

Range Use of the Forest Chimpanzees of Kibale: Implications for the Understanding of Chimpanzee Social Organization

COLIN A. CHAPMAN AND RICHARD W. WRANGHAM
Peabody Museum, Harvard University, Cambridge, Massachusetts

We contrast the range use patterns of male and female chimpanzees (*Pan troglodytes*) based on repeated sightings over three years of 19 individuals in the Kanyawara community of Kibale Forest Reserve, Uganda. Depending on how home range size was calculated, male chimpanzees used an area that was 1.5 to 2 times greater than that of females. There was no difference between the sexes in whether their home ranges were used in a clumped or uniform fashion. However, males were more likely to be seen in boundary areas than females. These results are discussed in light of previously proposed models of chimpanzee social organization. It is concluded that the scenario in which females have smaller core areas within the defended home range of the males is most strongly supported by the range use patterns observed in Kibale chimpanzees. © 1993 Wiley-Liss, Inc.

Key words: chimpanzees, range use, social organization, male–female strategies

INTRODUCTION

Field studies of chimpanzees (*Pan troglodytes*) have shown that adults spend their time either alone or in parties which frequently change size and composition [Goodall, 1986; Nishida, 1979; Wrangham, 1979; Boesch, 1991]. These parties consist of individuals from the same community [Goodall, 1986] or unit-group [Nishida, 1968], the members of which share a common home range. Interactions between adjacent communities can be aggressive, to the extent that conflicts between neighboring communities can result in the severe injury or death of the interactants [Goodall et al., 1979; Nishida & Kawanaka, 1972].

This form of social organization has been interpreted to be a delicate balance between social and ecological factors [Wrangham, 1979, 1986]. Females, whose reproductive potential is assumed to be limited by food intake, attempt to reduce feeding competition by travelling alone. In contrast, a male's reproductive potential seems to depend on critical male–male bonds. Thus, males spend much of their time in parties, patrolling territorial boundaries to exclude non-related competitors [Wrangham & Smuts, 1980; Goodall et al., 1979]. Unfortunately, few data

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Address reprint requests to Dr. Chapman's present address: Department of Zoology, University of Florida, Gainesville, FL 32611.

have been available on the socioecology of males and females from different types of habitats to test and develop these ideas [see Baldwin et al., 1982; Goodall, 1986; Wrangham, 1986; Nishida & Hirawa-Hasegawa, 1987 for reviews of chimpanzee studies]. Past studies of habituated communities have tended to focus on gallery forest and woodland communities [Goodall, 1986; Nishida & Kawanaka, 1972; Wrangham, 1979; Kawanaka, 1984; Nishida, 1990], although there is some information available from partially or non-habituated communities in a variety of habitats [woodland: Kano, 1971, 1972; savanna: Baldwin et al., 1982; forest: Sugiyama, 1969; Suzuki, 1971; Reynolds & Reynolds, 1965; Ghiglieri, 1984].

The study of sex differences in ranging behavior can reveal differences in the strategies of males and females and is important in two respects. First, the quantification of sex differences in home range size can help us understand differences in the foraging strategies and association patterns of the sexes. Second, the documentation of sex differences in the location of home ranges within the community's range can provide an understanding of sex differences in territoriality and community membership.

In this study, we examine the range use patterns of male and female chimpanzees from the Kibale Forest Reserve in Western Uganda, focusing on the differential use of boundary areas. Since Kibale is a forest site, the study of chimpanzees at Kibale offers an opportunity to examine factors that have been proposed to underlie chimpanzee social structure under ecological conditions quite different from those in which the models were proposed.

METHODS

Study Site

Kibale Forest Reserve is located in western Uganda (0° 13'–0° 41' N and 30° 19'–30° 32' E) near the base of the Ruwenzori Mountains. The study community inhabits a region known as Kanyawara which consists of a series of moderately undulating hills and valleys and sits at an elevation of approximately 1,500 m. Between 1977 and 1983 the daily maximum and minimum temperatures were 23.3°C (S.D. = 0.06) and 16.2°C (S.D. = 0.4), respectively, and the mean annual rainfall (1977–1984) was 1,570 mm (S.D. = 200 mm) [Butynski, 1990].

The forest in the region is transitional between lowland rainforest and montane forest [Struhsaker, 1975; Skorupa, 1988]. The canopy averages 20 to 30 m in height, although some trees exceed 50 m. Throughout the study area trees such as *Diospyros abyssinica* (12.3% of 2111 enumerated trees), *Markhamia platycalyx* (11.8%), *Celtis durandii* (10.9%), *Uvariopsis congensis* (9.8%), and *Bosqueia phoberus* (8.7%) are common. The forest is a mosaic of pristine forest, secondary forest (following logging which took place in the 1960s), grassland, swamps, and exotic pine plantations.

The chimpanzees in the Kanyawara area have been studied since 1983 [Isabirye-Basuta, 1987; Wrangham et al., 1992], providing both valuable background information and the habituation necessary for individual identification and behavioural observations. In this paper we report observations that were made between August 1988 and October 1991. During this period the community members were relatively well habituated [see Wrangham et al., 1992 for details of the level of habituation and times of study], and reliable individual identification was available. In the study area there is approximately 140 km of trails which provided access to an area of approximately 11 km² (Fig. 1).

Since September 1987, the Kanyawara community contained eight adult males and five subadult males. "New" females continue to be observed in the community, thus the numbers of females is uncertain. Some of these "new" females

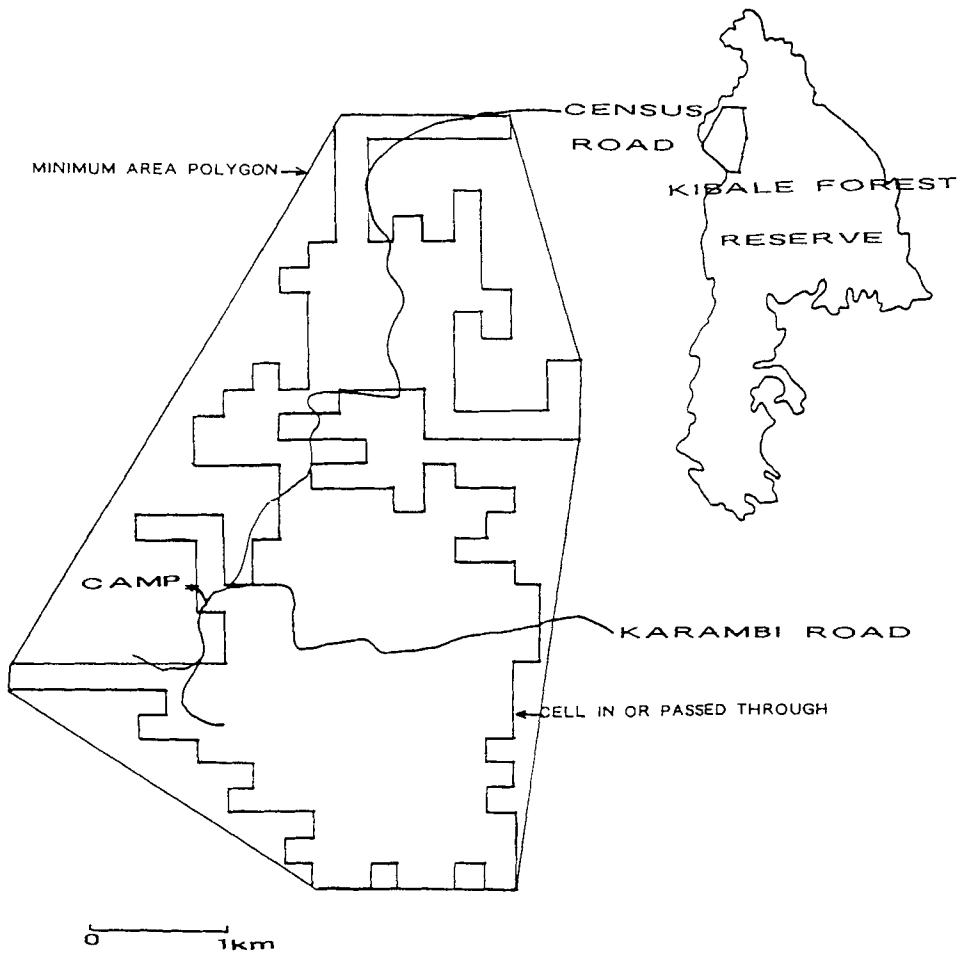


Fig. 1. A map of the area used by the study community of chimpanzees in the Kibale Forest Reserve, Uganda.

may represent new immigrants to the study community, while others may be females that habituated to observers, thus permitting individual recognition and routine observation. In 1989–1990, the community contained at least 41 individuals: 8 adult males, 5 subadult males, 14 adult females, 2 subadult females, 1 juvenile, and 11 dependent offspring. Not all individuals were observed sufficiently often or over a long enough period to permit a reliable estimate of home range size. There were 19 individually recognizable adult or subadult animals for which we had a sufficient number of sightings to make a reliable estimate of home range size (Table I). Individuals with insufficient sightings were primarily females that were seen irregularly, or appear to have recently moved into the area used by the community. For example, three adult females and their offspring have been seen at regular intervals since February 1989 in the northern end of the community's home range when the males were using that area. These females were not included in the overall analyses because the number of sightings were too few to make a

TABLE I. Characteristics of the Home Range of Known Individual Chimpanzees (*Pan troglodytes*) From the Kibale Forest Reserve, Uganda*

	Home range size			Residuals	Number of sightings	CD
	Cells in	Cell through	Polygon			
Adult male						
1 (ST)	4.3	5.4	12.8	+0.029	391	0.83
2 (SY)	4.7	5.8	13.1	+0.349	391	0.94
3 (TU)	3.2	5.6	12.6	+3.442	179	0.77
4 (BF)	3.8	4.8	12.3	+1.469	276	0.93
5 (BB)	2.9	4.2	9.9	+0.575	190	0.74
6 (LM)	3.1	4.0	9.4	-0.570	229	0.86
7 (LB)	3.7	4.5	10.4	-0.360	273	0.76
Adult female						
1 (LP)	3.1	4.5	9.6	-1.960	320	1.09
2 (FG)	3.1	4.0	9.7	-0.790	256	0.79
3 (KL)	1.8	2.6	6.6	-1.512	120	0.82
4 (CE)	1.6	2.5	8.6	+1.169	80	0.52
5 (AR)	1.3	2.1	5.2	-2.356	85	0.66
Subadult male						
1 (YB)	3.0	4.0	10.4	+0.714	210	0.94
2 (MS)	3.8	4.8	11.8	+0.859	286	0.87
3 (NJ)	3.0	4.2	9.8	-0.278	233	0.84
4 (AJ)	4.6	5.5	11.8	-1.317	409	0.83
5 (RZ)	2.9	4.2	11.7	+1.380	239	0.85
Subadult females						
1 (YJ)	0.9	2.1	6.6	-0.297	44	0.82
2 (AK)	0.9	2.4	6.8	-0.575	75	0.76

*See the text for explanation of the methods used to calculate home range size. Home range size is given in km².

realistic estimate of their ranging patterns (average $n = 18$). However, when they were seen, they interacted and travelled with the other members.

Home Range Size and Use

Chimpanzees were located using a number of different methods: by searching the area and encountering parties, by hearing calls and searching where the calls were heard, and by regularly visiting fruiting trees that the chimpanzees were known to visit. These techniques (particularly monitoring fruiting trees) may not produce results directly comparable to those obtained at different study sites using different methods (e.g., all day follows of specific individuals) but should produce reliable comparisons between individuals within the Kanyawara community.

A map of the area used by the community was divided into grid cells which were 200 m by 200 m in size. All sightings were placed on these maps as accurately as possible. Since much of the area used by the study community lies within the trail system and trails are rarely more than 200 m apart, it is believed that the accuracy of locating parties on these maps is high. For the purpose of constructing home range maps, we considered a sighting as occurring whenever an individual was seen to use a grid cell on a particular day. Thus, if an animal stayed in the same area all day, it represented one sighting, but if the animal returned to the same area the next day, it was considered as two sightings. This definition may

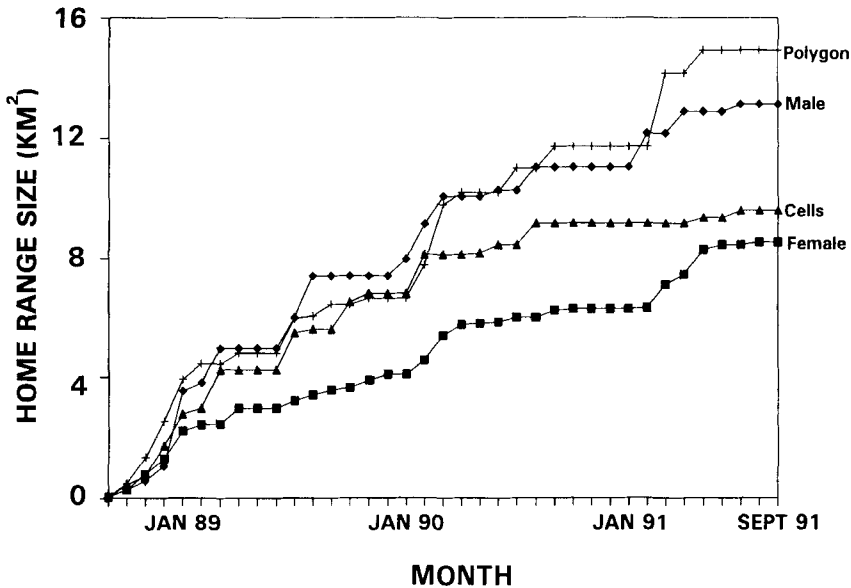


Fig. 2. A cumulative plot of the home range size of 1) the entire community of chimpanzees at the Kanyawara study site in Kibale Forest Reserve, calculated using the minimum area polygon (+), 2) the community's home range calculated using the sum of the 200 m by 200 m grid cells that a member of the community was seen to use or would have had to travel through to get from the location of one sighting to the next (triangles), 3) the cumulative home range size of a representative adult male (diamonds, polygon method), and 4) the cumulative home range of a representative adult female (squares, polygon method).

elevate the number of observations of easily followed animals, since they could be followed to their nest and then followed the subsequent morning.

Different methods of calculating home range size can produce marked variation in the results obtained [Lehner, 1979], thus home range size was calculated using three different methods. First, home range was calculated as the sum of the 200 m by 200 m grid cells in which an individual was seen. Second, it was calculated as the sum of the 200 m by 200 m grid cells that the individual used and those grid cells that it would have had to travel through to get from the location of one observation to the next. Third, home range size was calculated using the minimum area polygon method [Lehner, 1979].

We know the present estimate of community home range size is smaller than the actual value, since known individuals were commonly followed out of the trail system and lost as they travelled out of the area known to be used. To examine if home range size had reached an asymptote in relation to observation time, we plotted the cumulative monthly home range size for the community as a whole and for each individual (minimum polygon method). There was little evidence of an asymptote for any of the individuals examined (Fig. 2). To calculate a relative measure of home range size that was independent of observation time, we regressed home range size for each individual at the end of the study against the number of sightings for each individual. The residuals from this regression were used to represent the degree to which an individual's home range size was above or below the expected size based on the number of times it was observed.

Although the size of the home ranges of different individuals might be similar, their pattern of use of that area might be very different [Hasegawa, 1990]. For

example, while two individuals could use areas of the same size, one animal might use its entire home range in a uniform fashion, while the other individual might use a core area very frequently and only rarely enter the more peripheral regions. To examine the patterns of home range use, the coefficient of dispersion (CD) of grid cell use was calculated (variance of the number of times cells were used/mean) [Southwood 1966]. The calculation of CD allow the assessment of whether an individual used its home range in a clumped, random, or uniform pattern. The CD is sensitive to the size of the cells used in the calculation [Southwood 1966], so calculations were made using cell size of 200 m by 200 m and cells that were 400 m by 400 m.

Individuals may also exhibit differential use or avoidance of boundary areas where the study community's home range overlaps with that of another community. The communities neighboring the Kanyawara community are not yet habituated. Thus, the boundary of the Kanyawara community's home range cannot be rigidly defined. For the purpose of this analysis, the boundary was considered as the last row of 200 m by 200 m grid cells that any recognizable member of the community was observed to use. Since the size of the community's home range has not reached an asymptote with observation time, this will not be the absolute boundary, but it can be considered as an area where contact with neighboring communities is more probable. To evaluate this arbitrary definition of the community's boundary, analyses were conducted to examine differential use of the last 2, 3, and 4 rows of grid cells.

Following Clark [1991], the dominance of individuals was assessed by constructing a matrix of two classes of diadic agonistic interactions: 1) "pants," "grunts," and "pant-grunts" and 2) displacements. Goodall [1986] and Nishida [1989] state that these vocalizations are always given by an individual of lower rank to one of higher rank. Although displacements are not as unidirectional as pant-grunting [Bygott, 1979], we include these interactions in our assessment of dominance because grunting was rarely observed between adult males and subadult males. Clark [1991] provides a detailed discussion of the dominance hierarchy of the chimpanzees of the Kanyawara community and the addition of subsequent observations to the matrix Clark constructed does not alter the pattern. Analyses with dominance classes (high ranking, mid-ranking, and low ranking) revealed similar trends as the analyses using the linear dominance hierarchy. Since a correlational analysis does not reduce the variance among individuals to classes, only the results of analyses of the linear hierarchy are reported.

RESULTS

The size of the community's home range was 14.9 km² as calculated by the minimum polygon method (Fig. 1), 8.5 km² as determined by the sum of the 200 m by 200 m cells used or those assumed to have been passed through, and 7.8 km² estimated as the sum of all cells in which known individuals were observed. The home range of the community included a number of different habitats. Identifiable individuals were most frequently seen in relatively pristine forest in which only a few trees (3–4 stems/km²) have been removed by pitsawyers. This logging has had relatively little impact on the forest as a whole [Skorupa, 1988]. However, they also used areas which were selectively harvested in late 1960s [Skorupa, 1988]. The chimpanzees also used swamp forest, fed in papyrus swamp, and travelled through and ate terrestrial herbs in pine plantations.

Over the 3 years of this study, the number of sightings for the 19 individuals averaged 226 (range between individuals 44–409, Table I). The average size of an individual's home range varied depending on which method was used (Table II).

TABLE II. Descriptive Statistics of the Size (km²) of Individual Home Ranges as Calculated Using Different Methods for Individual Chimpanzees Found in the Kanyawara Study Community of the Kibale Forest Reserve

	Average size	Range	Standard deviation
Cells in	2.9	0.9-4.7	1.15
Cells in or through	4.9	2.1-5.8	1.20
Polygon	9.5	5.2-13.1	2.33

The estimated home range size for an individual increased with the number of times that the individual was seen (polygon $r = 0.807$, $P < 0.0001$; cells in $r = 0.953$, $P < 0.0001$; cells in or through $r = 0.887$, $P < 0.0001$). There was little evidence of an asymptote in the cumulative plot of home range size versus number of sightings (Fig. 2).

There was no difference in the home range size between adults and subadults of the same sex (males $t = 0.79$, $P = 0.448$; females $t = 0.10$, $P = 0.922$). Thus for the subsequent analyses adults and subadults of the same sex are considered together. In all methods of calculating home range size, males had significantly larger home ranges than females (cells in $t = 4.76$, $P = 0.0002$; cells in or through $t = 5.10$, $P = 0.0001$; minimum polygon $t = 5.41$, $P < 0.0001$, Table I). However, these analyses do not consider the influence of the number of sightings on estimates of home range size. This is particularly important in comparisons between sexes, since males were sighted more frequently than females ($t = 3.17$, $P = 0.006$), and there was a positive relationship between home range size and the number of sightings. To control for sample size differences, we compared the residuals of males and females from the regression of the number of sightings on home range size (Fig. 3). The significantly larger residuals of males than females ($t = 2.46$, $P = 0.025$) indicates a larger home range size for males than females, independent of the number of times they were sighted.

While two individuals could use areas of the same size, one animal might use its entire home range in a uniform fashion, while the other individual could use a core area very frequently and only rarely enter the more peripheral regions. For the Kanyawara chimpanzees, there was no difference between males and females in the pattern of home range use (average CD for males = 0.85; females = 0.78; Table I; $t = 1.153$, $P = 0.265$, 200 m by 200 m cells; $t = 0.686$, $P = 0.708$, 400 m by 400 m cells). As with home range size, CD was related to the number of sightings of an individual ($r = 0.557$, $P = 0.013$). To control for the number of sightings, we examined the residuals from the regression of an individual's CD value on the number of sightings. There were no differences in these residuals between males and females ($t = 0.373$, $P = 0.714$), again indicating no sex difference in the pattern of home range use.

If the boundary of the community's home range is considered as the last two rows of grid cells, there was a significant difference between males and females in boundary use ($t = 4.99$, $P < 0.0001$). Males were seen in the boundary areas four times as often as females. However, when one considers the boundary as the last three rows of grid cells ($t = 0.217$, $P = 0.830$), or the last four rows of grid cells ($t = 0.063$, $P = 0.954$) the sex difference in use disappears. This suggests that females tend to avoid only the edge of the community's range.

Dominant males had larger home ranges than subordinate males (Table III). However, for females there was no relationship between dominance and home

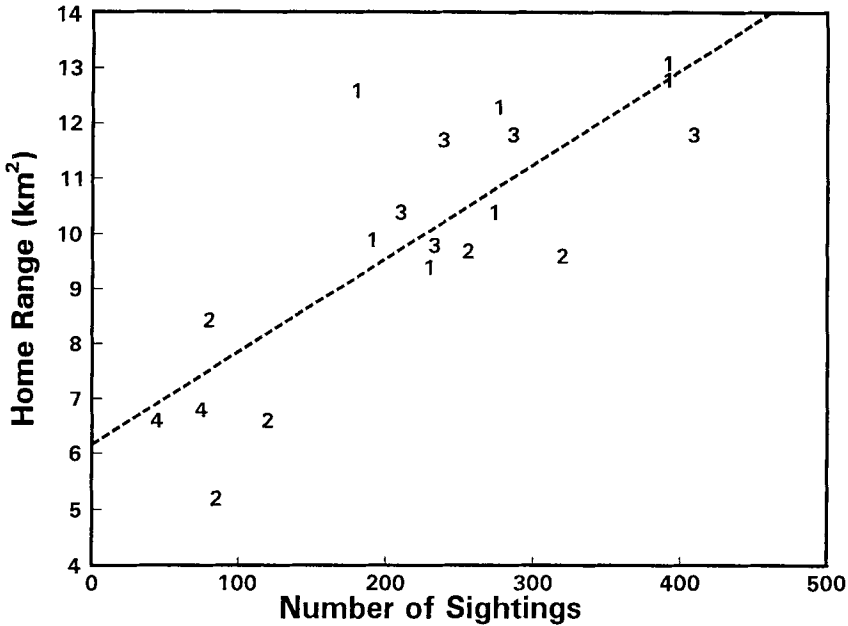


Fig. 3. The relationship between the number of sightings for each individual at the end of the study and their home range size. Each sex is depicted separately to illustrate the sex differences in home range size that is independent of the number of sightings (1, adult males; 2, adult females; 3, subadult males; 4, subadult females).

TABLE III. The Relationship Between Dominance and Home Range Size and the Number of Sightings for Males and Females in the Kanyawara Study Community of Chimpanzees in the Kibale Forest Reserve*

Method	Males	Females
Cells in	$r = -0.816, P = 0.025$	$r = +0.022, P = 0.971$
Cells in or through	$r = -0.917, P = 0.004$	$r = +0.042, P = 0.946$
Polygon	$r = -0.933, P = 0.002$	$r = +0.529, P = 0.359$
Number of sightings	$r = -0.630, P = 0.129$	$r = +0.094, P = 0.879$

*See the methods for a description of the methods used to calculate home range size.

range size. For both sexes, there was no relationship between dominance and the number of sightings.

There was a relationship between adult male dominance and the frequency of use of boundary areas ($r = -0.776, P = 0.040$). However, for adult females ($r = -0.390, P = 0.516$) and subadult males ($r = 0.312, P = 0.599$) there was no evidence of dominant animals using boundary areas more than subordinates.

DISCUSSION

There are three lines of evidence from Kibale which reflect the general strategies of male and female chimpanzees and have implications for how we view chimpanzee societies. First, male chimpanzees used an area that was 1.5 to 2 times

greater than that of females. Second, there was no difference between the sexes in whether their home ranges were used in a clumped or uniform fashion. Third, adult males were more likely to be seen in boundary areas than females.

We consider these findings in light of the models of chimpanzee society that are discussed by Wrangham [1979]. The original model suggests that males and females share their home range equally [Itani & Suzuki, 1967]. The findings from Kibale that females have smaller home ranges than males and avoid the boundary areas, argues against this interpretation of chimpanzee social organization.

The second model suggests females have smaller core areas within the male home range and are dispersed relative to males within the defended area. In the third scenario females have core areas that are independent of the area of use of the males and may or may not be within areas defended by the males of the community. The observation that the female chimpanzees in Kibale avoid the boundary areas of the community's home range suggests that the third model is not an adequate representation of the chimpanzee's community. Female core areas are within an area encompassed by a set of males.

Pusey [1980] argued against the third hypothesized model by presenting evidence that peaceful interactions between males and females of different communities are very rare and males show unusually violent aggression to females from adjacent communities except when these females are in estrus. Also, the observations from Gombe that females accompany males on border patrols and attempt to evict immigrating females suggests that females do experience a group identity. Kawanaka [1984] suggested that the data supporting the third model were biased by not including cycling females. Nishida et al. [1985] showed that females behave as if they have a sense of community and cited the evidence that the annual ranges of immigrant females roughly coincide with those of the resident adult males of the community. The observations by these researchers, and the data presented here, suggest that chimpanzee social organization involves females moving within an area that is dependent on a group of males supporting the second model. Nonetheless, in a recent review of much of this evidence, Rodman [1991] noted that conclusive data to reject the third model in favour of the second is not as yet available.

The range use patterns reported here pose interesting questions for future studies. How much is the sex difference in the size of home ranges a result of females avoiding boundary areas? What is the effect of avoiding boundary areas on female party size and association patterns? Do females leave parties that approach boundary areas? Does a female's use of the boundary change prior to emigration to a new community?

At Tai, Boesch [1991] describes females as ranging extensively across the whole community's range, in dispersed groups that include on average 72% of the members and have a sex ratio that varies between 3 to 4 in favor of adult females. At Tai, female-female coalitions are common. At Kibale, under similar forested conditions, females use much smaller areas, the sex ratio of parties typically favors males, and parties typically do not include such a large proportion of the community. Here female coalitions have not been observed. It is possible that factors that permit or create differences in the party sizes and range use patterns underlie differences in behaviors such as coalitions. For example, it may not be sufficiently profitable for females at Kibale to form coalitions with other females, since in comparison to females at Tai, they range separately more often and are in smaller parties.

CONCLUSIONS

1. The size of the Kanyawara chimpanzee community's home range was 14.9 km² (minimum area polygon), 8.5 km² (sum of the 200 m by 200 m cells used or assumed to have been passed through), and 7.8 km² (sum of all cells used).
2. Male chimpanzees used an area that was 1.5 to 2 times larger than that of females.
3. There was no difference between males and females in the general pattern of use of their home ranges, however males were seen in the boundary areas 4 times as often as females.
4. These findings are discussed in terms of the behavioral strategies of males and females and are viewed with respect to previously proposed models of chimpanzee society.

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