RANGING BEHAVIOR AND TERRITORIALITY IN CHIMPANZEES AT NGOGO, KIBALE NATIONAL PARK, UGANDA

by

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To the Ngogo chimpanzees

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Abstract

Chimpanzees are well known for their territorial behavior. Males defend heavily-used core areas and routinely patrol the periphery of their territories, apparently seeking signs of or contact with individuals from neighboring communities. In this research, I add to our understanding of chimpanzee territoriality via a study of an unusually large community of chimpanzees at Ngogo, Kibale National Park, Uganda.

Using 19 months of observations, I estimated the sizes of the Ngogo chimpanzee territory and core area, the most heavily used portion of the territory. Different methods produced similar estimates, though subsampling data to reduce autocorrelation substantially reduced estimates calculated using nonstatistical techniques. I found that a biologically meaningful estimate of the core area represented an area about 1/3 of total territory size.

Food availability and intercommunity relations are frequently hypothesized to influence territory use and size. I assessed their effects, but found little evidence that either affected the ranging patterns of the Ngogo chimpanzees.

Patrolling chimpanzees cover long distances, and patrols are likely to involve energetic costs for participants. To evaluate these costs, I compared observations of travel and feeding during patrols and matched control periods. Chimpanzees covered longer distances, spent more time traveling, and spent less time feeding during patrols than during control periods. These results suggest that ecological factors may constrain the ability of chimpanzees to patrol.

I also investigated factors affecting where chimpanzees patrol. Nest counts of neighboring chimpanzees did not predict patrolling locations, suggesting that chimpanzees do not respond to power imbalances between themselves and neighbors when choosing areas to patrol. Over the long but not short term, Ngogo chimpanzees patrolled more frequently in peripheral areas where they experienced more intercommunity encounters. In the most heavily patrolled areas, intercommunity encounter and patrol frequency were also positively correlated over the short-term. I found evidence that Ngogo chimpanzees defended some boundary areas of their territory more keenly than others, apparently adjusting their territorial activities in response to different neighbors in various ways.

These chapters present a picture of how chimpanzee communities use and defend their territories, and contribute to our arsenal of methods for assessing ranging and territoriality.

CHAPTER 1

Introduction

BACKGROUND

Chimpanzee Territoriality

Territorial animals defend an area against conspecifics [Burt 1943; Noble 1939]. In its most common form, displayed by many bird species, territorial defense involves one or both members of mated pairs defending areas associated with nests or other reproductive activity [e.g. Hyman et al. 2004; Noble 1939; Sergio and Newton 2003; Stamps and Krishnan 1999]. Less commonly, groups of animals compete over territories. Although group territoriality has been observed in many species of tropical birds [Gaston 1978], it is comparatively rare among mammals, only having been reported in social carnivores [e.g. cheetahs: Caro and Collins 1987; lions: Grinnell et al. 1995; spotted hyenas: Henschel and Skinner 1991; Kruuk 1972; wolves: Mech et al. 1998; Mech and Boitani 2003; Packer et al. 2005; Schaller 1972], and some species of primates [e.g. spider monkeys: Aureli et al. 2006; Wallace 2008; bonnet macaques: Cooper et al. 2004; blue monkeys: Cords 2007; white-faced capuchins: Crofoot 2007; Gros-Louis et al. 2003; vervet monkeys: Struhsaker 1967].

Chimpanzees provide one of the best examples of group territoriality in primates. Chimpanzees live in large communities that include multiple adult males, adult females, and immature individuals. Male chimpanzees of the same community jointly defend heavily-used areas and routinely patrol peripheral areas in large parties, occasionally making deep incursions into the territories of their neighbors [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Herbinger et al. 2001; Mitani and Watts 2005; Watts and Mitani 2001].

During boundary patrols and incursions, chimpanzees appear to seek contact with or information about individuals in other communities. Behavior during patrols is characterized by the striking silence of males as they travel in a closely spaced, single-file line. Chimpanzees on patrol appear particularly tense and attentive, move in a directed fashion, and engage in reassurance behavior when startled [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001].

In most cases, patrolling chimpanzees return to their home territory without having made contact with neighbors, but about 1/3 of the time, patrollers encounter neighbors [26% of patrols at Taï: Boesch and Boesch-Achermann 2000; 39% of patrols at Ngogo: Mitani et al. 2002b]. Auditory contacts, in which the patrolling party hears the calls of a party from the neighboring community, are the most common type of intercommunity encounter [Boesch and Boesch-Achermann 2000; Watts and Mitani 2001; Wilson and Wrangham 2003]. Patrolling chimpanzees who hear neighbors will sometimes approach or stalk them, usually in a silent, quick, and directed fashion [Boesch and Boesch-Achermann 2000; Goodall et al. 1979; Watts and Mitani 2001; Wilson and Wrangham 2003]. These approaches can result in visual contact, during which parties from the two communities meet, call, display, and engage in chasing or fighting [Boesch and Boesch-Achermann 2000; Goodall et al. 1979; Watts and Mitani

2001]. Occasionally these encounters result in an attack by the larger party, leading to some individuals sustaining severe or fatal injuries [review in Wilson and Wrangham 2003]. A recent study on lethal coalitionary aggression at Ngogo reports that 12/95 patrols and 8/68 intercommunity encounters not associated with patrols included physical aggression during 41 months in 1997-2003 [Watts et al. 2006]. Eighteen fatalities have been observed at Ngogo from 1999 to 2008 [Mitani personal communication].

Chimpanzee territorial behavior is dramatic and has major fitness consequences for participants, making it an important topic of study. While a growing number of reports have added to our understanding of the proximate and ultimate factors underlying territoriality and boundary patrols, several gaps in knowledge remain [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001; Watts et al. 2006; Williams et al. 2004; Wilson et al. 2002; Wilson et al. 2001; Wilson and Wrangham 2003; Wrangham 1999]. For instance, recent research has clarified some of the fitness benefits accrued by patrolling chimpanzees [Goodall et al. 1979; Mitani and Watts 2005; Mitani et al. 2002a; Watts and Mitani 2001; Watts et al. 2006; Williams et al. 2004; Wilson and Wrangham 2003], but their costs have been largely unexplored. Moreover, few data exist regarding the spatial distribution of and whether and why chimpanzees patrol in some areas more than others.

Chimpanzee Use of Space

Understanding chimpanzee territoriality depends on quantifying how they use space. By definition, boundary patrols occur along the periphery of or outside the usual range. Thus many studies of chimpanzee patrolling behavior include representations of territory size and shape [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Watts and Mitani 2001; Williams et al. 2004; Wilson et al. 2001; Wilson et al. 2007; Wilson et al. 2004]. Several methods are available to estimate territory size. Different techniques may produce dramatically different results, and there is little agreement on which method should be used.

Previous studies, employing a variety of different methods of estimating space use parameters, have revealed considerable intercommunity variation in territory size and ranging patterns [e.g. Baldwin et al. 1982; Basabose 2005; Chapman and Wrangham 1993; Doran 1997; Emery Thompson et al. 2007; Herbinger et al. 2001; Lehmann and Boesch 2003; Lehmann and Boesch 2005; Mitani and Amsler 2003; Murray et al. 2008; Newton-Fisher 2000; Newton-Fisher 2001; Newton-Fisher 2003; Williams et al. 2004; Wilson et al. 2007; Wrangham et al. 2007]. Several factors, including body size, group size, food availability, and intergroup relationships have been hypothesized to influence this variability. Different studies yield contradictory findings, and as a consequence, the factors that affect space use patterns in chimpanzees are still not entirely clear.

GOALS OF THIS DISSERTATION

In this thesis, I attempt to resolve some of the problems outlined above, by investigating space use and territoriality in chimpanzees at Ngogo, Kibale National Park, Uganda. Obtaining accurate and reliable estimates of territory size is critical to understand territorial behavior as well as other questions regarding the behavior, ecology and conservation of chimpanzees. Accordingly, I begin in Chapter 2 by estimating the size of the Ngogo chimpanzees' territory and their core area using several frequently adopted techniques. I discuss methodological problems associated with estimating territory size and compare my results to those reported for other chimpanzee communities. In Chapter 3, I investigate the factors that affect the size of chimpanzee territories, specifically examining the influences of fruit availability and intercommunity relations. In Chapters 4 and 5, I move from issues of territory size to how chimpanzees defend their territories against conspecifics. Chapter 4 addresses the costs of territorial defense with an examination of the energy costs involved with boundary patrols. In Chapter 5, I ask whether chimpanzees defend particular parts of their territory by patrolling there frequently and why they might do so.

STUDY SITE

The Kibale National Park is located in western Uganda along the eastern edge of the western Great Rift Valley, 24 km east of the Rwenzori Mountains [Lwanga 1994; Struhsaker 1997] (Fig. 1.1). Designated a national park in 1993, Kibale has been subject to fluctuating levels of government regulation and conservation since it was gazetted as a crown forest in 1932 and as a central forest reserve in 1948 [Lwanga 1994; Lwanga et al. 2000; Struhsaker 1997]. The park covers 766 km^2 of mixed old growth and colonizing forest. It consists of a mosaic of vegetation types, including montane tropical forest, grassland, woodland thicket, colonizing forest, papyrus swamp, and exotic tree plantation. Tall evergreen forest composes most (60%) of the park [Chapman et al. 1997; Ghiglieri 1984; Lwanga 1994; Struhsaker 1997]. Although it is generally warm and rainy with two wet and two dry seasons annually, Kibale is somewhat cooler and drier than other tropical rain forests due to its higher elevation [Struhsaker 1997]. Soils in the Kibale National Park are of particularly high quality and fertility compared to other tropical rainforests, resulting in lower levels of secondary compounds in the leaves of its trees, which in turn permits a high biomass of primates, particularly folivores [Struhsaker 1997]. In fact, the density of primates there is among the highest anywhere [Oates et al. 1990; Struhsaker 1997].

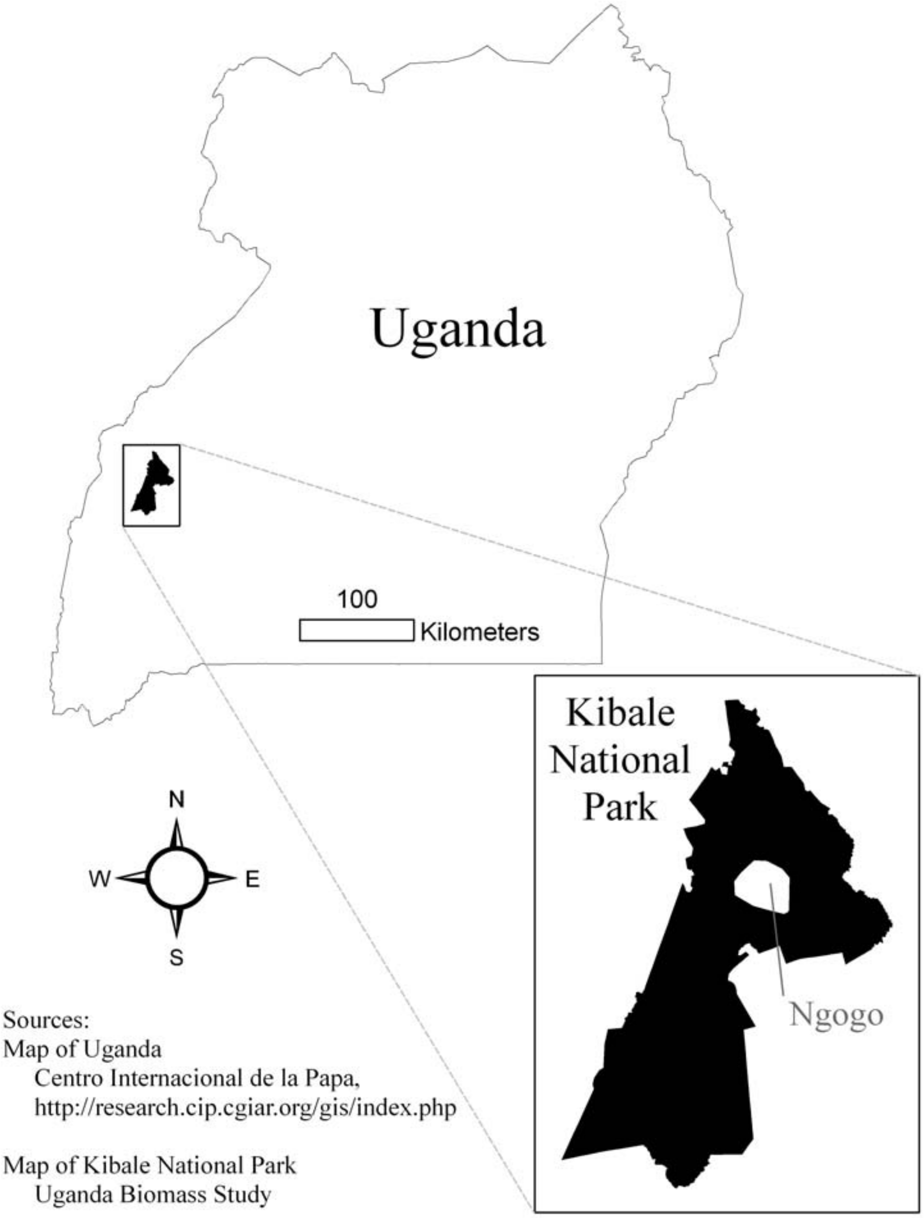

Fig. 1.1. The location of Kibale National Park in Uganda, and the location of the Ngogo study site within the park (inset).

Kibale also boasts high faunal diversity, with at least 300 bird species and at least 70 species of mammals, including 11 primate species. This diversity is due in part to the location of Kibale National Park at the interface of Central and East African habitats, as well as its mosaic of habitats [Ghiglieri 1984; Lwanga 1994; Struhsaker 1997]. The Makerere University Biological Field Station (MUBFS) maintains two research sites within the Kibale Park. The vast majority of previous ecological and behavioral research has been conducted at Kanyawara, located in the northwest of the park where commercial logging has occurred. Ngogo, where I observed chimpanzees for this dissertation, is more centrally located within the park, about 10 km southeast of Kanyawara.

The Ngogo Nature Reserve was established within Kibale in 1975, and has been the site of behavioral research on primates since around that time [Mitani et al. 2000; Mitani and Watts 1999; Struhsaker 1997] (Fig. 1.1). M. Ghiglieri [1984] carried out the first studies of chimpanzees at Ngogo in 1976-1978 and 1981. Subsequent habituation and observations of chimpanzees were made there by Wrangham et al. [1992; 1991] from 1988-1995, B. Grieser-Johns from 1992-1993, and D. Watts in 1993. Long-term observations were initiated by D. Watts and J. Mitani in 1995, and chimpanzees have been observed continuously since then [Mitani 2006; Mitani et al. 2000]. The Ngogo research site consists of a mix of old growth and colonizing forest, dotted with *Pennisetum purpureum* grasslands. Lying about 1350 m above sea level, Ngogo is characterized by its hilly topography [Ghiglieri 1984; Lwanga 1994; Lwanga et al. 2000; Struhsaker 1997]. Long-term weather data from 1998-2007 indicate that the mean annual rainfall at Ngogo was 1397 mm (SD = 174 mm, n = 10 years). The average minimum and maximum daily temperatures during the same period were 16.7° C (SD = 0.29) and 24.7°

C (SD = 0.79), respectively. Ngogo has not experienced mechanized logging and contains large patches of old growth forest, the preferred habitat of chimpanzees [Lwanga 2006].

Ngogo offers ideal conditions for studying space use and territoriality in chimpanzees. The site is well established with more than 220 km of trails covering the 30 km^2 study area. Chimpanzees at Ngogo have never been provisioned, and as a result of prior research, they are habituated to and individually identifiable by human observers [Mitani et al. 2000]. Ngogo males tolerate humans following at short distances, even during boundary patrols, and observers have routinely followed patrolling males since 1997 [Watts et al. 2006]. The central location of Ngogo within the park not only protects the community somewhat from human activities, but also means that the Ngogo chimpanzees are surrounded on all sides by neighboring communities of chimpanzees. Thus, intercommunity encounters and boundary patrols can occur in any direction, which contributes to their frequency of occurrence. The Ngogo chimpanzees do, in fact, patrol at high rates, thereby optimizing the amount of data available to investigate territorial activities [Mitani 2006; Watts and Mitani 2001].

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CHAPTER 2

Estimating the Territory: Review and Methods

ABSTRACT

Obtaining accurate and reliable estimates of territory size is important to understand the behavior, ecology, and conservation of chimpanzees. Various methods have been used to estimate chimpanzee territory size, but the extent to which estimates from different studies can be productively compared has been an open question. In this study I estimated the territory and core area size of the chimpanzee community at Ngogo, Kibale National Park, Uganda using three frequently adopted techniques: the minimum convex polygon (MCP), grid cell, and fixed kernel. Estimates produced by different methods were similar and showed high overlap. Core areas defined by 75-80% of observations accounted for 33-39% of the total territory area. I suggest that an 80% core area is biologically relevant for the Ngogo chimpanzees. I discuss methodological problems related to estimating chimpanzee territories and core areas. Subsampling data to reduce autocorrelation substantially reduced estimates calculated using nonstatistical methods, while the kernel method was more robust to sample size changes. I compare my results to territory and core area estimates made for other chimpanzee communities, and conclude by making suggestions about how to improve comparability among studies.

INTRODUCTION

The home range represents the area habitually traversed by an individual or group of animals during normal daily activities such as feeding, resting, and reproductive behavior [Burt 1943]. Home ranges are usually assessed with reference to specified periods, such as days or years, because ranges may change size or shift over time [Newton-Fisher 2003]. Individuals or groups that defend their range against conspecifics are said to occupy *territories*, rather than home ranges [Burt 1943; Noble 1939].

An understanding of how animals use space is essential when addressing many fundamental questions about behavior, ecology and conservation. Predator-prey relationships, territorial activities, and reproductive behaviors may all influence the size, shape, and location of an animal's home range or territory [Horne and Garton 2006b]. Ranging patterns may also be affected by ecological variables such as rainfall or habitat productivity [Cushman et al. 2005]. Understanding the spatial requirements of threatened and endangered species provides information about the size and ecological attributes of areas that need protection [Durbian et al. 2008; Irwin 2008; Yamagiwa 1999; Yeiser et al. 2008]. In sum, the ability to accurately measure the extent of home ranges and territories and to spatially represent patterns in the way animals use these areas is important for several reasons.

Recent advances in GPS (Global Positioning Systems) and GIS (Geographic Information Systems) technology have revolutionized our ability to track the movement of animals and to characterize their ranging patterns in probabilistic ways [Moorcraft and Lewis 2006; Nilsen et al. 2008]. Once the positions of animals have been plotted using this technology, various methods are available to represent and estimate ranges and territories. Polygon methods, such as the minimum convex polygon (MCP), are frequently used to estimate size but cannot represent differential use. Other methods, such as the grid cell and kernel estimation techniques, can be applied not only to estimate range size, but also to measure varying intensity of use throughout that area. Each of these methods has its advantages and drawbacks, and estimates may vary greatly depending upon which is used [Barg et al. 2005; Herbinger et al. 2001; Jennrich and Turner 1969; Moorcraft and Lewis 2006; Nilsen et al. 2008; Schoener 1981].

Different researchers often define territory boundaries differently due to disagreement over which method is most biologically relevant [Shivik and Gese 2000]. Moreover, the use of different methods complicates comparisons among studies [Anderson 1982]. Other factors such as sampling effort, study length, and sampling regime may also affect results [Börger et al. 2006], and it is often difficult to standardize these factors across studies. An awareness of how estimation methods and other variables influence results is important, particularly when comparing estimates among different study populations.

In addition to estimating the extent of the home range or territory, many researchers find it useful to specify boundaries of a core area. First introduced by Kaufmann [1962], the core area is the area within the territory or home range which is used most intensely [Samuel et al. 1985]. The existence of a core area makes sense as a way to quantify space use patterns, and many researchers have identified core areas within the territories of their study species. The same estimation methods used to estimate home ranges and territories have been employed to delineate core areas; however, there is no consensus on how to define core area boundaries.

Autocorrelation between successive points is another issue that has been of concern when estimating animal home ranges and territories. Autocorrelation occurs when an animal's position at one sample point is influenced by its position at the previous sample point. Statistical methods of home range estimation require that points be independent [Swihart and Slade 1985a; Swihart and Slade 1985b]. As a result, many researchers employ techniques intended to eliminate dependence between consecutive points, such as subsampling positions. Unfortunately, because animal ranging is a non-independent phenomenon, these techniques may lead to inaccurate or misleading representations of home ranges and territories [Barg et al. 2005; Blundell et al. 2001; Cushman et al. 2005; De Solla et al. 1999]. Understanding the space use patterns of animals requires knowing where animals actually range, and statistical purity may be less important than the inclusion of all biologically meaningful data, even if it entails the use of autocorrelated points.

Chimpanzees are a territorial species that lives in large communities composed of multiple adult males, adult females, and immature individuals. Our understanding of chimpanzee behavior, ecology, and conservation has been enhanced by several recent studies investigating chimpanzee ranging patterns [Baldwin et al. 1982; Basabose 2005; Chapman and Wrangham 1993; Herbinger et al. 2001; Lehmann and Boesch 2003; Newton-Fisher 2000; Newton-Fisher 2001; Newton-Fisher 2003; Williams et al. 2004; Wilson et al. 2007; Wrangham et al. 2007]. For example, territory estimates collected over time at Gombe National Park, Tanzania have shed light on how territorial behaviors such as patrolling and lethal coalitionary aggression are related to reproduction [Williams et al. 2004]. Reliable and accurate territory size estimates also provide insight into how chimpanzees satisfy daily needs, such as feeding [Baldwin et al. 1982; Basabose 2005]. While between site comparisons can be useful to examine several aspects of behavior and ecology [Herbinger et al. 2001; Newton-Fisher 2003], methodological differences often complicate such comparisons. Chimpanzee researchers have used a variety of techniques to estimate territory size, and estimates vary widely. Although these studies have used multiple methods, facilitating comparisons between sites, there is no agreement regarding how to measure this important parameter in the lives of chimpanzees.

In this paper, I use observations of ranging behavior of chimpanzees living at Ngogo, Kibale National Park, Uganda, to investigate several problems associated with estimating the size of animal territories and core areas. I begin by comparing estimates of territory size and core areas generated using different methods. I then examine the effects of subsampling as a means to address the problem posed by autocorrelation. I conclude by reviewing methods used to estimate the sizes of territories and core areas in other chimpanzee communities and suggest how different estimates between sites produced via different techniques might be meaningfully compared.

METHODS

Study Site and Animals

I observed chimpanzees at Ngogo, Kibale National Park, Uganda. This site is covered primarily by tall, moist evergreen forest, with areas of swamp, grassland, woodland thicket, and colonizing forest. More than 230 km of trails cover the approximately 30 km^2 study area. I used a handheld GPS to map the entire trail system, which facilitated plotting the locations of chimpanzees. Struhsaker [1997] provides a detailed description of the site.

Ngogo has been the site of behavioral research on several primate species [review in Struhsaker 1997], and chimpanzees there have been observed continuously since 1995 [Mitani 2006; Mitani et al. 2000; Mitani et al. 2002a; Mitani et al. 2002b; Watts et al. 2006]. As a result of prior research, the chimpanzees of Ngogo are habituated to human observers. The Ngogo chimpanzee community is the largest that has been described in the wild [Mitani 2006; Mitani and Amsler 2003; Watts 2002; Watts 2004; Watts and Mitani 2000; Watts and Mitani 2001; Watts et al. 2006]. Community size ranged from 137 to 148 individuals over the course of the present study.

Field Methods

I observed chimpanzees at Ngogo for a total of 19 non-consecutive months. To capture unpredictable seasonal and between-year variation in fruit availability [Mitani unpublished data; Struhsaker 1997], I divided my observation period into 4 periods: June – August 2003, July – November 2004, February – June 2005, and September 2005 – February 2006.

Chimpanzees live in fission-fusion societies. Individuals form temporary parties whose membership changes throughout the day [Nishida 1968]. I observed focal male chimpanzees for 2 hours at a time, recording their locations and activities. I focused on males because they range over the entire territory, while females tend to use smaller core areas within the territory [Chapman and Wrangham 1993; Emery Thompson et al. 2007;

Williams et al. 2002; Wrangham and Smuts 1980]. During times that I was not following a focal male, I usually attempted to remain with the party containing the largest number of adult males. I recorded locations of focal males or the approximate center of parties during scans at 30-minute sample intervals, made every hour and half-hour. I took geographic coordinates with a Magellan 315 GPS receiver. When the unit was unable to track enough satellites to obtain a fix, I estimated the direction and distance in meters from known locations, such as trail intersections, or previous GPS readings.

Territory Size Estimation

I calculated the size of the Ngogo community's territory using the minimum convex polygon and grid cell methods, the two most commonly employed techniques in previous chimpanzee studies [Basabose 2005; Boesch and Boesch-Achermann 2000; Chapman and Wrangham 1993; Hasegawa 1990; Herbinger et al. 2001; Lehmann and Boesch 2003; Lehmann and Boesch 2005; Mitani and Amsler 2003; Newton-Fisher 2003; Williams et al. 2004; Wilson et al. 2007]. I also estimated the size of the Ngogo territory using the fixed kernel technique, the method generally considered in the ranging literature to be the best available [Barg et al. 2005; Börger et al. 2006; Kernohan et al. 2001; Seaman and Powell 1996; Swihart and Slade 1997; Worton 1987; Worton 1995b]. Territory estimates were based on locations derived from 30-minute scans. Territorial boundary patrols involve movements at or outside the boundaries of the territory [Boesch and Boesch-Achermann 2000; Goodall 1986; Watts and Mitani 2001]. I therefore excluded all locations recorded on days when the Ngogo chimpanzees patrolled, as they were likely to be outside the areas typically used. Included in the territory size estimates were locations from 4459 scans collected on 251 observation days between June 2003 and February 2006.

Minimum Convex Polygon Estimates

I estimated the Ngogo territory using a 100% minimum convex polygon (MCP). The MCP has been the most commonly used home range estimator in animal ranging studies [Harris et al. 1990; Seaman et al. 1999] since early research showing its utility [e.g. Mohr 1947]. An MCP is calculated from a set of locations by connecting peripheral points into a convex polygon, whose internal angles measure less than 180 degrees [Worton 1987]. The 100% MCP is the smallest convex polygon containing all locations. This method remains appealing because it is easy to understand and simple to calculate. Because it has been widely applied, it also affords the opportunity for cross-study comparisons. However, the MCP method has its limitations. First, MCP estimates vary as a function of sample size, with estimated territory sizes increasing with the number of locations. They are also sensitive to outlying points, so that occasional excursions may contribute unduly to the estimate. Sample size and sensitivity to outliers can be addressed by “peeling” away points based on their distance from the arithmetic center of all x- and y-coordinates, resulting in percentage MCP estimates [Mizutani and Jewell 1998; Schoener 1981; Worton 1987; Worton 1995a]. The MCP method additionally constrains the shape of the territory to a convex polygon, which may result in the inclusion of unused areas and thus an overestimation of territory size [Anderson 1982; Barg et al. 2005; Börger et al. 2006; Herbinger et al. 2001; Kenward et al. 2001; Nilsen et al. 2008; Worton 1995a]. In a ranging study of roe deer and kestrels, Börger et al. [2006] found the

MCP to be considerably more biased in various and unpredictable ways than other estimation methods. Finally, while the MCP can be used to represent the extent of territories, it says nothing about intensity of use of different parts of territories [Worton 1987]. Despite these drawbacks, the MCP method continues to be widely applied in ranging studies and commonly used in studies of chimpanzees [Boesch and Boesch-Achermann 2000; Herbinger et al. 2001; Lehmann and Boesch 2003; Newton-Fisher 2003; Williams et al. 2004; Wilson et al. 2007].

I calculated the 100% MCP for all locations in my sample using the Animal Movement extension to ArcView 3.3 [Hooge and Eichenlaub 1997].

Grid Cell Estimates

I also estimated the size of the Ngogo territory using the grid cell method, another method often used in studies of chimpanzee ranging [Basabose 2005; Chapman and Wrangham 1993; Herbinger et al. 2001; Lehmann and Boesch 2003]. In contrast to the MCP, the grid cell reveals how intensity of use varies over the territory [Bailey and Gatrell 1995; Mizutani and Jewell 1998]. In this method, a grid is superimposed over the area, and locations are counted in each quadrat. Counts per quadrat summarize the pattern of range use. Territory estimates typically include cells with positive counts as well as any cells that animals must pass through to reach cells with positive counts. While the grid cell method is also relatively easy to implement, it too has limitations. First, the territory size estimate is quite sensitive to grid cell size. Second, interpreting patterns of use is also dependent on cell size. Detail is lost at larger sizes while high variability in quadrat counts becomes difficult to interpret at smaller sizes [Bailey and Gatrell 1995;

Herbinger et al. 2001; Mizutani and Jewell 1998]. Finally, the grid cell method does not provide a good way to remove outliers [Mizutani and Jewell 1998]. It has, however, proven useful for representing territory use, particularly when it is necessary to quantify the overlap in the intensity of use between two animals or groups [Doncaster 1990].

I estimated the Ngogo territory size as the total of all 500 X 500 meter grid cells, which contained at least one observation from scan samples. 500 X 500 meter grid cells are commonly used in chimpanzee studies because they are relatively small compared to the large territories occupied by chimpanzees [Herbinger et al. 2001; Lehmann and Boesch 2005]. This size appropriately balances the risk of excluding many small areas when overly small cells are used against the possibility of including too many unused areas with overly large cells [Amsler unpublished data].

Kernel Estimates

I used kernel density as a third way to estimate the Ngogo community's territory size. Kernel density estimation methods have increasingly gained favor over other methods such as MCP and grid cell [Barg et al. 2005; Blundell et al. 2001; Börger et al. 2006; Horne and Garton 2006a; Kernohan et al. 2001; Worton 1987]. Like the grid cell method, kernel density methods provide a way to measure varying intensity of use within the territory. A statistical method, the kernel is based on the utilization distribution (UD), which gives the probability of finding a community member at any given location based on the distribution of locations over time [Anderson 1982; Blundell et al. 2001; Seaman and Powell 1996; Worton 1987; Worton 1995b]. Estimating territory size with a kernel involves superimposing a fine grid over the study area and estimating the intensity of use at each grid intersection based on the number of observations within a specified "window" [Bailey and Gatrell 1995; Worton 1989]. Percent volume contours are formed by interpolating between these estimated values and connecting areas of equal density [Kenward et al. 2001; Seaman and Powell 1996]. Multiple kernel functions can be implemented, but neither the kernel function nor the grid cell size greatly affects results. Kernels make no assumptions about the underlying distribution of locations, allow for multiple centers of activity, and provide more accurate and less biased estimates than the MCP [Barg et al. 2005; Blundell et al. 2001; Börger et al. 2006; Kenward et al. 2001; Seaman et al. 1999; Swihart and Slade 1997; Worton 1987]. Compared to the grid cell method, kernels result in a smoother territory estimate, and percent volume contours provide a way to address outliers [Bailey and Gatrell 1995; Dixon and Chapman 1980; Kenward et al. 2001; Samuel et al. 1985; Seaman and Powell 1996; Worton 1989; Worton 1995b].

The only drawback to the kernel method is its sensitivity with respect to bandwidth, the radius of the "window" [Bailey and Gatrell 1995; Barg et al. 2005; Gitzen and Millspaugh 2003; Horne and Garton 2006a; Kenward et al. 2001; Seaman and Powell 1996]. A larger bandwidth may obscure detail because it increases the region around each point from which observed events influence the estimated value. In contrast, a small bandwidth may result in a spurious level of detail, reducing the ability to see large-scale patterns of use intensity [Silverman 1986; Worton 1989]. Despite the issue of bandwidth selection, kernel methods are generally agreed to be the best available means to estimate territory size [Kernohan et al. 2001].

I estimated the Ngogo territory size using the fixed kernel method with least squares cross validation (LSCV). A fixed kernel uses the same bandwidth at all locations. Seaman and Powell [1996] have found it to be more accurate than the alternative adaptive kernel, which adjusts the bandwidth to density on a local basis. LSCV selects a bandwidth for a given kernel and sample size by minimizing the mean integrated square error value of the estimate. Although debate still exists over the best process for choosing bandwidths, LSCV has proven more accurate with less bias than other bandwidth choices in most studies [Börger et al. 2006; Gitzen and Millspaugh 2003; Seaman et al. 1999; Seaman and Powell 1996; but see Blundell et al. 2001; De Solla et al. 1999; Horne and Garton 2006a].

I generated kernel density estimates using Hawth's Analysis Tools for ArcGIS 9.1 [Beyer 2004] after first calculating the LSCV bandwidth using the Animal Movement extension to ArcView 3.3 [Hooge and Eichenlaub 1997]. Hawth's Analysis Tools does not provide the LSCV bandwidth option, while Animal Movement does. A comparison of multiple kernel calculation programs revealed that the Animal Movement extension underestimated the probability contours compared with other computer programs [Mitchell 2006]. Therefore I combined the desirable features of each program to produce kernel estimates. To estimate territory size, I calculated the 95% and 99% percent volume contours for the locations of chimpanzees recorded during scan samples.

Subsampling of Locations to Reduce Autocorrelation

To address the extent to which subsampling affects territory size calculations, I estimated the size of the Ngogo territory using two subsamples of scan locations. Based on Swihart and Slade's [1985b] proposal that the time-to-independence between consecutive locations should be based on the time it takes to traverse the territory, Newton-Fisher [2003] estimated that it took four hours to achieve independent locations for chimpanzees at Budongo. To calculate the same for the Ngogo chimpanzees, I determined that 2.52 km/hr is the average travel rate of adult males in my sample and that the farthest distance between any 2 points in the 100% MCP territory is ca. 7000 m. Using these figures, a constantly traveling adult male could move between any two locations within the Ngogo territory within 2.78 hours. I generated MCP, kernel, and grid cell territory estimates using only scan locations at 800, 1230, and 1700 hours, for a time lag of 4.5 hours between successive locations, which is longer than estimates for both Budongo and Ngogo and therefore should result in independence. This subsampling regime reduced the sample size to 569 locations. Other chimpanzee studies have more conservatively used one location per day to reduce autocorrelation [Herbinger et al. 2001; Mitani and Amsler 2003]. I therefore also created territory estimates with each of the three methods based on one randomly selected location per day. I used a random choice program to choose one scan from each of the 251 observation days (http://jklp.org/public/html/choose.html).

Core Area Estimation

I also delineated a core area using various methods, to compare with results from other studies and to ascertain the best way to determine the core area. The core area is the portion of a territory with the highest probability of use [Samuel et al. 1985]. An arbitrary percentage is typically chosen, and the portion of the territory that accounts for this percentage of use is identified as the core area. Chimpanzee researchers often define the core area as the area encompassing 75% of observations, while 50% appears to be commonly chosen in studies of other animals [e.g. Boesch and Boesch-Achermann 2000; Cimino and Lovari 2003; Herbinger et al. 2001; Lehmann and Boesch 2003; Nielsen and Woolf 2001].

For comparison with other studies, I calculated the areas encompassing 75% and 50% of all scans using the MCP and kernel methods. To generate percentage MCPs, I used the floating arithmetic mean method to choose a subset of all scan locations. This method drops locations sequentially by calculating the arithmetic mean of all points, dropping the farthest point, recalculating the mean, dropping another point, and so on, until the desired percentage of the original set of locations remains [Rodgers and Carr 1998]. I used the Home Range Extension to ArcView 3.3 to calculate percentage MCPs [Rodgers and Carr 1998]. Using the LSCV fixed kernel, I also estimated the core area with the 75% and 50% probability contours using Hawth’s Analysis Tools for ArcGIS 9.1 [Beyer 2004].

In addition to these arbitrary determinations of core area using subsets of observations, some researchers have defined the core area based on biologically meaningful criteria. The crux of the core area concept is that ranging within the territory is not uniform or random, but rather clumped. Samuel et al. [1985] therefore proposed that areas of the territory that “exceed an equal-use pattern” should be considered the core area. Using the grid cell method, I defined the core area as the cells that exceed equal use. All grid cells whose frequencies of use were higher than the average were regarded as part of the core area. I then determined the proportion of scans included in this set of grid cells. This method provided a way to determine the appropriate percentage of observations to define an area that exceeds an equal use pattern for the Ngogo chimpanzees. I then used this percentage of locations to delineate MCP and kernel core areas boundaries.

In another attempt to create an objective definition of core area, others have calculated areas at progressively smaller percent volume contours and chosen as the core area boundary the point at which the area changes most dramatically [e.g. Barg et al. 2005; Clutton-Brock et al. 1982]. Although I also searched for discontinuities in the area represented by successive kernel contours, none were apparent, so this method could not be applied to determine the core area of the Ngogo chimpanzees.

Because a clumped pattern of territory use by chimpanzees, with a centrally-located core area, is thought to reflect relations with neighbors [Herbinger et al. 2001; Wrangham et al. 2007], recent studies of chimpanzees have sought to determine core areas using measures that incorporate knowledge of intercommunity associations and territorial behavior. Wilson et al. [2007], for example, defined the core area based on where chimpanzees built night nests, assuming those locations indicated areas where the chimpanzees felt secure against raids from neighbors. Herbinger et al. [2001] calculated not only 75% and 50% core areas, but also exclusive 75% and 50% core areas, which were the portions of the 75% and 50% MCPs where neighboring chimpanzees were not observed. Because chimpanzees neighboring Ngogo have not been habituated, observations of where they range are not available. In an attempt to define the core area in a similar way, I recorded *ad libitum* the locations of all aural and visual encounters Ngogo chimpanzees had with members of other communities. These intercommunity encounters provide a way to assess the degree to which the Ngogo community territory overlaps with those of their neighbors. I used the innermost intercommunity encounters to form the “maximum internal convex polygon”. I connected these locations to form the largest polygon possible such that all external angles measured at least 180 degrees. Although it may not reflect territory use patterns, this polygon, representing an area where neighbors are not encountered, can be considered an area of exclusive use. I calculated the area of overlap between this exclusively used internal polygon and the 50% and 75% MCP core areas for comparison with the exclusive 50% and 75% core areas estimated by Herbinger et al. [2001] at Taï.

Comparing Territory and Core Area Estimates

I compared territory size estimates generated by MCP, grid cell, and LSCV fixed kernel methods. To evaluate the similarity between estimates derived using different methods, I calculated the degree of overlap between each pair of estimates. I also compared patterns of territory use illustrated by the grid cell and kernel methods.

To evaluate the effect of subsampling, I compared estimates generated using the entire sample of scans with those obtained using the subsample of scans at 4.5 hour intervals and the subsample containing one randomly selected scan per day.

Finally, I compared estimates of the core area using MCP, grid cell, and kernel methods. Using each method I calculated the core area size and its percentage of the total territory.

Comparing Chimpanzee Territory Size Estimates from Different Sites

I reviewed the literature from 1990-2007 for studies which estimated territory and core area size for chimpanzee communities. I started my review in 1990 because the reporting of estimation methods before 1990 was less explicit and standardized than in more recent research. Only those studies which explained the methods used for territory estimation were included. I obtained territory size estimates from 11 studies, for 9 chimpanzee communities at 6 sites located in 4 African countries. I obtained community core area estimates from 5 studies, for 3 communities at 3 sites in 3 countries. I report the range of territory and core area sizes estimated by different methods in these studies and compare the percents of the total territory size represented by core area estimates. Because community size and range size may be associated in group-living animals [Boesch and Boesch-Achermann 2000; Clutton-Brock and Harvey 1977; Dias and Strier 2003; Dunbar 1988; Lehmann and Boesch 2003; Milton and May 1976; Struhsaker 1967], I also compare territory size estimates for different communities by plotting community size against territory size.

RESULTS

Territory Estimation

Using the sample of 4459 scan locations across 251 days, territory size estimates for the Ngogo community ranged from 19.5 km^2 to 29.25 km^2, depending on the method used (Table 2.1). Regardless of method, territory size estimates reached an asymptote after approximately 2500 locations, collected over 164 days. Excluding the 95% fixed kernel, which is much smaller than the others, the estimates did not differ greatly and overlapped considerably (Fig. 2.1). For example, the area of overlap between the 100% MCP estimate and the grid cell estimate was 26.37 km^2, which represents 95.27% of the MCP area and 90.15% of the grid cell area (Table 2.2). The overlap within pairs of estimates (excluding the 95% fixed kernel estimates) represents between 88% and 97% of the area of either one of them.

TABLE 2.1. Estimates of the territory size of the Ngogo chimpanzee community.

Estimation Method	*Territory Estimate (km^2)*
100% MCP	27.7
Grid Cell (500 X 500 meter quadrats)	29.3
95% Fixed Kernel with LSCV	19.5
99% Fixed Kernel with LSCV	26.4

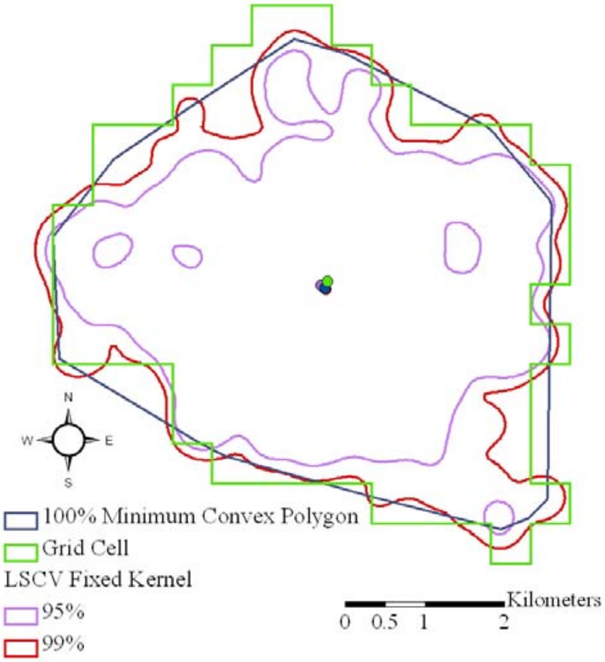


Fig. 2.1. Ngogo chimpanzee community territory boundaries generated using the MCP, grid cell, and fixed kernel estimation methods. The centroid of each polygon is indicated in a point of the same color as the border outline.

TABLE 2.2. Overlap between different territory estimates. For each method listed on the left, the first column reports the area of overlap, or shared area, with the method in the top row, while the second reports the percent of the total area estimate represented by that overlap. For example, 90.15% of the grid cell estimate area and 95.27% of the MCP estimate area is represented in the 26.37 km^2 overlap between the grid cell and MCP estimates.

	Area of overlap with MCP (km^2)	*% Overlap with MCP*	*Area of overlap with Grid Cell (km^2)*	*% Overlap with Grid Cell*	*Area of overlap with 95% Kernel (km^2)*	*% Overlap with 95% Kernel*	*Area of overlap with 99% Kernel (km^2)*	*% Overlap with 99% Kernel*
MCP	-		26.37	95.27%	19.40	70.09%	25.10	90.68%
Grid Cell	26.37	90.15%	-		19.41	66.36%	25.64	87.66%
95% Kernel	19.40	99.28%	19.41	99.33%	-		19.54	100%
99% Kernel	25.10	95.18%	25.64	97.23%	19.54	74.10%	-	

The grid cell and kernel methods also illustrate how the intensity of use varies across the territory (Fig. 2.2). The two different methods present a similar picture. Both indicate that most peripheral areas show little activity, except for the southwest periphery, which is used more intensively than other border regions. Additionally, both methods show the portion of territory slightly south of the center as a central focus of activity.

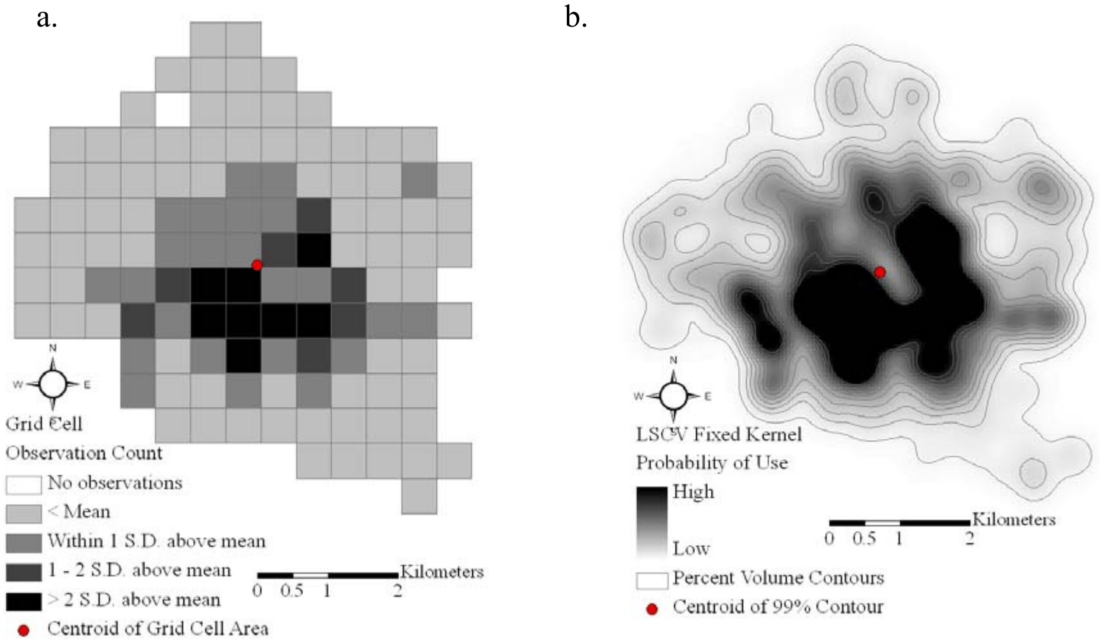


Fig. 2.2. Variation in intensity of use of the territory as represented by the grid cell and fixed kernel methods. (a) Grid cell method. Observation count refers to the number of scan locations per quadrat. The mean number of observations per quadrat was 37.8 (SD = 51; range = 1 – 267; n = 4459). The lightest grey quadrats had observation counts below the mean. The darkest quadrats are those whose observation counts were more than 2 standard deviations above the mean. (b) Kernel method. The areas with highest probability of use are shown in black, and the color fades to white as probability decreases. Percent volume contours are shown for 99% and at 5% intervals from 95% to 50%.

The Effect of Subsampling Locations

Subsampling data, by definition, resulted in reduced sample sizes. Selecting three locations per day, separated by 4.5 hours, reduced the sample size from 4459 to 569 locations, and selecting one location per day reduced the sample to 251 locations. Sampling three times per day yielded fewer than one third of the total 4459 sampled locations because I did not collect locations at all three designated times on all days. Compared to territory estimates made with the entire sample, these subsamples produced progressively smaller estimates using the MCP and the grid cell methods. The 95% kernel remained fairly consistent regardless of subsampling regime, and the 99% kernel estimate was affected to a lesser degree than the MCP or the grid cell estimates (Table 2.3, Fig. 2.3).

TABLE 2.3. Territory size estimates (km^2) based on three different samples of locations.

	All scans	*3 scans per day*	*1 scan per day*
Sample size	**4459**	**569**	**251**
100% MCP	27.7	25.6	22.8
Grid Cell	29.3	26.3	21.3
95% Kernel	19.5	19.4	19.3
99% Kernel	26.4	25.5	25.0

Core Area

The core area comprised between 11 and 39% of the total territory estimated using the same method (Table 2.4). The 75% core areas were about 34% of the total territory area, which is similar to estimates produced for other chimpanzee communities (Fig. 2.4a). The 50% core areas were about 15% of the total territory area (Fig. 2.4b), which is higher than Herbinger et al.’s [2001] 50% MCP estimates at Taï. The exclusive 75% and 50% core areas were also larger than those calculated by Herbinger et al. [2001], though the method used here was different in that I defined the area using intercommunity encounters rather than researcher observations of neighbors (Fig. 2.4e,f).

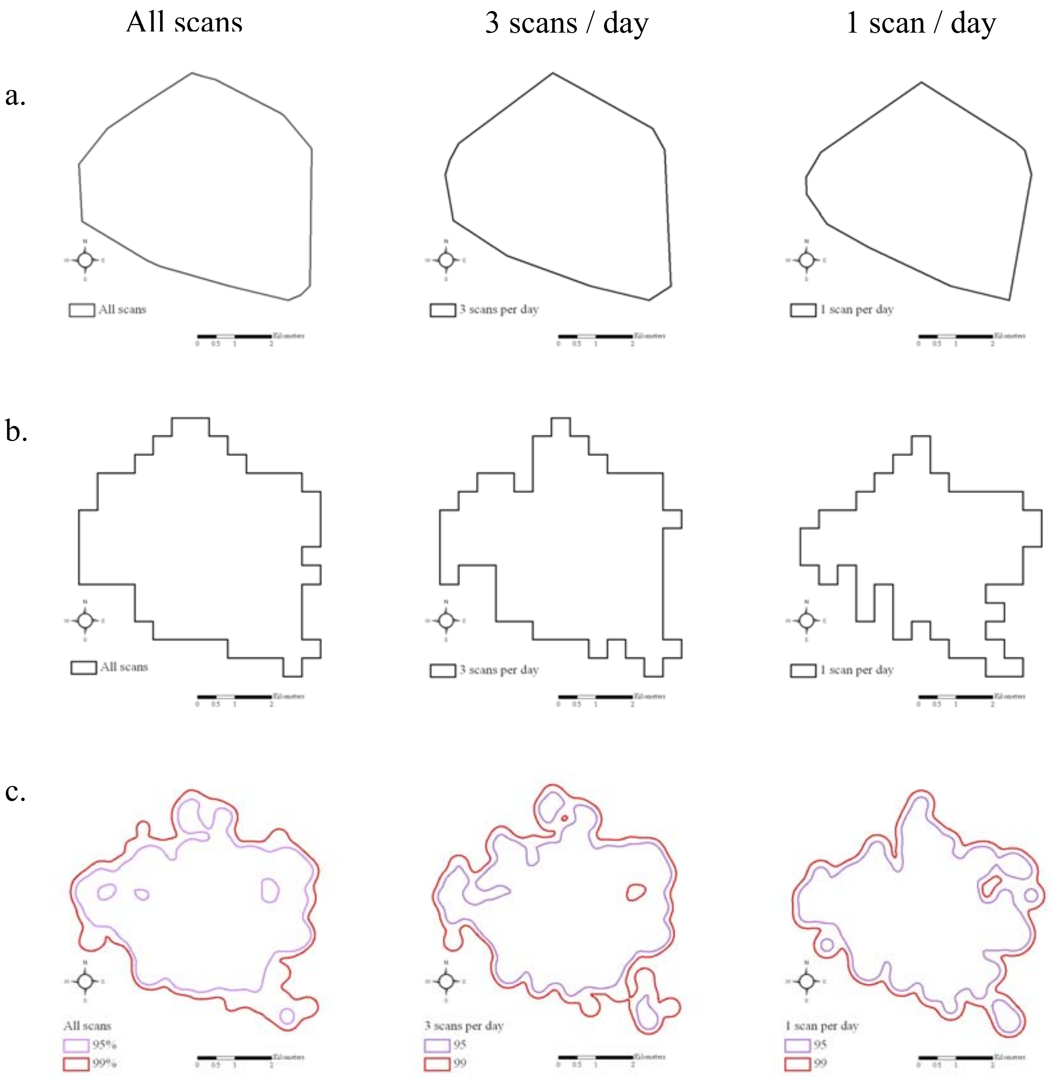


Fig. 2.3. Territory boundaries based on three different samples of locations. Territory boundaries based on the full sample of points are displayed in the first column (All scans); territory boundaries based on locations at 800, 1230, and 1700 h are displayed in the second column (3 scans / day); and territory boundaries based on one randomly selected location per day are displayed in the third column (1 scan / day). (a) MCP boundaries are shown in the first row; (b) grid cell boundaries are shown in the second row; and (c) kernel boundaries (99% in red, 95% in purple) are shown in the third row. Table 2.3 reports the corresponding territory size estimates.

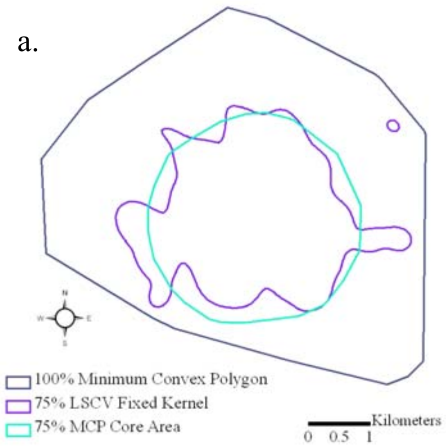
Using the grid cell method, 39 of 118 cells had scan location counts above the mean, so the area that exceeded an equal use pattern was 9.75 km^2 (Fig. 2.4c). Thirty eight quadrats were contiguous; the one disconnected quadrat was included in the core area estimate, as it represented an area that was heavily used by the Ngogo chimpanzees. This core area encompassed 80% of all scan locations, suggesting one way to define the core area for the Ngogo in a biologically meaningful way. This corresponds with Wrangham's [1979] suggestion that an individual chimpanzee's core area be considered the area in which he spends 80% of his time. Therefore I calculated the 80% MCP and 80% probability contour core areas (Fig. 2.4d).

TABLE 2.4. Core area estimates (km^2) and their percentages of total territory area (in parentheses), calculated with different methods and usage percentages.

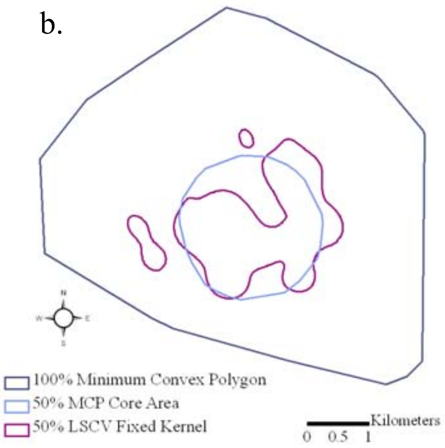
Estimation Method	*Core Area & Percent of Territory*
75% MCP	9.3 (33.6%)
75% Fixed Kernel with LSCV	8.9 (33.7%)
Grid Cell (> equal use: 80%)	9.75 (33.3%)
80% MCP	10.8 (39.0%)
80% Fixed Kernel with LSCV	10.4 (39.4%)
50% MCP	4.2 (15.2%)
50% Fixed Kernel with LSCV	4.0 (15.2%)
Exclusive use internal polygon	12.0 (43.2%)
Exclusive 75% MCP	6.3 (22.7%)
Exclusive 50% MCP	3.2 (11.6%)

Fig. 2.4. Core areas calculated using different methods. (a) The 75% MCP and kernel core areas, shown with the 100% MCP territory outline. (b) The 50% MCP and kernel core areas, shown with the 100% MCP territory outline. (c) The core area as determined by the 500 m X 500 m quadrats that exceed an equal use pattern. The black quadrats had location counts above the mean and include 80% of scan locations. (d) The 80% MCP, kernel, and grid cell core areas, shown with the 100% MCP territory outline. (e) The polygon formed by connecting the innermost intercommunity encounters represents the area exclusively used by the Ngogo chimpanzees. Shown with the 100% MCP territory outline. (f) The exclusive 75% (solid green polygon) and exclusive 50% (solid blue polygon) core areas, formed from the area of overlap between the exclusive use interior polygon and the 75% and 50% MCP core areas respectively.

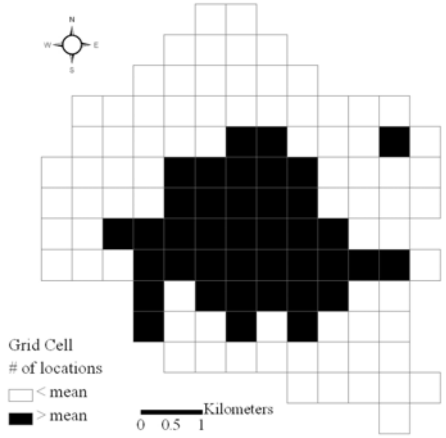
a.


N
W
E
S
100% Minimum Convex Polygon
75% LSCV Fixed Kernel
75% MCP Core Area
Kilometers
0
0.5
1

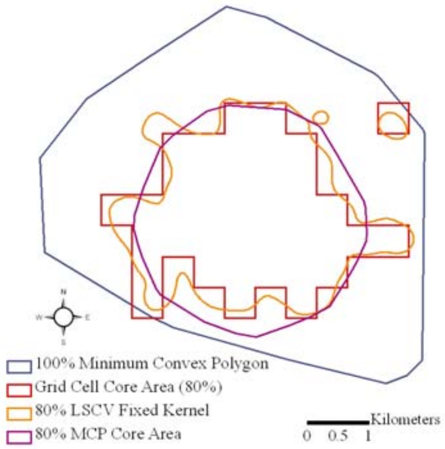
b.


N
W
E
S
100% Minimum Convex Polygon
50% MCP Core Area
50% LSCV Fixed Kernel
Kilometers
0
0.5
1

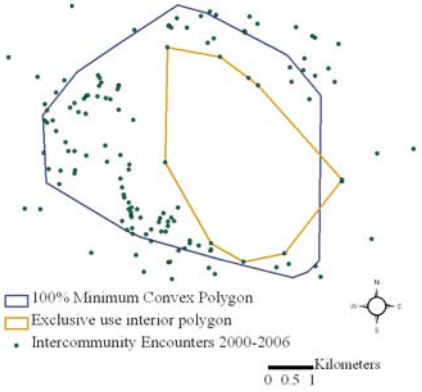
c.


N
W
E
S
Grid Cell
# of locations
< mean
> mean
Kilometers
0
0.5
1

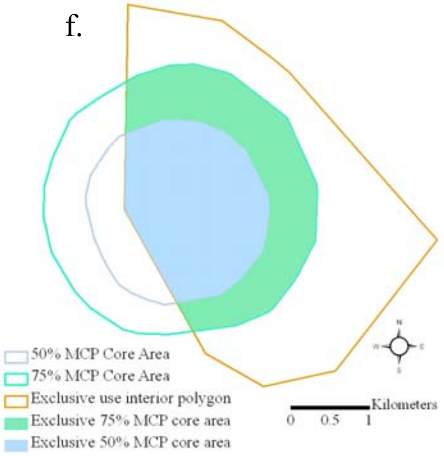
d.


N
W
E
S
100% Minimum Convex Polygon
Grid Cell Core Area (80%)
80% LSCV Fixed Kernel
80% MCP Core Area
Kilometers
0
0.5
1

e.


N
W
E
S
100% Minimum Convex Polygon
Exclusive use interior polygon
Intercommunity Encounters 2000-2006
Kilometers
0
0.5
1

f.


N
W
E
S
50% MCP Core Area
75% MCP Core Area
Exclusive use interior polygon
Exclusive 75% MCP core area
Exclusive 50% MCP core area
Kilometers
0
0.5
1

Comparing Chimpanzee Territory Size Estimates from Different Sites

I reviewed eleven studies, seven of which estimated chimpanzee territory size using polygon methods (MCP or similar) and six of which utilized grid cell methods with quadrat sizes ranging from 200 X 200 meters to 500 X 500 meters. Only one study calculated the territory size using kernel methods, while one used the Fourier estimation method, a statistical method based on the utilization distribution similar to the kernel method (Table 2.5). Most studies compared estimates using more than one method. Polygon estimates of chimpanzee territories ranged from 6 to 38 km^2; grid cell estimates ranged from 8 to 29 km^2; and statistical methods resulted in estimates of 3 to 15 km^2.

Community core areas were estimated in 5/11 studies. The majority (3) used a percentage of the MCP to estimate core area, two studies used only the grid cell method with quadrat sizes of 250 X 250 meters and 500 X 500 meters, and one of the studies that used the MCP also used the statistical Fourier method to estimate core area (Table 2.6). 75% total usage was commonly employed in these studies to define the core area [Boesch and Boesch-Achermann 2000; Herbinger et al. 2001; Lehmann and Boesch 2003]. In an attempt to make the core area biologically relevant, Herbinger et al. [2001] compared 75%, exclusive 75% (the portion of the 75% MCP not used by other communities), 50%, and exclusive 50% core areas. Under the assumption that chimpanzees will only build their night nests in areas where they feel secure, Wilson et al. [2007] defined the core area as the 100% MCP encompassing all nesting locations within park boundaries.

Core areas determined using 75% of locations resulted in estimates ranging from 19 – 38% of the total territory area. Core areas determined using 50% of locations resulted in estimates ranging from 5 – 12% of total area using the MCP, and from 23 -

31% using the Fourier method. Reducing the 75% and 50% MCP core areas to only those exclusively used by the community resulted in much smaller percentages of overall territory: 2 – 14% [Herbinger et al. 2001]. On the other hand, the method of using nesting locations resulted in a core area that was 36% of the total area, in the range of the 75% usage core areas, although it accounted for 85% of observation time [Wilson et al. 2007].

TABLE 2.5. Comparison of territory estimates from 11 studies of chimpanzee ranging patterns, organized by the estimation method employed. Sources: [1]Wilson et al. 2007; [2]Boesch and Boesch-Achermann 2000; [3]Lehmann and Boesch 2003; [4]Newton-Fisher 2003; [5]Herbinger et al. 2001; [6]Williams et al. 2004; [7]Chapman and Wrangham 1993; [8]Basabose 2005; [9]Hasegawa 1990; [10]Mitani and Amsler 2003; [11]Lehmann and Boesch 2005. *When the percentage MCP was not reported in the original source, it was most likely 100%. **The minimum polygon method is essentially the same as the MCP. [§]The restrictive polygon method "peels" away outlying points from the MCP by restricting each polygon side length to no more than the mean of the distances of all points from the polygon center [Todd 1992]. [†]The size of the grid cells is indicated as "Xm" for cells that are X by X meters.

Research Community and Time Period	*Estimation Method*	*Territory area (km^2)*	*Community Size*
	Polygon Methods		
Kibale, Kanyawara 1996-1998[1]	MCP*	37.80	50
Taï, North 1982[2]	MCP	19.50	74
Taï, North 1989[2]	MCP	26.90	66
Taï, North 1992[3]	MCP	26.42	46.5
Taï, North 1993[3]	MCP	17.81	41.5
Taï, North 1994[3]	MCP	21.30	36
Taï, North 1995[2]	MCP	16.50	29
Taï, North 1995[3]	MCP	16.08	32
Taï, North 1996[3]	MCP	17.10	33
Taï, North 1997[3]	MCP	14.95	32
Taï, North 1998[3]	MCP	13.90	31
Taï, North 1999[3]	MCP	18.03	26.5
Taï, North 2000[3]	MCP	20.45	22.5
Taï, North 2001[3]	MCP	21.36	22
Budongo, Sonso 1994-1995[4]	MCP (100%)	6.78	38-46
Taï, Middle 1996-1997[5]	MCP (100%)	12.10	11
Taï, North 1996-1997[5]	MCP (100%)	16.80	35
Taï, South 1996-1997[5]	MCP (100%)	26.50	63

Taï, Middle 1996-1997[5]	MCP (95%)	9.00	11
Taï, North 1996-1997[5]	MCP (95%)	10.50	35
Taï, South 1996-1997[5]	MCP (95%)	13.50	63
Gombe, Kasekela 1975-1992[6]	MCP (99%)	6.00-14.00	32-60
Kibale, Kanyawara 1988-1991[7]	Minimum Polygon**	14.90	41
Taï, Middle 1996-1997[5]	Restrictive Polygon[§]	9.60	11
Taï, North 1982[2]	Restrictive Polygon	18.10	74
Taï, North 1989[2]	Restrictive Polygon	23.70	66
Taï, North 1995[2]	Restrictive Polygon	15.50	29
Taï, North 1996-1997[5]	Restrictive Polygon	14.80	35
Taï, South 1996-1997[5]	Restrictive Polygon	20.60	63
	Grid Cell Methods		
Kibale, Kanyawara 1988-1991[7]	Grid Cell (200m[†]) - used and passed through	8.50	41
Kibale, Kanyawara 1988-1991[7]	Grid Cell (200m) - used only	7.80	41
Kahuzi-Biega, Kaboko 1994-2000[8]	Grid Cell (250m)	12.81	23
Mahale, M Group 1980-1982[9]	Grid Cell (400m)	14.90	not reported
Kibale, Ngogo 1999-2002[10]	Grid Cell (500m)	17.50	150
Taï, Middle 1996-1997[5]	Grid Cell (500m)	13.00	11
Taï, North 1996-1997[5]	Grid Cell (500m)	18.30	35
Taï, North 1997[11]	Grid Cell (500m)	17.50	32
Taï, North 1998[11]	Grid Cell (500m)	17.00	31
Taï, North 1999[11]	Grid Cell (500m)	20.50	26.5
Taï, North 2000[11]	Grid Cell (500m)	22.00	22.5
Taï, North 2001[11]	Grid Cell (500m)	21.00	22
Taï, South 1996-1997[5]	Grid Cell (500m)	23.30	63
Taï, South 2000[11]	Grid Cell (500m)	27.00	50-57
Taï, South 2001[11]	Grid Cell (500m)	29.00	50-57
	Statistical Methods		
Budongo, Sonso 1994-1995[4]	Adaptive Kernel (100%)	14.51	38-46
Budongo, Sonso 1994-1995[4]	Fixed Kernel (100%)	6.89	38-46
Taï, Middle 1996-1997[5]	Fourier (95%)	3.10	11
Taï, North 1996-1997[5]	Fourier (95%)	7.50	35
Taï, South 1996-1997[5]	Fourier (95%)	9.50	63

TABLE 2.6. Comparison of methods used to estimate chimpanzee community core areas and the percent of total territory size represented by each core area estimate. Sources: see Table 2.5 legend. †The size of the grid cells is indicated as "Xm" for cells that are X by X meters.

Research Community and Time Period	*Estimation Method*	*Definition of Core Area*	*% of Territory*
	Polygon Methods		
Taï, Middle 1996-1997[5]	MCP (exclusive 75%)	75% of all locations, reduced to exclusive use area	4
Taï, North 1996-1997[5]	MCP (exclusive 75%)	75% of all locations, reduced to exclusive use area	14
Taï, South 1996-1997[5]	MCP (exclusive 75%)	75% of all locations, reduced to exclusive use area	13
Taï, Middle 1996-1997[5]	MCP (exclusive 50%)	50% of all locations, reduced to exclusive use area	2
Taï, North 1996-1997[5]	MCP (exclusive 50%)	50% of all locations, reduced to exclusive use area	12
Taï, South 1996-1997[5]	MCP (exclusive 50%)	50% of all locations, reduced to exclusive use area	6
Taï, Middle 1996-1997[5]	MCP (75%)	75% of all locations	19
Taï, North 1996-1997[5]	MCP (75%)	75% of all locations	29
Taï, South 1996-1997[5]	MCP (75%)	75% of all locations	20
Taï, North 1982[2]	MCP (75%)	75% of all locations	38
Taï, North 1989[2]	MCP (75%)	75% of all locations	32
Taï, North 1995[2]	MCP (75%)	75% of all locations	35
Taï, Middle 1996-1997[5]	MCP (50%)	50% of all locations	5
Taï, North 1996-1997[5]	MCP (50%)	50% of all locations	12
Taï, South 1996-1997[5]	MCP (50%)	50% of all locations	8
Kibale, Kanyawara 1996-1998[1]	MCP (100%)	all nesting locations within park boundaries	36
	Grid Cell Methods		
Taï, North 1992-2001[3]	Grid Cell (500m†)	75% - the minimum # cells that account for 75% usage	~35
Kahuzi-Biega, Kaboko 1994-2000[8]	Grid Cell (250m)	cells used for 51.7-81.7% of all observation months	5
	Statistical Methods		
Taï, Middle 1996-1997[5]	Fourier (50%)	50% of all locations	23
Taï, North 1996-1997[5]	Fourier (50%)	50% of all locations	31
Taï, South 1996-1997[5]	Fourier (50%)	50% of all locations	24

Comparisons among Sites

Although sampling methods differ among chimpanzee studies, the same territory estimation methods have been used at several different sites. There were too few statistical methods (e.g. kernel) used in the reviewed studies to compare with my results at Ngogo. However, I found MCP and grid cell estimates for multiple chimpanzee sites. Plots of the community size and territory size for multiple sites are shown in Fig. 2.5. To avoid issues of dependence I did not include multiple estimates for the same site, even if they included observations for different time periods. This practice resulted in sample sizes too small for regression analysis. However, the trend lines show that in general as community size increases, territory size also increases. The Ngogo territory size estimated by the MCP falls within the usual range of forest-living chimpanzee territory sizes despite an unusually large community size. Using the grid cell estimate, both territory size and community size at Ngogo are larger than those observed at other chimpanzee research sites, but territory size is much closer to the range of other estimates.

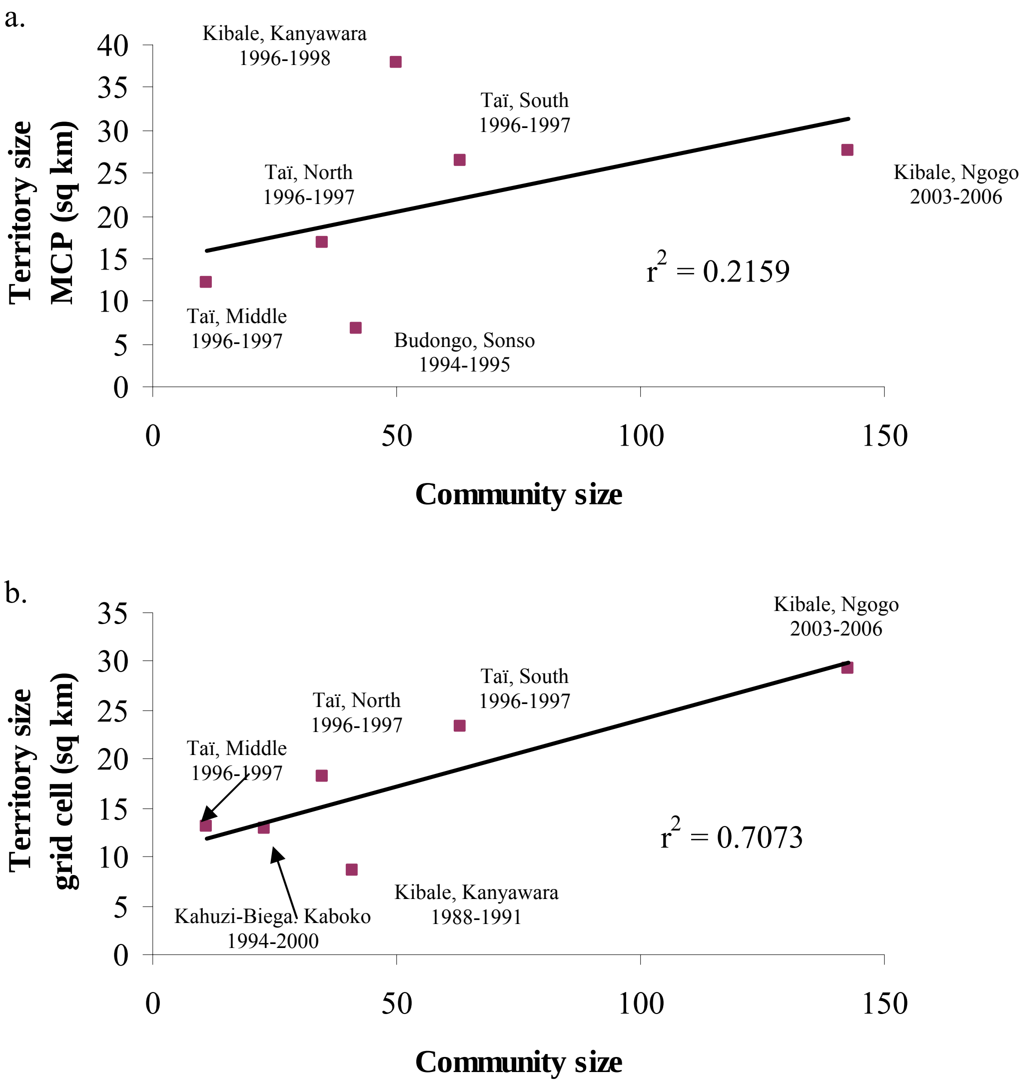


Fig. 2.5. The relationship between community size and territory size across chimpanzee communities. Values are based on the published studies reviewed in Table 2.5 and the data from this chapter. Only one estimate per community is shown for each method to reduce dependence among data points. Trend lines based on regression analysis are shown through the data points. The r^2 value for each trend line is displayed. (a) 100% MCP estimates. (b) grid cell estimates. Sources are listed in Table 2.5.

DISCUSSION

My results demonstrate that with a large and unrestricted sample size, the various territory estimation techniques perform similarly. Minimum convex polygon, grid cell, and fixed kernel territory size estimates for the Ngogo community were similar and showed high overlap. Intensity of use was also represented in a similar way by both the grid cell and kernel methods. Subsampling data to reduce autocorrelation substantially reduced the estimates calculated using nonstatistical methods, while the kernel was more robust to sample size changes. The grid cells that exceeded an equal use pattern represented 80% of the Ngogo territory, suggesting that an 80% core area is a biologically relevant way to quantify the pattern of territory use by Ngogo chimpanzees. A review of recent chimpanzee studies revealed that the MCP and grid cell were the most commonly applied estimation methods, while kernels were rarely used to estimate chimpanzee territories or core areas.

Territory Size Estimation

Obtaining accurate and reliable estimates of territory size is an important goal if such estimates are to be used to better understand the behavior, ecology, and conservation of chimpanzees. The extent to which estimates from different studies can be productively compared has been an open question. Results presented here are encouraging for comparing studies that employ different techniques because they suggest that different methods yield similar results. However, the preceding analyses also indicate that several methodological factors must be considered before comparisons are made. First, a similar percentage of the territory should be calculated. Ninety-five percent kernels are often used and may sometimes be appropriate. For example, occasional forays are often not picked up using this technique, and in situations where these forays are unimportant, this method may prove useful. However, the 95% kernel can result in considerably smaller estimates, and should therefore not be compared with estimates generated by 99-100% kernels.

Another important consideration is the sample of points used to determine territory size. By including locations recorded at short intervals throughout the day, territory estimates computed in this study encompassed nearly all places chimpanzees actually ranged during observations. A concern with autocorrelation has led some researchers, on the other hand, to subsample their data. This practice has its roots in a decades-old discussion in the ranging literature about independence of locations [e.g. Dunn and Gipson 1977; Schoener 1981; Swihart and Slade 1985a; Swihart and Slade 1985b]. Swihart and Slade [1985a; 1985b] pointed out that statistical methods of range estimation, such as kernels, require that locations be independent. They proposed, based on Mitani and Rodman [1979], that the time to independence (TTI) for primates should be based on the time it takes to traverse the territory or home range, resulting in a likely TTI of less than a day for territorial primates, such as chimpanzees, and a TTI of more than 24 hours for non-territorial primates [Swihart and Slade 1985b]. Much of the chimpanzee ranging literature has taken this suggestion to heart, subsampling data in an attempt to achieve independence of locations [Herbinger et al. 2001; Newton-Fisher 2003].

More recently, considerable attention has been devoted to refuting the idea that independence is required. Animal ranging is a non-independent phenomenon, and autocorrelation can be informative [Blundell et al. 2001; Cushman et al. 2005; De Solla et al. 1999]. Studies of several taxa have shown that subsampling available locations changes the distribution of locations. With the loss of biologically relevant information, a misleading representation of range use patterns results [e.g. Cerulean warblers: Barg et al. 2005; river otters: Blundell et al. 2001; African elephants: Cushman et al. 2005; snapping turtles and antler flies: De Solla et al. 1999].

The findings presented here demonstrate that the improvement of estimates with autocorrelated points is largely a matter of sample size. When a study is conducted over a short period, a trade-off exists between sample size and independence of location data points [Hansteen et al. 1997; Seaman et al. 1999]. Subsampling data in the attempt to attain TTI tends to result in an underestimation of range size. In this study, sampling regime had its largest effect on grid cell estimates, with those based on 3 scans per day and 1 scan per day reduced to 90% and 73%, respectively, of the area calculated using the entire sample. The statistical kernel technique was the most resistant to reductions in sample size. The 99% kernels based on 3 scans per day and 1 scan per day represented 97% and 95%, respectively, of the area calculated using the entire sample. Territory estimates in a previous chimpanzee study were similarly affected by sample size. Subsampling locations once per day, from data points recorded every 30 minutes, resulted in a 70% reduction in chimpanzee territory size estimates using nonstatistical methods in the Taï National Park, Côte d'Ivoire [Herbinger et al. 2001]. Thus, when nonstatistical methods are employed, I recommend including locations collected at short time intervals so that the territory estimate covers all areas where chimpanzees range.

Finally, results presented here suggest that territory size estimates for chimpanzees should be based on data collected over a relatively long period of time. Using all three methods, territory size estimates reached an asymptote after approximately 2500 locations, collected across 164 days during 10 months. Territory sizes based on fewer locations underestimated the territory size of Ngogo chimpanzees.

Core Area Estimation

One way to quantify the pattern of space use by animals is to identify a core area, which is the area with the highest probability of use [Samuel et al. 1985]. Here I employed a method based on one used by Samuel et al. [1985] and determined that the grid cells exceeding an equal use pattern contained 80% of all observations. Eighty percent is quite close to the 75% of observations often chosen in chimpanzee studies, and validates the use of a percentage of this magnitude for this species. The 75% core area estimate at Ngogo represented 34% of the total territory area. Depending on method used, the 80% core area represented a slightly larger portion of the territory (39% using the MCP and kernel methods, 33% using grid cells). This means that Ngogo chimpanzees spent 75-80% of their time in about one third of their territory. The 75% core area for chimpanzees at Taï composed a similar or somewhat smaller portion of the overall territory, depending on the study [Boesch and Boesch-Achermann 2000; Herbinger et al. 2001; Lehmann and Boesch 2003].

I also used a biologically meaningful criterion to define the core area by employing a method similar to that used by Herbinger et al. [2001], who calculated an exclusive core area. Here I found that the intersection of the exclusive use area and the 75% MCP core area represented about 23% of the total territory area, more than twice the percent covered by exclusive core areas for communities at Taï [Herbinger et al. 2001]. It is interesting that, though the Ngogo territory is not as large as might be expected for such a large community, the exclusive core area covered a larger portion of the territory than a similarly defined area at Taï. One of the reasons that a large community can be supported on a smaller territory may be that it has exclusive control over a larger portion of that territory.

I did not define the core area based on the area where Ngogo chimpanzees built night nests, as Wilson et al. [2007] did. Chimpanzees at Ngogo, particularly when in large parties, do not show an avoidance of peripheral areas at the end of the day [see chapter 3, this dissertation].

The core area was offset to the southwest of the area of exclusive use. The lack of alignment means that Ngogo chimpanzees spent more time in the overlap zone in the southwest portion of their territory than they did in other areas that were not shared with neighbors. This space use pattern may set the Ngogo chimpanzees up for conflict with neighbors to the southwest. In fact, patrols by the Ngogo chimpanzees are clustered in this southwest border region that is used frequently but not exclusively [see chapter 5, this dissertation]. It seems likely that such areas are particularly resource rich, making them worth fighting for. On the other hand, the exclusive core area represents an important portion of the territory to the Ngogo chimps, as they used that area heavily while remaining safe from intercommunity encounters.

As GPS and GIS technology permit researchers to pinpoint chimpanzee observations on a map, our ability to use these locations to compare ranging among communities is also improving. This study explored methodological issues related to estimating chimpanzee territories and core areas, compiled recent territory and core area estimates made for chimpanzee communities, and suggested ways to improve comparability among studies.

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CHAPTER 3

Ranging Patterns of the Ngogo Community

ABSTRACT

Chimpanzee territories vary widely in size. Two factors hypothesized to influence territory size are food availability and intercommunity relations. I assessed the effects of fruit availability and encounters with neighboring communities on the monthly territory size of chimpanzees at Ngogo, Kibale National Park, Uganda. I also examined the extent to which territory use patterns were constrained by neighbors. I found little evidence that ranging was affected by either the food supply or relations with neighboring communities. Monthly territory size was larger when the fruit supply was good, but not significantly so. Neither territory size nor patterns of use suggested that the Ngogo chimpanzees' ranging was significantly constrained by neighboring communities. Some of these results are consistent with research on other chimpanzee communities. However, a consistently high fruit supply at Ngogo may ease the pressure to adjust territory size to fluctuations in the food supply while the unusually large size of the Ngogo community may decrease their vulnerability in intercommunity interactions.

INTRODUCTION

The home range represents the area habitually traversed by an individual or group of animals during normal daily activities such as feeding, resting, and reproductive behavior [Burt 1943]. When this range is defended against conspecifics it is referred as a territory [Burt 1943; Noble 1939]. Quantification of this area enables a better understanding of animals' space and habitat use. Several factors, including body size, group size, food availability, and intergroup relationships have been hypothesized to influence variation in home range or territory size.

Range size is primarily determined by metabolic requirements [McNab 1963]. Because body weight influences energy expenditure, which in turn affects the amount of food an animal must ingest, body weight shows a strong association with range size in mammals [Harestad and Bunnell 1979; Leonard and Robertson 2000; McNab 1963; Milton and May 1976; Swihart et al. 1988]. For social species, group size also contributes to range size [Clutton-Brock and Harvey 1977; Dias and Strier 2003; Dunbar 1988; Milton and May 1976]. Increased feeding competition is a well-known cost of group-life, and social mammals must range over a larger area than that needed by a solitary individual to satisfy their energetic requirements [red colobus monkeys: Gillespie and Chapman 2001; primates and carnivores: Wrangham et al. 1993].

In addition to body size and group size, two primary hypotheses have been proposed to explain variation in home range size. The first of these involves the available food supply. Resource availability should affect how far individuals must range to obtain sufficient food. Modeling by South [1999] suggests that a decrease in food density should increase the range area of individual foragers. However, empirical results are mixed as to the effects of food availability on range size. In a review of territorial species, Adams [2001] reports that while the majority of studies demonstrate the predicted negative correlation, fully 35% fail to find a relationship between food abundance and territory size.

Intergroup relations are also hypothesized to affect variation in range size and shape. In territorial species, neighbors apply pressure on one another, and boundaries between adjacent residents emerge as a result of disparities in competitive ability as well as movement patterns of individuals in each group [Adams 2001]. In general, power asymmetries resulting from relative group size also mean that larger groups can defend larger territories [e.g. social insects, cooperatively breeding birds, and social mammals; review in Adams 2001].

Chimpanzees furnish a model system to investigate the factors that contribute to variation in range size. Chimpanzees are a territorial primate species in which parties of males defend the community range against members of other communities. Many studies have addressed ranging in chimpanzees, revealing considerable variation in chimpanzee territory size and ranging patterns [e.g. Baldwin et al. 1982; Basabose 2005; Chapman and Wrangham 1993; Doran 1997; Emery Thompson et al. 2007; Herbinger et al. 2001; Lehmann and Boesch 2003; Lehmann and Boesch 2005; Mitani and Amsler 2003; Murray et al. 2008; Newton-Fisher 2000; Newton-Fisher 2001; Newton-Fisher 2003; Williams et al. 2004; Wilson et al. 2007; Wrangham et al. 2007]. As is true of mammals in general, body size in primates is a good predictor of range size [Leonard and Robertson 2000; Milton and May 1976]. The group size hypothesis has also been investigated for chimpanzees and other primates. However, variation in community size does not always predict variation in territory size [chimpanzees: Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2003; vervet monkeys: Struhsaker 1967], suggesting that other factors, such as food availability and intercommunity relations, may play a role.

The food availability hypothesis has received mixed support when tested in chimpanzees and other primates. As frugivores, chimpanzees rely primarily on sugar-rich fruits, the availability of which varies in time and space [Wrangham et al. 1996; Wrangham et al. 1998]. As a result, the food supply may vary among sites as well as seasonally at any one site [Chapman et al. 1995; Wrangham et al. 1998]. The responses of frugivorous primates to changes in habitat quality vary. In some cases primates range over greater areas when food is scarce [chimpanzees: Basabose 2005; Yamagiwa 1999; red colobus monkeys: Gillespie and Chapman 2001; guenons: Kaplin 2001; vervet monkeys: Struhsaker 1967], while other studies have found that primate ranges do not increase, or even decrease, when fruit is less abundant [woolly monkeys: Di Fiore 2003; gibbons: Raemaekers 1980; gorillas: Yamagiwa 1999].

Studies in the Taï National Park, Côte d'Ivoire have found that chimpanzees reduced their day range size during rainy seasons, which may be associated with food scarcity [Doran 1997; Herbinger et al. 2001]. In contrast, when fruit abundance was quantified at the same site based on phenological observations, basal area, and density, it did not significantly correlate with chimpanzee territory size [Lehmann and Boesch 2003]. The ranging response to food scarcity may also vary as animals have multiple mechanisms for coping with changes in habitat quality. In another example, Kaplin [2001] found that frugivorous blue monkeys faced with low fruit availability either increased their dietary diversity, thereby increasing their range size, or decreased dietary diversity, which resulted in a more concentrated pattern of space use. Zhang [1995] reports that capuchins reduced their range size in response to both fruit scarcity and abundance, with the widest ranging occurring during average fruit availability. For chimpanzees, both unusually large and unusually small territory sizes have been attributed to high fruit availability [Herbinger et al. 2001; Newton-Fisher 2003].

Some of the contradictory results arising from these analyses stem from the fact that few chimpanzee studies have adequately quantified resource density or distribution to examine the association between food supply and territory size. Though quantification of food availability has been undertaken recently [e.g. at Taï: Anderson et al. 2002; Lehmann and Boesch 2003], further research is clearly needed to test the hypothesis that resource availability, critical to energetic requirements of chimpanzees, affects territory size.

Intercommunity relations are also hypothesized to influence variation in chimpanzee territory size. Chimpanzees living in larger territories benefit through access to additional resources [Williams et al. 2004]. To this end, parties of chimpanzees routinely patrol territory boundaries and make incursions into the territories of neighbors. Intercommunity interactions among chimpanzees are typically hostile and can result in injury or death [Wilson and Wrangham 2003]. Such interactions with neighboring communities therefore likely constrain the territory size that a chimpanzee community can defend.

The intercommunity relations hypothesis predicts that intruder pressure should negatively affect territory size. Goodall [1986] reported that the Kasakela community territory in the Gombe National Park, Tanzania shrunk as invasions from the south began in 1979. Later the territory expanded to the north and south as more Kasakela males participated in border patrols. Similarly in the Mahale Mountains National Park, Tanzania, the smaller K group avoided use of the overlap zone whenever the larger M group began using seasonally available resources there [Nishida and Kawanaka 1972]. Intruder pressure can be measured by intercommunity encounter rates. At Taï, intercommunity encounter rates account for some of the variation in territory size [Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2003].

If intercommunity interactions influence territory size, larger community size is predicted to confer an advantage. Although variation in chimpanzee community size does not always predict territory size [Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2003], results are currently mixed concerning whether the absolute number of males in a community affects territory size. Because males are the primary participants in chimpanzee territorial activities, the number of males is a measurable proxy for the fighting strength of a community relative to its neighbors and a better measure than overall community size. Studies at both Gombe and Taï have suggested that the number of adult males predicts territory size [Boesch and Boesch-Achermann 2000; Goodall 1986; Lehmann and Boesch 2003], however a subsequent analysis of data from Gombe revealed no such relationship [Williams et al. 2004].

Predictions about the pattern of space use also follow from the intercommunity relations hypothesis. Animals may use their territory in a concentrated, even, or random fashion. A concentrated pattern of use is often quantified by determining a core area, the area with the highest probability of use [Samuel et al. 1985]. If chimpanzee ranging is constrained by pressure from neighboring communities, a concentrated pattern of use is predicted, with a centrally-located core area at a distance from territory borders or other areas where neighbors are commonly encountered. Studies at Taï suggest a clumped range use pattern in which the core area is concentrated in the center of the territory and remains stable over time, even as territory and group size shift [Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2003]. If such a core area exists, the intercommunity relations hypothesis additionally predicts that, though chimpanzees may range into the periphery of the territory during the day, by the end of the day they will return to the core area, where they are more secure from detection and attack by neighbors [Wilson et al. 2007].

In this paper, I investigate the factors influencing variation in chimpanzee territory size by testing the food availability and intercommunity relations hypotheses using data from an unusually large community of chimpanzees at Ngogo, Kibale National Park, Uganda. Specifically, I test a critical prediction of the food availability hypothesis that monthly community territory size is related to measures of resource availability. Furthermore, I test five predictions derived from the intercommunity relations hypothesis: 1) monthly home range size will change with the intercommunity encounter rate; 2) the size and strength of a community is related to its territory size; 3) the pattern of territory use will be centered with a clearly defined core area some distance from borders with other communities; 4) the core area of the territory will be located primarily in the area where Ngogo chimpanzees do not encounter neighbors; and 5) peripheral areas will be used during the middle of the day, but individuals will return to the core area to make night nests.

METHODS

Study Site and Animals

I observed chimpanzees at the Ngogo study site in the Kibale National Park, Uganda. This site is covered primarily by tall, moist evergreen forest, with areas of swamp, grassland, woodland thicket, and colonizing forest. Struhsaker [1997] provides a detailed description of the site.

Ngogo has been the site of behavioral research on several primate species [review in Struhsaker 1997], and chimpanzees there have been observed continuously since 1995 [Mitani 2006; Mitani et al. 2000; Mitani et al. 2002b; Mitani et al. 2002c; Watts et al. 2006]. As a result of prior research, the chimpanzees of Ngogo are habituated to and individually identifiable by human observers. The Ngogo chimpanzee community is the largest that has been described in the wild [Mitani 2006; Mitani and Amsler 2003; Watts 2002; Watts 2004; Watts and Mitani 2000; Watts and Mitani 2001; Watts et al. 2006]. Community size ranged from approximately 140 to 150 individuals during the period considered here, including 40-45 adult females, 5-15 adolescent females, 26-29 adult males, and 12-21 adolescent males.

The Ngogo study area is well established with more than 230 km of trails covering the ~30 km^2 study area. I used a handheld GPS to map the entire trail system, which facilitated plotting the locations of chimpanzees.

Behavioral Observations

Observations were collected during 19 months over 4 field seasons: June – August 2003, July – November 2004, February – June 2005, and September 2005 – February 2006.

Chimpanzees exhibit fission-fusion social organization, in which temporary parties of variable size and composition join and dissolve throughout the day [Nishida 1968]. I defined parties according to the 50 m chain rule, including individuals within 50 m of at least one other chimpanzee [Smolker et al. 1992]. I recorded party membership during scans made at 30-minute sample intervals, every hour and half-hour throughout observations.

In addition to party membership, I also recorded the location of the party during scans. I attempted to record the location of the center of the party. However, this was not always possible because, for other research questions, I was often following target individuals within the party. Thus, the recorded location during focal individual follows reflects where that individual was observed. Because I selected focal subjects by giving priority to those individuals who had been sampled less recently, most adult males in the community are represented in each month's data. I took geographic coordinates with a Magellan 315 GPS receiver. When the unit could not track enough satellites to obtain a fix, I estimated the direction and distance in meters from known locations or previous GPS readings.

I also recorded *ad libitum* all auditory and visual encounters with members of other communities. Because I predicted that intruder pressure would affect the ranging patterns of the Ngogo chimpanzees, I considered here only those intercommunity encounters that occurred when the Ngogo chimpanzees were not actively patrolling themselves.

Fruit Availability

To assay the availability of fruit, field assistants collected phenological data each month on a sample of 20 individuals of the top 20 fruit tree species in the diet of Ngogo chimpanzees [Mitani and Watts 2005; Mitani et al. 2002a]. Diameter at breast height (dbh) was used to estimate average tree sizes. For 15 tree species, dbh was measured on the 20 trees included in the phenological sample plus an additional 10 randomly selected individuals. For the remaining 5 tree species, a sufficient number of individuals could not be located, and dbh samples ranged from 22 to 28 trees. The densities of tree species were recorded in 263 5 X 50 m plots placed randomly throughout the territory [Mitani and Watts 2005; Mitani et al. 2002a]. Phenological observations were made between the sixth and tenth days of calendar months. At this time, field assistants noted the presence or absence of ripe fruit.

The phenology, density, and size of trees were combined to compute the following composite index:

$$\sum_{i=1}^{20} = p_i \cdot d_i \cdot s_i;$$

where p_i is the percentage of the *i*th tree species possessing ripe fruit; d_i is the density of the *i*th tree species (trees/hectare), and s_i is the mean size of the *i*th species (cm dbh) [cf.

Anderson et al. 2002; Mitani and Watts 2005; Mitani et al. 2002a]. A higher score indicates more available fruit than a lower score.

Territory Size and Core Area

I plotted the locations of parties at all half-hour scans to estimate the territory size and core area used by the Ngogo chimpanzees between 2003 and 2006. Days on which chimpanzees conducted territorial boundary patrols were excluded from territory size estimates because they were likely to include locations outside the area typically used. Locations included data from 4459 scans collected on 251 observation days. Territory size can be estimated using a variety of methods, which can result in widely disparate estimates [Chapter 2 of this dissertation; Barg et al. 2005; Herbinger et al. 2001; Jennrich and Turner 1969; Moorcraft and Lewis 2006; Nilsen et al. 2008; Schoener 1981]. For the purposes of these analyses, I estimated territory size three ways using 500 m X 500 m grid cells [Siniff and Tester 1965], the 100% minimum convex polygon (MCP) method [Mohr 1947], and 99% fixed kernels [Worton 1989].

I estimated monthly territory size using spatial data centered on the period of phenological data collection, from the 22nd of the previous month through the 21st of the month. For example, I estimated the March 2005 territory size using the scan locations of chimpanzees between February 22 and March 21, 2005. I chose to use the grid cell method for analyses requiring monthly territory size, because the territory estimates were least likely to include lacunas, or areas that were not used by chimpanzees that month. For the grid cell method, I plotted all scan locations where chimpanzees were observed in a given month, totaled the number of 500 X 500 m grid cells that contained those points, and calculated the summed area of those cells. Because I was interested in the cells actually used during the month, I did not include those that chimpanzees would have had to travel through to access utilized cells. The kernel and MCP methods, used over the short time span of a month, tended to result in larger monthly estimates than the grid cell method, because they include unused areas that connect disjointed areas of use. To ensure that territory estimation method did not affect the results, I conducted all analyses using monthly territory sizes calculated from all 3 methods separately. Because results did not differ, I report here only those using the grid cell method. The number of observation days varied from month to month, and I computed corrected territory sizes by dividing by the number of observation days.

The core area of a territory has typically been defined in previous studies of chimpanzees as the area accounting for 50, 75, or 80% of total usage frequency [Herbinger et al. 2001; Lehmann and Boesch 2003; Williams et al. 2002; Wrangham 1979]. Alternatively, the core area can be defined to include those portions of the territory that "exceed an equal-use pattern" [Samuel et al. 1985]. Like territories, core areas can be estimated using the MCP, fixed kernel, or grid cell methods. Using the grid cell method and the 4459 scans of locations, I determined that 80% of grid cells were used more often than the average; that is, 80% of territory grid cells exceeded an equal use pattern. This result confirmed that core areas that include 80% of observations are biologically relevant for Ngogo chimpanzees. Because other recent chimpanzee studies have considered the community core area to be the area where community members spend 75% of their time [Boesch and Boesch-Achermann 2000; Herbinger et al. 2001; Lehmann and Boesch 2003], and 75% is very similar to the 80% that is biologically relevant, I calculated 75%

core areas using both the fixed kernel and MCP methods. Core areas estimated using the different methods resulted in very similar core area size estimates (75% MCP: 9.3 km^2; 75% fixed kernel: 8.9 km^2; 80% grid cell: 9.75 km^2). Core area estimates also overlapped considerably: the area of overlap within pairs of estimates represented 70-80% of the area of either one of them.

In the following analyses, I delineated the Ngogo chimpanzees' core area using the 75% MCP of all scans of locations. The 100% MCP represents the territory as the smallest polygon containing *all* locations where animals were observed, with all internal angles less than 180 degrees [Worton 1987]. To generate a 75% polygon, I used the floating arithmetic mean method to choose a subset of all scans of locations. This method drops locations sequentially by calculating the arithmetic mean of all points, dropping the farthest point, recalculating the mean, dropping another point, and so on, until 75% of the original set of locations remains [Rodgers and Carr 1998]. I used the Home Range Extension in ArcView 3.3 to calculate percentage MCPs [Rodgers and Carr 1998].

Analyses

To test the hypothesis that the community territory size is related to measures of resource availability, I compared territory size estimates with fruit availability indices for each month. To investigate whether neighboring communities constrain ranging patterns, I compared territory size estimates with intercommunity encounter rates for each month. The intercommunity encounter rate was calculated as the number of encounters divided by the number of observation days in each month. Only encounters that did not occur as a result of a patrol were included. I used the nonparametric Spearman's rank correlation to evaluate the strength of the relationship between monthly fruit availability score and territory size as well as between monthly intercommunity encounter rate and territory size.

To further tease apart the relative contributions of fruit availability and intercommunity encounters to variation in territory size, I performed a nested linear regression. The dependent variable was monthly territory size, and the predictor variables were average monthly party size, monthly resource availability, and monthly intercommunity encounter rate. Party size was included in the model as a potential confound because it may be related to the other variables. Fruit availability may be positively related to party size [Boesch 1996; Doran 1997; Matsumoto-Oda et al. 1998; Mitani and Watts 2005; Mitani et al. 2002a], and party size may also affect the likelihood of intercommunity encounters, as larger parties are more likely to range close to territory boundaries where the opportunity to encounter neighbors is higher [Wilson et al. 2007]. I log transformed the values of fruit availability to achieve a normal distribution.

The current study lacked sufficient time depth to include changes in community size and composition. I was therefore unable to directly address the prediction that increases in the community size or adult male numbers result in larger territory size at Ngogo. However, in an indirect test, I compared the relationship between community strength and territory size at Ngogo with those of other chimpanzee communities. Using a review of chimpanzee research from Chapter 2 of this dissertation, I plotted the relationship between community size and territory size for multiple chimpanzee communities. I also plotted the relationship between the number of adult males, a measure of community strength, and territory size for these same communities. The territory size of some communities has been estimated in multiple studies at different times. To allay concerns about potentially dependent data points in this review, I created additional scatterplots for both community size and male numbers using only one estimate per community. I used Microsoft Excel 2003 (v. 11) regression analysis to draw trend lines through the data points.

To test the prediction that the portion of territory used most often by the Ngogo chimpanzees is centrally located at some distance from territory borders, I determined the distance between the centroid of the 75% MCP core area and the centroid of the 100% MCP territory. The centroid of a polygon is its geographical center. If the centroid of the 75% core area and the centroid of the 100% MCP territory were perfectly aligned, then the 75% core area would be absolutely centrally-located.

To generate a test statistic, I superimposed a grid of points, spaced at 100 m intervals, over the study area. I then moved a polygon the shape and size of the 75% core area around the grid so that its centroid fell at every point in this grid. This process resulted in 356 polygons located entirely within the 100% MCP territory borders and represents the 356 possible locations of a core area of that shape and size based on the 100 m X 100 m grid (Fig. 3.1). I calculated the distance between the centroid of each polygon and the centroid of the 100% MCP, which generated a distribution of possible centroid distances. The proportion of these distances that was higher than that of the actual 75% core area centroid represents the p-value.

I tested in a similar manner the prediction that the core area of the territory will be located primarily in the area where Ngogo chimpanzees do not encounter neighbors. Here I examined the overlap of the 75% MCP core area with the area of exclusive use. To determine the area of exclusive use I recorded *ad libitum* the locations of all aural and visual encounters Ngogo chimpanzees had with members of other communities. These intercommunity encounters provide a way to assess areas where the Ngogo territory may intersect with the territories of neighbors. I used the innermost intercommunity encounters to form the “maximum internal convex polygon.” I connected the internal intercommunity encounter locations into the largest polygon possible such that all external angles measured at least 180 degrees (Fig. 3.1). This area, inside of which the Ngogo chimpanzees never encountered strangers, represented the area of exclusive use. I then calculated the area of overlap between this area of exclusive use and each of the 356 polygons that represent the possible core area locations within the 100 m X 100 m grid. By this process I generated a distribution of possible overlap values for a core area the size and shape of the 75% core area. Higher overlap values represent core area locations that overlap most with the area where Ngogo chimpanzees do not encounter neighbors. The p-value is the proportion of overlap values that fall below the observed overlap between the actual core area and the exclusive use area.

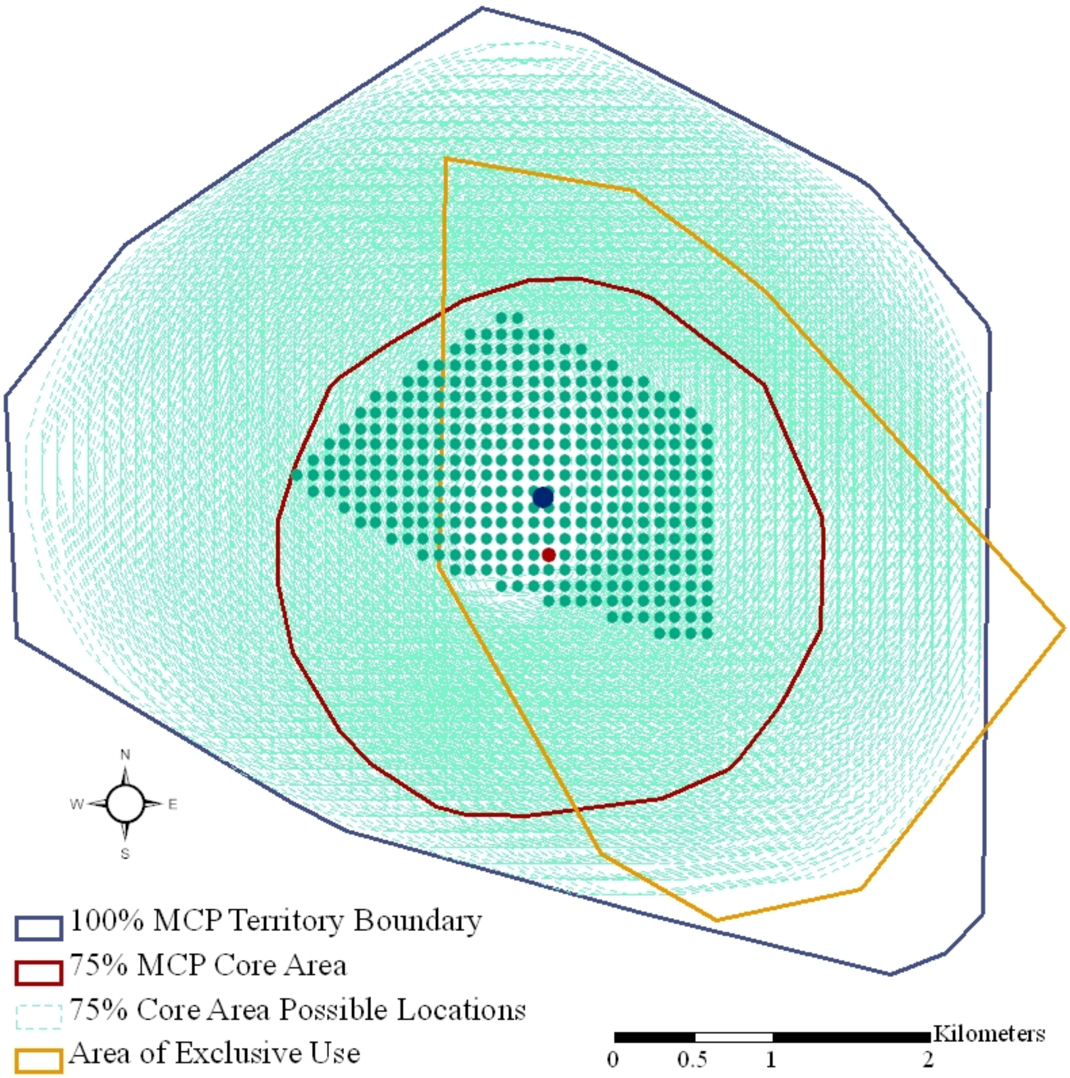


Fig. 3.1. Map of possible locations for a core area the size and shape of the actual 75% MCP core area (in red). Possible core areas were located by moving the core area polygon over a grid of centroids spaced at 100 meter intervals within the Ngogo territory border (in blue). Borders of possible core areas are displayed with green dotted lines. Centroids of polygons are displayed in the same color as their outlines. The area of exclusive use is outlined with yellow.

To test the prediction that chimpanzees range near territory boundaries in the middle of the day, but return to the core area at night, I plotted the locations of chimpanzee parties at 1300 hours for every day of observation (n = 266). I also plotted the location of the last scan of the day for all observation days that lasted until at least

1730 hours (n = 184). I identified each location as being either in the core area, as defined by the 75% MCP, or the periphery, all locations outside the 75% MCP. I performed the G-test of independence [Sokal and Rohlf 1995] to determine whether mid-day and end-day locations showed a different frequency of core versus peripheral area use by chimpanzees. The G-test was implemented using Proc Freq for a chi square test in SAS [McDonald 2007].

All statistical tests were performed using SAS release 9.1.3.

RESULTS

Monthly territory size averaged 9.3 km^2 using the grid cell method (SD = 3.6, range = 4.5 – 14.8, n = 17 months), 10.6 km^2 using the 100% MCP (SD = 5.2, range = 3 – 19.1, n = 17 months), and 12.1 km^2 using the 99% volume contour lines of the kernel (SD = 5.4, range = 4.5 – 21, n = 17 months). The estimates resulting from different methods were highly correlated (Intra-class correlation = 0.91), but nonetheless the mean values differed significantly by method (F = 17.22, $p < 0.0001$), and post-hoc tests also showed that mean territory size was significantly different between each pair of methods (Tukey-Kramer multiple comparison procedure, $p \leq 0.01$ for all three pairs).

Because the number of observation days varied by month, I divided these monthly estimates by the number of days observed each month to ensure that territory size estimates were comparable among months. I observed chimpanzees an average of 14.4 days per month (SD = 4.7, range = 7 – 22, n = 17 months), which excluded those days on which territorial boundary patrols took place. The corrected estimates, representing territory size in the following results, were also highly correlated (Intra-class correlation

= 0.85), though the mean values differed significantly by method in the overall test ($F = 14.83$, $p < 0.0001$). However, post-hoc tests comparing the mean territory size between each pair of methods, indicated that the 99% kernel produced a significantly different estimate than both the MCP and grid cell (Tukey-Kramer multiple comparison procedure, $p = 0.01$ and $p < 0.0001$ respectively), but that the MCP and grid cell did not yield significantly different monthly mean territory size estimates from one another ($p = 0.067$).

Effects of Food Supply and Intruder Pressure on Territory Size

In contrast to the expectation of the food availability hypothesis, there was no significant relationship between monthly fruit availability scores and territory sizes, regardless of the territory estimation method employed. I found a non-significant positive relationship (grid cell method: $\rho = 0.36$; $p = 0.16$; Fig. 3.2a).

If neighboring communities constrain ranging patterns, intruder pressure as assayed by intercommunity encounter rates should predict territory size. However, no relationship exists between these two variables regardless of territory size estimation method (grid cell method: $\rho = 0.003$; $p = 0.99$; Fig. 3.2b).

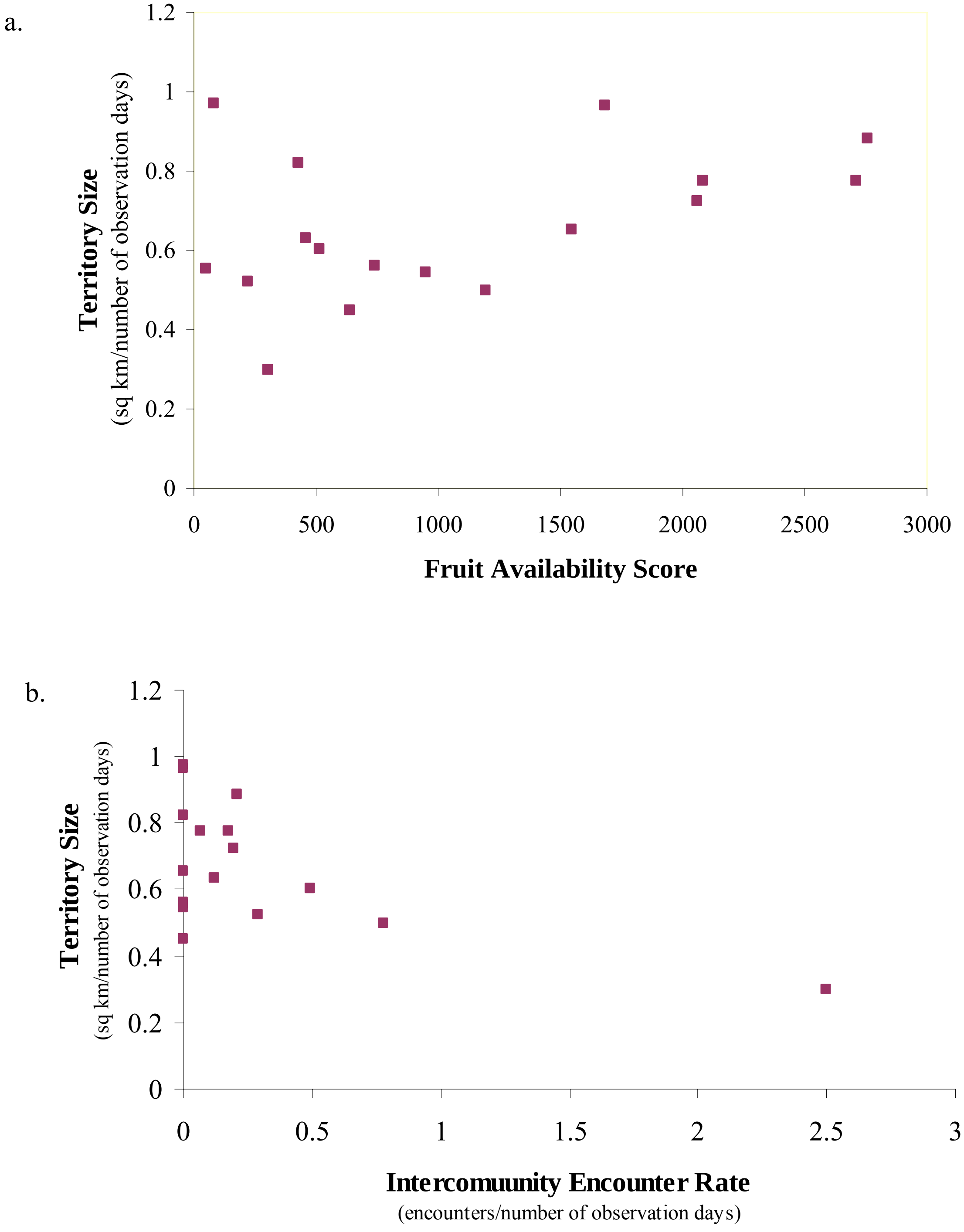


Fig. 3.2. Relationships between monthly territory size and (a) fruit availability and (b) intercommunity encounter rate. Territory size was estimated using the grid cell method and corrected for the number of observation days in the month (n = 17 months).

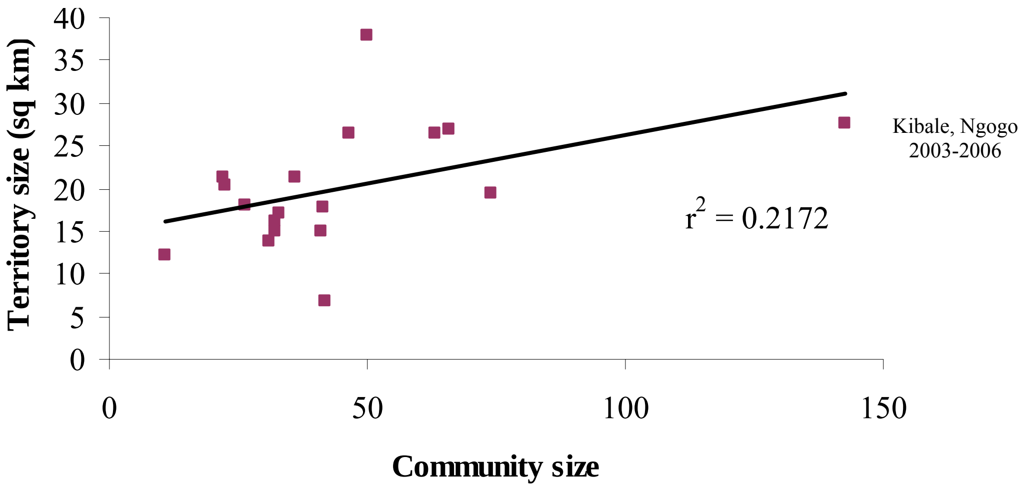
The regression analysis shows that, although the overall model is not significant ($r^2 = 0.18$), some of the variation in territory size was explained. Because party size is a potentially confounding variable, this was entered with the first variable of interest, fruit availability, in the initial model of the nested regression. These two variables accounted for 16% of the variation in territory size ($r^2 = 0.16$). When I added the other variable of interest, intercommunity encounter rate, in Model II, only an additional 2% of the variance in territory size was explained (Table 3.1). The small sample size (n = 17 months) may account for the non-significant result. A power analysis showed that the sample size of 17 months provided only 9% power, and 324 months would be required to achieve 80% power. Thus, though this model explained relatively little of the variation in territory size, considering the small sample size, it is nonetheless interesting that some of the variation was explained.

TABLE 3.1. Results of nested regression. ß = parameter estimate, SE = standard error, ICE = intercommunity encounter rate, FAI = fruit availability index.

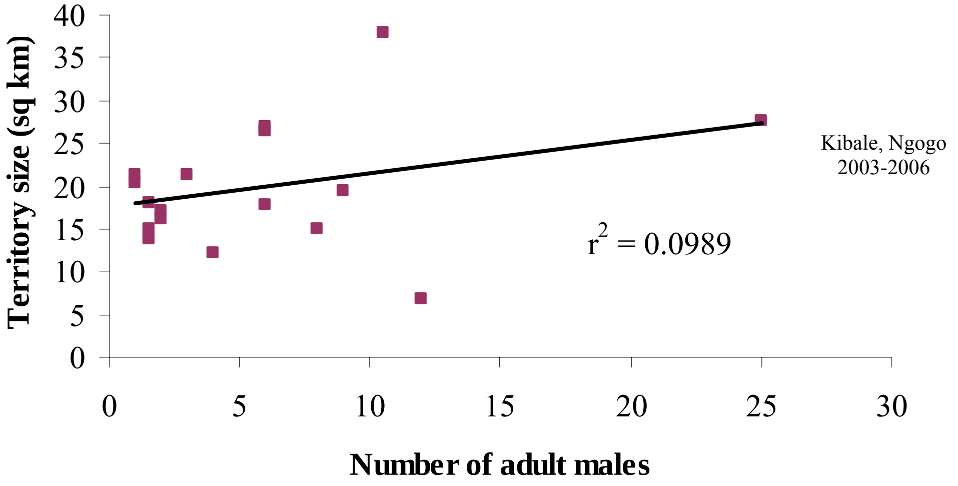
	ß	SE	p	r^2	Δr^2
Model I				16%	
Party Size	0.017	0.012	0.17		
logFAI	-0.05	0.041	0.23		
Model II				18%	2%
Party Size	0.019	0.012	0.16		
ICE rate	0.410	0.750	0.60		
logFAI	-0.057	0.043	0.21		

Stronger communities are expected to outcompete weaker ones. The size of a community and its number of males have been used as proxies for community strength [Boesch and Boesch-Achermann 2000; Goodall 1986; Lehmann and Boesch 2003; Williams et al. 2004]. An intercommunity comparison reveals that, while Ngogo is an unusually large community, with 140-150 members and more than 20 adult males, its territory size falls within the usual range of forest-living chimpanzee communities. In a review of published ranging research from other chimpanzee sites, community size elsewhere was considerably smaller than at Ngogo, ranging from 11-74, with no more than 12 adult males [chapter 2 of this dissertation]. The territory size estimates for these communities, assessed using similar methods to those in this study, ranged from 3 – 38 km^2. Depending on the territory estimation method, the Ngogo chimpanzees' territory is between 19.5 and 29.25 km^2 [chapter 2 of this dissertation], near the upper end of, but within, the range of other communities despite a community size twice as large as the next largest reviewed (Fig. 3.3). This data set includes more than one estimate for some sites (Taï, North and Kibale, Kanyawara), assessed in different studies at different times. However, even when the data set is reduced to include only one estimate per community, the trend lines demonstrate the same thing: Ngogo's territory size is not nearly as big as it would be if either community size or male numbers predicted territory size across sites.

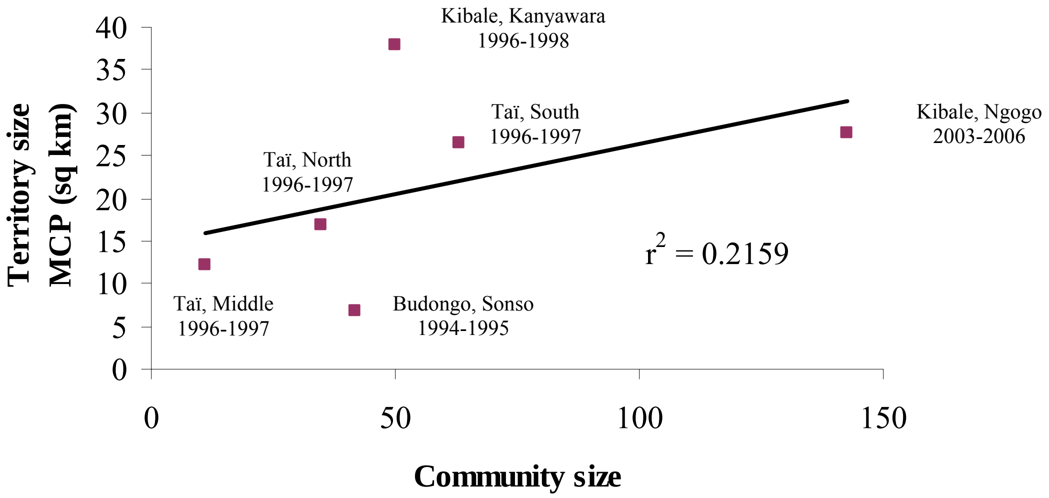
a.


Territory size (sq km)
40
35
30
25
20
15
10
5
0
0
50
100
150
Community size
Kibale, Ngogo
2003-2006
$r^2 = 0.2172$

b.


Territory size (sq km)
40
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
Number of adult males
Kibale, Ngogo
2003-2006
$r^2 = 0.0989$

c.



d.

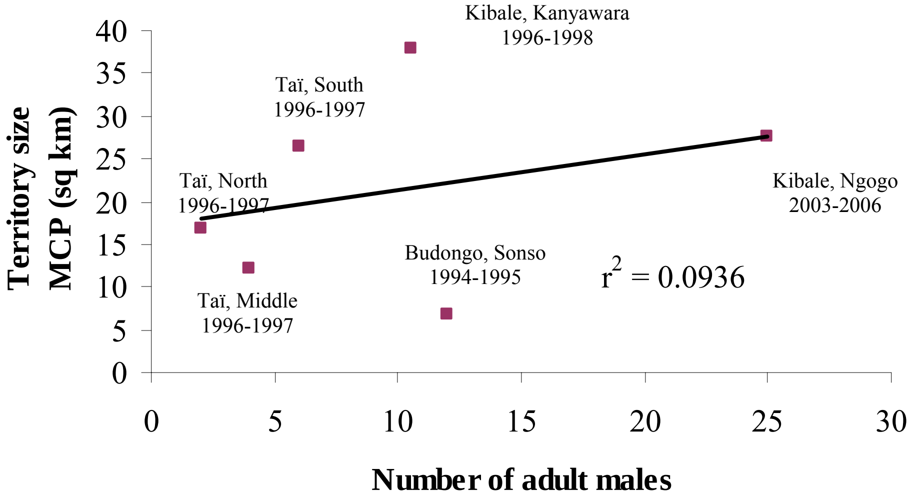
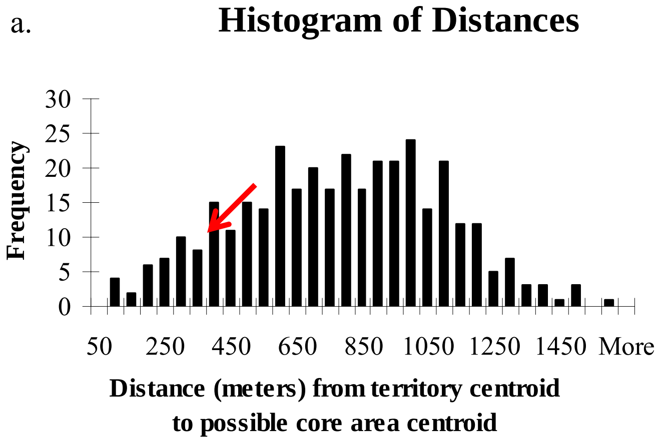


Fig. 3.3. The relationship between community size/strength and territory size across chimpanzee communities. Values are based on published studies. For comparability across sites, only 100% MCP estimates are included. Trend lines based on regression analysis are shown through the data points. The r^2 value for each trend line is displayed. (a) Community size and territory size. (b) Number of adult males and territory size. (c) A smaller sample of community size and territory size. Only one estimate per community is included. (d) A smaller sample of adult male numbers and territory size. Only one estimate is included per community. Sources in (c) and (d): Ngogo: chapter 2 of this dissertation; Kanyawara: Wilson et al. 2007; Sonso: Newton-Fisher 2003; Taï: Herbinger et al. 2001. Additional sources in (a) and (b): Taï, North 1992, 1993, 1994, 1995, 1996, 1997, 1998, 1999, 2000, 2001: Lehmann and Boesch 2003; Taï, North 1982, 1989: Boesch and Boesch-Achermann 2000; Kanyawara 1988-1991: Chapman and Wrangham 1993.

The core area should be located in the center of the territory and overlap extensively with the exclusive use area if ranging is constrained by the activities of neighbors. In contrast to these expectations, the area used by the Ngogo chimpanzees during 75% of observation time was not significantly central nor did it overlap significantly with the area of exclusive use when compared to a distribution of possible core area locations. The core area centroid was located 356 m south of the territory centroid (Fig. 3.1). In the distribution of distances from 356 possible core area centroids to the territory centroid, 11% of possible core area centroids were closer than 356 m to the territory centroid, while 89% were further (Fig. 3.4). While the trend is in the predicted direction, with the core area closer to being centered than not, the difference does not achieve statistical significance ($p = 0.11$). The area of overlap between the core area and the exclusive use area was 6.3 km^2. This value falls roughly in the middle of the distribution of 356 possible overlaps, with 46% having higher overlap values than the actual core area and 54% having lower values ($p = 0.46$; Fig. 3.4). The core area was west of the area of exclusive use (Fig. 3.1).

a.



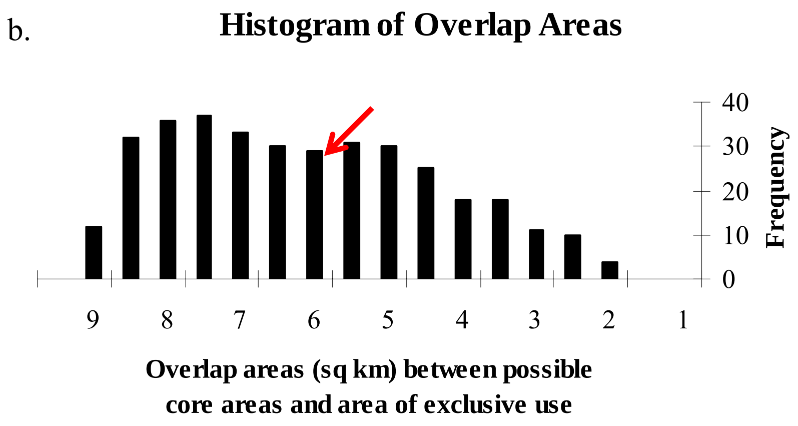


Fig. 3.4. Histograms showing the distribution of distances (a) and overlap areas (b) for all possible locations of the core area. Distances are from the centroid of the territory to the centroid of the possible core area locations. Overlap values are the area of overlap between the area of exclusive use and the possible core area locations. Red arrows show the value for the observed core area.

I predicted that peripheral areas would be used during the middle of the day, but that individuals would return to the core area before nightfall. Although chimpanzees were observed more often in the core area than the periphery at both times of day, mid-day and end of day locations did show a different frequency of core versus peripheral area use. However, contrary to the predicted effect, chimpanzees were more likely to be observed in the periphery at the end of the day than during the middle of the day (Table 3.2). This result is significant (G = 3.82; p = 0.05).

TABLE 3.2. The number of scans that occurred in the core area and the periphery at two different times of day. The percent of scans represented by that number for each time is indicated in parentheses.

Time of Day	*# of Core Area Scans*	*# of Periphery Scans*
End of Day	119 (64.67%)	65 (35.33%)
Mid-day	195 (73.31%)	71 (26.69%)

To explain this unexpected result, I examined the effect of party size on daily ranging patterns. Chimpanzees are likely to find safety in numbers [Mitani and Watts 2005; Wilson et al. 2001; Wilson and Wrangham 2003], and an overrepresentation of large parties in my dataset might have skewed the results. Using the interquartile range, I defined large parties as those above the upper quartile value of 17 independent individuals, and small parties as those below the lower quartile value of 4 independent individuals. I performed a G-test of independence separately on these 2 subsets of the data.

Large parties were found in peripheral areas of the territory at the end of the day more often than they were found in the core area (Table 3.3). In contrast, large parties ranged equally often in the periphery and core area during the middle of the day (Table 3.3). Although the pattern of ranging for large parties matches that in the total sample, chimpanzees in large parties used the core area and periphery similarly during different times of day (G = 3.24; p = 0.73). Small parties avoided the periphery at both times of day (Table 3.3). Thus time of day did not affect the pattern of territory use by small parties either (G = 1.66; p = 0.20).

TABLE 3.3. The number of scans that occurred in the core area and the periphery at two different times of day for large and small parties. The percent of total scans for each time and party size are indicated in parentheses.

Party Size	*Time of Day*	*# of Core Area Scans*	*# of Periphery Scans*
Large	End of Day	15 (37.5%)	25 (62.5%)
Large	Mid-day	34 (55.7%)	27 (44.3%)
Small	End of Day	33 (80.5%)	8 (19.5%)
Small	Mid-day	45 (90%)	5 (10%)

DISCUSSION

Although food availability and intercommunity relations are two factors predicted to influence ranging patterns in territorial animals [Adams 2001], neither affected the territory size of chimpanzees at Ngogo. First, at Ngogo, chimpanzees' monthly territory size was unrelated to monthly fruit availability. This result is consistent with that of Lehmann and Boesch [2003], who also quantified fruit availability when examining the relationship between these variables for chimpanzees at Taï. In their study, fruit availability did not predict daily travel paths or other measures of territory use. Although most territorial species use a smaller area when food is abundant [Adams 2001], at Ngogo, territory size actually increased with increasing fruit availability, though not significantly so.

Though this result contrasts with the prediction of the food supply hypothesis, the relationship between resource availability and ranging may depend on the overall productivity of the habitat. For example, chimpanzees living in marginal savanna habitats range over much larger territories than those in more productive forest environments [Baldwin et al. 1982; Hunt and McGrew 2002]. However, for communities with ample food that is consistently available, as may be the case at Ngogo [Mitani and Watts 2005; Potts 2008], the food supply may never be low enough to necessitate a dramatically larger range. The trend found here, toward expanded territory use with high fruit availability, may be explained through the increased energy gained from a good fruit crop. The territorial nature of chimpanzees may induce them to increase their ranging to monitor neighboring communities whenever their energy balance allows. Although patrol days were excluded from territory size estimations, even in the absence of patrolling there may be a benefit to ranging as widely as possible to monitor and prepare to respond to the territorial activities of neighbors.

A fission-fusion subgrouping pattern may additionally reduce the need to use a larger area when times are tough. Chimpanzees appear to offset food shortfalls by forming smaller parties [Basabose 2004; Boesch 1996; Chapman et al. 1995; Matsumoto-Oda et al. 1998; Mitani et al. 2002a; Wrangham 2000]. This ability to modulate party size according to the food supply may provide an alternative to adjusting ranging patterns, explaining why the Ngogo chimpanzees' territory size did not increase when fruit availability was low.

Contrary to the prediction of the intercommunity relations hypothesis, intruder pressure, as measured by the monthly intercommunity encounter rate, also did not influence territory size. Monthly territory size tended to be small when the intercommunity encounter rate was high, but this trend was not significant. Research at Taï similarly indicates that the average annual number of intercommunity encounters alone was not a significant predictor of territory size; however, it improved the fit of a model which included the number of adult males [Lehmann and Boesch 2003]. In their research, changes in territory size were best predicted by these two variables.

In general, power asymmetries resulting from relative group size mean that larger groups can defend larger territories [e.g. social insects, cooperatively breeding birds, and social mammals; review in Adams 2001]. In chimpanzees, the outcome of intercommunity contests generally depends more on the number of males involved than on the size of the community per se. The willingness of a party of chimpanzees to engage neighbors is therefore a function of its male numbers [Boesch and Boesch-Achermann

2000; Watts and Mitani 2001; Wilson et al. 2001]. Stronger communities can be defined as those able to form parties with more males. Chimpanzee researchers have thus suggested that territory size is sensitive not only to the size of the community, but also to its strength, measured by the number of adult males. Although that prediction could not be directly tested here given the time frame of my research, the Ngogo territory area falls within the usual range of forest-living chimpanzee territory sizes despite an unusually large community size and a large cohort of adult males. Changes in adult male numbers may contribute to variation in territory size within a community [e.g. at Taï, Lehmann and Boesch 2003], but intercommunity comparisons including data from Ngogo suggest that more is involved in the determination of territory size than simply demographic differences. A consistently good food supply at Ngogo is likely to explain the higher density of chimpanzees there compared with chimpanzees in other forests [Potts 2008].

Chimpanzees whose ranging is constrained by the activities of neighbors should demonstrate a concentrated pattern of space use. The core area is predicted to be centered so as to be at a distance from borders with neighboring communities and to be located in the area where neighbors are not encountered. Although the 75% core area of the Ngogo chimpanzees did not abut the territory borders, it was neither perfectly central nor did it overlap highly with the area of exclusive use. The core area was south of center and west of the area of exclusive use. Habitat quality is a likely explanation for this location. The eastern portion of the exclusive use area includes large tracts of swamp and grassland, making this area less suitable for chimpanzee activities. The northern part of the territory similarly contains a fair amount of swamp. The southwest portion of the Ngogo territory, on the other hand, has a high concentration of many of the chimpanzees' favorite fruit trees (Wakefield, Potts, and Amsler, unpublished data).

Because chimpanzees are expected to feel more secure in the core area of their territory, the intercommunity relations hypothesis additionally suggests that though they may use peripheral areas during the middle of the day, they will tend to return to the core area before nightfall [Wilson et al. 2007]. I did not, however, observe this predicted pattern at Ngogo. Chimpanzees were more likely to be in the periphery than the core area at the end of the day than at mid-day. When parties of different sizes were considered separately, the mid-day and end of day locations for neither large nor small parties showed a different frequency of core versus periphery use. Interestingly, at the end of the day larger parties were actually more likely to be in the periphery (62.5% of scans) than the core area (37.5% of scans). Small parties, on the other hand, were much more likely to end the day in the core area (80.5% of scans) than the periphery (19.5% of scans), and in fact were more likely to spend time in the core area regardless of time of day. These results from Ngogo agree with a recent study at nearby Kanyawara, which found that chimpanzee parties ranging near boundaries contained more males than those in the core area [Wilson et al. 2007].

These results suggest that party size mediates the way in which neighboring communities affect ranging patterns. Although there was no overall time-of-day effect on whether the Ngogo chimpanzees were willing to range near neighbors, larger parties were likely to end the day in peripheral areas even though they used both core and peripheral areas during the middle of the day. Sleeping in peripheral areas may be beneficial when chimpanzees are in large parties because they can make their presence known to neighboring communities. Calls made early in the morning by a large party of chimpanzees may deter neighboring chimpanzees from approaching boundary regions during that day. In accord with this idea, Wilson et al. [2007] found that individual males produced more pant hoots early in the morning in the periphery than the core, although they called more frequently in the core area than the periphery at other times of day. When in small parties, on the other hand, chimpanzees are wise to stay away from areas where they are likely to meet strangers, thus the tendency of small parties to remain in the core area both at mid-day and toward nightfall.

The fact that none of the predictions of the intercommunity relations hypothesis were supported indicates that the Ngogo chimpanzees' ranging patterns are not particularly constrained by neighboring communities: 1) territory size was not significantly smaller during months that neighbors were encountered frequently; 2) the Ngogo core area was not absolutely centered within the territory, nor was it located mostly within the area used exclusively by the Ngogo chimpanzees; and 3) the Ngogo chimpanzees did not necessarily avoid peripheral areas at night, when they are most vulnerable. The unusual size of the Ngogo community may provide an explanation for some of these perplexing results. If membership and male numbers are high relative to neighbors, the Ngogo chimpanzees may have little to fear by ranging widely even when and where intercommunity encounters are frequent. Future comparative research is needed to investigate whether the relative size and strength of chimpanzee communities affect the extent to which their ranging patterns are constrained by the activities of neighbors.

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CHAPTER 4

Energetics of Territorial Boundary Patrols

ABSTRACT

Chimpanzees are well known for their territorial behavior. Males who belong to the same community defend heavily-used areas, routinely patrol the periphery of their territories, and occasionally make deep incursions into the territories of their neighbors. Males may gain several fitness benefits by participating in territorial boundary patrols, but patrolling is also likely to involve fitness costs. Patrollers risk injury, and patrols may be energetically costly and may involve opportunity costs. Although territorial patrols have been reported at all long-term chimpanzee study sites, quantitative data on their energetic costs have not previously been available. I measured the energy costs of patrolling for male chimpanzees at Ngogo, Kibale National Park, Uganda during 14 months of observation between July 2004 and February 2006. In 29 patrols and matched control periods, I recorded the distances covered and time spent traveling and feeding by chimpanzees. I found that male chimpanzees covered longer distances, spent more time traveling, and spent less time feeding during patrols than during control periods. These results support the hypothesis that chimpanzees incur energetic costs while patrolling and suggest that ecological factors may constrain the ability of chimpanzees to patrol.

INTRODUCTION

Territorial animals defend an area against conspecifics [Burt 1943; Noble 1939]. In its most common form, displayed by many bird species, territorial defense involves one or both members of mated pairs defending areas associated with nests or other reproductive activity [e.g. Hyman et al. 2004; Noble 1939; Sergio and Newton 2003; Stamps and Krishnan 1999]. Less commonly, groups of animals compete over territories. Although group territoriality has been observed in many species of tropical birds [Gaston 1978], it is comparatively rare among mammals, only having been reported in social carnivores [e.g. cheetahs: Caro and Collins 1987; lions: Grinnell et al. 1995; spotted hyenas: Henschel and Skinner 1991; Kruuk 1972; wolves: Mech et al. 1998; Mech and Boitani 2003; Packer et al. 2005; Schaller 1972], and some species of primates [e.g. spider monkeys: Aureli et al. 2006; Wallace 2008; bonnet macaques: Cooper et al. 2004; blue monkeys: Cords 2007; white-faced capuchins: Crofoot 2007; Gros-Louis et al. 2003; vervet monkeys: Struhsaker 1967]. Chimpanzees provide one of the best examples of group territoriality in primates. Male chimpanzees of the same community jointly defend heavily-used areas and routinely patrol peripheral areas in large parties, occasionally making deep incursions into the territories of their neighbors [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Herbinger et al. 2001; Mitani and Watts 2005; Watts and Mitani 2001].

During boundary patrols and incursions, chimpanzees appear to seek contact with or information about other communities. Behavior during patrols is characterized by the striking silence of males as they travel in a closely spaced, single-file line. Chimpanzees on patrol appear particularly tense and attentive, move in a directed fashion, and engage in reassurance behavior when startled [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001].

Boundary patrolling is even rarer among mammals than group territoriality. Spotted hyenas, wolves, and spider monkeys are among the only other mammals to similarly patrol border regions and make incursions into the territories of neighboring groups, although it is not clear in these species that the goal of patrols is to contact conspecifics [Aureli et al. 2006; Henschel and Skinner 1991; Kruuk 1972; Mech 1994]. Although rare in mammals, patrols occur universally at all chimpanzee study sites where multiple communities exist [Wilson et al. 2004; Wrangham 1999].

Boundary patrolling may furnish several benefits to participants. Possible benefits include recruitment of females [Goodall et al. 1979; Mitani et al. 2002a; Watts and Mitani 2001; Watts et al. 2006; Wilson and Wrangham 2003], resource defense [Williams et al. 2004], defense of the community against threats by outside males [Mitani and Watts 2005; Mitani et al. 2002a; Watts and Mitani 2001; Watts et al. 2006], elimination of rival males [Watts et al. 2006; Wilson and Wrangham 2003], and a way for individuals to signal value as a cooperative partner to other males in the community [Watts and Mitani 2001]. Evidence remains scant for many of these hypothesized benefits, though long-term data from Gombe strongly support the resource defense hypothesis, which posits that males patrol to maintain and increase territory size to provide better resources and thus improve reproduction by community members [Williams et al. 2004].

Despite these benefits, territorial boundary patrols are relatively infrequent, occurring at intervals of 10-23 days at various study sites [Boesch and Boesch-

Achermann 2000; Goodall 1986; Mitani and Watts 2005; Watts and Mitani 2001]. The rarity of patrols suggests that they are costly to participants. Three potential costs include injury or death, opportunity costs, and energetic costs. First, there is an obvious potential risk of serious injury or death during intercommunity conflict. Lethal attacks are not uncommon during encounters between neighboring communities, and chimpanzees exhibit fear and hostility when they encounter members of neighboring communities [Wilson and Wrangham 2003]. However, parties of males appear to reduce the risk of injury by modulating their willingness to engage neighbors based on relative party size [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001; Wilson et al. 2002; Wilson et al. 2001]. By taking the offensive, patrollers are in a good position to assess power imbalances before initiating encounters, thereby minimizing such risks. Probably as a result of this advantage, males who participate in attacks rarely display obvious injuries [Watts et al. 2006].

Second, patrollers may also experience opportunity costs. The sometimes lengthy time spent on patrol is time that cannot be used to pursue other important activities, such as mating with estrous females. With an interbirth interval of 5-6 years and few postpartum estrous cycles before conception [Boesch and Boesch-Achermann 2000; Nishida et al. 2003; Sugiyama 2004; Wallis 1997], it is to his advantage for a male to be present when each cycling female is potentially fertile. Nevertheless, previous research at Ngogo suggests that the opportunity costs of losing the chance to mate do not reduce the probability that males will patrol [Mitani and Watts 2005].

Energetic factors constitute a third cost associated with patrolling. Many discussions of patrols have assumed that energy costs constrain territorial activity [e.g. Herbinger et al. 2001; Mitani and Watts 2005; Watts and Mitani 2001; Wilson and Wrangham 2003]. Patrolling chimpanzees engage in prolonged movements accompanied by little or no feeding [Boesch and Boesch-Achermann 2000; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001]. Lengthy directed travel and losing chances to feed should increase the energetic costs of patrolling. The magnitude of these costs has remained undetermined, however, as no quantitative measurement has been attempted.

In addition to the energetic effects of caloric intake and output through feeding and travel, travel rate may also contribute to the energetic cost of patrols. Because energy expenditure increases with increasing running speed in mammals independent of body mass, faster travel during patrols would exact an additional energetic cost [Taylor et al. 1982].

Despite the widespread occurrence of patrolling behavior by chimpanzees, quantitative data on the energetic costs of patrols do not exist [Mitani et al. 2002a; Watts and Mitani 2001]. In this paper I investigate these costs using observations of travel and feeding during patrols and comparing these with similar observations made on control days when patrols did not take place. I predict that patrolling chimpanzees will feed less, travel more, cover more distance, and travel faster than they do when not on patrol. In addition, using published values for chimpanzee energy expenditure during locomotion [Sockol et al. 2007], I predict that patrolling significantly increases transport costs compared with normal daily travel.

METHODS

Study Site and Subjects

I collected behavioral observations of chimpanzees during 14 months of fieldwork in 2004 – 2006 at Ngogo, Kibale National Park, Uganda. The site is covered primarily by tall, moist evergreen forest, with areas of swamp, grassland, woodland thicket, and colonizing forest. Struhsaker [1997] provides a detailed description of the study area. Ngogo has been the site of behavioral research on several primate species (*ibid*), and chimpanzees there have been observed continuously since 1995 [Mitani 2006; Mitani et al. 2000; Mitani et al. 2002a; Mitani et al. 2002b; Watts et al. 2006]. As a result, the chimpanzees of Ngogo are habituated to and individually identifiable by human observers. Approximately 230 km of trails cover the ~30 km^2 Ngogo study area. I used a handheld GPS to map the entire trail system. The resulting map facilitated plotting the locations of chimpanzees.

The Ngogo chimpanzee community is the largest described in the wild and includes many males [Mitani 2006; Mitani and Amsler 2003; Watts 2000a; Watts 2000b; Watts 2002; Watts 2004; Watts and Mitani 2000; Watts and Mitani 2001; Watts et al. 2006]. Community size ranged from 137 to 148 individuals with 26-29 adult males over the course of the present study.

Behavioral Observations

I recorded four variables to determine the energetic costs of patrols: 1) the proportion of time spent traveling; 2) the proportion of time spent feeding; 3) distance covered, controlling for observation time, and 4) travel rate (distance covered per unit travel time). I recorded these data during patrols and during control observations.

I located chimpanzee parties each day by checking food trees, listening for calls, walking the trail system, or returning to individuals followed the previous day. Once chimpanzees were located, I conducted two-hour focal animal samples of adult males, continuously recording data on their feeding behavior and travel. I selected focal subjects on a pseudorandom basis, with priority given to those individuals who had been sampled infrequently.

For each feeding bout by a focal male, I recorded the time spent feeding. During travel bouts, I recorded time spent traveling. I also took geographic coordinates with a Magellan 315 GPS receiver. When the unit was locked into satellites, I recorded GPS readings at the start of travel, every two minutes during travel, and when travel stopped or paused. When the unit could not track enough satellites to obtain a fix, I noted trails and the times they were crossed. In these cases, I estimated the direction and distance in meters from known locations or previous GPS readings. I used the coordinates to create travel paths for patrols and focal follows.

I also conducted scan samples at 30-minute sample intervals, in which I recorded party membership. I defined parties according to the 50 m chain rule, including individuals within 50 m of at least one other chimpanzee [Smolker et al. 1992].

Observations during Patrols

Patrols are easily recognizable. Patrolling chimpanzees move toward and along borders, and sometimes travel into the territories of others. Patrols also involve a distinctive set of behaviors. Patrollers are unusually quiet, maintain close proximity, and travel in single-file. They pause frequently and are unusually alert and attentive to their surroundings. Patrolling chimpanzees sometimes stand bipedally or climb trees to scan the area. They frequently sniff the ground and vegetation, and inspect any signs of chimpanzees that they find, such as nests, food wadges, or feces. Chimpanzees rarely feed while on patrol [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001].

To address my four predictions, I calculated the proportion of time spent traveling and feeding during patrols, the distance traveled on complete patrol paths, and travel rates. During patrols, I typically followed a single-file line of chimpanzees, and often I could only observe the behavior of individuals toward the back of the line. Because males closely coordinate their behavior during patrols, start and stop travel times usually applied to all individuals, so I could continue focal animal samples even when my view of the focal individual was obscured by others. I recorded *ad libitum* feeding by any visible participant rather than just focal subjects, which likely inflates the feeding time above that of focal animals. This measure thus represents a conservative choice for comparison with control observations. To correct for unequal observation times, I divided the distance traveled by the total time spent on patrol. To determine travel rates, I calculated the distance covered per unit of travel time. To match patrols to control observations, I also recorded the number of participating males.

I recorded complete patrol paths and travel times, which included both the trip out and the return. I defined the start time of the patrol as the moment chimpanzees first began to exhibit distinctive patrol behavior, including silence, cohesive and directed travel, frequent attentive pauses, and sniffing of the ground, vegetation or signs of chimpanzees [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001]. For many patrols the start time was clear because a cohesive party of mostly male chimpanzees quickly formed when its members abruptly and simultaneously stopped feeding or resting as they jumped up and quickly moved off together, sometimes separating from females and their young as they did so. This sudden gathering and movement was generally accompanied by fear grimaces and embracing among party members. It was sometimes precipitated by a far-off call from a neighboring group. For other patrols, chimpanzees were already traveling, making it more difficult to identify start times. In these cases, I defined start times of patrols in one of three ways, after: 1) the last audible call was uttered; 2) the last feeding bout; or 3) most females dropped out of the party.

I considered patrols to continue until the Ngogo chimpanzees returned to their territory and either made considerable noise by calling loudly and displaying, including buttress drumming displays, or simply resumed normal feeding and calling behavior. When patrollers did not meet neighbors or only made auditory contact with them, they generally remained cohesive as they returned to the Ngogo territory. In these situations, chimpanzees called and displayed once they returned to their territory, and I could record data that applied to all patrol participants. When the patrolling individuals encountered other chimpanzees, however, the patrollers often scattered and moved back to the Ngogo territory in smaller parties that traveled in parallel. In these cases, I followed one of the subgroups, and continued noting the patrol path and events for those individuals only. I considered patrols to be over when the individuals that I followed resumed normal feeding and calling behavior.

I also collected data *ad libitum* on events during patrols. Events included sniffing the ground, vegetation, nests, feces, or other signs of chimpanzees from neighboring communities; unusually tense or alert behavior; fear grins; embraces between patrol members; calls, most notably screams and whimpers; reactions to hearing chimpanzees from other communities; displays and drumming; battles, consisting of visual contact, confrontation, charges, and chases between Ngogo patrollers and members of the opposing party [Boesch and Boesch-Achermann 2000; Goodall 1986]; attacks on other chimpanzees; infanticides; consumption of killed infants; and any other distinctive or unusual behavior.

Control Observations

I compared observations of patrolling behavior with control observations, which were focal animal samples of adult males that I collected on days that did not include a patrol. I used a matched-pairs design to compare behavior during patrols with control observations. I selected controls that occurred within a window that started 10 days before a patrol and ended 10 days after it (mean difference = 5.7 days, SD = 2.6, range = 1 – 10, n = 29 pairs) at a similar time of day and that contained a similar number of males as patrol periods, to control for the effects of food availability, time of day, and party size on travel. Because all control follows were two hours while patrols varied in length, I used the midpoint time of control periods and patrols to match time of day (mean difference = 53 minutes, SD = 62, range = 0 – 280, n = 29 pairs). Party scans were taken every half hour during each control follow and patrol, and I used the maximum number of males present during scans for each control period and patrol to match the number of males in parties (mean difference = 1.9 males, SD = 2.0, range = 0 – 9, n = 29 pairs).

For each two-hour control sample, I calculated the proportion of time the focal individual spent traveling and feeding. I also calculated the distance covered on travel paths of focal samples. As I did with patrols, I divided this distance by the total number of minutes in the focal follow, while I determined travel rates based on the distance covered during travel only.

Cost of Transport

Based on the distance traveled, I calculated energy expenditure during patrols and control observations using published values for the cost of transport in chimpanzees. Sockol et al. [2007] calculated the cost of quadrupedal walking for adult male chimpanzees to be 0.19 ml O_2 per kg of body weight per meter moved. I reported energy expenditure in kilocalories (kcal) rather than O_2. Consumption of a liter of O_2 corresponds to about 4.83 kcal of energy [Campbell et al. 1999]. I estimated adult male body mass at 42.7 kg, a value based on known masses of 21 wild shot East African chimpanzees (*Pan troglodytes schweinfurthii*) [Smith and Jungers 1997]. This value may underestimate the weight of male chimpanzees in the Kibale National Park, which were estimated at 45 – 55 kg based on skeletal measurements of the remains of 3 individuals [Kerbis Peterhans et al. 1993]. However, I follow Pontzer and Wrangham [2004] in using the lower figure because it was based on a larger sample of individuals of known body mass.

I also estimated the daily cost of transport for adult male chimpanzees at Ngogo. I calculated the average distance traveled per hour for all focal observations of at least 2 hours that occurred on days that the chimpanzees did not patrol. I estimated daily transport costs by calculating kcal consumption per hour based on the average hourly travel distance and multiplying that value by 12 hours. Using the distances covered on the 29 patrol paths, I also determined the cost of transport for each patrol. I subtracted the time spent on each patrol from 12 hours, and multiplied the remaining number of hours in the day by the average hourly transport cost for non-patrol days. This provided an estimate for energy expenditure during the part of the day that the chimpanzees did not patrol. I added this figure to the cost of transport for the patrol to obtain total cost of transport for each day that the chimpanzees patrolled.

Statistical Analysis

For each patrol and matched control I calculated the proportion of time spent traveling, the proportion of time spent feeding, the distance covered per unit observation time, and the actual travel rate (distance covered/time spent traveling). I plotted the distribution of values of each variable separately for patrols and control periods. Values were not normally distributed, and I used the nonparametric Wilcoxon signed rank test to examine whether variables differed between patrol and control conditions.

I performed a t-test to assess whether chimpanzees increase their daily transport costs by patrolling. I compared the mean of the sample of daily transport costs for the 29 patrol days with the estimated daily transport cost for days on which the chimpanzees did not patrol.

Other researchers recorded data on patrols that are included in these analyses. In the cases where I was not present at a patrol (n = 8), some data were not collected. Patrols without sufficient data for any given variable were eliminated, resulting in differences in sample sizes among the four analyses.

I performed all statistical tests using SAS release 9.1.3.

RESULTS

I collected observations of feeding and travel during 29 boundary patrols. Fig. 4.1a shows the travel paths for these patrols. I recorded data on distances covered for 29 patrols, on the proportions of time spent traveling and travel rates for 25 patrols, and on the proportions of time spent feeding for 23 patrols (Table 4.1).

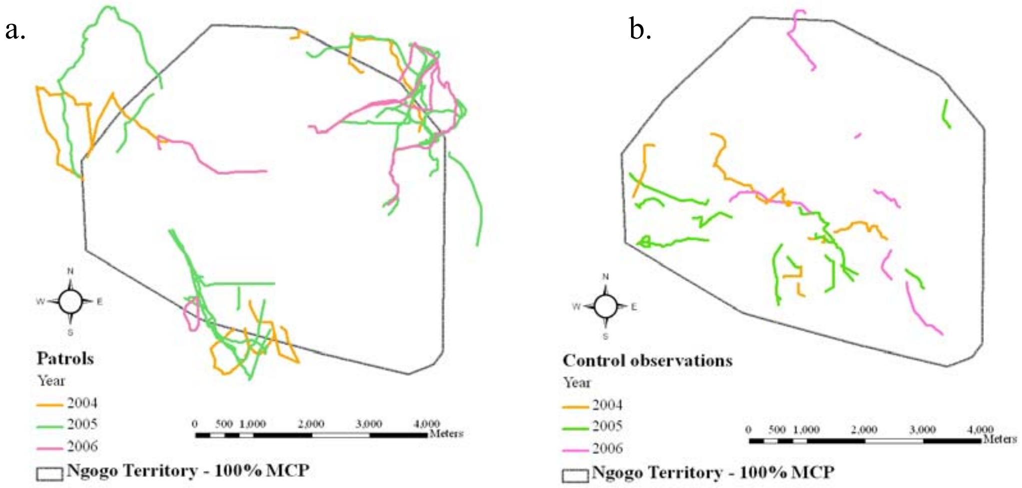

Fig. 4.1. Maps showing the paths followed during patrols (a) and control periods (b).

TABLE 4.1. Durations, distances, travel rates, activity budgets and participants for the 29 patrols analyzed here.

Date M/D/Y	*Total time (minutes)*	*Proportion of time spent traveling*	*Proportion of time spent feeding*	*Distance (meters)*	*Distance covered (per unit patrol time - meters/min)*	*Travel rate (meters/ min)*	*Party Size*	*# of Males*
8/1/04	164	0.50	0	3318	20.23	40.46	12	11
8/6/04	47	No data	No data	2271	48.32	No data	15	15
9/14/04	15	1.00	0	428	28.53	28.53	12	12
10/5/04	45	No data	No data	1057	23.49	No data	20	20
10/6/04	198	0.36	0.30	2147	10.84	29.82	32	27
10/12/04	322	0.43	0	3918	12.17	28.09	28	27
11/9/04	185	0.45	0.44	2582	13.96	30.92	32	29
2/12/05	38	0.95	0	932	24.53	25.89	20	18
2/18/05	82	0.66	No data	2352	28.68	43.56	16	15
2/21/05	170	0.75	0.01	4547	26.75	35.66	20	20
2/22/05	165	No data	No data	1813	10.99	No data	10	10
2/28/05	43	0.51	0	994	23.12	45.18	20	19
3/2/05	264	0.64	0.003	5374	20.36	31.89	20	19
3/10/05	155	0.85	0	3878	25.02	29.38	16	16
3/25/05	49	0.85	No data	1482	30.24	35.71	12	10
4/13/05	84	0.71	0.04	2360	28.10	39.66	20	19
4/13/05	47	0.49	0	567	12.06	24.65	11	10
4/23/05	86	0.64	0	2304	26.79	41.89	14	12
4/23/05	173	0.51	0.02	2746	15.87	30.85	12	12
5/4/05	70	0.81	0	1944	27.77	34.11	19	17
10/12/05	137	0.30	0.09	1274	9.30	30.70	19	18
10/13/05	125	0.62	0.33	3096	24.77	39.95	25	23
12/27/05	36	0.25	0	407	11.31	45.22	21	18
12/28/05	348	0.42	0.28	5482	15.75	37.81	23	23
1/23/06	266	0.52	0.29	5020	18.87	36.38	15	14
1/30/06	164	0.28	0	2375	14.48	51.08	11	10
2/1/06	181	0.66	0.39	4270	23.59	35.88	9	9
2/3/06	86	0.41	0	1396	16.23	39.32	20	20
2/5/06	135	No data	No data	899	6.66	No data	14	14

Behavior during patrols

Patrollers usually started out moving quickly and in a directed fashion, though sometimes pausing after a few minutes to wait for stragglers to catch up. After this initial rapid travel, they usually interspersed longer travel bouts with shorter rest bouts, apparently listening for other chimpanzees during pauses. Patrolling chimpanzees often stopped on ridges, where calls and other sounds made by conspecifics can be heard over long distances. They also paused to sniff vegetation or signs of chimpanzees. When patrollers heard other chimpanzees, they excitedly embraced each other, fear-grimaced, and sometimes uttered low amplitude screams that did not carry far before moving quickly in the direction of the calls.

Return trips generally involved more continuous and directed travel than trips out, especially in cases where patrollers made deep incursions into the territories of neighbors. When patrollers met one or few females and committed an infanticide, they tended to stay in the area for an hour or more before traveling back to the Ngogo territory. If they met a large group from another community, the encounter was generally over within 25 minutes, followed by direct and rapid travel back to the Ngogo territory.

Travel Costs

Patrols lasted an average of 134 minutes and varied from 15-348 minutes (SD = 88 minutes, n = 29). Chimpanzees traveled more than half the time on average while on patrol (mean = 58%; SD = 21%; range: 25 – 100%; n = 25 patrols), while during control periods they spent about 14% of their time traveling (SD = 9%; range: 0 – 35%; n = 25 controls). Thus chimpanzees spent significantly more time traveling during patrols than during control periods (Wilcoxon signed-rank test, T = 163, $p < 0.0001$; Fig. 4.2).

Because chimpanzees spent considerable time traveling during patrols, patrollers were likely to cover long distances. In fact, travel distances during patrols ranged from short (c. 0.5 km) “checks” near border areas to much longer treks of more than 5 km (mean = 2456 m; SD = 1492 m, n = 29; Table 4.1; Fig. 4.1a). These distances were longer than those covered during 2-hour control periods, correcting for observation time (Wilcoxon signed-rank test, T = 216.5, $p < 0.0001$; Fig. 4.3). Patrollers moved a mean distance of 21 m per minute of observation time (SD = 9; range: 7 – 48; n = 29 patrols). In contrast, the mean distance covered during control periods was only 6 m per minute of observation time (SD = 4; range: 0 – 14; n = 29 controls).

Based on the distances covered, adult male chimpanzees consumed an estimated 0.81 kcal per minute during patrols (SD = 0.34; range = 0.26 – 1.89; n = 29 patrols), compared with 0.24 kcal per minute during control observations (SD = 0.15; range: 0 – 0.54 kcal; n = 29 controls). In 452 focal observations of at least 2 hours that occurred on days that the chimpanzees did not patrol, the average distance traveled per hour was 302 m (SD = 260; range: 0 – 1608 m; n = 452), which requires consumption of 11.82 kcal (SD = 10.20; range: 0 – 63.0 kcal; n = 452). In a 12 hour day this translates to 141.84 kcal consumed to support transport costs. Chimpanzees expended an average of 96.25 kcal per patrol (SD = 58.48; range: 15.95 – 214.82 kcal; n = 29 patrols). Their average estimated total daily transport cost for patrol days was 194.62 kcal (SD = 45.24; range: 150.57 – 300.49 kcal; n = 29 patrol days), which was significantly greater than the usual 141.84 kcal expended on a day without patrolling activity (t-test, t = 8.33, $p < 0.0001$).

Despite traveling long distances during patrols, the mean travel rate, computed as the distance traveled per unit travel time, was actually faster during control periods (44 m/minute; SD = 18; range: 0 – 94; n = 25 controls) than patrols (36 m/minute; SD = 7; range: 25 – 51; n = 25 patrols). This difference was significant (Wilcoxon signed-rank test, T = 80.5, $p < 0.05$; Fig. 4.3), and indicated that chimpanzees traveled slower but more steadily while on patrol than other times.

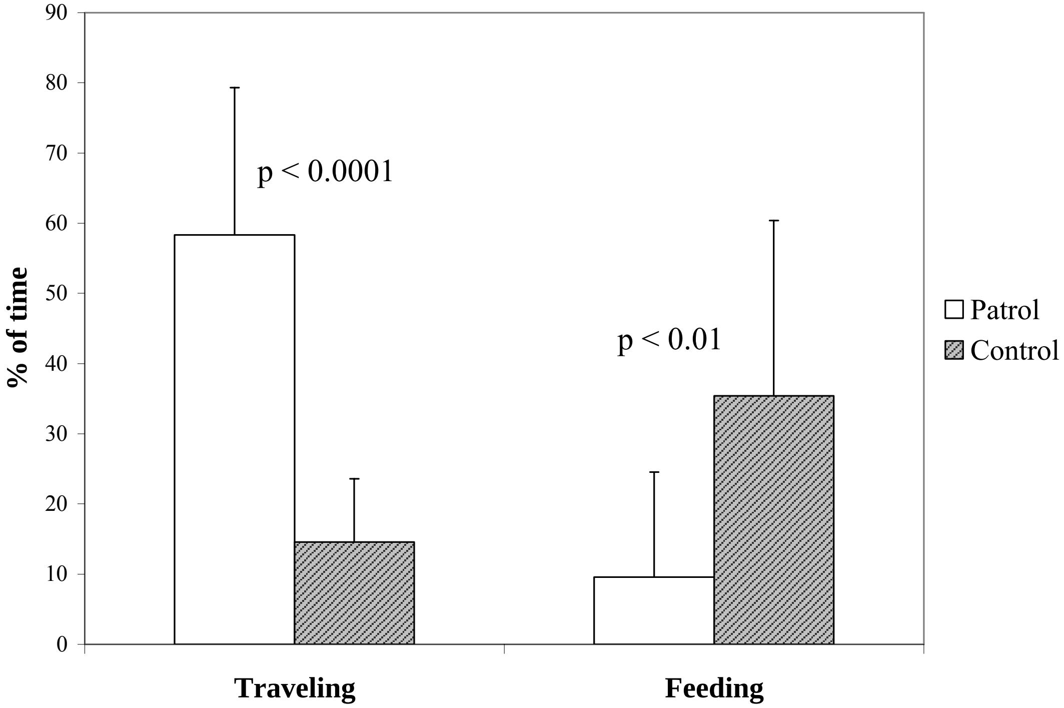

Fig. 4.2. Comparison of the average time spent traveling and feeding during patrols and control periods. Means + 1 SD are displayed.

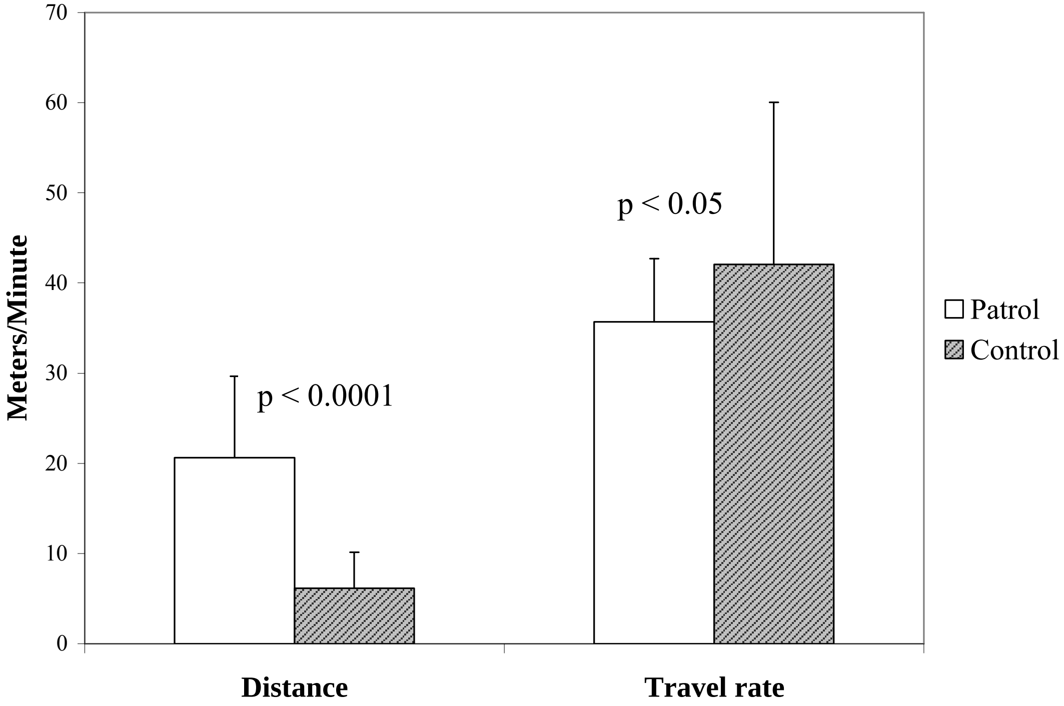

Fig. 4.3. Comparison of distance covered and travel rate during patrols and control periods. Distance is represented by the meters covered per minute of observation time. Travel rate is the actual travel rate expressed in meters covered per minute of travel time. Means + 1 SD are displayed.

Feeding Costs

I rarely observed feeding by patrolling chimpanzees. Patrollers occasionally fed on one or two fallen fruits as they paused to sniff broken branches and vegetation under food trees in a neighbor's territory. In these cases, only one or two individuals typically fed. During other times, chimpanzees ate the leaves of saplings while pausing, often on a ridge, apparently listening for other chimpanzees.

I recorded sustained feeding bouts during patrols in only two contexts. Three times patrolling chimpanzees encountered and hunted red colobus or black and white colobus monkeys that they subsequently consumed. Twice patrollers killed and consumed infant chimpanzees from other communities, and those in possession of dead infants fed on them for a long time. Following one of these infanticides, several chimpanzees fed on the ripe fruit of *Morus mesozygia* for almost an hour and a half while one male cannibalized the infant.

Excluding these five patrols, chimpanzees spent only about 3% of their time feeding during patrols (mean = 2.7%; SD = 7.9%; range: 0 – 32.8%; n = 19 patrols). In contrast, they spent 40% of their time feeding during matched control periods (SD = 23.6%; range: 0 – 82.5%; n = 19 controls). Chimpanzees thus spent significantly less time feeding during patrols than during control periods (Wilcoxon signed-rank test, T = 74.5, $p < 0.0001$).

Including the five exceptional cases had no appreciable effect on the analysis as chimpanzees still spent significantly less time feeding during patrols than during control periods (Wilcoxon signed-rank test, T = 83.5, $p < 0.01$; Fig. 4.2). Chimpanzees spent less than 10% of their time feeding during patrols (mean = 9.6%; SD = 15%; range: 0 – 44%;

n = 23 patrols) compared to 35% of their time feeding during matched control periods (SD = 25%; range: 0 – 82.5%; n = 23 controls).

DISCUSSION

The results of the preceding analyses reveal that patrols have tangible effects on travel and feeding. During territorial boundary patrols, chimpanzees at Ngogo spent more than half of their time traveling, on average, but less than 10% of their time feeding. The opposite pattern emerged during normal activities; with chimpanzees spending about twice as much time feeding (33%) as traveling (16%) during control sessions. Consistent with these time budget differences, chimpanzees traveled three times as far during patrols than control periods, despite traveling more slowly, on average, while patrolling. Traveling longer distances involved appreciably greater energy expenditure.

Although chimpanzees clearly spent less time feeding when on patrol than during other times, the difference in feeding time is probably even greater than reported here. Data collection was biased against finding the hypothesized result: feeding records for controls included only the focal individual, but records during patrols included feeding by all visible individuals. The bias introduced by using *ad lib* data particularly affected the results when an infanticide resulted in cannibalism by one or few patrollers, while the others ate nothing. In addition, the minimum feeding time recorded was 1 minute; shorter bouts were rounded up to this length. Thus if an individual ate only one fruit, I counted it as 1 minute of feeding time. This was far more likely to occur during patrols, when one or two patrollers might have grabbed a fruit or two as they passed under and investigated a food tree in the neighbor’s territory.

Chimpanzees covered long distances while patrolling, but they traveled relatively slowly. The cautious manner in which chimpanzees moved during patrols probably accounted for this slow rate. Just as they interspersed short resting bouts between longer periods of travel to listen for chimpanzees in other communities, they also moved slowly while patrolling, watching and listening for signs of neighbors to direct their travel. During normal travel within their own territory chimpanzees traveled directly from one spot to another between food trees and social groups. They moved faster because their travel depended more on the locations of known destinations than attentiveness to their surroundings.

The cost of travel is positively related to speed [Taylor et al. 1982], but slow travel during patrols may not compensate for energy deficits that result from reduced caloric intake and increased caloric output. Chimpanzees pay transport costs while both foraging and patrolling, but net activity costs appear to differ. Normal foraging presumably leads to net energy gains, or at least energy balance, because chimpanzees take in energy while traveling relatively little compared to patrols. Patrolling chimpanzees ate almost nothing while spending a lot of time covering considerable distances. The energy savings from slow travel probably do not compensate for these net activity costs.

These results support the hypothesis that male chimpanzees incur energetic costs during territorial boundary patrols and suggest that ecological factors may constrain the ability of male chimpanzees to patrol. Previously at Ngogo, Mitani and Watts [2005] found that while both fruit availability and party size predict the tendency to patrol, party size accounts for most of the variation. Although fruit availability scores tended to be higher on patrol days than on days that the chimpanzees did not patrol, patrols occurred even when there was a paucity of fruit [Mitani and Watts 2005]. Ecological conditions may generally be favorable enough at Ngogo to reduce the energetic impact of fruit scarcity [Potts 2008]. This accords with the suggestion that frequent territorial behavior at Taï may result from high food availability [Herbinger et al. 2001]. Feeding efficiency should be high when fruit is abundant; this would permit more time to invest in territorial activities, because individuals can readily replenish energy spent.

Frequent patrols also suggest that Ngogo chimpanzees enjoy a positive energy balance. They were observed to patrol 30 times during the 280 days that I followed chimpanzees for more than 6 hours in 2003-2006. Thus they patrolled, on average, every 9.3 days (weekly patrol rate of 0.75). This rate is similar to that found by Watts and Mitani [2001] in 1998-1999, when Ngogo chimpanzees patrolled every 9.7 days (weekly patrol rate of 0.72) and approximately twice as high as rates at Gombe [~ every 22 day, 1977-1982, Goodall 1986] and Taï [≤ every 14 days, 1984-1991, Boesch and Boesch-Achermann 2000].

Mitani and Watts [2005] pointed out that due to the unusually large number of males at Ngogo, the per capita patrol rate does not differ between sites. However, overlap in patrol participation is high. For the 25 adult males who were alive throughout my study period, each participated in about half of all patrols (mean = 52%, SD = 10%, range = 37-70%). Such high patrol participation suggests that many individual males at Ngogo do, in fact, participate in more patrols than males at other sites. For individual male chimpanzees, frequent participation in patrols exacts energetic costs that must be sustained by available food resources.

Territorial boundary patrols, like other behaviors, are considered adaptive if fitness benefits outweigh fitness costs. Researchers interested in the fitness value of a behavior frequently focus on identifying its potential benefits. In the case of territorial boundary patrolling in chimpanzees, several non-mutually-exclusive benefits have been hypothesized: recruitment of females, rival coalition reduction, resource defense, community defense, and costly signaling [Goodall 1986; Goodall et al. 1979; Mitani and Watts 2005; Mitani et al. 2002a; Nishida et al. 1985; Watts and Mitani 2001; Watts et al. 2006; Williams et al. 2004]. Although several of these benefits may play a role in maintaining patrolling behavior, there is emerging consensus around the resource defense hypothesis, which suggests that males maintain and try to increase territory size to increase the quality and quantity of food available to the entire community [Williams et al. 2004].

While chimpanzees may derive benefits via patrols, costs are another important part of the fitness equation. Sufficiently low costs may favor patrolling even when the fitness benefits are weak [Wilson and Wrangham 2003]. The costs of boundary patrolling are generally assumed to be low [Manson and Wrangham 1991; Wilson and Wrangham 2003; Wrangham 1999]. Patrolling chimpanzees seem to reduce the most severe risk, that of serious injury or death, by modulating their willingness to engage rival chimpanzees based on relative party size [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001; Wilson et al. 2002; Wilson et al. 2001]. Chimpanzees tend to patrol in large parties, thereby minimizing the risks. Patrols in my sample contained a minimum of 9 males (mean = 16, SD = 6, range = 9-29, n = 29 patrols).

Patrols also exact energetic and opportunity costs [e.g. Herbinger et al. 2001; Mitani and Watts 2005; Watts and Mitani 2001; Wilson and Wrangham 2003], but these, too, have been thought to be sufficiently low that even with weak potential benefits, territorial boundary patrolling behavior remains adaptive [Wilson and Wrangham 2003]. Until now, however, no attempt has been made to quantify the energetic costs of patrolling behavior. As this study demonstrates, energetic costs may not be negligible. Patrolling chimpanzees incur nontrivial energetic costs, spending significantly more of their time budgets traveling and moving over significantly longer distances, while feeding much less than they do normally.

As similar quantitative data from other chimpanzee research projects become available, it will be possible to assess the extent to which variability across study sites reflects underlying ecological differences bearing on energetic constraints of patrolling. This study represents a first step toward resolving an outstanding problem concerning a striking behavior in our closest living relatives.

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CHAPTER 5

Spatial Distribution of Territorial Boundary Patrols

ABSTRACT

Chimpanzee males regularly patrol the boundaries of their territories in large parties, apparently seeking contact with members of neighboring communities. Such contact occasionally results in lethal aggression. Although the proximate and ultimate factors affecting when and whether chimpanzees patrol have been the focus of recent research, the spatial distribution of these patrols has received little attention. Here I investigated the factors affecting where chimpanzees patrol through a study of the unusually large community of chimpanzees at Ngogo, Kibale National Park, Uganda. The population density of neighboring chimpanzees, as assayed by nest counts, did not predict where Ngogo chimpanzees patrolled, suggesting that they do not respond to power imbalances between themselves and neighbors when choosing patrol directions. Over the long but not short term, Ngogo chimpanzees patrolled more frequently in peripheral areas where they experienced more intercommunity encounters. However, in the most heavily patrolled areas, intercommunity encounter density and patrol density were also positively associated over the short-term. Intercommunity encounters were more often passively experienced than actively sought, and the ratio of active to passive encounters varied as a function of location, suggesting that the Ngogo chimpanzees defended some boundary

areas more keenly than others. In sum, these results suggest that the Ngogo chimpanzees adjusted their territorial activities in response to different neighbors in various ways.

INTRODUCTION

Chimpanzees are a territorial species. Members of the same community jointly defend their territory, and routinely form large parties to patrol territory peripheries and areas where the ranges of neighboring communities overlap. Some patrols involve deep incursions into the territories of neighboring communities [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Herbinger et al. 2001; Mitani and Watts 2005; Watts and Mitani 2001]. Boundary patrols have been described at all long-term chimpanzee field sites where chimpanzee communities occupy adjacent territories [Wilson et al. 2004; Wrangham 1999], but are nonetheless a relatively infrequent event, occurring at intervals of 10-23 days [Boesch and Boesch-Achermann 2000; Goodall 1986; Mitani and Watts 2005; Watts and Mitani 2001].

Despite its rarity, territorial boundary patrolling by chimpanzees can have major fitness consequences [Boesch and Boesch-Achermann 2000; Goodall 1986; Mitani and Watts 2005; Watts and Mitani 2001]. During intercommunity encounters, severe and sometimes lethal coalitionary aggression may result if the patrollers greatly outnumber the neighbors [Goodall 1986; Manson and Wrangham 1991; Wilson et al. 2001; Wilson and Wrangham 2003; Wrangham and Peterson 1996; Wrangham 1999]. Patrolling appears to be adaptive for participating males because it leads to acquisition of more territory, which translates into improvement in female reproduction within the community [Williams et al. 2004]. At the proximate level, recent research at Ngogo in the Kibale National Park, Uganda suggests that fruit availability and male party size are two ecological and social factors that predict the tendency to patrol [Mitani and Watts 2005].

While the ultimate and proximate factors affecting the tendency to patrol have become increasingly clear, scant attention has been paid to another salient aspect of patrolling behavior: where chimpanzees patrol. Just as the frequency with which chimpanzees patrol varies across time due to shifting ecological and social conditions [Mitani and Watts 2005], the frequency with which they patrol in different directions may also vary. For example, chimpanzees in the Taï National Park, Côte d'Ivoire, patrolled more frequently in some directions than others [Boesch and Boesch-Achermann 2000], while in the Gombe National Park, Tanzania, patrols by the Kasakela community occurred equally to the north and to the south [Goodall 1986]. Previous research at Ngogo suggests that patrols are unevenly distributed around the territory boundary, and locations of patrols may even shift over time [Watts and Mitani 2001]. There is considerable variation in the spatial distribution of patrols, and the factors underlying this variation are unclear. Several factors are likely to play a role.

The imbalance-of-power hypothesis provides one possible explanation for variation in the spatial distribution of patrols. According to this hypothesis [Manson and Wrangham 1991; Wilson and Wrangham 2003; Wrangham 1999], lethal coalitionary aggression in chimpanzees is facilitated by their fission-fusion social system, which creates size disparities between parties from rival communities. Differences in party size furnish low-cost opportunities for lethal coalitionary aggression when large coalitions of males search for and attack small parties or lone individuals from other communities

[Manson and Wrangham 1991; Watts et al. 2006; Wilson and Wrangham 2003; Wrangham 1999]. A favorable imbalance-of-power is most likely when one community is considerably larger than another, resulting in larger party sizes on average and increased frequency of patrols [Boesch and Boesch-Achermann 2000]. As a result, this hypothesis predicts that chimpanzee communities will direct their territorial activities toward smaller communities, leading to spatial variation in patrol frequency. Over the long term, patrols are expected to be more frequent in peripheral areas where chimpanzees experience a favorable imbalance-of-power.

Social and ecological factors may also affect where chimpanzees patrol. In particular, intruder pressure may vary in different boundary areas and affect spatial patterns of patrolling over the short term. Chimpanzee territories can overlap extensively (30-60%) with those of their neighbors [Boesch and Boesch-Achermann 2000; Herbinger et al. 2001; Nishida and Kawanaka 1972], and as a result, encounters with members of other communities occur frequently. Chimpanzees encounter parties from adjacent communities either aurally or visually on 3 – 12% of observation days during patrols or in the course of foraging in overlap zones [summarized in Wilson and Wrangham 2003]. If patrols serve to protect females and offspring against the attacks by intruding neighbors, then male chimpanzees might increase their patrolling effort to deter threats posed by these intrusions. In a previous study at Ngogo, Mitani and Watts [2005] found that chimpanzees did not systematically increase the frequency of patrols in response to intruder pressure, but the spatial proximity of patrols to intercommunity encounters was not considered.

Ecological factors may also affect the frequency and location of patrols over the short term. At Ngogo, most intercommunity encounters occur in peripheral areas near seasonally abundant food sources [Watts et al. 2006]. Prior research suggests that the Ngogo chimpanzees may patrol overlap zones heavily just prior to seasonal periods of fruiting activity in those areas to gain priority of access to food [Mitani and Watts 2005]. Thus patrolling behavior may "clear-out" contested areas along the boundary that experience large seasonal crops of food. Feeding following such "clearing-out" events may correspond to what Goodall [1986; 1979] called *excursions*, in which large mixed-sex parties at Gombe visited peripheral areas occasionally in times of abundant food. Excursions were sometimes immediately preceded by calls and vigilance as though the chimpanzees were checking for others, while at other times the chimpanzees moved directly into the overlap zone without apparent trepidation [Goodall 1986; Goodall et al. 1979]. It is unclear whether the excursions involving less vigilance followed recent patrols to the area.

In this study, I investigate the factors that affect the spatial distribution of territorial patrols by chimpanzees at Ngogo, Kibale National Park, Uganda. Specifically, I evaluate the effects of three social and ecological factors hypothesized to influence patrolling. First, I examine whether long-term patterns of patrolling direction and frequency relate to the imbalance of power between the Ngogo community and its neighbors by assessing the local population density of chimpanzees around territory borders. Second, I investigate whether the spatial distribution of territorial patrols correlates over the short-term with the spatial distribution of intercommunity encounters.

Finally, I determine whether chimpanzees patrol boundary zones frequently prior to exploiting a large fruit crop in the area.

METHODS

Study Site and Subjects

I collected behavioral observations of chimpanzees at Ngogo, Kibale National Park, Uganda. The site is covered primarily by tall, moist evergreen forest, with areas of swamp, grassland, woodland thicket, and colonizing forest. Struhsaker [1997] and Lwanga et al. [2000] provide detailed descriptions of the study area. Ngogo has been the site of behavioral research on several primate species [review in Struhsaker 1997], and chimpanzees there have been observed continuously since 1995 [Mitani 2006; Mitani et al. 2000; Mitani et al. 2002a; Mitani et al. 2002b; Watts et al. 2006].

The Ngogo community is the largest that has been described in the wild and includes an exceptionally large number of males [Mitani 2006; Mitani and Amsler 2003; Watts 2000a; Watts 2000b; Watts 2002; Watts 2004; Watts and Mitani 2000; Watts and Mitani 2001; Watts et al. 2006]. Community size at Ngogo ranged from 140-150 individuals between 2000 and 2006, with 22-29 adult and 12-22 adolescent males at any given time.

Behavioral Observations and Use of Space

I collected behavioral observations during four field seasons: June – August 2003, July – November 2004, February – June 2005, and September 2005 – February 2006, for a total of 17 months. Additional data on patrols and intercommunity encounters from the long-term records at Ngogo were collected primarily by David Watts and John Mitani during field seasons between 2000 and 2006.

I estimated the size and extent of the Ngogo community territory based on observations made between June 2003 and October 2005. I defined the territory as the 100% minimum convex polygon (MCP) encompassing all geographic coordinates collected while following the Ngogo chimpanzees on days that they did not patrol (Fig. 5.1). I observed parties of chimpanzees between 0700 and 1800 hours, often following target males during two hour focal follows. During observations of focal males and chimpanzee parties I recorded geographic coordinates during travel and at locations where chimpanzees stopped to rest or feed.

To facilitate analyses, I superimposed a system of 500 X 500 meter quadrats over the Ngogo territory and surrounding area (Fig. 5.1).

Territorial Patrols

I collected data on patrols *ad libitum*. I identified patrols by a distinctive suite of behaviors exhibited by chimpanzees as they moved toward or along territorial borders or into the territories of others. Behavior during patrols is characterized by the striking silence of males as they travel in a cohesive, single-file line. Patrolling chimpanzees appear particularly tense and attentive, move in a directed fashion, and engage in reassurance behavior when startled. They pause frequently to look and listen, sometimes standing bipedally or climbing a tree to scan the area. They frequently sniff the ground, vegetation, or signs of chimpanzees, such as nests, food wadges, or feces, that they find

[Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001].

I defined the start time of a patrol as the moment chimpanzees first began to exhibit distinctive patrol behaviors. For many patrols the start time was clear because a cohesive party of mostly male chimpanzees quickly formed when its members abruptly and simultaneously stopped feeding or resting as they jumped up and quickly moved off together, sometimes separating from females and their young as they did so. This sudden gathering and movement was generally accompanied by fear grimaces and embracing among party members. It was sometimes precipitated by a far-off call from a neighboring group. For other patrols, chimpanzees were already traveling, making it more difficult to identify start times. In these cases, I defined start times of patrols in one of three ways, after: 1) the last audible call was uttered; 2) the last feeding bout; or 3) most females dropped out of the party.

I considered patrols to continue until the Ngogo chimpanzees returned to their territory and either made considerable noise by calling loudly and displaying, including buttress drumming displays, or simply resumed normal feeding and calling behavior [Goodall 1986]. When patrollers did not meet neighbors or only made auditory contact with them, they generally remained cohesive as they returned to the Ngogo territory. In these situations, chimpanzees called and displayed once they returned to their territory, and I could record data that applied to all patrol participants. When the patrollers encountered other chimpanzees, however, they often scattered and moved back to the Ngogo territory in smaller parties that traveled in parallel. In these cases, I followed one of the subgroups, and continued noting the patrol path and events for those individuals only. I considered patrols to be over when the individuals that I followed resumed normal feeding and calling behavior.

During patrols I collected geographic coordinates with a Magellan 315 GPS receiver. When the unit was locked into satellites, I recorded GPS readings at the start of travel, every 2 minutes during travel, and when travel stopped or paused. When the unit was unable to track enough satellites to obtain a fix, I noted trails and the times they were crossed. In these cases, I estimated the direction and distance in meters from known locations or previous GPS readings. I used these coordinates to create travel paths for patrols (Fig. 5.1).

Some patrols in the long-term records at Ngogo contained sufficient spatial information for inclusion with patrols I observed in analyses requiring travel routes. Therefore, for analysis I had a total of 61 patrols with complete travel paths (Fig. 5.1). Others could be identified by the sector of the periphery in which they occurred (see *Effects of Direction* section and Fig. 5.4 below.)

Intercommunity encounters

I also recorded intercommunity encounters *ad libitum* (Fig. 5.1). In some encounters members of the Ngogo community and individuals of another community came into visual contact, occasionally including physical contact. In these cases, I recorded the locations where interactions took place. Other intercommunity encounters involved only auditory contact with neighbors. For these, I plotted the location of the calling neighbors using their estimated distance and direction from the party of Ngogo chimpanzees that I followed.

Nest Count Transects

To assess the power differential between the Ngogo community and its neighbors, I assayed relative population density of surrounding communities using the standing crop nest count (SCNC) technique. Although the SCNC method may not produce absolute estimates of chimpanzee population densities, it is a useful and efficient way to determine relative densities [Plumptre and Reynolds 1997].

I established 15 east-west 1.5-km transect lines around the periphery of the Ngogo chimpanzees' territory. Each transect bisected a block of three 500 X 500 m quadrats (Fig. 5.1). An extremely large swamp directly to the north of the Ngogo chimpanzee territory precluded placing any transects in that area. Transects were spaced 1-km apart in the north-south direction, with their center points averaging 1.5 km from the edge of the MCP territory boundary. Where the planned locations for transects cut through grassland or the trail system, they were moved, because nest count censuses at other sites have revealed that unhabituated chimpanzees tend to build nests away from human activity zones like trails [Plumptre and Reynolds 1997] and because chimpanzees do not nest in savannas [Poulsen and Clark 2004]. I attempted to locate all transects in tropical high forest, as designated by the Uganda Forest Department National Biomass Study. This is the primary land cover type surrounding the territory of the Ngogo chimpanzees. Nonetheless, several transects passed through short sections of swamp that were not visible on available maps. I also placed three 1.5-km transects within the Ngogo territory for comparison with the results from peripheral areas.

The starting coordinates for each transect were predetermined using GIS. I then walked the transects with an assistant, following a fixed compass bearing at a pace of 1 km/hour [following Furuichi et al. 2001; Plumptre et al. 2003]. A second assistant walked ahead of us with a machete, cutting a minimal amount of vegetation to help us keep our bearing while looking for nests. My assistant and I separately walked each 50 m segment of transect counting individual nests; we then compared notes to ensure all nests sighted by each of us were counted. We walked each transect line once, with all transects completed within 3 months (October 2005 – January 2006) spanning the transition from the wet to the dry season.

Although the patrol data cover a longer period (2000-2006), the nest count data from 2005-2006 were likely to accurately reflect the demography of the communities surrounding Ngogo since 2000. This assumption is based on the fact that three chimpanzee communities habituated to humans within Kibale National Park, at Ngogo, Kanyanchu, and Kanyawara, have not experienced dramatic demographic fluctuations or territory shifts during this period [Ngogo: J. Mitani personal communication; Kanyanchu: J. Lloyd personal communication; Kanyawara: Gilby and Wrangham 2007].

For purposes of the following analyses, the nest counts for each transect were assigned to the centroid of the center quadrat of the three-quadrat block bisected by the transect (Fig. 5.1). I estimated nest counts in unsampled quadrats using simple kriging, as implemented in the Geostatistical Analyst extension in ArcMap 9.1. Kriging is an unbiased geostatistical interpolation method that uses statistical probabilities based on sampled values to create a map of predicted values in unsampled locations. It relies on spatial autocorrelation, with values that are close in space more similar to each other than values that are farther apart. Kriging is controlled by the semi-variogram, which illustrates the spatial autocorrelation between pairs of measured values [Rosenbaum and

Söderström 1996]. Through kriging, I interpolated nest count values for the centroids of other quadrats around the outside of the Ngogo territory, extending out to one quadrat beyond the set of transects.

Graphical Representation of Data

All data used in spatial analyses are graphically illustrated in Fig. 5.1. These include:

1. The Ngogo chimpanzee community territory boundary, using a 100% MCP based on all GPS points taken between June 2003 and October 2005.
2. A system of 500 X 500 meter quadrats superimposed over the Ngogo study area, extending out to one cell beyond the nest count transects.
3. Travel paths for the 61 patrols with sufficient geographic data for analysis.
4. Locations of all intercommunity encounters that I observed between June 2003 and February 2006 (n = 30) and all intercommunity encounters from the long-term data since 2000 (n = 104).
5. The 15 east-west 1.5-km nest count transect lines around the periphery of the Ngogo chimpanzees' territory and the 3 transect lines within the Ngogo territory.

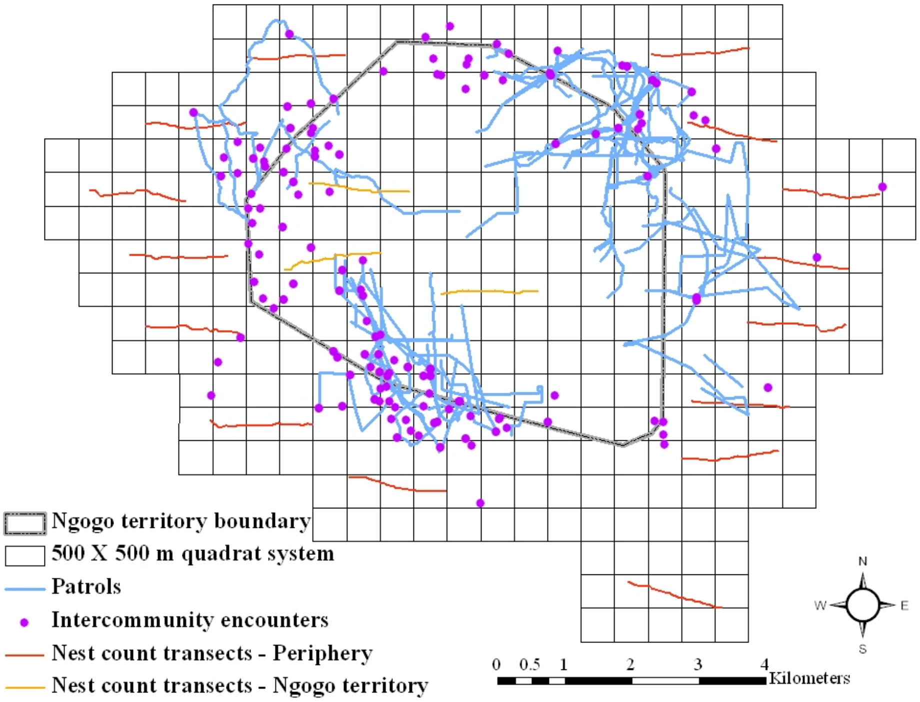


Fig. 5.1. Data used in spatial analyses.

Spatial Analyses

Hypothesis 1: Imbalance of Power

I used the nest count data and locations of patrols to investigate whether the density of chimpanzees in outlying areas predicts where Ngogo chimpanzees patrol. Employing the 500 X 500 m quadrat as the unit of analysis, I determined whether a correlation existed between nest counts and patrol counts. Patrols were closer to territory boundaries than were nest count transects. As a result, I needed to take into account whether patrols occurred in the direction of the quadrat, as they rarely passed through a quadrat where nests had been counted. I therefore drew a circular buffer with a 1500 m radius around the centroid of each quadrat. A 1500 m radius balanced the need to (1) maximize the distance to include patrols that occurred in the direction of the quadrat, and

(2) minimize the area to the sides, where patrols in different directions or more distant chimpanzee density values might be encompassed in the circle. The diameter of these circular buffers (3000 m) approximates the estimated day range of the Ngogo chimpanzees [3600 m, see chapter 4 of this dissertation]. The maximum possible distance within one circle between a nest count and a patrol that occurred in the same direction is the diameter of the circle. Therefore, using a diameter that is similar to the day range makes this circle size biologically relevant. I truncated the quadrat system to create a ring of quadrats whose innermost cells were along the Ngogo territory boundary and whose outermost cells had buffer circles that covered the furthermost edge of patrols (Fig. 5.2). This truncation method resulted in 193 buffer circles.

To determine whether chimpanzee density and patrol locations were correlated, buffer circles required values for both variables. I determined chimpanzee density values for quadrats based on nest counts using the simple kriging technique described above. I selected the highest nest count captured by each buffer circle as its chimpanzee density value. I calculated a patrol count for each buffer circle as the number of patrols that fell within it.

Because these 193 circles overlapped one another, both patrol counts and nest counts were spatially autocorrelated, and standard correlation techniques were not appropriate. To account for the spatial dependence of data, I analyzed patrol counts as a function of chimpanzee density using a linear mixed model, with spatial correlation of residuals [Littell et al. 2006]. The analysis was carried out using SAS Proc Mixed [SAS release 9.1.3].

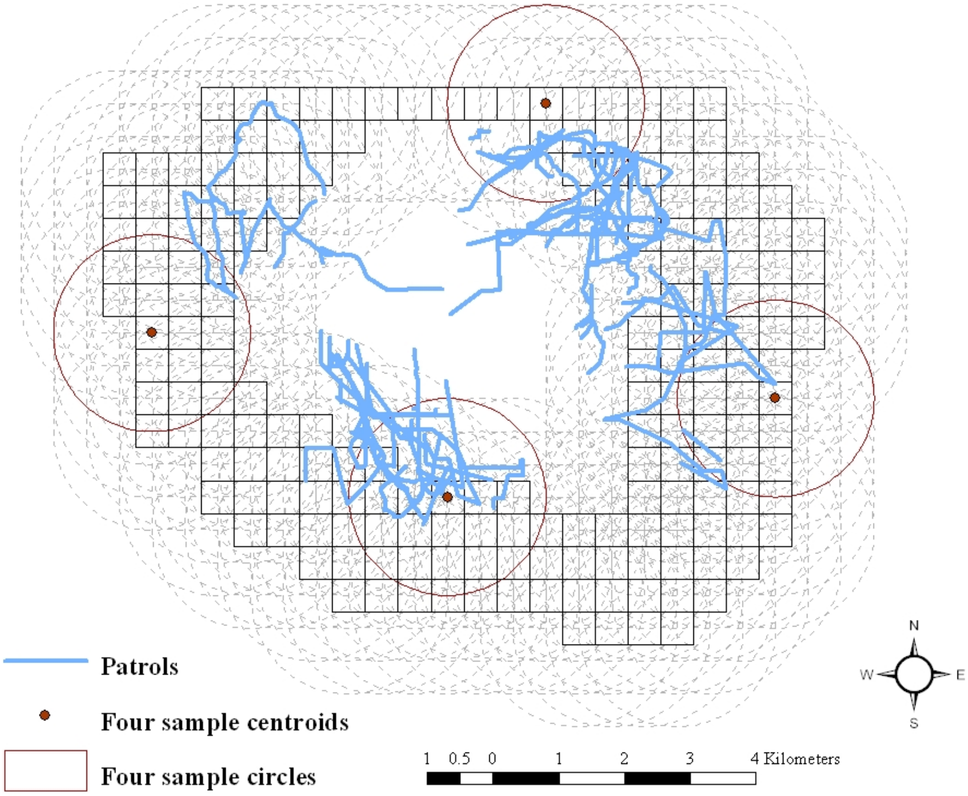


Fig. 5.2. The truncated quadrat system used to analyze patrol count as a function of chimpanzee density. This system includes the 193 quadrats whose buffer circles, radius 1500 meters, lie along the Ngogo territory boundary to the far edge of where patrols occurred. The full set of 193 overlapping buffer circles are outlined with grey dotted lines, and four circles with their centroids are shown in red as examples.

Hypothesis 2: Intercommunity Encounters

To investigate whether the spatial distribution of territorial patrols correlates over the short-term with the spatial distribution of intercommunity encounters, I mapped all patrol paths (n = 61) and all intercommunity encounters. Only those encounters not associated with patrols were analyzed (n = 92). For direct encounters, I plotted the locations where the Ngogo chimpanzees contacted their neighbors. For encounters that involved only auditory contact, I plotted the estimated locations of neighboring individuals. I estimated the density of both patrols and intercommunity encounters for each quadrat using a kernel density function, which used the density of observations to produce a smooth probability estimate of the actual density [Silverman 1986]. I created kernel density estimates using the Spatial Analyst extension in ArcMap 9.1, which measures the density of lines, such as these patrols, in meters of line per square km and the density of points, such as intercommunity encounters, as the number of points per square km. I set the bandwidth to 800 m, such that the density estimate for each quadrat was based on the number of patrols or intercommunity encounters within 800 m of the centroid of the quadrat. This distance was chosen to be biologically meaningful, as it approximates the distance over which a chimpanzee pant hoot can be heard [Mitani, personal communication]. Thus, 800 m represents a distance over which chimpanzees can be detected. I conducted an analysis on all quadrats that the MCP border passed through, plus one full quadrat to either side (Fig. 5.3). This set of quadrats (n = 132) encompassed most patrols and intercommunity encounters. To account for the spatial dependence of data (quadrats that are near one another will have similar density values while those farther apart will have dissimilar values), I analyzed patrol density as a function of intercommunity encounter density using a linear mixed model, with spatial correlation of residuals [Littell et al. 2006]. The analysis was implemented using SAS Proc Mixed (SAS release 9.1.3).

Because I hypothesized that the intercommunity encounter rate would affect the patrol rate on a short-term basis, I also analyzed the data separately by field season, to examine whether intercommunity encounter density predicted patrol density during each field season. For this analysis I used data from my four field seasons and data from Ngogo records for field seasons the previous three years. Density values for quadrats were based on 9 patrols and 13 encounters in 2000, 9 patrols and 13 encounters in 2001, 8 patrols and 17 encounters in 2002, 2 patrols and 4 encounters in 2003, 9 patrols and 4 encounters in 2004, 13 patrols and 7 encounters in 2005, and 11 patrols and 4 encounters in 2006. The field season labeled "2006" actually includes data from my observations that spanned September 2005 – February 2006, while "2005" represents the earlier field season in 2005.

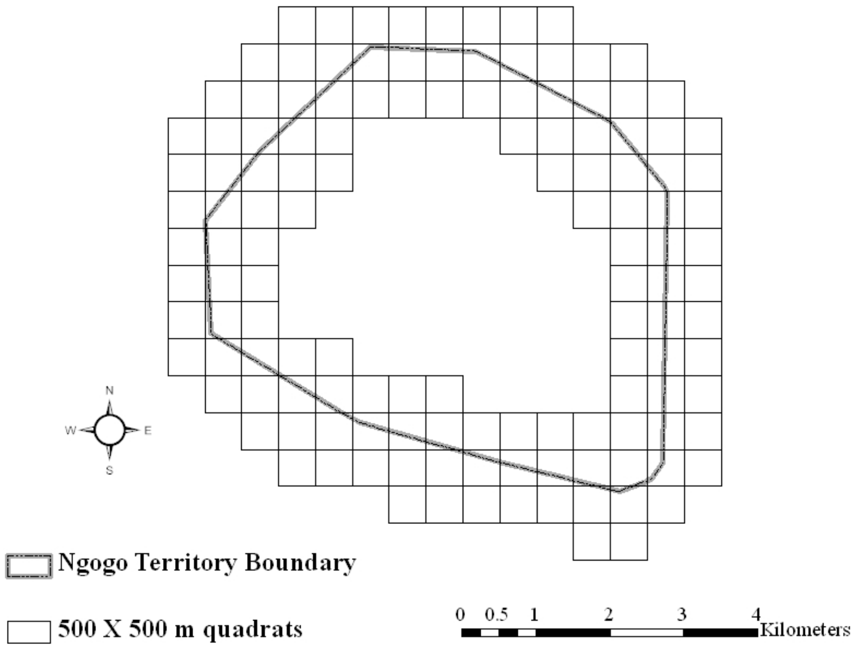


Fig. 5.3. The quadrat set used to analyze patrol density as a function of intercommunity encounter density. This set includes the 132 quadrats falling within 1 full quadrat of the MCP border.

Effects of direction

The tendency to patrol may be influenced by different factors along different borders, depending on the characteristics of the neighbors who occupy various peripheral areas. Therefore, I also conducted an analysis to determine whether the population density of neighbors and density of intercommunity encounters affect patrol rates differently in different directions. Given the distribution of patrols, I operationalized direction with northwest, northeast, southeast, and southwest sectors, by running a straight north-south and a straight east-west line through the centroid of the Ngogo territory (Fig. 5.4). These analyses used a linear mixed model with a term for the sector of the periphery, a term for density, and a term for the interaction of sector and density. The interaction term was used to determine whether the regression slopes of different sectors were significantly different from each other. I also fit a model separately by sector to determine whether the regression slope of any given sector was significantly different from zero.

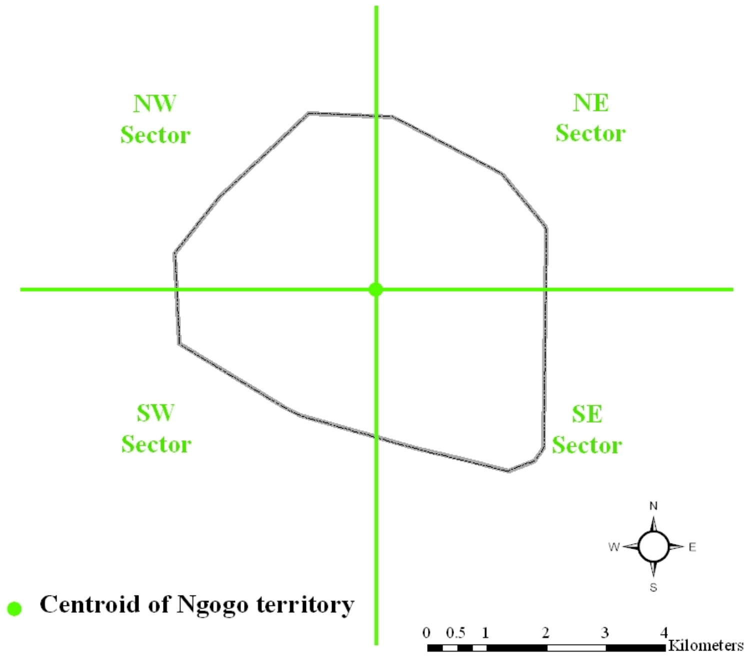


Fig. 5.4. The Ngogo territory and periphery divided into four sectors. The effects of neighbor population density and density of intercommunity encounters on patrols were compared by sector.

I conducted a final analysis by sector using a larger sample of patrols, including those with less precise data for the patrol route (n = 94). I identified the sector and field season in which each patrol and intercommunity encounter occurred. I conducted a simple correlation (Pearson’s r) within each sector, pairing the patrol and encounter data within field seasons. For each sector I examined the relationship between the number of intercommunity encounters and the number of patrols (n = 7 field seasons).

Passive versus active intercommunity encounters

Some intercommunity encounters occurred while the Ngogo chimpanzees were on patrol, and thus were actively sought by the Ngogo chimpanzees (“active”). Other encounters were experienced by the Ngogo chimpanzees when they were not patrolling (“passive”). Some passive encounters precipitated a patrol, even though the Ngogo chimpanzees were not engaged in territorial behavior at the time they heard or met the neighbors. Elevated frequency of active encounters in one direction may indicate that the Ngogo chimpanzees were keenly defending or attempting to expand boundaries there. On the other hand, a higher frequency of passive encounters in a given direction would suggest a balance between the two communities, more of an overlap zone, and/or an area that requires regular territorial defense. I used chi square tests to determine whether the proportions of active and passive encounters differed by location.

Hypothesis 3: Clearing-out

My third hypothesis examined whether chimpanzees patrol boundary zones frequently prior to exploiting a large fruit crop there. To test this hypothesis, I used feeding and spatial data collected during scan samples made every 30 minutes throughout the day. During each scan, I recorded all state behaviors observed by visible party members. I used these records to determine the number of times at least one member of the party fed. I also noted the location of the chimpanzees at these times, allowing a designation for each scan of either core area or periphery, as defined below.

Fruit crops included a single plant species, or a combination of two species, which produced fruits eaten by the chimpanzees over one fruiting season. I defined peripheral fruit crops as those found outside the 50% MCP core area, used on at least 20% of observation days during one fruiting period, and accounting for greater than 10% of all half-hour scans that included feeding during that period. For each identified peripheral fruit crop, I calculated the proportion of patrols during the previous month that occurred in the same area as the crop.

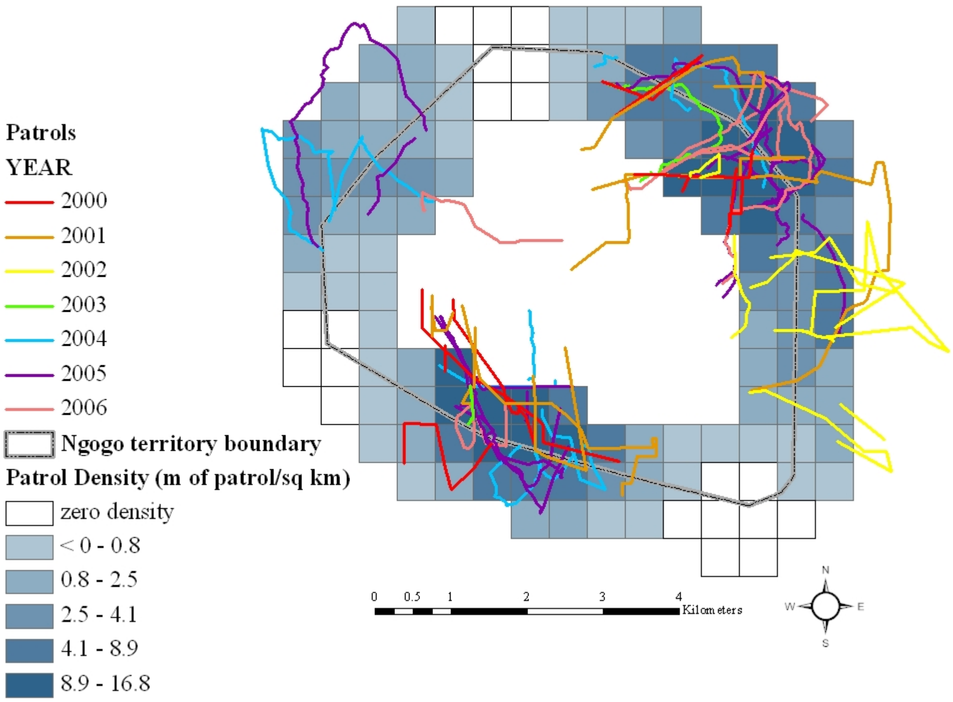
RESULTS

Patrols

Ngogo chimpanzees were observed to patrol 30 times during the 280 days that I observed chimpanzees in 2003-2006; thus they patrolled, on average, every 9.3 days (weekly patrol rate of 0.75). This rate is similar to that found by Watts and Mitani [2001] in 1998-1999, when Ngogo chimpanzees patrolled every 9.7 days (weekly patrol rate of 0.72), and approximately twice as high as rates at Gombe [0.31 between 1977 and 1982, Goodall 1986] and Taï [0.5 between 1984 and 1991, Boesch and Boesch-Achermann 2000]. There was, however, considerable heterogeneity in the rate of patrolling over time, ranging from 0.11 patrols per week in 2003 to 0.8 patrols per week in 2005.

I observed 25 patrols between June 2003 and February 2006. An additional 36 patrols from the long-term data collected at Ngogo had sufficient spatial information for inclusion in the analyses. Combined, these 61 patrols were distributed into four spatial clusters, to the northwest, northeast, east/southeast, and southwest (Fig. 5.5a). No patrols were observed directly north, directly south, or directly west. The density estimate per quadrat ranged from 0 to 16.8 m of patrol path per km^2 (mean = 3.3, SD = 3.9, n = 132 quadrats). Patrol density was highest in the northeast and southwest (Fig. 5.5a and Table 5.1).

a.



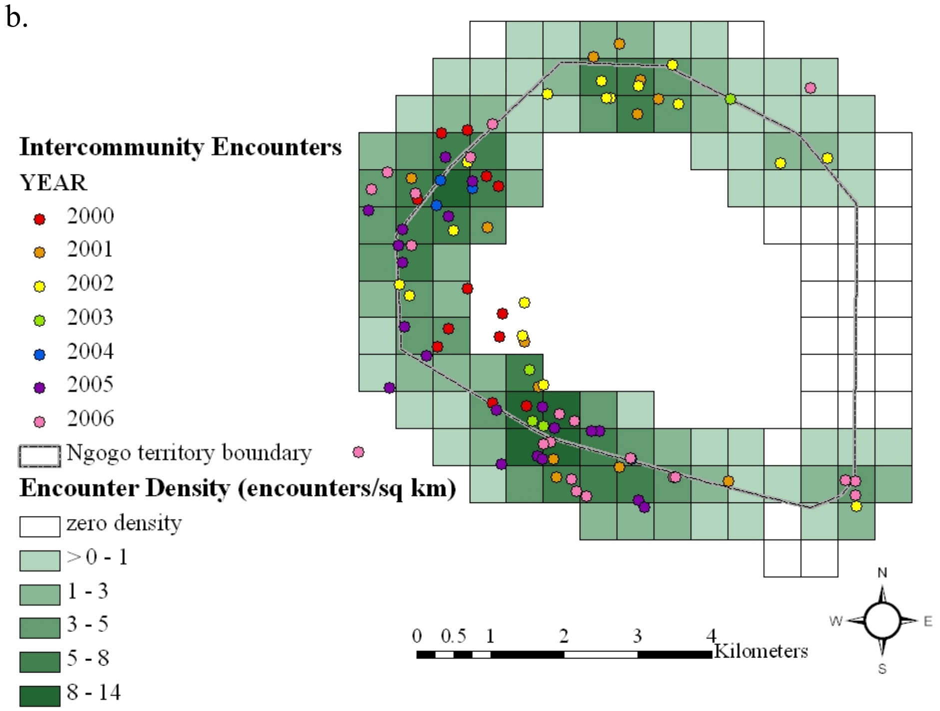


Fig. 5.5. Map of the 132 quadrats used in the analysis of patrol density and intercommunity encounter density. (a) Kernel density of patrols. Darker blue quadrats have higher patrol density values than lighter blue quadrats. Quadrats with a value of zero are not colored. (b) Kernel density of intercommunity encounters. Only intercommunity encounters not associated with patrols were included. Darker green quadrats have higher encounter density than lighter green quadrats. Quadrats with a value of zero are not colored.

TABLE 5.1. Distribution of patrols across years and spatial clusters. The first column displays the total number of patrols in each year. Subsequent columns show the number of patrols and percent of the total for individual years in the four spatial clusters of patrols. Totals for each spatial cluster across all years are shown in bold in the bottom row.

	Total Patrols	***Patrols in Northwest***		***Patrols in Northeast***		***Patrols in East/southeast***		***Patrols in Southwest***	
	#	#	%	#	%	#	%	#	%
2000	9	0	0%	5	56%	0	0%	4	44%
2001	9	0	0%	3	33%	0	0%	6	67%
2002	8	0	0%	1	12.5%	7	87.5%	0	0%
2003	2	0	0%	1	50%	0	0%	1	50%
2004	9	2	22%	2	22%	0	0%	5	56%
2005	17	2	12%	8	47%	1	6%	6	35%
2006	7	1	14%	4	57%	0	0%	2	29%
TOTAL	**61**	**5**	**8%**	**24**	**39%**	**8**	**13%**	**24**	**39%**

Intercommunity Encounters

I recorded intercommunity encounters 30 times during 17 months of observations. An additional 104 intercommunity encounters were available from the long-term data. Intercommunity encounter density was mapped based only on the 92 encounters that occurred when the Ngogo chimpanzees were not patrolling. The kernel density estimate for intercommunity encounters is shown in Fig. 5.5b. The estimated intercommunity encounter density per quadrat ranged from 0 to 14 encounters/km^2 (mean = 2.5, SD = 3.0, n = 132 quadrats).

Nest counts

Nest counts for transects in peripheral areas are shown in Fig. 5.6a. The surface of interpolated values, created using simple kriging, and based on these measured nest count values, is shown in Fig. 5.6b. The highest number of nests (105) was counted on a transect to the southwest of the Ngogo territory. A medium to high concentration of nests is represented by 2 consecutive transects to the southeast (45 and 29 nests) and by one transect to the west (41 nests). All other nest count values are relatively low, ranging from 1 to 16. The three transects placed within the Ngogo territory (not shown in Fig. 5.6) yielded nest counts of 10, 49, and 61, two of which are in the medium to high range.

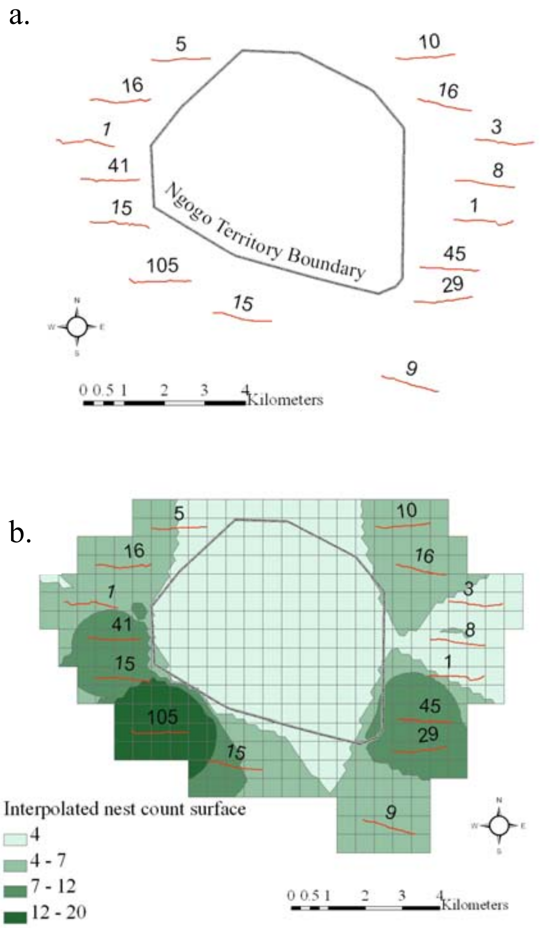


Fig. 5.6. Nest counts in peripheral areas. (a) The number of nests counted is displayed above each transect. (b) The surface created by simple kriging. Interpolated values for nest counts ranged from 4 to 20 and are displayed in a graduated color scheme with darker colors indicating higher predicted values.

Hypothesis 1: Imbalance of Power

Using a linear mixed model that accounted for spatial dependence of the residuals, the maximum kriged nest count value, a measure of chimpanzee density, does not predict patrol count (estimated slope (β) = -0.015, t = -0.16, p = 0.87, n = 193 quadrats). Fig. 5.7 illustrates the lack of relationship between the two variables.

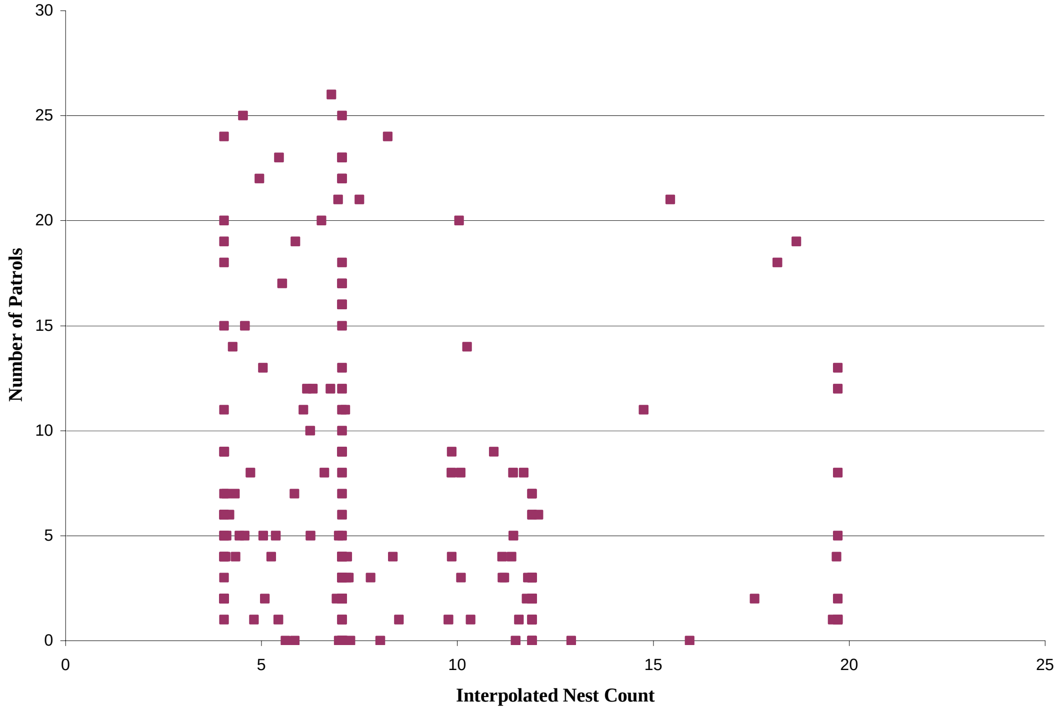


Fig. 5.7. Patrol count plotted against maximum interpolated nest count, a measure of the density of neighboring chimpanzees. Each data point represents one of 193 overlapping circles formed around the centroids of the quadrats as shown in Fig. 5.2. There was no relationship between the two variables.

A possible reason for this negative result is that I may not have measured nests on a sufficient number of transects for kriging to produce accurate interpolated values, resulting in values that were too homogenous. While the range of measured values was 1 – 105, the range of kriged values was 4.0 – 19.7. For example, for the quadrat where the measured value was 105, the corresponding interpolated value was only 19.7 (Fig. 5.6b). Therefore, I also analyzed the data using only 15 circles around the centroids of the quadrats for which I had counted nests. In this smaller sample of circles measured nest counts again did not predict the number of patrols (estimated slope (β) = 0.012, t = 0.34, p = 0.74, n = 15 quadrats; Fig. 5.8 and 5.9).

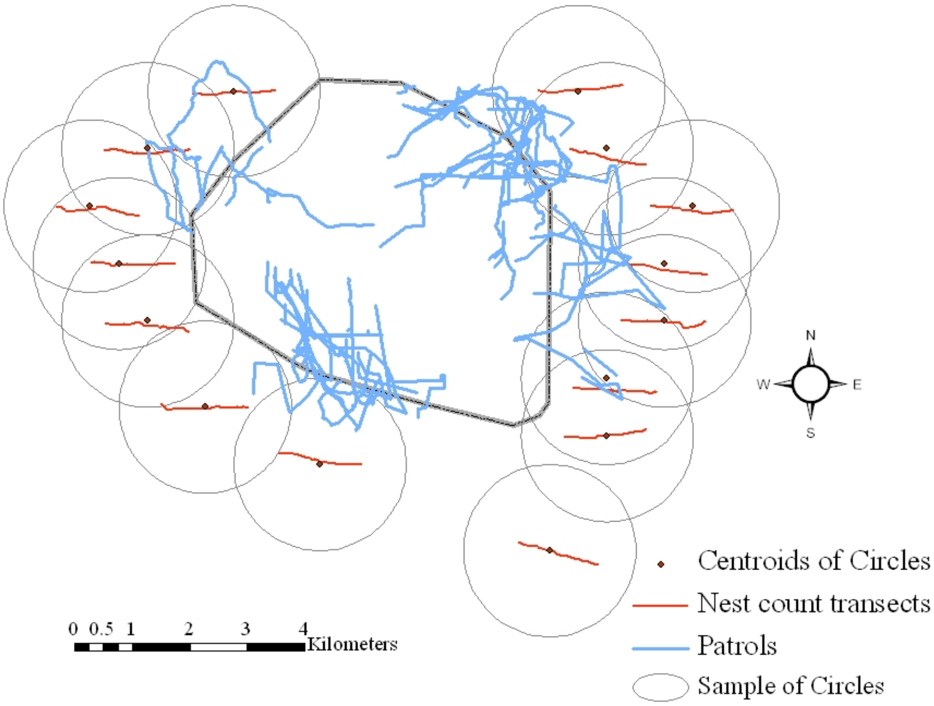


Fig. 5.8. The sample of circles (n = 15) created around centroids, which represent the center of the transects along which nests were counted.

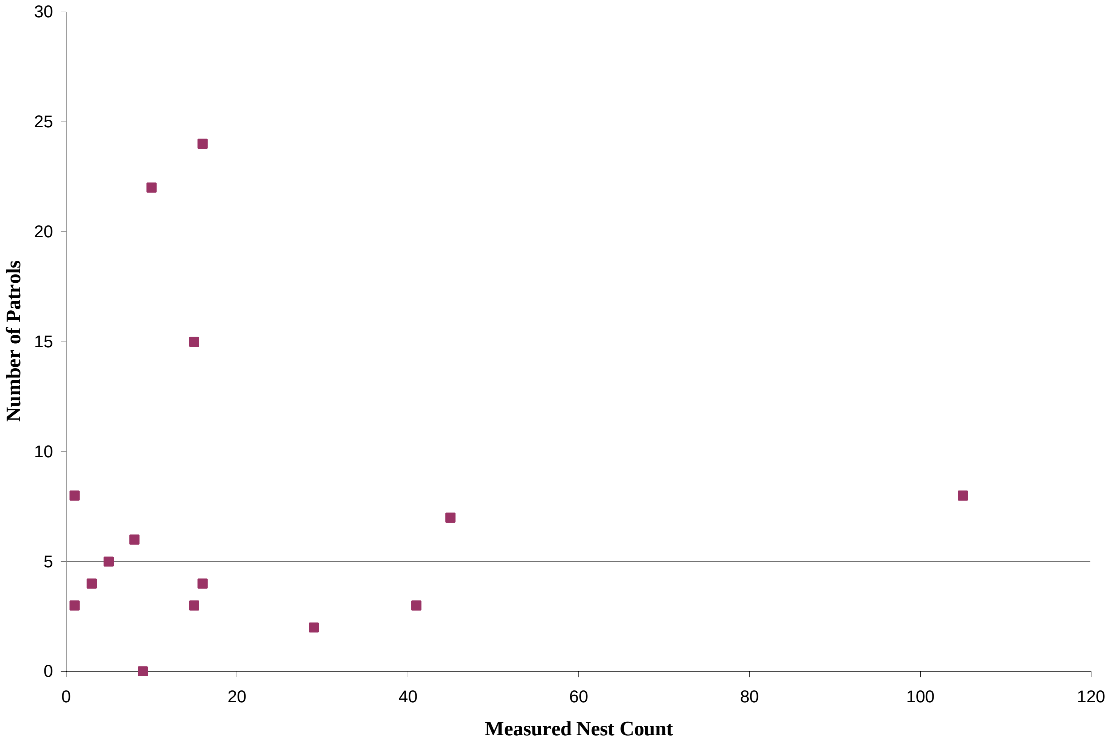


Fig. 5.9. Patrol count plotted against measured nest count. Each data point represents one of 15 circles formed around the centroids of the quadrats with measured nest count values. There was no relationship between the two variables.

The effect of the density of chimpanzee neighbors on patrol rate may not be uniform in all directions. The distribution of patrols and nest counts on the maps in Fig. 5.5a and 5.6 suggests a difference between the northeast and southwest, the two sectors with the highest patrol rates. In the northeast, the Ngogo chimpanzees patrolled heavily, with 39% of all patrols occurring there (Table 5.1), and nest counts were fairly low (mean = 10, SD = 7, range = 3-16, n = 3 transects). On the other hand, in the southwest, another direction in which the Ngogo chimpanzees patrolled often, with another 39% of all patrols taking place there (Table 5.1), nest counts were relatively high (mean = 44, SD = 42, range = 15-105, n = 4 transects). One nest count in particular was much higher in the southwest sector than anywhere else.

These differences suggest that in the northeast, Ngogo chimpanzees may be taking advantage of numerical superiority to push the territory boundary in that direction. If so, then an analysis by sector would show a negative relationship between nest count and patrol rate in the northeast. In contrast, the Ngogo chimpanzees may patrol in the southwest simply to try to maintain their territory there against a stronger community, trying to push its boundary into the Ngogo territory. This dynamic would result in a positive relationship between nest count and patrol rate in the southwest sector. If these two opposing factors were operating in the two different sectors, their results would cancel each other out in the overall analysis. I therefore analyzed the data separately in the four sectors of the periphery.

The results of the by-sector analysis, however, do not support this hypothesis. The regression slopes in different sectors were not significantly different from each other (F = 0.58; df = 3,185; p = 0.63), which suggests that the population density of neighbors does not affect the rate of patrolling differently in different areas. Also, regression slopes were not significantly different from zero for any of the individual sectors (southwest: estimated slope (β) = 0.06, std err = 0.21, t = 0.28, df = 1, 44, p = 0.78; northeast: estimated slope (β) = 0.21, std err = 0.42, t = 0.5, df = 1, 41, p = 0.62; northwest: estimated slope (β) = -0.09, std err = 0.09, t = -1.04, df = 1, 37, p = 0.31; and southeast: estimated slope (β) = -0.14, std err = 0.15, t = -0.91, df = 1, 63, p = 0.37). These results indicate that patrol frequency was not related to the density of neighboring chimpanzees as assayed by nest counts within any individual sector.

Hypothesis 2: Intercommunity Encounters

Results of the linear mixed model that accounted for spatial dependence of the residuals show that the density of intercommunity encounters predicts patrol densities for data from all years combined (n = 132 quadrats, estimated slope (β) = 0.29, standard error = 0.10, t = 2.82, df = 1, 130, p = 0.006; Fig. 5.5 and 5.10).

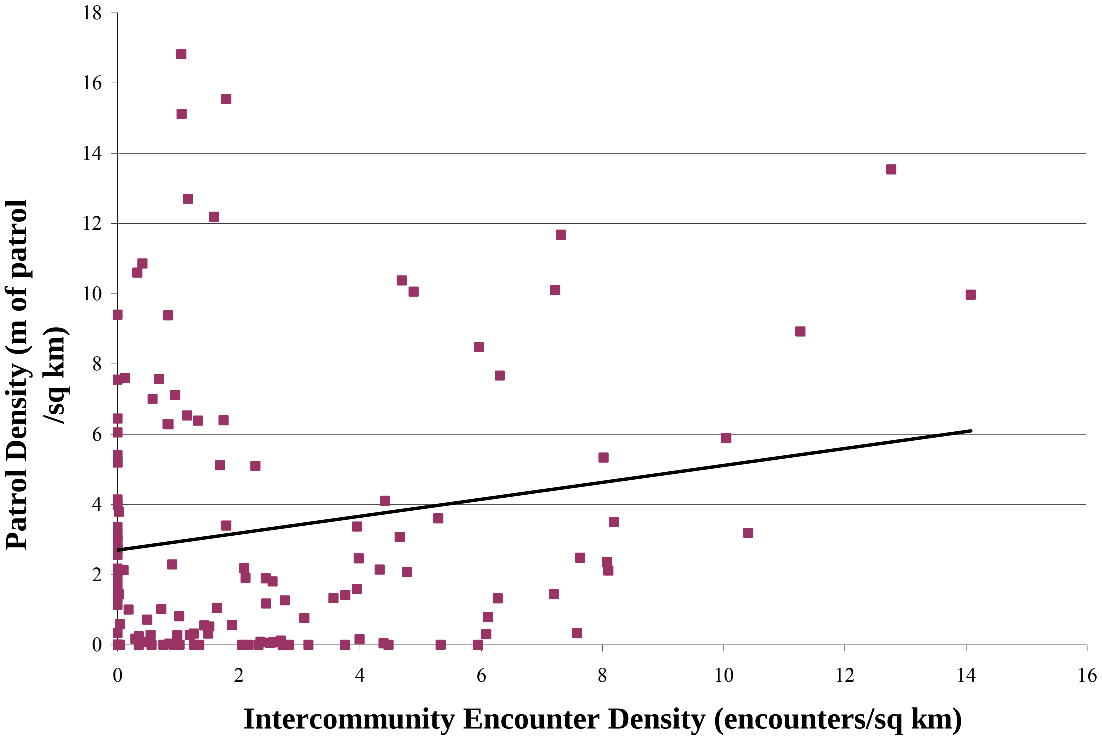


Fig. 5.10. Relationship between patrol density and intercommunity encounter density, all years combined. Each data point represents the density values for one quadrat (n = 132 quadrats).

However, intercommunity encounters were hypothesized to influence patrols over the short-term. Ngogo chimpanzees may increase patrol rates in certain peripheral areas on an as-needed basis, when the threat-level is perceived as higher, based on the encounter rate. When the same analysis was performed on the data from each field season separately, the slope was positive for 5 of 7 field seasons, but only significant for 2003 and 2004. Thus there was no consistent relationship between intercommunity encounter density and patrol density over short periods of time (Table 5.2; Fig. 5.11).

TABLE 5.2. The relationships between intercommunity encounter density and patrol density by quadrat across 7 field seasons. * denotes a result significant at the 0.05 level.

Year	*Parameter estimate (Standard Error)*	*DF*	*t-value*	*p-value*
2000	-0.033 (0.093)	1, 130	-0.35	0.7237
2001	0.073 (0.08)	1, 130	0.92	0.3606
2002	0.0096 (0.069)	1, 130	0.14	0.8895
2003	0.28 (0.047)	1, 130	5.95	<0.0001 *
2004	0.23 (0.092)	1, 130	2.52	0.0130*
2005	-0.023 (0.076)	1, 130	-0.31	0.7585
2006	0.12 (0.067)	1, 130	1.73	0.0853

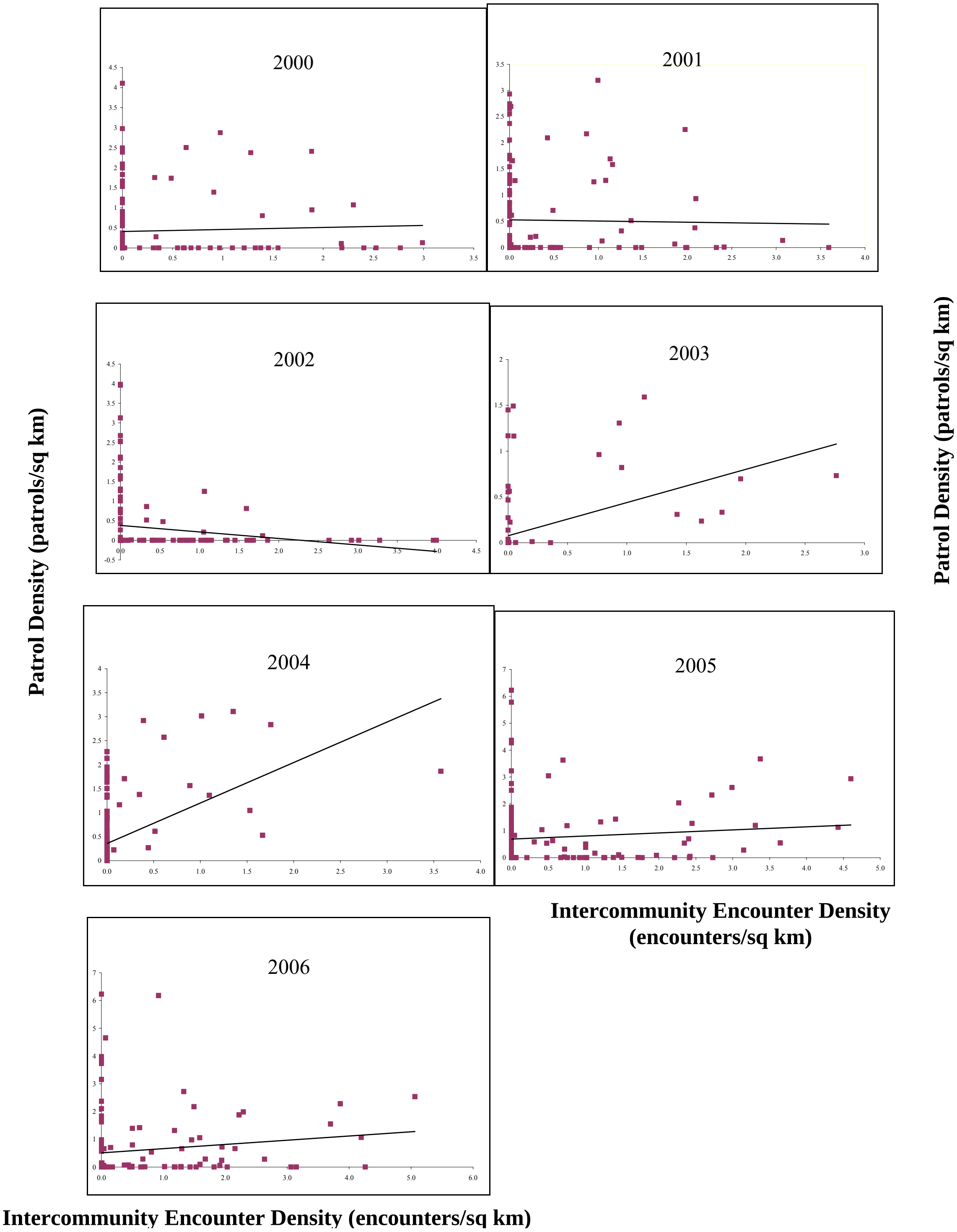


Fig. 5.11. Relationship between patrol density and intercommunity encounter density. Field seasons are presented separately. Data points represent density values for quadrats (n = 132 quadrats). Significant relationships were obtained in 2003 and 2004 only.

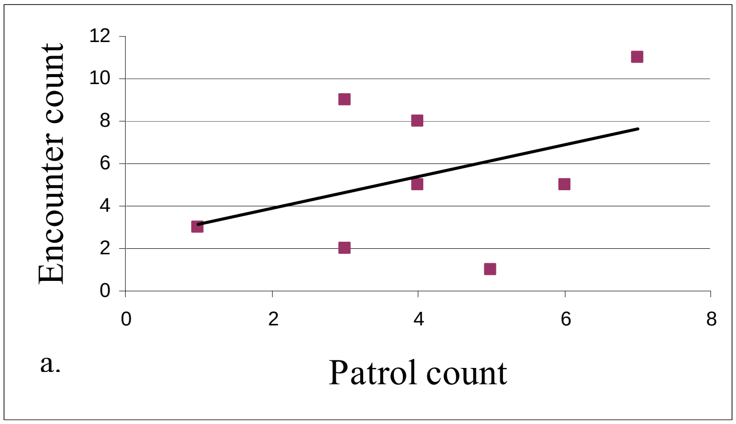
The slopes of the relationship between intercommunity encounter density and patrol density did not differ by sector (F = 0.42; df = 3, 124; p = 0.74). In the separate analysis of each sector, however, both the southwest and northwest sectors had regression slopes significantly different from zero (southwest: estimated slope (β) = 0.54, std err = 0.12, df = 1, 29, t = 4.39, p = 0.0001; northwest: estimated slope (β) = 0.13, std err = 0.05, df = 1, 33, t = 2.71, p = 0.01) while the northeast and southeast did not (northeast: estimated slope (β) = 0.96, std err = 0.52, df = 1,30, t = 1.85, p = 0.07; southeast: estimated slope (β) = 0.12, std err = 0.15, df = 1, 32, t = 0.80, p = 0.43). In both the southwest and northwest, then, intercommunity encounter rates were positively associated with patrol rates.

Short-term relationship between intercommunity encounters and patrols within sectors

A larger dataset of patrols (n = 94) included the 61 patrols used in the preceding analyses, and 33 others with insufficient data to map exact routes, all of which could be assigned to one of the four sectors of the territory periphery. To further investigate the possibility that intercommunity encounters and patrols in particular sectors were associated over the short-term, I used this larger dataset to conduct correlational analyses in each sector. The patrols were distributed across 8 field seasons: 2000, 2001, 2002, 2003, 2004, early 2005, late 2005-early 2006, and 2006. As was true in the smaller dataset of patrols, the southwest and northeast sectors had the highest patrol count across all years (Table 5.3). For the two sectors with the highest number of patrols, I found moderately strong correlations between the intercommunity encounter count and the patrol count (southwest: r = 0.40; northeast: r = 0.64; n = 8 field seasons; Table 5.3; Fig. 5.12). However, in the northeast there were many patrols but few intercommunity encounters across all years, while in the southwest both patrols and encounters were high. Interestingly, the northwest sector is the only sector showing a negative relationship between intercommunity encounter count and patrol count, with many encounters but few patrols.

TABLE 5.3. The overall counts per sector for intercommunity encounters and patrols. For each sector, the r-value is shown representing the correlation between encounter count and patrol count across 8 field seasons.

Sector	*Encounter Count (all field seasons)*	*Patrol Count (all field seasons)*	*Correlation (n = 8 field seasons)*
SW	44	33	0.40
NE	7	37	0.64
NW	34	6	-0.31
SE	7	18	0.23



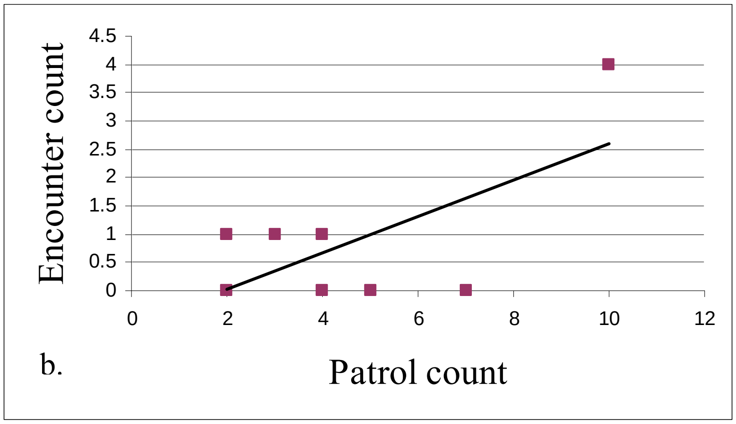


Fig. 5.12. The relationship between patrol count and intercommunity encounter count in the two most heavily patrolled sectors. Each data point represents one field season (n = 8). (a) southwest sector; r = 0.40. (b) northeast sector; r = 0.64.

Passive versus active intercommunity encounters

Ngogo chimpanzees experienced passive intercommunity encounters more often (n = 97) than they encountered others actively (n = 33). The distribution of active and passive encounters was not random with respect to sector, however (Fig. 5.13). A chi square test revealed a significant relationship between sector and the ratio of passive to active intercommunity encounters (chi square = 32.28, df = 3, $p < 0.0001$). To determine where the differences were, I also performed chi square tests between each pair of sectors. The proportion of passive to active encounters in the northeast sector (6:15) was significantly lower than the proportion of passive to active encounters in each of the other sectors (southeast: 9:5; southwest: 47:10; northwest: 35:3; Table 5.4). I also found a significant difference between the southeast and northwest sectors (chi square = 6.08, p = 0.01, df = 1): the Ngogo chimpanzees had more active and fewer passive encounters in the southeast compared with the northwest.

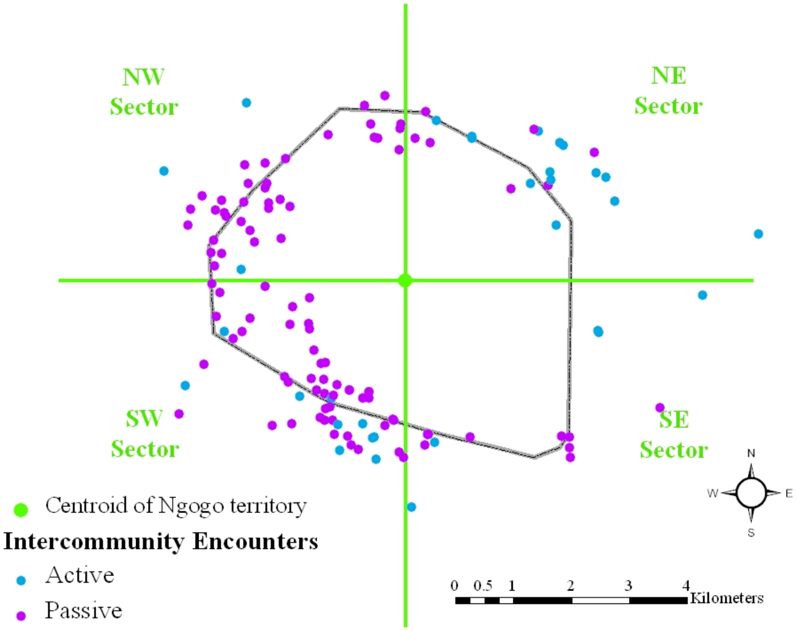


Fig. 5.13. A map of the distribution of active and passive intercommunity encounters across the 4 sectors of the periphery.

TABLE 5.4. Significant differences between sectors in the proportions of passive and active intercommunity encounters. Chi square values are shown in bold with the p-values below.

	NE	SE	SW	NW
NE	*	**4.38** 0.04*	**20.50** < 0.0001*	**25.75** < 0.0001*
SE	*	*	**2.23** 0.14	**6.08** 0.01*
SW	*	*	*	**1.80** 0.18

Hypothesis 3: Clearing-out

Six peripheral fruit crops ripened during my study. For three of these six I observed chimpanzees for the majority of the preceding month (17-20 observation days), allowing me to examine patrol activity prior to the crop (Fig. 5.14). From July 3-27, 2003, the Ngogo chimpanzees fed on *Aningeria altissima* in the western periphery of their range on 23.8% of observation days, accounting for 12.7% of all feeding scans during that period; between October 20 and November 16, 2004 *Monodora myristica* and *Ficus mucuso* in the eastern periphery of their range were utilized on 52.4% of observation days and accounted for 41.6% of feeding scans; and from March 28 to April 6, 2005 they fed in the southwest periphery on *Mimusops bagshawei* on 87.5% of observation days, accounting for 44.1% of feeding scans.

Patrol activity during the month prior to the crops does not suggest that chimpanzees were trying to clear these areas out before utilizing them. Almost no patrols during months preceding peripheral fruit crops occurred in the same peripheral area as the crop (Range: 0 – ¼ of patrols; Table 5.5; Fig. 5.14).

TABLE 5.5. Peripheral fruit crops utilized by the Ngogo chimpanzees and their patrol activity during the preceding month.

Dates of fruiting season for peripheral crop	***Location with regard to the Ngogo core area***	***Resource***	***Total patrols in previous month***	***Patrols to crop area in previous month***	***# of obs days in previous month***
7/3/03-7/27/03	West	*Aningeria altissima*	2	0	20
10/20/04-11/16/04	East	*Monodora myristica/ Ficus mucuso*	3	0	17
3/28/05-4/6/05	Southwest	*Mimusops bagshawei*	4	1	22

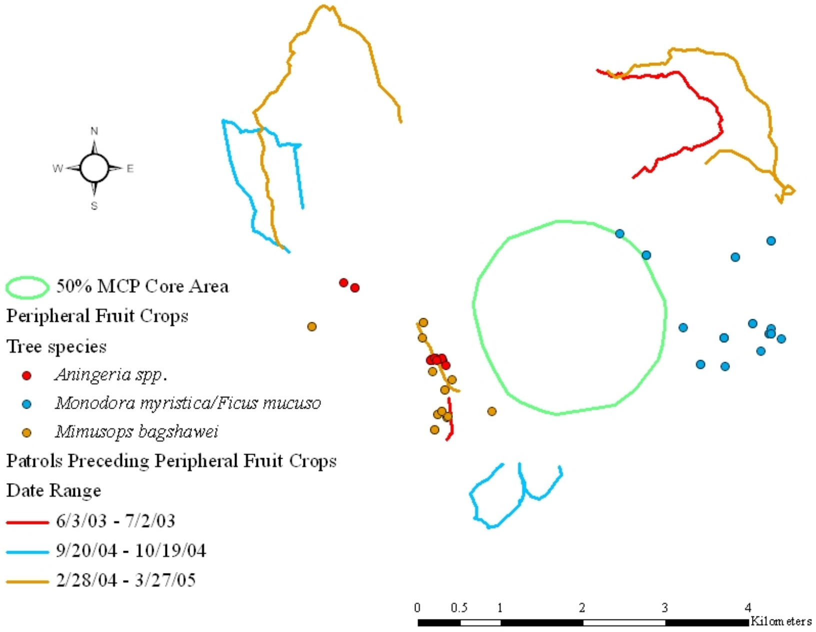


Fig. 5.14. Locations of peripheral fruit crops and patrols during the preceding month. Patrols are displayed in the same color as the fruit crop they precede.

DISCUSSION

Patrols were spatially clustered and territorial activities clearly varied depending upon location around the periphery of the Ngogo territory. The density of chimpanzees around the periphery of the Ngogo territory, as assayed by nest counts, did not predict the spatial distribution of patrols over the long-term as hypothesized. This result held regardless of whether I used the measured nest counts or predicted values based on kriging. There did not appear to be directional effects either. When the periphery of the Ngogo territory was divided into 4 sectors, there was no relationship between the distribution of patrols and the estimated nest counts within any sector.

My failure to support the hypothesis that chimpanzees patrol in areas where they outnumber their neighbors may be due to limitations of the data. The nest count method may have been an inadequate way to assay relative population density of surrounding communities. Time constraints limited the number of transects that could be established, as well as the frequency with which transects could be walked. A larger sample of the area around the Ngogo territory might yield more accurate density estimates. In addition, local density should vary over time in response to fluctuating food availability, so nests counted at a single point in time may not reflect longer-term patterns of peripheral area use by neighbors. Chimpanzees probably maintain a general knowledge about the location and demography of their neighbors, which they incorporate into considerations of power imbalances that then influence territorial activity [Boesch 2007]. However, until more of the Ngogo community's neighbors are habituated, researchers do not possess the same knowledge that the Ngogo chimpanzees have about their numbers and the extent of their territories. Given presently-available data, the imbalance of power hypothesis does not appear to explain the spatial distribution of the Ngogo chimpanzees' territorial patrols.

The investigation of effects of intruder pressure on the spatial distribution of territorial patrols yielded mixed results. Although intercommunity encounter density predicted patrol density when data from all field seasons were combined, a consistent significant relationship did not exist over the short term, as was hypothesized. However, in a larger sample of patrols, with less precise location data, a short-term relationship between intercommunity count and patrol count was found in the two sectors of the periphery with the highest patrol rates. In addition, when I analyzed directional effects over the long-term, I found that intercommunity encounter density predicted patrol density in the northwest and southwest, but not in the northeast and southeast sectors. This result suggests that Ngogo chimpanzees may respond differently to intruder pressure depending on where it occurs, or which neighbors are involved.

An interesting distinction existed between actively sought and passively experienced intercommunity encounters. The northeast was the only sector in which the Ngogo chimpanzees had more active than passive encounters with neighbors. The relationship between sector and ratio of passive to active encounters was significant when the northeast sector was paired with each of the other sectors. This result suggests that the Ngogo chimpanzees were more actively defending or expanding their boundary to the northeast than in other directions. Another possibility is that the community to the northeast does not use the overlap zone with the Ngogo community as much as communities in other directions, and they may be less likely to intrude into the Ngogo territory than other surrounding communities. One or both factors would result in fewer passive encounters there.

The northwest sector, in contrast, had the highest passive to active intercommunity encounter ratio. This could suggest that both the Ngogo community and the community to the northwest use the overlap zone regularly or that the northwest community moves into the Ngogo territory more often than the reverse. In fact, the number of patrols in the northwest sector was quite low, while the number of intercommunity encounters was high. An adult male from Ngogo was found dead from wounds inflicted by other chimpanzees in the northwest sector in February 2006. Two other Ngogo males were killed just south of the northwest sector in the southwest sector in July 2005. Since my sectors are arbitrary and do not reflect knowledge of where other chimpanzee communities actually range, at least one, but maybe all three, deaths could have been perpetrated by a community to the northwest.

Oddly, the nest counts in both the northeast and northwest sectors were fairly low. If my nest counts accurately reflected the density of chimpanzees in those directions, then it is not immediately clear why the Ngogo chimpanzees appeared to be on the offensive in the northeast but on the defensive in the northwest.

Nest counts suggest that the community to the southwest of Ngogo, where the nest count was 105, may be even larger than, or at least as large as, Ngogo, where two out of three nest counts were in the moderately high range. However, the Ngogo community seems to be comparably sized to or larger than all other surrounding communities. Therefore, the largest threat to the Ngogo chimpanzees as assayed by my nest counts, if community size is correlated with the number of males and the number of males determines the outcome of intercommunity interactions, is clearly the community to the southwest. The highest rate of intercommunity encounters also occurred in the southwest sector, with the majority of them passive, and perhaps as a consequence, the Ngogo chimpanzees patrolled there frequently.

The third hypothesis, that the Ngogo chimpanzees patrol frequently before exploiting a large peripheral fruit crop, was not supported. Of six identified peripheral fruit crops, I only had patrol data from the preceding month for three. This paucity of data prevented a quantitative investigation, but almost none (0/2, 0/3, and 1/4) of the patrols during the month preceding each peripheral fruit crop were conducted in the same peripheral area as the crop. Thus patrolling behavior does not seem to serve to “clear-out” contested areas of the periphery that experience large seasonal fruit crops, although the question is still open until more data become available.

Several factors appear to be involved in determining where Ngogo chimpanzees patrol. In particular the spatial distribution of their territorial activities seems to be responsive to characteristics of specific neighboring communities. Over the long term, Ngogo chimpanzees patrolled more frequently in peripheral areas where they experienced more intercommunity encounters. In the most heavily patrolled areas, intercommunity encounter density and patrol density were also positively associated over the short-term. Furthermore, the ratio of active to passive encounters varied as a function of location, suggesting that the Ngogo chimpanzees defended some boundary areas more keenly than others. However, based on currently available nest count data, they do not respond to power imbalances between themselves and neighbors when choosing patrol directions. Better knowledge about the ranging activities of neighbors would facilitate future investigations of this question.

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CHAPTER 6

Summary and Discussion

Although territorial boundary patrols have been the subject of considerable research, the energetic costs and spatial distribution of patrols have not been widely investigated. In this dissertation I examined these issues using observations of an unusually large community of chimpanzees at Ngogo in the Kibale National Park, Uganda. I set out to address the energetic costs of chimpanzee patrolling and to determine the factors that affect where chimpanzees patrol. These two topics formed the basis of Chapters 4 and 5. In the process of investigating these problems, I conducted additional studies of chimpanzee ranging behavior. Boundary patrols occur along the periphery of or outside the territory, and asking questions about where chimpanzees patrol requires a spatial representation of the territory. A brief review of chimpanzee ranging studies showed that several methods have been used to estimate territory size and to depict differential use of the territory. These studies also revealed that different chimpanzee communities inhabit territories that vary considerably in size. Chapter 2 emerged out of work to determine which methods are most accurate and reliable. In Chapter 3, I assessed two factors hypothesized to influence variation in territory size, food availability and intercommunity relations.

In Chapter 2, I compared different methods used to estimate the size of animal territories and core areas and implemented them using observations of the Ngogo chimpanzees. Territory size estimates for the Ngogo community varied between 19.5 and 29.25 km^2, depending on the method used. Although the Ngogo chimpanzee community is unusually large, these territory size estimates fall within the range of those calculated for other forest-living chimpanzee communities. In general, estimates calculated using different methods overlapped considerably and did not differ greatly. Different techniques also yielded similar depictions of how the Ngogo chimpanzees used their territory. Estimates created with subsamples of the data, intended to reduce autocorrelation between data points collected successively, were substantially lower, particularly when implementing non-statistical techniques. These results lend credence for comparisons between studies that typically employ different techniques to estimate territory size, especially in cases utilizing large samples that encompass all places chimpanzees actually range. Regardless of method, territory size estimates reached an asymptote after approximately 2500 locations, collected over 164 days during 10 months. Subsampling data at locations separated by longer time intervals resulted in smaller territory size estimates, an unsurprising result as biologically relevant information about where animals spent their time was lost [cf. Barg et al. 2005; Blundell et al. 2001; Cushman et al. 2005; De Solla et al. 1999].

One way to quantify the pattern of space use by animals is to identify a core area, which is the area with the highest probability of use [Samuel et al. 1985]. In Chapter 2, I determined that grid cells exceeding an equal use pattern contained 80% of all observations. This figure is quite close to the 75% of observations often chosen to represent the core area in chimpanzee studies [Boesch and Boesch-Achermann 2000; Herbinger et al. 2001; Lehmann and Boesch 2003]. The 75 – 80% core areas, calculated using multiple methods, represented about 1/3 of the Ngogo territory, a figure similar to core areas estimated for other chimpanzee communities [Boesch and Boesch-Achermann 2000; Herbinger et al. 2001; Lehmann and Boesch 2003]. I also defined an exclusive core area akin to that calculated for chimpanzees at Taï [Herbinger et al. 2001]. The intersection of the 75% core area with the area used only by the Ngogo chimpanzees represented about 23% of the total Ngogo territory. This area is more than twice that covered by exclusive core areas computed for chimpanzee communities in the Taï National Park, Côte d'Ivoire [Herbinger et al. 2001]. Although the Ngogo chimpanzees' territory is not as large as might be expected for such a large community, they had exclusive access to a larger portion of their territory than a similarly defined area at Taï. The exclusive control over a large area may be one reason why a relatively small territory can support the large number of chimpanzees at Ngogo.

I applied the information in Chapter 2 about the territory size and core area of the Ngogo chimpanzees in subsequent analyses. In Chapter 3, I tested the hypotheses that resource availability and intercommunity relations influence ranging patterns. Specifically, I assessed the effects of fruit availability and intercommunity encounters on the monthly territory size of the Ngogo chimpanzees and the extent to which use of the territory was constrained by neighbors. Although many territorial species use small portions of their territories when food is abundant [Adams 2001], fruit availability did not correlate with territory size at Ngogo. Local conditions at Ngogo and the fission-fusion grouping pattern of chimpanzees provide two possible reasons for this negative result. Recent research shows that the habitat at Ngogo may be unusually productive [Potts 2008]. Thus, chimpanzees there may never be so food-stressed to necessitate wider ranging to acquire enough food to satisfy their nutritional needs. Alternatively, chimpanzees offset food shortfalls by forming smaller parties [Basabose 2004; Boesch 1996; Chapman et al. 1995; Matsumoto-Oda et al. 1998; Mitani et al. 2002a; Wrangham 2000], and adjusting party size in response to a fluctuating food supply may provide another option to altering ranging patterns.

I also found little evidence that relations with neighboring communities affected chimpanzee ranging patterns at Ngogo. Although monthly territory size tended to be small when the intercommunity encounter rate was high, this trend was not statistically significant. I additionally predicted that the core area would be centrally located, but instead found that the core area was not perfectly central and did not overlap substantially with the area exclusively used by Ngogo chimpanzees. Other predictions of the intercommunity relations hypothesis were also not upheld. For example, the Ngogo chimpanzees did not seek security from their neighbors by reliably returning to the core area of their territory each night. In sum, although food availability and intercommunity relations have frequently been shown to influence ranging patterns in territorial animals [Adams 2001], the results I presented in Chapter 3 suggest that neither affect the territory size of chimpanzees at Ngogo.

I examined how chimpanzees defend their territories against conspecifics in Chapters 4 and 5. Chimpanzee males regularly patrol territory boundaries in large parties, apparently seeking information about or contact with members of neighboring communities. Some patrols involve deep incursions into the territories of neighboring communities [Boesch and Boesch-Achermann 2000; Goodall 1986; Goodall et al. 1979; Herbinger et al. 2001; Mitani and Watts 2005; Watts and Mitani 2001]. In Chapter 4, I asked whether chimpanzees incur costs by patrolling. Several studies have investigated the potential benefits derived by patrollers [Goodall et al. 1979; Mitani and Watts 2005; Mitani et al. 2002b; Watts and Mitani 2001; Watts et al. 2006; Williams et al. 2004; Wilson and Wrangham 2003]. Patrols nevertheless occur infrequently, a fact that suggests they are also costly to participants. Patrolling chimpanzees engage in prolonged movements accompanied by little or no feeding, and patrollers are likely to suffer energetic costs as a consequence [Boesch and Boesch-Achermann 2000; Goodall et al. 1979; Mitani and Watts 2005; Watts and Mitani 2001]. Prior to my research it has been unclear whether energy costs constrain territorial boundary patrol activity [e.g. Herbinger et al. 2001; Mitani and Watts 2005; Watts and Mitani 2001; Wilson and Wrangham 2003]. My results suggest that they do, as I found that male chimpanzees covered longer distances and spent more time traveling and less time feeding during patrols than during control periods. Traveling longer distances involved appreciably greater energy expenditure. These findings represent the first empirical demonstration that chimpanzees suffer nontrivial energetic costs by participating in territorial boundary patrols.

Patrols occur non-randomly around territory boundaries, and their locations may shift over time [Watts and Mitani 2001]. The factors underlying this variation have not been investigated. In Chapter 5, I evaluated the effects of three social and ecological factors hypothesized to influence where chimpanzees patrol. First, I examined whether long-term patterns of patrolling direction and frequency can be explained by an imbalance of power between the Ngogo community and its neighbors. In contrast to a prediction of this hypothesis, I found that relative population density, as assayed by nest counts, did not affect where the Ngogo chimpanzees patrolled. My failure to support this hypothesis may be due to limitations of the data. Specifically, I was able to survey only a limited number of nest count transects, and the relatively small sample may have led to an imprecise picture of the population density of neighbors surrounding the Ngogo community. Habituating neighboring chimpanzees to the presence of human observers will be required to assess power differentials more accurately, and until this is done, it will remain unresolved whether chimpanzees incorporate knowledge regarding power imbalances into decisions about where to patrol [Boesch 2007].

Second, I investigated whether the spatial distribution of territorial patrols correlated with the spatial distribution of intercommunity encounters. Results indicated that there was no association between the locations of patrols and encounters over short periods of time. These were, however, positively associated over the short-term when analysis was restricted to the most heavily patrolled areas of the territory periphery. Moreover, patrol density and encounter density also showed a significant relationship across all peripheral areas when considered together over longer periods of time. Finally, analyzing directional effects over the long-term, I found that intercommunity encounter density predicted patrol density to the northwest and southwest, but not in the northeast and southeast sectors of the periphery.

Third, I sought to determine whether chimpanzees patrolled boundary zones frequently prior to exploiting a large fruit crop in the area. Limited data precluded me from testing this hypothesis rigorously, but my observations indicated that the Ngogo chimpanzees patrolled rarely in the periphery of their territory before feeding on large quantities of fruit in the same area. These observations suggest that patrolling behavior does not serve to “clear-out” contested areas prior to their use, although the question will remain open until more data become available.

While examining the intercommunity encounter data in Chapter 5, I found that some intercommunity encounters occurred while the Ngogo chimpanzees were on patrol, and thus were actively sought by them. Others were experienced passively while the Ngogo chimpanzees engaged in their normal activities and were not patrolling. The Ngogo chimpanzees had more active than passive encounters with their neighbors in only the northeast sector of the periphery of their territory. This result suggests that the Ngogo chimpanzees were actively defending or expanding their territory in the northeast more than in other directions. Another possibility is that the chimpanzee community to the northeast does not use their area of overlap with the Ngogo chimpanzees as much as communities in other peripheral areas. Thus, chimpanzees to the northeast may be less likely to intrude into the Ngogo territory than other surrounding communities. One or both factors would result in fewer passive encounters.

The area to the northwest of the Ngogo chimpanzee territory had the highest passive to active intercommunity encounter ratio. This may mean that both the Ngogo chimpanzees and their neighbors to the northwest use their overlap zone regularly or that the latter moves into the Ngogo territory more often than the reverse. In fact, the number of patrols to the northwest was quite low, while the number of intercommunity encounters was high. An adult male from Ngogo was found dead from wounds inflicted by other chimpanzees in the northwest in February 2006. Two other Ngogo males were killed just south of the northwest sector in July 2005. Since these sectors are arbitrary and do not necessarily reflect the areas used by other chimpanzee communities, at least one, and perhaps all three, deaths could have been perpetrated by a community to the northwest.

In sum, results in Chapter 5 were not entirely consistent with any of the three proposed hypotheses. My findings nonetheless suggest that the Ngogo chimpanzees adjusted their territorial activities in response to their neighbors in various ways by: 1) increasing patrols in the most heavily patrolled border regions when intruder pressure there was high; 2) patrolling more often in areas of frequent intercommunity encounters over the long-term, particularly in certain peripheral areas; and 3) defending some boundary areas more actively than others. The Ngogo chimpanzees appear to respond differently to intruder pressure depending on the identity of neighbors and where they encounter them.

CONTRIBUTIONS AND DIRECTIONS FOR FUTURE RESEARCH

With this project I have made important inroads into understanding the ranging patterns and territoriality of the Ngogo chimpanzees. A persistent question about the Ngogo chimpanzee community concerns its unusually large size. As my work demonstrates, the Ngogo chimpanzee territory is not particularly large, and as a result, the population density is extremely high. To compensate, the Ngogo chimpanzees control exclusive access to a large portion of their territory, an area considerably larger than that which has been reported for chimpanzees living at one other site in the Taï National Park, Côte d’Ivoire. Habitat quality may also explain how a large number of chimpanzees can be supported on a smaller-than-expected territory. Recent research indicates that the habitat at Ngogo provides considerably more chimpanzee food than that of

Kanyawara, which is 10 km away in the Kibale National Park [Potts 2008]. The Kanyawara community, with about 50 individuals, is relatively small, but ranges over a larger territory than chimpanzees at Ngogo [Wilson et al. 2007]. Additional research will be necessary to clarify how and why the Ngogo chimpanzee community maintains its large size.

It became apparent during my research that more information about surrounding communities is required to answer questions about space use and territoriality. Although I was able to estimate the territory size and core area utilized by the Ngogo chimpanzees, I was unable to assess overlap with territories occupied by neighboring chimpanzees. Knowledge of how neighboring communities use their territories would greatly improve my ability to evaluate the extent to which the Ngogo chimpanzees control access to an exclusively used area.

The results of Chapter 5, while intriguing, were nevertheless incomplete. My measure of other communities involved counting nests in a systematic way around the periphery of the Ngogo territory. This process was designed to provide data about how the relative density of chimpanzees varied around the periphery of the Ngogo chimpanzee territory. It failed, though, to furnish specific knowledge about the strength, location, or number of neighboring chimpanzee communities. As discussed above, these nest counts may also have been an inadequate way to assay relative population density of surrounding communities as local nest densities are likely to vary considerably over time depending on variation in fruit abundance and distribution.

Thus if I could revisit this part of my study, I would establish a larger number of transects and walk them repeatedly over a longer period of time. A larger sample would improve my ability to discern approximate territory boundaries of specific neighbors through kriging. Repeated nest counts would be more likely to capture fluctuations in local density over time in response to changing food availability. The large nest count in the southwest is especially intriguing in this regard. Repeated nest counts over time, as well as additional counts in nearby areas, would help to determine whether the chimpanzees in this area live in a particularly large community or whether large parties gather there seasonally.

Habituating neighboring communities would provide a direct way to evaluate how relationships with neighbors influence the spatial distribution of patrols. With knowledge of the demography, ranging patterns, and territorial activities of these other chimpanzees, I could calculate territory and core area estimates, determine overlap zones, and assess power imbalances. These data could be used to test hypotheses about the factors affecting where chimpanzees patrol. Recent research on the Kanyanchu community to the south of Ngogo has included the collection of GPS data [Lloyd personal communication]. These data will permit estimating the extent of overlap between the two chimpanzee communities.

Research questions with a spatial component present unique analytical challenges. Although several recent chimpanzee studies have included data on ranging behavior and territory size [e.g. Baldwin et al. 1982; Basabose 2005; Chapman and Wrangham 1993; Herbinger et al. 2001; Lehmann and Boesch 2003; Newton-Fisher 2000; Newton-Fisher 2001; Newton-Fisher 2003; Williams et al. 2004; Wilson et al. 2007; Wrangham et al. 2007], I found myself in uncharted territory when it came to several analyses using spatial data, and I had to use considerable creativity to address several questions. For example, determining whether a core area is centrally-located with a territory in a statistical sense was not straightforward because this question had not been asked and analyzed before. Similarly, no precedent existed to analyze the relationship between intercommunity encounter and patrol locations. GIS (Geographic Information Systems) programs provide many useful analytical tools, but determining which were most applicable to my specific questions was a seemingly endless task. A major contribution of my research is that I have provided new ways to analyze spatial data to address questions about chimpanzee, primate, and animal behavior. I expect to refine and continue to use these methods to address additional hypotheses about how chimpanzees use space in the future.

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