiding response to intruders. Female lions living in the densely populated Ngorongoro Crater approached even when outnumbered, and female lions who lacked a territory failed to approach at all (Heinsohn 1997). Future experiments with chimpanzees in different populations may reveal similar sensitivity to population density and other ecological factors. The chimpanzee population density at Kanyawara, approximately 1 adult / km^2, is somewhat less than the maximum of roughly 4/km^2 (reported for the

Ngogo study site, 12 km southeast of Kanyawara (Watts 1998)), and much higher than in savanna sites (0.1/ km2: (Baldwin 1982)). Chimpanzees in extremely dense populations might enter contests at a lower ratio of defenders to intruders, and chimpanzees in extremely sparse populations might avoid such contests altogether.

Experiment Location

In contrast to many territorial species, chimpanzees did not modify their response to an intruder based on location. At least three explanations for this pattern are possible. First, the sample size is small, reducing statistical power. Although I attempted to balance the number of trials towards the center and edge of the nesting range, few trials were conducted outside the nesting range. It is possible that tests far outside the nesting range would reveal some effect, such as an increase in caution. Nevertheless, the trials I did conduct outside the nesting range elicited approach and counter-calling, and there was no tendency for decreased speed or distance of travel.

Second, if males in general attempt to defend females rather than a geographical boundary (van Schaik et al. 1992), males should always seek to repel outsiders. This model seems appropriate for many primate species, in which males and females travel together in cohesive groups. It is not clear whether this model applies to species such as chimpanzees, in which females generally travel alone or in small scattered parties and tend to avoid border areas (Chapman & Wrangham 1993). Given the spatial distribution of female chimpanzees, the best strategy for mate defense might indeed be to defend a territorial boundary, or at least increase intensity of defense towards the territory center.

Third, the lethal raiding hypothesis predicts that the payoff for intergroup aggression should be independent of location. Although the small sample size warrants caution, the results presented here are consistent with this prediction.

Variation Among Individuals and Mechanisms of Cooperation

One surprising result of this study was the similarity of response across individuals. Theoretical considerations suggest that high ranking males should be more willing to participate in intergroup conflict (Nunn 2000). This prediction finds some support in the (non-significant) tendency for low-ranking males to travel towards the rear of progressions. Nonetheless, low ranking males behaved remarkably like high ranking males, in that they counter-called and approached whenever they had numerical superiority. The willingness of low ranking males to participate in intergroup contests suggests that cooperation in chimpanzees does not depend on asymmetrical benefits or privileged groups.

The tendency for some males to travel towards the rear when approaching resembles the case for lions (Heinsohn & Packer 1995), in which some females consistently lagged behind by 50-200 m. Heinsohn and Packer (1995) argue that leading and lagging are fixed strategies for female lions. In contrast with lions, chimpanzees showed greater flexibility. As discussed above (Results), male chimpanzees sometimes defected by staying behind while others approached. Nevertheless, individuals who defected in some trials joined or even led approaches in other trials. Defection appeared to depend on immediate circumstances, such as the presence of an estrous female. The greater flexibility apparent in chimpanzees may result from cognitive differences between the species, or may simply represent variability revealed by a greater number of trials conducted within a single social group.

At least four alternative explanations exist for the similarity of response among individuals. First, it is possible that high ranking males benefit more from intergroup contests and are more willing to approach intruders, but low ranking males join the approach for selfish reasons: the safest place to be during an intergroup encounter is with the largest available party. Nevertheless, low ranking males approached the speaker even when no high ranking males were present. In nine trials with 1-2 males, four parties approached. Only one of the approaching parties contained a male with higher than median dominance rank, whereas four of the non-approaching parties contained high ranking males.

Second, cooperation in male chimpanzees is generally thought to depend on kinship resulting from male philopatry (e.g. Goodall 1986). In support of this males at Gombe are related to one another on the order of half-siblings (Morin et al. 1994). However, genetic study of one West African community did not replicate this finding (Gagneux et al. 1999). Additionally, at Kanyawara, maternal relatedness failed to predict affiliation patterns (Goldberg 1997), and in the Ngogo study site, 12 km from Kanyawara, maternal relatedness failed to predict cooperative behaviours including alliances, meat-sharing and border-patrolling (Mitani 2000). In light of these recent findings, it is perhaps not surprising that maternal relatedness did not have a strong effect on whether males cooperated in response to playbacks. In playbacks to parties with two males, males who shared a maternal haplotype did not always approach, and males who probably did not share a maternal haplotype did approach together (Table 4.1). Although the genetic data for this population are still incomplete, sharing a maternal haplotype was a poor predictor of whether paired males approached the speaker. Kinship may facilitate cooperation among males, but specific instances of cooperation, such as alliances and response to intruders, appear to depend on additional factors.

Third, low- and high-ranking males might actually receive similar benefits from territory defense. Current mating success may be skewed towards high-ranking males, but rank varies over a male’s life (Goodall 1986). Males may defend a territory to protect offspring they sired in the past. In support of this, the two former alpha males, BB and SY, had the highest mean approach ranks. Young but still low-ranking males may participate in defense to protect the territory for a future in which they expect to be high ranking. Additionally, the varied mating strategies of chimpanzees, including consortships, may help moderate reproductive skew and give all males an incentive for territory defense. Such spreading of benefits, however, may actually result in a collective action problem, in which no single individual has enough to gain from territory defense to undertake such risks (Nunn 2000).

Table 4.1 Kinship and approach to speaker for parties with two males. In parties with two adult males, approaching the simulated speaker together did not depend on whether the males were matrilineal relatives (Fisher's exact test: NS; mtDNA sequence data from Goldberg & Wrangham 1997). LK's mtDNA has not been sequenced yet, but observations of AJ's association patterns when he was younger suggest LK and AJ are maternal brothers.

Date	Males present	Maternal haplotype shared?	Maternal haplotype shared? (If LK's = AJ's)	Approach together?	Males who app-roached	Latency to 100m (min.)
13 May 97	BB LK	UNK	No	No	None	NA
18 Jun 98	MS LB	No	No	No	None	NA
07 May 97	SY LK	UNK	No	Yes	SY LK	10
16 Nov 97	YB LK	UNK	No	No	YB	4
06 Nov 97	MS YB	Yes	Yes	No	None	NA
23 Jul 97	MS YB	Yes	Yes	Yes	MS YB	4
14 May 98	LB LK	UNK	Yes	Yes	LB LK	13

Fourth, if cooperation in male chimpanzees depends on mutualism, as Grinnell et al. (1995) argue for male lions, each male might indeed have a similar interest in territory defense. The conditions for cooperation through 'mutual dependencies' (Lima 1989) involve low probability of success when alone and coalition partners who will participate in many interactions and are difficult to replace. These conditions apply to male chimpanzees as well: they probably cannot defend territories when alone, they spend their entire lives with their coalition partners, and partners can only be replaced through birth and maturation of community males. Testing this possibility clearly requires additional research, in which playback experiments would prove extremely helpful.

In conclusion, I found that male chimpanzees counter-called and approached strangers whenever they faced favorable odds. The decision to enter an intergroup contest depended on favorable numerical asymmetries, rather than range location or other factors known to affect response in other territorial species. Additionally, males showed a striking similarity in their pattern of response, regardless of dominance rank. This pattern of response suggests that males may expect similar benefits from territorial defense, despite differences in rank and mating success, and is consistent with cooperation through mutualism.

CHAPTER FIVE

CHIMPANZEES AND THE MATHEMATICS OF BATTLE

5.1 SUMMARY

Recent experiments have demonstrated the importance of numerical assessment in animal contests. Nevertheless, few attempts have been made to model explicitly the relationship between the relative number of combatants on each side and the costs and benefits of entering a contest. One theoretical framework that may be especially suitable for making such explicit predictions is Lanchester's theory of combat, which has proven useful for understanding combat strategies in humans and several species of ants. In collaboration with Nicholas Britton and Nigel Franks, I tested whether a model derived from Lanchester's "square law" predicted willingness to enter intergroup contests in wild chimpanzees (Pan troglodytes), re-examining data from a recent series of playback experiments. We found that chimpanzees approached more quickly, the greater the net benefits predicted by the square law. Furthermore, the model predicts that in contests with multiple individuals on each side, chimpanzees in this population should be willing to enter a contest only if they outnumber the opposing side by a factor of 1.5. I discuss these results in light of existing data on intergroup encounters in chimpanzees, and also discuss potential applications of the square and linear laws for understanding combat strategies in other species.

5.2 INTRODUCTION

Recent experimental studies have demonstrated that for several species, individuals are more willing to enter an intergroup contest the more they outnumber their opponents (Adams 1990; McComb et al. 1994; Wilson et al. 2001). Few attempts have been made, however, to model explicitly the relationship between numerical assessment and willingness to enter a contest. Lanchester's theory of combat (Lanchester 1916) provides an explicit model for human battles, which should be applicable to intergroup contests in other species. Franks & Partridge (1993) were the first to show that Lanchester's theory of combat could be applied to animals other than humans. For instance, they showed that the contrasting patterns of attrition described by Lanchester's two models, the square law and the linear law, explain contrasting combat strategies among different ant species. Specifically, combat strategies may focus on either numerical strength or individual fighting value, with the square law applying to the former and the linear law applying to the latter. The predictions of Franks & Partridge have been tested for certain ants (Whitehouse & Jaffe 1996; McGlynn 2000). Here we re-examine one set of data (Wilson et al. 2001) to test whether the willingness of wild chimpanzees (Pan troglodytes) to approach a simulated intruder follows the predictions of the square law. We also discuss potential applications of the square and linear laws for understanding combat strategies in other species.

5.3 METHODS AND RESULTS

Chimpanzees live in groups of 20 to more than 140 individuals and travel in temporary parties of varying size, ranging from one to more than 20 individuals (Goodall 1986; Chapman et al. 1994; Watts 1998). Males breed in their natal group, defend group territories and sometimes kill members of neighbouring groups. Such lethal intergroup aggression likely benefits the attackers by reducing the fighting strength of the victim's group. The attackers thereby increase their chances of success in future battles, resulting in increases in territory size, access to females, food, and safety from neighbouring groups (Nishida et al. 1985; Goodall 1986; Wrangham 1999).

Chimpanzee intergroup contests appear to satisfy the conditions for Lanchester's square law, which assumes that all individuals on both sides are equally vulnerable to attack from every individual on the opposing side, that battle is potentially to the death, and that attack proceeds without recruitment of new combatants. Observed lethal attacks in chimpanzees involved concentrated attack by many individuals on one victim (reviewed in Wrangham (1999)). During fights with multiple participants on both sides, attempts to isolate individuals for concentrated attack have been observed (Goodall 1986; Boesch & Boesch-Achermann 2000). Recruitment of new combatants may occur in chimpanzee intergroup contests, but observations suggest that such recruitment is rare, probably because distinct parties are typically scattered over a large home range (10-38 km^2 in forest sites (Goodall 1986; Wilson et al. 2001).

Recent theoretical discussions of intergroup aggression in chimpanzees have focused on the importance of numerical imbalances in reducing the cost of aggression to the attackers (Manson & Wrangham 1991; Wrangham 1999), but no attempt to model explicitly the costs and benefits of aggression has been made. Lanchester's square law provides a framework for making such predictions. Actual intergroup encounters occur with low frequency and are difficult to observe systematically. Playback experiments provide an opportunity to collect systematic data appropriate for testing explicit models.

A recent series of playback experiments (Wilson et al. 2001) was conducted to determine the factors underlying response to the call of a foreign intruder. In each trial, a single pant-hoot vocalization of a single foreign male was played through a speaker (which was immediately removed so that no chimpanzees saw the speaker in operation). Response variables recorded by the observers included the time it took a group of males to travel 100 m towards the speaker (i.e. the latency time) and the party composition of the focal party and any other parties known to be within acoustic range of the speaker. These playbacks elicited cooperative responses, with the nature of the response depending on the number of adult males in the party. Parties with three or more males consistently joined in a chorus of loud vocalizations and approached the speaker together. Parties with fewer adult males usually stayed silent, approached the speaker less often, and traveled more slowly if they did approach. (Table 5.1.)

Table 5.1. Summary of responses of chimpanzees to playback experiments in which the call of a single foreign male was played to parties of varying size and composition (from Wilson et al. in press). Whether a party approached depended on the number of males in the focal party, which differed in some cases from the number of males within acoustic range.

# adult males in focal party	# focal parties observed	# parties approaching	% parties approaching
0	4	0	0
1	3	1	33
2	7	4	57
3	2	2	100
4	2	2	100
5	3	3	100
6	3	2	67
7	2	2	100
8	1	1	100
9	1	1	100

The response depended primarily on the number of adult males in the focal party, but the presence of nearby allies also affected the response. For instance, the one case in which a male from a one-male party approached the speaker, that male initially moved away from the speaker and was lost from view, but within 37 min of the playback he was seen at the speaker site with four males from a nearby party.

Using stepwise multiple linear regression, Wilson and colleagues (in press) found that latency to 100 m depended on both the number of adult males within acoustic range and the number of adult females in the immediate party ($n = 15$ trials, $r^2 = 0.58$, $p = 0.005$). Although this linear model provides a reasonably good fit to the data, it predicts a measurable latency for parties with one male (about 8 min in this case), whereas lone males did not in fact approach the speaker. A model based on the square law should provide a better qualitative fit.

We postulate that these playback experiments emulate potential battles, which meet the assumptions of Lanchester's square law. The square law assumes all individuals on both sides are equally vulnerable to attack from every individual on the opposing side, and that individuals are killed at a rate proportional to the numbers on the opposing side. The following equations describe the rates of attrition of the two sides:

$$\begin{aligned} dm/dt &= -\alpha n \\ && (1) \\ dn/dt &= -\beta m \end{aligned}$$

where m and n are the numbers of survivors remaining at time t since the start of the battle; α and β are constants representing the relative fighting values of individuals on the two sides. Every individual on the numerically weaker side finds itself the focus of concentrated attack by more than one individual on the opposing side. The disparity between the fighting forces increases through time as the larger side focuses more and more of its attacking strength upon the dwindling opposition. Dividing the two equations to eliminate time and integrating gives:

$$\beta(m_0^2 - m^2) = \alpha (n_0^2 - n^2) \qquad (2).$$

Rearranging for m when n = 0 gives:

$$m = (m_0^2 - (\alpha/\beta)n_0^2)^{1/2} \qquad (3)$$

where m_0 and n_0 represent the numbers on sides m and n at the start of the battle. For m to win, therefore, $m_0^2 > (\alpha/\beta)n_0^2$;

or

$$\beta m_0^2 > \alpha n_0^2 \qquad (4).$$

Either side of equation (4) is proportional to the fighting strengths of one of the two groups. The square terms highlight the relative importance of superior numbers over individual fighting value. If (4) holds, the losses incurred by either side are n_0 and $(m_0-(m_0^2-(\alpha/\beta)n_0^2)^{1/2})$ respectively.

Not all battles between opposing groups of chimpanzees are to the death. In applying the square law to chimpanzees we shall therefore assume that the expected losses incurred by either side are proportional to — rather than equal to — the losses predicted by the square law, and are δn_0 and $\delta(m_0^2-(\alpha/\beta)n_0^2)^{1/2})$ respectively, where δ is a constant. We shall neglect any differences (such as asymmetries in ownership, e.g. (Davies 1978)) between groups and assume that $\alpha = \beta$. Let the cost of losing a coalition member be 1, and the benefit of killing a member of an opposing coalition be γ, where $\gamma < 1$.

In the playback experiments there is one (virtual) opponent. The expected loss incurred by the opponents is δ, and by the focal group $\delta(M_a - (M_a^2 - 1^2)^{1/2})$ where M_a is the initial number of males within acoustic range.

Using the number of adult males within acoustic range for M_a satisfies the condition of no recruitment. In practice, for all but two of the trials for which latency was measured, the males in the focal party were the only males known to be within acoustic range. The choice of M_a (males in acoustic range or focal party) has little effect on the results (Table 5.2). To avoid pseudoreplication, we used a single focal party for each trial. Only in Trial

Table 5.2 Summary of how two choices (whether focal party A or B is chosen from the one trial in which latencies were determined for two parties, and whether M_a is defined as the males in acoustic range or in the focal party) affect the resulting values for γ and Minimum M_a (the predicted minimum numerical advantage required for entering an intergroup contest), based on the slope and intercept of the least squares fit of 1/L vs. ($M_a - (M_a^2 - 1^2)^{1/2}$).

Focal party chosen for Trial 96.01	Choice of M_a	Slope ($-k\delta$)	Intercept ($k\delta\gamma$)	γ	Minimum M_a	r^2
A	Acoustic	-7.2	2.9	0.40	1.5	0.42
A	Focal	-6.6	2.9	0.44	1.4	0.34
B	Acoustic	-9.6	3.5	0.36	1.6	0.36
B	Focal	-8.4	3.3	0.39	1.5	0.23
Mean values		-8.0	3.2	0.40	1.5	0.34

96.01 were latencies measured for multiple focal parties, and the choice of party does not substantially affect the results (Table 5.2).

Hence net benefit = benefit – cost = $\delta(\gamma.1 - 1.(M_a - (M_a^2 - 1^2)^{1/2}))$

We hypothesize that the speed of approach (1/Latency time) provides a measure of propensity to attack and is proportional to expected net benefit.

Hence $1/L = k\delta(\gamma - (M_a - (M_a^2 - 1^2)^{1/2}))$

$-k\delta$ is the slope, and $k\delta\gamma$ is the intercept of the least squares fit of 1/L vs. $(M_a - (M_a^2 - 1^2)^{1/2})$.

Hence γ can be determined, and we predict that a plot of 1/L vs. $(\gamma - (M_a - (M_a^2 - 1^2)^{1/2}))$ will be a straight line through the origin. Such is the case (Fig. 5.1).

Now suppose that there are n_0 opposing males,

benefit – cost = $\delta(\gamma n_0 - (M_a - (M_a^2 - n_0^2)^{1/2}))$.

This is zero when $\delta(\gamma n_0 - ((M_a - (M_a^2 - n_0^2)^{1/2})) = 0$, which can be solved to give

$M_a = ((1+\gamma^2)/(2\gamma))n_0$.

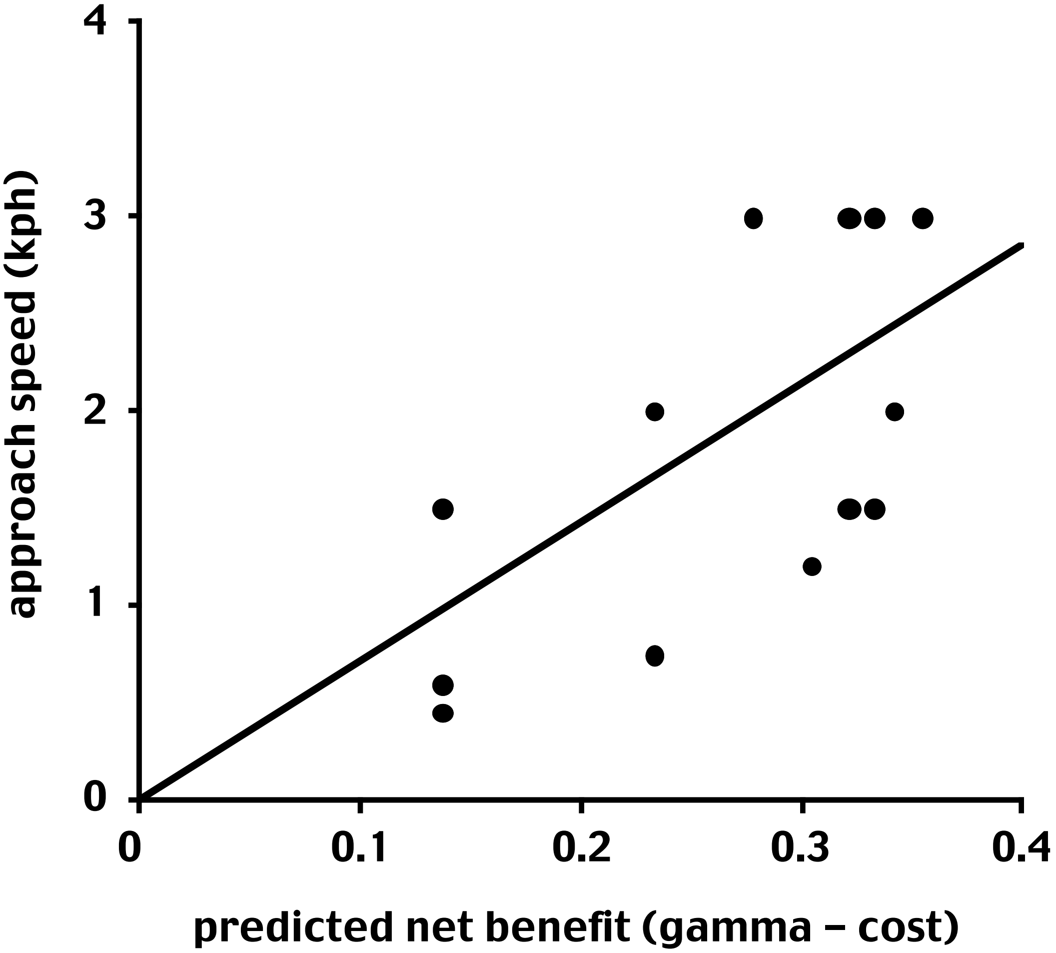


Figure 5.1 Plot of speed of approach versus the net benefits of attacking as predicted by Lanchester's square law, based on the total number of males in acoustic range. The regression equation is: approach speed = 0.0 + 7.1 (gamma–cost); $r^2 = 0.423$; $p < 0.01$. Trial 96.01 had ten males in acoustic range divided into two parties. This figure shows the approach speed for Party A; Party B had an approach speed of approximately 6 kph.

Calculated as shown above from the slope and intercept of the least squares fit of 1/L vs. $(M_a - (M_a^2 - 1^2)^{1/2})$, $\gamma = 0.40$, and thus $M_a = 1.5\ n_0$. We can therefore predict that in this population, male chimpanzees should be willing to enter a contest against more than one opponent only if the total number of nearby allies is more than 1.5 times the number in the opposing group.

To test which factors best predicted the speed of approach, we ran backward stepwise logistic regressions using Stata 6.0 (Stata Corporation 1999) with the following independent variables: number of adult males within acoustic range of the speaker, number of adult females in the immediate party, and the net benefits predicted by the square law; we used a p-level-to-retain of 0.10. Depending on which party from Trial 96.01 was included, the only variable to be retained was either the predicted net benefit ($F_{1,13} = 9.52$, $r^2 = 0.42$, $p<0.01$) or the number of males within acoustic range ($F_{1,13} = 14.34$, $r^2 = 0.52$, $p<0.005$).

5.4 DISCUSSION

Lanchester's square law provides an explicit model for numerical assessment in intergroup contests. Wilson and colleagues (in press) found that male chimpanzees were more likely to approach a simulated intruder — and approached more quickly — the more they outnumbered the intruder. This pattern of approach is generally consistent with Lanchester's square law. Here we show that one measure of willingness to enter an intergroup contest, the speed of approach, increased with increases in the specific net benefits predicted by a model based on the square law. With the small sample size we were unable to determine whether the predicted net benefits or the raw number of males present better predicted the speed of approach. Nevertheless, the square law model has the advantage of explaining rather than merely describing the pattern of approach. Additionally, the square law correctly predicted that lone males should be unwilling to approach.

The square law model predicts that for this population, male chimpanzees should be willing to fight a group of foreign males whenever they outnumber their rivals by a factor of 1.5. This result is consistent with the results of the playbacks, in which parties with one male did not approach until joined by allies, and parties with two males approached in 4 out of 7 cases. In practice, however, wild chimpanzees seem to require at least three males to successfully kill an adult (Wrangham 1999). In support of this, male chimpanzees approaching playbacks did not vocally advertise their presence unless in parties with three or more males (Wilson et al. 2001). The quiet approaches by males in smaller groups suggest they perceived greater risk and/or a lower probability of successful attack. In one case in captivity, one male was killed by two males, but this case may be anomalous in that the confines of a night cage likely restricted the victim's ability to escape or to recruit allies (de Waal 1989). The low minimum ratio determined here may result from using data from playbacks rather than actual lethal attacks. Although approach to a stranger's call probably correlates with willingness to attack, such an attack is not inevitable. Individuals approaching a stranger's call may simply be interested in a closer look; the presence of at least one ally may provide sufficient safety to make such an inspection worthwhile.

Recent discussions of intergroup aggression in chimpanzees have focused on the role of imbalances of power, arguing that chimpanzees kill because variation in party size permits them to kill at low cost when they sufficiently outnumber their rivals (Manson & Wrangham 1991; Wrangham 1999; Boesch & Boesch-Achermann 2000). For instance, Wrangham (1999) distinguished between "battles" (multiple combatants on each side) and "raids" (many males attacking a single victim), and argued that for chimpanzees, fatalities were much more likely in raids than in battles. The square law model supports the importance of relative numbers in chimpanzee combat, and also makes a more general prediction: lethal killing should be possible whenever the attackers have a sufficiently large ratio. In contrast to this prediction, observed chimpanzee battles have rarely resulted in fatalities. Instead, encounters between parties with many males on each side typically result in mutual chasing and displaying, followed by retreat of one party before any serious injuries result (Goodall 1986; Boesch & Boesch-Achermann 2000). In one case at Gombe, Tanzania, three attacking males did isolate and kill a victim from a party of three males (two adult and one subadult) who watched from a distance before retreating (Goodall 1986). Additional observations at sites with neighbouring habituated groups, as well as detailed analysis of existing long-term records, are needed to test this prediction adequately. Observations of neighbouring habituated groups at two Tanzanian sites in the 1970s provided the best observations of intergroup encounters, but at both sites, one of the study groups appears to have been exterminated by the other (Nishida et al. 1985; Goodall 1986). Recent improvement in habituation of neighbouring communities at several long-term study sites is beginning to provide opportunities for detailed observations again (Stanford 1998; Boesch & Boesch-Achermann 2000; Watts & Mitani in press). Willingness to enter battles could also be tested with playback experiments simulating multiple foreign male intruders, in contrast to the single intruder experiments of Wilson and colleagues (in press).

The model used here assumes that the benefit of battle increases with the number of opponents ($\delta\gamma n_0$). Gaining the full benefit would thus require that all opponents be destroyed, something never observed in a single chimpanzee battle. To achieve full destruction, chimpanzees would have to systematically isolate and kill each individual. With their limited weapons (teeth and hands), chimpanzees take tens of minutes to kill an enemy, and therefore might be unable to fight true Lanchester battles against multiple opponents — the enemy is likely to escape or regroup before the attackers disable the first victim. Moreover, with their small group sizes and low reproductive rate (Kaplan et al. 2000), chimpanzees are probably incapable of inflicting or sustaining the levels of attrition seen in human or insect armies. Although chimpanzee battles may rarely or never result in multiple casualties, the square law nevertheless appears to accurately model the relative costs and benefits of approaching a single rival.

Lanchester's laws of combat provide useful predictions for understanding intergroup aggression in humans, ants, and chimpanzees, and show promise for wide application to other species. For instance, the laws permit a refinement of the general expectation that resource holding potential depends on individual fighting value in one-on-one contests and relative numbers in intergroup contests (McComb et al. 1994).

Apart from social insects, most examples of potentially lethal animal contests appear to be duels fought between individuals (e.g. several species of mantis shrimp, gladiator frogs Hyla rosenbergi, red deer Cervus elaphus, musk ox Ovibos moschatus, pronghorn antelope Antilocapra americana, gorillas Gorilla gorilla (Wilkinson & Shank 1976; Kluge 1981; Clutton-Brock et al. 1982; Dingle 1983; Fossey 1983; Byers 1997); see review in Huntingford & Tuner (1987), or concentrated gang attacks (e.g. lions Panthera leo, wolves Canis lupus, spotted hyenas Crocuta crocuta, cheetahs Acinonyx jubatus, western red colobus Procolobus badius, chimpanzees (Kruuk 1972; Caro & Collins 1986; Goodall 1986; Packer et al. 1988; Starin 1994; Mech et al. 1998). Duels can be considered a special case of the linear law, where $M_0 = n_0 = 1$. In duels, success depends on individual fighting value, as seen by huge investments in body size and weaponry in species in which males fight duels for access to females. In contrast, species with concentrated gang attacks seem likely to follow the square law, and are hence predicted to show relatively less investment in weaponry. Plavcan and colleagues found that among primate species in which the outcome of fights is typically determined by coalitionary fighting, selection for weaponry (canines) is reduced (Plavcan et al. 1995). In particular, male chimpanzees have relatively small canines for their body size, consistent with other evidence that success in battle for chimpanzees depends on coalition size rather than individual weaponry.

In addition to duels and concentrated attacks, some animals should be expected to fight linear law battles, in which groups fight one another in a series of duels. In such species, fighters should be expected to invest in fighting value, as Franks & Partridge (1993) showed for slave-making ants. Such linear law battles appear to be rare, partly because lethal intergroup aggression is rare, and partly because linear battles require some method of reducing the effectiveness of concentrated attack. Slave-making ants accomplish this by dispersing the rival forces with “propaganda substances” (Franks & Partridge 1993). In at least one vertebrate species, intergroup battles do potentially follow the linear law. In the naked mole-rat, Heterocephalus glaber, narrow burrows constrain the battlefront to a small number of individuals on each side. Consistent with the prediction of the linear law, individuals most active in experimentally induced intercolony battles were significantly larger than other members of the colony (Lacey & Sherman 1991).

Detailed observational and experimental work with lions provides an opportunity to test whether Lanchester’s square law applies to other species with concentrated gang attacks. Both male and female lions are vulnerable to lethal attack, particularly when outnumbered (Packer et al. 1988). Consistent with the square law, larger groups tend to defeat smaller groups (Packer et al. 1990; Grinnell et al. 1995). Playback experiments have found that both male and female lions approach the roars of simulated same-sex intruders faster the more they outnumber the intruders (McComb et al. 1994; Grinnell et al. 1995). However, in contrast to the predictions of the square law, defenders sometimes approached the playback even when outnumbered by simulated intruders. For example, females always approached when they had cubs in the pride (McComb et al. 1994), and males approached even when outnumbered 3:1 (Grinnell et al. 1995). Willingness to enter an intergroup contest also varied with local population density (Heinsohn 1997).

At least four possible explanations exist for the willingness of lions to approach playback when outnumbered. First, an unknown number of these playbacks violated Lanchester's assumption of no recruitment. McComb and colleagues (1994) state that female lions in groups below maximum pride size were more likely to roar following playback, and when they did so, in nearly half the cases they were joined by other pride members. The number of individuals in acoustic range is not explicitly reported for any of the lion experiments. Second, the playback distance for all of the lion experiments (200 m) was shorter than the median playback distance for chimpanzees (300 m), even though natural lion roars can travel much further than chimpanzee pant-hoots (lions: up to 8 km (Schaller 1972); chimpanzees: at least 1-2 km (Reynolds & Reynolds 1965) For both lions (e.g. Heinsohn (1995)) and chimpanzees, the shortest latency to 100 m was close to 1 minute (6 kph). For male chimpanzees, this appeared to be close to top speed over rough terrain (pers. obs.), whereas lions can sprint much faster (48-59 kph), though they can only maintain this for 100 m or so (Schaller 1972). The lion playbacks might therefore simulate an intruder-defender distance which is shorter for lions and hence more threatening. Third, the square law model assumes that there is no cost to not challenging an intruder, an assumption which may be untrue for chimpanzees but is almost certainly so for lions, especially females defending cubs, or for males, in which any failure to defend their territory against rival males could result in eviction, with complete loss of lifetime reproductive success (Packer et al. 1988). Fourth, the decision to enter an intergroup contest surely depends on additional costs and benefits, including asymmetries in ownership (e.g. Davies 1978) and the value of the future (Enquist & Leimar 1990). Lanchester's model seems most appropriate when numerical assessment is the overriding factor. The population variation revealed by the lion experiments suggests that the particular value of γ for a particular population of chimpanzees may also depend on local ecology and demography.

In summary, male chimpanzees responded to playbacks in a manner consistent with Lanchester's square law. This relatively neglected theoretical perspective shows promise for applications for other cases of animal combat.

CHAPTER SIX

DISCUSSION

6.1 INTRODUCTION

To increase our understanding of lethal intergroup aggression in chimpanzees and other animals, I tested predictions of the imbalance-of-power hypothesis (Manson & Wrangham 1991; Wrangham 1999). Intergroup aggression can have profound fitness consequences for chimpanzees (Goodall 1986; Williams 2000), but occurs infrequently and is difficult to observe when it does occur. Instead of waiting for such rare events to occur, I used systematic observations, playback experiments, and mathematical models to examine behavior during two types of elevated intergroup threat. First, I tested whether ranging, grouping and vocal behavior changed near the boundaries of other communities. Second, I conducted playback experiments to test factors underlying response to a simulated intruder. In the following sections, I summarize the results described in Chapters Two through Five. I then discuss some implications of these results for understanding coalitionary killing in humans, and conclude with suggestions for future research.

Chapter Two: Ranging and Grouping Behavior

I tested three predictions of the imbalance-of-power hypothesis relating to ranging behavior. First, the increased mortality risks posed by borders should result in border avoidance. Second, if the sexes differ in coalitionary bonds, the sex that forms bonds should visit borders more often. Third, since success in intergroup encounters depends primarily on relative numbers, larger parties should be more likely to visit boundaries. Overall, chimpanzees in this population responded as predicted to the increased risks posed by intercommunity boundaries. They appeared to avoid border areas, with 90% of observations occurring in the central 40% of their total range. Males ranged more widely than females, using home ranges 1.3 to 1.7 times larger than females' home ranges, depending on the percentage of observations included for analysis. Females used home ranges located towards either the center or the periphery of the total range. Males visited border areas more often than central females, but less often than peripheral females. Males differed from both central and peripheral females in that each male visited most or all of the range, whereas females rarely visited borders far from their home ranges. Parties with more males were more likely to visit the territory edge and were also more likely to raid crops outside the park.

Chapter Three: Vocal Suppression

The imbalance-of-power hypothesis predicts that chimpanzees should stay quiet when in border areas, both to reduce risks of being detected and attacked by members of neighboring groups and to increase chances of conducting surprise attacks. Testing this prediction is complicated by the likelihood that chimpanzees visit borders for different reasons, and different vocal behavior might be predicted accordingly. Goodall (1986) distinguished two types of border visit: boundary patrols, which are primarily for territorial defense, and excursions, which are primarily for feeding. In contrast to the silence expected during border patrols, during feeding excursions chimpanzees might be expected to maintain or increase production of loud calls in order to advertise territory claims or coalitionary strength. Distinguishing the different types of border visit proved beyond the scope of this thesis, but I was able to examine vocal behavior in one context in which suppression of loud calls is clearly advantageous: crop-raiding. Using both focal and party follows, I found that chimpanzees produced fewer pant-hoots when in Crops than in either the Core or Edge of their range, independent of time of day. Chimpanzees also tended to produce fewer pant-hoots when at the Edge compared to the Core, but this difference failed to reach statistical significance. Further work will be required to distinguish among different types of border visits, such as feeding excursions versus patrols.

Chapter Four: Playback Experiments

I conducted a series of playback experiments to test whether males were more willing to approach the call of a foreign male intruder if they outnumbered the intruder, and if willingness to approach diminished towards the edge of the study group's range. I found that male chimpanzees counter-called and approached strangers whenever they faced favorable odds. The decision to enter an intergroup contest depended on favorable numerical asymmetries, rather than range location or other factors known to affect response to intruders in other species. During progressions towards the speaker, higher-ranking males tended to travel towards the front, but both high- and low-ranking males modified their response according to their party size, with approach more likely in parties with more males.

Chapter Five: Mathematical Models

The imbalance-of-power hypothesis focuses on the importance of numerical advantage, but does not explicitly specify how the net benefits of entering an intergroup contest should relate to the relative numbers on each side. In collaboration with Britton and Franks, I tested an explicit model based on Lanchester's square law. Using the approach speed data from the playback experiments, I found that chimpanzees approached more quickly with increasing net benefits, as predicted by the square law. Furthermore, the model predicts that in contests with multiple individuals on each side, chimpanzees in this population should be willing to enter a contest only if they outnumber the opposing side by a factor of 1.5. Although parties with one to two males did approach at least half the time, males were unlikely to counter-call before approaching unless they had at least three males in their party, suggesting that at least three males were needed for a safe approach.

6.2 TESTING THE IMBALANCE-OF-POWER HYPOTHESIS

Of the various hypotheses tested in this study, Table 6.1 lists the seven predictions most directly related to the imbalance-of-power hypothesis. The results are clearly consistent for five of these predictions. Two other predictions, (2) and (4), received qualified support: males traveled more widely than females, visiting more borders, and parties tended to pant-hoot less often in border areas. Overall, therefore, the results of this study support the specific predictions of the imbalance-of-power hypothesis.

Table 6.1 Summary of results.

Prediction	Imbalance-of-power hypothesis	Results of this study	Source
1. Avoid borders	Yes	Yes	Ch. 2
2. Males visit borders more than females	Yes	Qualified yes	Ch. 2
3. Travel in larger parties at borders	Yes	Yes	Ch. 2
4. Stay quiet at borders	On patrols	Possibly	Ch. 3
5. Call and approach when numerical advantage	Yes	Yes	Ch. 4
6. Call and approach regardless of range location	Yes	Yes	Ch. 4
7. Approach faster when net benefits are greater	Yes	Yes	Ch. 5

Table 6.2 Comparison of predicted behavior if the mechanism underlying intergroup aggression depends on "human influence," "male philopatry," or "imbalance of power."

	Mechanism underlying aggression		
Prediction	Human Influence	Male Philopatry	Imbalance of Power
1. Avoid borders	No	Yes	Yes
2. Males visit borders more than females	No	Yes	Yes
3. Travel in larger parties at borders	No	Yes	Yes
4. Stay quiet at borders	No	On patrols	On patrols
5. Call and approach when numerical advantage	No	Yes	Yes
6. Call and approach regardless of range location	No	No	Yes
7. Approach faster when net benefits are greater	No	Yes (if benefit = food, females)	Yes (if benefit = killing rivals)

As discussed in the Introduction, explanations of lethal intergroup aggression can be divided into at least four categories: “Cultural Bias”, “Human Influence,” “Male Philopatry,” and “Imbalance-of-Power.” Table 6.2 lists the predictions of these hypotheses, assuming that the first two categories lead to similar predictions (Sussman 1997). In the following sections, I discuss how the results of this study relate to each of these explanations.

Cultural Bias and Human Influence

Sussman (1997) accepts that chimpanzees sometimes behave aggressively but does not attempt to explain how often or under what circumstances they should do so, except to cite Power’s (1991) explanation for the observed lethal attacks. Power (1991) argues that chimpanzee violence is the result of human influence. Specifically, by provisioning chimpanzees with bananas for several years and then suddenly limiting the supply of bananas, scientists at Gombe frustrated their study subjects, who then vented their frustration by killing their neighbors. Powers (1991) predicts that in the absence of provisioning, chimpanzees should have relaxed and peaceful relations both within and between groups. Kanyawara chimpanzees have never been provisioned, but in contrast to Power’s (1991) prediction, all observed interactions between communities in this population have been hostile. In a little over a decade (1988-1998), at least two and possibly three adult chimpanzees were killed by chimpanzees along Kanyawara's borders (Wrangham & Peterson 1996; Wrangham 1999).

During the present study, Kanyawara chimpanzees appeared to avoid their borders, traveled in parties with more males when visiting borders, and tended to produce fewer pant-hoots during border visits despite the greater number of males in their parties. Males traveled more widely than females. In principle, this sex difference in range size could result from males increasing travel to monitor the reproductive state of females. Although males surely do expend a great deal of effort to find and follow mates, the fact that male home ranges showed nearly complete overlap suggests that they were also defending a shared territory. Playback of foreign male calls elicited strong responses consistently related to the number of males in the party. The quiet, cautious approach to the speakers by males in small parties would be difficult to interpret if chimpanzees had nothing to fear from their neighbors. Even if we had not found Kanyawara males beating on and displaying around the freshly killed and mutilated corpse of a neighboring male (Wrangham 1999; Wrangham et al., in prep), the results of this study would clearly indicate that chimpanzees in this population do not behave as Power predicted.

Male Philopatry and Imbalance-of-Power

The Male Philopatry and Imbalance-of-Power hypotheses lead to similar predictions for chimpanzee behavior. This is not surprising since both models were developed by researchers who accepted the validity of the existing chimpanzee data and attempted to explain the observed patterns. Wrangham distinguishes two possible proximate mechanisms underlying intergroup aggression: resource competition and dominance drive (Wrangham 1999). Although these mechanisms are not necessarily mutually exclusive, the male philopatry hypothesis predicts that fighting should be driven by competition for specific resources such as food, females and territory. The imbalance-of-power hypothesis is more consistent with the dominance drive mechanism, in which attacks should occur whenever they are economically feasible . Testing these hypotheses fully requires consideration of both the species distribution of coalitionary killing and the analysis of long-term chimpanzee data, examining whether the frequency and intensity of intergroup aggression depend on the distribution of resources or on the opportunities for low-cost attacks. As discussed in the Introduction, the species distribution of coalitionary killing supports the Imbalance-of-Power hypothesis. All species compete for resources, but few species kill their neighbors.

Table 6.2 lists the two possible points of difference between the male philopatry and imbalance-of-power hypotheses for this study: predictions (6) and (7).

Regarding prediction (6), the male philopatry model predicts that response to an intruder call should depend on range location. The center of the territory should be more valuable than the edge; therefore, response to intruders should decrease with distance from the center. In contrast, the imbalance-of-power model predicts that chimpanzees should take advantage of any opportunity to attack, regardless of range location. In this case, the benefits of attacking derive from opportunities to kill rivals and thereby reduce the neighboring community’s coalitionary strength. The response to playback experiments did not depend on range location (Chapter Four), supporting the imbalance-of-power model in this case.

As for prediction (7), both models predict faster approach when net benefits are greater, but differ on how to measure benefits. The male philopatry model would predict faster approach in defense of specific resources, such as food or mates. The imbalance-of-power hypothesis predicts that a principle benefit is killing rivals, so approach should increase with increasing odds of doing so. The analysis in Chapter Five revealed that approach speed did increase with benefits measured in terms of odds of killing rivals. A thorough test of the male philopatry model in this case would require more detailed analysis of resource distribution. Notably, one case in which several males defected following a playback involved the guarding of a female with a full sexual swelling (Chapter Four).

6.3 IMPLICATIONS FOR HUMANS

The predictions of the imbalance-of-power hypothesis are generally supported both by the specific responses of chimpanzees to the threat of intergroup aggression and by the species distribution of coalitionary killing. Most, if not all, human societies satisfy the two conditions of hostile intergroup relations and imbalances of power (Rodseth et al. 1991). Coalitionary killing, therefore, should be ubiquitous in humans.

The extent to which pre-state societies engaged in destructive warfare and other forms of coalitionary killing remains the subject of intense debate. Otterbein (1999) describes how the debate has become polarized between "Hawks," who see war as part of human nature, and "Doves," who see war as the result of state organization. Otterbein lists among the Hawks archeologist Lawrence Keeley and primatologist Richard Wrangham, while the Doves include anthropologists R. Brian Ferguson and Leslie Sponsel (Otterbein 2000). Hawks emphasize the evidence for destructive warfare in the ethnographic (Ember 1978; Dentan 1988; Gat 1999) and archeological (Keeley 1996; LeBlanc 1999) record. Doves focus on societies that appear to be peaceful (Gregor 1996), or argue that contact with state-level societies exacerbates violent conflict in tribal societies (Ferguson 1992; Tierney 2000). Otterbein places himself as a critic of both extremes, arguing that "Some conditions lead to war, some do not. I see great variation in the nature and frequency of war. It is this variation and the reasons for it that researchers should be investigating" (Otterbein 2000).

Addressing the variation in rates and intensity of warfare should prove a fruitful way to progress beyond the Hawk-Dove debate. Warfare is ubiquitous today and throughout recorded history, but some societies are more warlike than others; also, the propensity to engage in warfare changes with time. Western Europe suffered frequent and destructive warfare during the first half of the 20th century but enjoyed nearly continuous peace for the next half century. In addition to such within-society variation, a great deal of variation exists among different societies. Table 6.3 lists data on rates of mortality from intraspecific conflict for various small-scale societies compiled by Gat (1999). These societies were selected based on having comparable data available, rather than having unusually high or low rates of war. This table illustrates two main points. First, intraspecific fighting commonly results in high levels of mortality for humans, including foragers in sparsely inhabited lands. Second, rates of overall mortality vary from 5 to 60 percent. An enormous amount of variation in the rate of killing remains unexplained.

In contrast to the widespread assertion that warfare is less destructive in “simple” societies, the societies listed in Table 6.3 experience higher mortality rates than many modern warlike nations. For instance, during the first three decades of the 20th century, France lost an estimated 6.3 percent of its population to war (Wright 1942), comparable to the mortality experienced by hunter-gatherers living in the Australian bush and much less than that suffered by horticulturists in New Guinea or the Amazon.

Does the imbalance-of-power hypothesis help us understand ourselves?

Whatever the distribution of warfare among and within societies, the question remains: does any of this have any real impact on how we understand humans? Many critics of biological explanations of intergroup aggression in humans point out that modern warfare depends on elaborate institutions, with individual soldiers killing because they are told to kill, not because their demonic nature urges them to kill (Keeley 1996). Institutional organization and technology clearly affect the way wars are conducted, and it is difficult to determine the extent to which biology affects behavior in modern warfare.

Table 6.3 Percent adult mortality from intraspecific killing (from Gat (1999))

Population	Males	Females	both
Murngin (Australia)	30	NA	NA
Tiwi (Australia)	10	NA	NA
Central Australia (arid)	NA	NA	5
Central Australia (well-watered)	NA	NA	6.5
Yanomamö (Amazon)	24	7	15
Waorani (Amazon)	NA	NA	60
Dani (New Guinea)	28.5	2.4	NA
Enga (New Guinea)	34.8	NA	NA
Gebusi (New Guinea)	35.2	29.3	NA
Median	29.3	7	10.75

A striking example of coalitionary killing in modern societies is what Horowitz (2001) terms the “deadly ethnic riot.” Riots between ethnic groups occur worldwide, erupt spontaneously, involve individuals acting voluntarily, without an organized system of command, and are generally fought with very simple weapons such as machetes. Horowitz argues that “ethnic riots are probably the most common form of collective violence, by some estimates the form that took more lives than any other in the twentieth century” (Horowitz 2001), a strong claim for a century that included two world wars. The spontaneous nature of ethnic riots suggests that they would be a particularly good test case for the imbalance-of-power hypothesis. Ethnic riots permit an investigation of the factors leading people to kill one another when they are neither compelled by officers nor removed from the killing by remote-control technology.

Horowitz does not cite Wrangham and generally appears uninterested in biological explanations of aggression. Nevertheless, the underlying variables that he describes as best explaining the occurrence of deadly ethnic riots include the two conditions that Wrangham (1999) argues are necessary and sufficient for coalitionary killing: hostile intergroup relations and low-cost of attacking (Horowitz 2001). The importance of relative numbers is clear from his descriptions: “the creation of overwhelming mass, the use of (usually bladed) weapons against unarmed civilians, and the leadership of local figures skilled in fighting all provide an initial advantage for the aggressors. (Small, unarmed crowds do not kill large numbers of victims)” (Horowitz 2001). Like chimpanzees and lions, human rioters appear to be skilled at assessing whether an attack will be costly. “There is not a single riot considered in this book in which rioters miscalculated their own tactics and power, the intentions of the police, or the response of their targets, such that the rioters suffered more casualties than the targets did" (Horowitz 2001).

Although Horowitz is able to make some empirical generalizations for which factors are important in starting deadly ethnic riots, why humans should be so willing to kill their neighbors remains mysterious, at least within the framework he considers. As Horowitz points out in a review of the social psychology literature: "Disappointingly little has come of the prodigious literature on violence. No theory is clearly supported by empirical evidence" (Horowitz 2001). In contrast, the imbalance-of-power hypothesis is supported by a growing body of empirical evidence, and seems a promising foundation for building a theory of intergroup aggression in humans.

Practical applications

The imbalance-of-power hypothesis suggests some means for reducing coalitionary killing in humans. If intergroup hostility and low-cost of killing are the two necessary and sufficient conditions for coalitionary killing, reducing either or both of those factors should reduce the rate of killing.

Intergroup hostilities may be reduced in a variety of ways. Horowitz argues that ethnic riots have declined in the Western world since World War II as a result of ideology that emphasizes the shared humanity of all people (Horowitz 2001). In contrast to chimpanzees, humans are motivated by ideology, and changes in ideology can have profound effects on rates of killing. Internationally, the spread of democracy might help to reduce warfare. Although democratic nations are perfectly willing to go to war, they rarely if ever go to war with other democracies (Fukuyama 1992).

Several mechanisms exist for reducing opportunities for low-cost killing. In modern human societies, the number of attackers and defenders on a given side often depends on how many outside parties are willing to get involved. For instance, in the American South, lynchings were common when local, white-controlled governments condoned such attacks. Lynchings became less common when federal forces became willing to intervene and when public mood shifted so that even on a local scale such attacks were not supported (Horowitz 2001). A state willing to enforce equal laws for all of its citizens can prevent ethnic riots. Punishing international violators of human rights (including genocide, ethnic cleansing, and wars of conquest) may also be effective, though as the history of the United Nations suggest, international punishment suffers from collective action problems. Just as higher-ranking male primates may be more willing to exclude extragroup males (Nunn 2000), more powerful nations are more willing and able to invest in punishment, and they typically choose to punish their enemies rather than their friends. For example, the United Nations generally depends upon the United States for any effective action, so that enemies but not friends of the United States are punished for invading their neighbors. Simple solutions are often difficult to implement in a complicated world.

6.4 QUESTIONS FOR FUTURE RESEARCH

Many questions remain about the evolution of coalitionary killing. In particular, we need a better understanding of how coalitionary killing is distributed among species, and how it varies within species. Testing the species-distribution predictions of the imbalance-of-power hypothesis requires continued long-term studies of species predicted to have coalitionary killing, particularly bottlenose dolphins, spider monkeys, and ruffed lemurs. Many of the predictions tested in this study should also apply to other species known to have coalitionary killing, such as lions and wolves. Do lions avoid borders? Do wolves travel in more cohesive packs during border visits? We need more information on rates of intraspecific killing across species so we can better assess whether a given species suffers a high rate of killing. We also need a better understanding of circumstances leading to coalitionary killing in species with stable groups, such as rhesus monkeys.

Concerning chimpanzees, we still have much to learn about the dynamics involved in intergroup encounters. Do larger groups always win encounters? What percent of "battles" with multiple fighters on each side lead to injury or death? What factors affect variation in the frequency and intensity of intergroup encounters? Why did Gombe and Mahale both experience group extinctions in the 1970s but not since then? Answering such questions requires long-term observation of habituated neighboring communities. Opportunities for such observations are currently improving at Gombe, Kibale (Ngogo), and Tai. The recent computerization of the long-term data from Gombe (Williams 2000) provides an especially rich database for addressing such questions; this will be the focus of my post-doctoral work.

The present study has demonstrated the feasibility of playback experiments. Such experiments will undoubtedly continue to expand and deepen our understanding of relations between and within groups. How do chimpanzees respond to multiple foreign males? Do they distinguish neighbors from unfamiliar callers? Do they respond differently to different within-community callers? Such experiments should be conducted with due caution, however, to reduce the risk of exacerbating existing intergroup hostilities.

6.5 CONCLUSIONS

In summary, I tested seven main predictions of the imbalance-of-power hypothesis using systematic observations, playback experiments, and mathematical models. I found clear support for five of these predictions: chimpanzees avoided borders, traveled in large parties when visiting borders, called and approached a simulated intruder whenever they had sufficient numerical advantage, called and approached a simulated intruder regardless of range location, and approached faster when predicted net benefits were greater. I found qualified support for two predictions. First, males were predicted to visit borders more often than females. Males did range more widely than females, but females with home ranges centered near the territory edge appeared to spend more time near borders than males. Second, chimpanzees were predicted to produce fewer pant-hoot calls during border patrols. I found clear evidence that chimpanzees stayed remarkably quiet in one context: raiding crops outside the park. I also found that chimpanzees tended to give fewer loud calls than expected when visiting borders, but more work is needed to distinguish different types of border patrols from other types of border visit, such as feeding excursions. Overall, these results support the imbalance-of-power hypothesis, and suggest that coalitionary killing should be ubiquitous in species with hostile intergroup relations and opportunities for low-cost attacks. Most human societies, including small-scale foraging societies, appear to satisfy these conditions. Future studies of the variation in the frequency and intensity of intergroup conflict will help further illuminate the mechanisms underlying lethal intergroup aggression.

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