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RESEARCH ARTICLE

Home-Range Use and Intergroup Encounters in Western Gorillas (*Gorilla g. gorilla*) at Lossi Forest, North Congo

M. BERMEJO[1,2]*
[1]*Animal Biology Department, Faculty of Biology, University of Barcelona, Barcelona, Spain*
[2]*Conservation and Rational Utilization of Tropical Forest Ecosystems in Central Africa (ECOFAC)-Congo (European Union)*

I present data on home-range use and types of intergroup encounters for one group (Apollo) of western gorillas (*Gorilla gorilla gorilla*) from a new study site in the Republic of Congo. The total home-range size of the focal group, which I calculated by superimposing a 100 m × 100 m grid over the mapped daily path traveled, was 11 km^2. The majority (73%) of the group's home range was used exclusively, although at the periphery it overlapped with the ranges of three other groups. Most encounters (86%) with other groups (n = 14) took place in the periphery of the home range, and appeared to involve access to fruit trees. The focal group silverback's encounters with solitary silverbacks occurred throughout the focal group's home range, did not involve access to fruit, and typically resulted in aggressive or avoidance behavior. The focal group silverback's response to other group males was more varied: it included tolerance (64%), avoidance (14%), and aggression (21%), and was dependent upon the identity of the extragroup male. The focal group exhibited an unusual form of tolerant behavior toward some other groups by occasionally forming ''nesting supergroups'' (two groups nested together overnight at distances of 30–50 m). The western gorillas at Lossi were somewhat fluid in their grouping. Subgrouping and supergrouping occurred, although more infrequently than reported previously, and with a new twist: subgrouping did not necessarily require a silverback's presence. I stress the need for intraspecific comparisons and more complete data sets on western gorilla social organization. Am J Primatol 64:223–232, 2004.

Key words: *Gorilla g. gorilla*; home range; social interactions; apes

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*Correspondence to: Magdalena Bermejo, Dpto. Biología Animal (Vertebrados) Facultad de Biología, Universidad de Barcelona, Avda. Diagonal 645, 08028 Barcelona, Spain. E-mail: berille@jazzfree.com

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INTRODUCTION

Little is known about western gorilla social organization because it has been especially difficult to habituate western gorillas to human observation. Research from indirect studies has documented that western gorillas eat a more frugivorous diet, travel longer daily distances, and use larger home ranges than the closely-related mountain gorilla [Bermejo, 1997; Doran & McNeilage, 1998, 2001; Doran et al., 2002; Goldsmith, 1996, 1999; Nishihara, 1995; Remis, 1997a, b; Rogers et al., 1990; Sabater-Pi, 1977; Tutin, 1996; Williamson et al., 1990] (Doran et al., this issue; Rogers et al., this issue). It has been argued that such differences may be associated with changes in sociality. For example, there have been persistent reports, based on trail follows, that western gorillas are more fluid in their grouping patterns than mountain gorillas, and exhibit sub- or super-grouping on a regular basis [Goldsmith, 1996; Doran & McNeilage, 1998; Remis, 1997a]. Additionally, intergroup encounters in western gorillas have been described as more varied, including more tolerant behavior between groups [Magliocca et al., 1999; Tutin, 1996; Vanleeuwe et al., 1998] (Doran et al., this issue; but see Cipolletta, this issue) than the typical aggressive response of mountain gorillas, whose intergroup encounters are related to the acquisition of females rather than to the defense of a group's range [Cheney, 1987; Sicotte, 1993; Yamagiwa, 1983]. However, prior to the complete habituation of western gorilla groups, it has not been possible to document the exact nature of these behaviors.

In this study, I report on the home-range use, grouping patterns, and intergroup encounters of one habituated western lowland gorilla group in the Lossi Forest, Republic of Congo, in order to augment our knowledge of gorilla social interactions. Specifically, I examine home-range overlap between groups, and the frequency and nature of intergroup encounters and grouping patterns within a group to readdress the issues of whether and how these behaviors occur.

MATERIALS AND METHODS

Study Area

The Lossi study area (0°14′N and 14°30′E), consisting of 25 km^2 of tropical rain forest, is located 50 km southwest of Odzala National Park, Republic of Congo. The habitat consists of Marantaceae forest [Letouzey, 1968], swamp forest along streams and secondary forests, and secondary forest in places that were affected by human activities 50 years ago. The mean annual rainfall was 1,007 mm at the site (SD = 629, n = 6 years), and typically there were 5 months per year (June–August and January–February) with <50 mm of rain.

Study Animals and Data Collection

Data were collected from 1995 through 2000, with uneven sampling between years (Table I). There were four gorilla groups in the study site, with an average group size of 17.4 (range = 15–35, SD = 8.6, n = 4; Table II). I focused primarily on one group (Apollo), although I regularly contacted the other groups during the first 2 years of the study, which provided the basis for an analysis of home-range overlap. The gorillas were located with the assistance of trackers who were skilled at finding and following subtle traces of gorilla activity. We tried to observe and measure complete daily follows (lead to the nest site). We observed gorillas for 4–30 days in each month (mean = 17.1 days, SD = 6.5, total hr of contact = 1,099) and followed their trails on 71.4% of days in the field (n = 912 days).

TABLE I. Data Sample sizes for Observations on Four Gorilla Groups (AP, AR, PO, and HE) at Lossi Study Area During the Study Period (1995–2000)

	1995 (n=10 months)			1996 (n=11 months)			1997 (n=6 months)			1998 (n=6 months)			2000 (n=5 months)		
Groups	Partial day trails	Complete day range	Obs (hr)	Partial day trails	Complete day range	Obs (hr)	Partial day trails	Complete day range	Obs (hr)	Partial day trails	Complete day range	Obs (hr)	Partial day trails	Complete day range	Obs (hr)
AP	96	10	137.5	130	47	279.5	2	65	131.6	38	95	256.5	68	28	196.3
AR	11	11	32.4	4	4	11.9	0	0	0	0	0	0	0	0	0
PO	5	7	16.2	11	3	15.4	0	0	0	0	0	0	0	0	0
HE	5	2	8.7	1	8	12.9	0	0	0	0	0	0	0	0	0
Total	117	30	194.8	146	62	319.7	2	65	131.6	38	95	256.5	68	28	196.3

TABLE II. Group composition of Four Gorilla Groups Regularly Studied at Lossi Study Area

	Group composition 1995–1996			
Age-class	Ares (AR)	Apollo (AP)	Poseidon (PO)	Hermes (HE)
Silverback	1	1	1	1
Blackback	2	2	1	
Adult female	8	8	4	5
Adult?	4		2	1
Subadult	6	1	2	2
Juvenile	7	3	4	3
Infant	7	5	3	3
Total	35	20	17	15

We measured group movements from a 1:20,000 map, upon which we plotted each contact, feeding tree, nest-site, and connecting trail. We determined their location by an extensive system of trails marked every 100 m, and by pacing distances, compass bearings, and GPS position. The whole system was later digitized with the use of Map Info software. We superimposed a 100 m $\times$ 100 m grid system onto the map to measure home-range size. We calculated the home range as the sum of all 100 m $\times$ 100 m quadrants entered by the group. Any quadrant entered six or more times was considered to be part of the core area. This cutoff point was selected because it was the natural cutoff in a distribution of frequency of use. For Apollo's group we recorded 245 complete daily path lengths (DPLs; mean = 7.4 days per month, range = 0–25 days, SD = 5.9, n = 38 months) and 334 partial days of trail. For other groups we recorded a total of 35 complete DPLs and 37 partial days of trail.

The response of the focal group silverback during encounters with other groups or lone males was classified as ''tolerant'' (remains in proximity without displays), ''avoid'' (moves quietly away from), or ''aggression'' (vocal displays, chest-beating, and/or physical fighting). Following Remis [1997a], the focal group (Apollo) was considered to be traveling or foraging as a single unit if individuals moved together or along parallel paths (maintaining vocal contact, usually within 300 m) and if by nightfall all members nested at one nest site. Subgroups were defined as spatial subsets of the AP group that moved as a single unit independently from the rest of the group (at least 500 m apart, and apparently often out of auditory range) and slept separately [Robinson & Janson, 1987]. Foraging parties fed together within a tree or cluster of trees separate from the main group, maintained vocal contact with the rest of the group, coordinated travel with the rest of the group, and rejoined it for sleeping. Foraging parties, which could be comprised of lone individuals or groups of females up to 500 m from the males, were more temporary, fluid, and less predictable in size and composition than the subgroups.

RESULTS

Home-Range Use

The total home-range size for the Apollo group during a 38-month period was 11 km^2. The home-range size continued to increase throughout the study period, although 80% of the current home-range size was reached within the first 2 years of the study (Fig. 1). The group's core area included 20% of the total home range

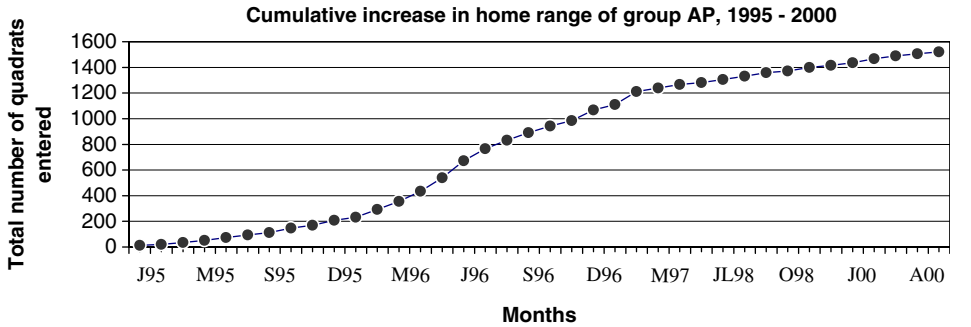

Fig. 1. Cumulative increase in the home range of group AP in 1995–1998 and 2000.

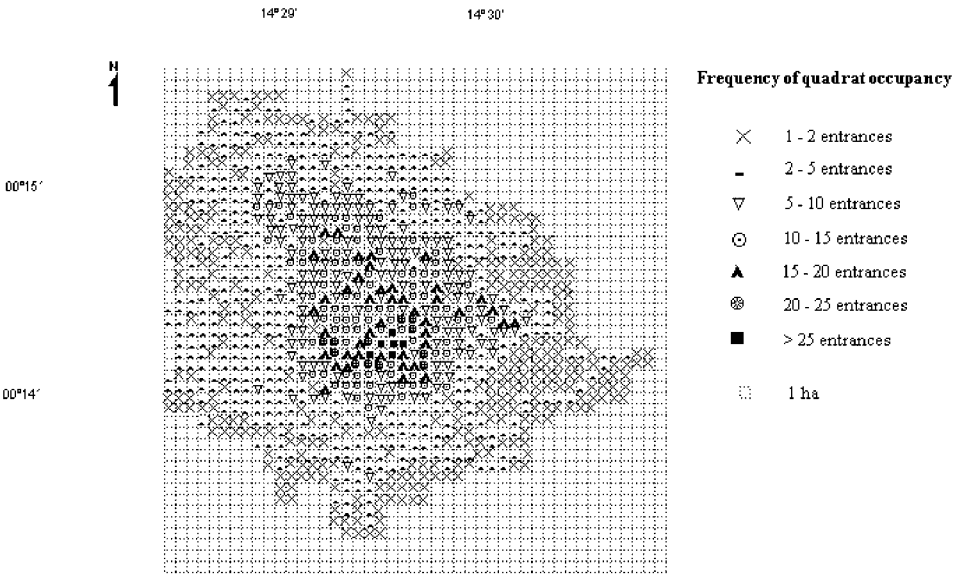

Fig. 2. Frequency of quadrat occupancy in 1995–1998 and 2000.

and was located within the center of their home range (Fig. 2). Three neighboring groups overlapped the periphery of the focal group range, although no other group was found in the core area of Apollo group (Fig. 3). Since data are available for all groups only from 1995–1996, I examined home-range overlap more closely during that period. The total home-range size of the AP group was 11 km^2, of which 73% was used exclusively by the Apollo group. Three other groups used a total of 27% of the home range on Apollo's periphery, either exclusively (AR = 11%, HE = 8%, and PO = 6%) or shared between them (AR + HE = 2%).

Encounters

During the study period, 22 encounters between the focal group and other groups or lone males were recorded. The encounters occurred at distances of 20–250 m and lasted an average of 164 min (SD = 271, range = 1–720), including

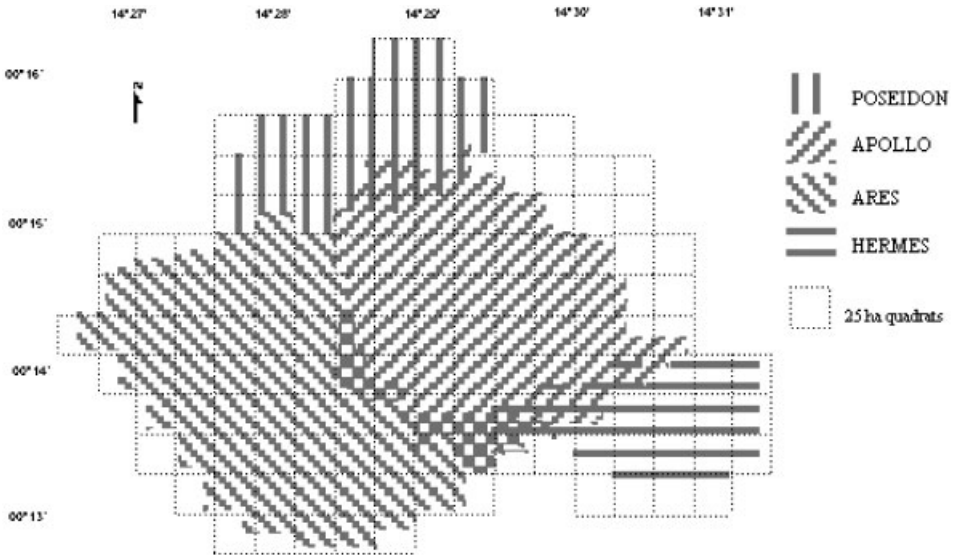

Fig. 3. Home range of the focal group (AP) in 1995–1998 and 2000, and its overlap area with three different groups (AR, PO, and HE).

encounters with co-nesting through the night. During 1,001 hr of daytime observations, 13.9 hr of encounters were observed, representing 1.4% of the time the focal group was under direct daytime observation. The probability and/or nature of the encounters were probably affected by the presence of observers, especially when the gorilla groups differed in their degree of habituation to human observers. However, most of the intergroup encounters reported in the study occurred when the observers were undetected by the nonfocal gorilla groups. Sixty-four percent of encounters were with other groups (n: AR = 8, PO = 4, unknown group = 2). Thirty-six percent of encounters were with lone males (n = 8), which occurred when lone males silently tracked groups, occasionally for as long as 2 consecutive days. The location of encounters differed depending upon whether they were with other groups or lone males. Encounters with other groups did not occur randomly throughout the focal group's home range: 86% of encounters with other groups (n = 14), including all cases of co-nesting, took place in the periphery of their home range. However, encounters with lone males occurred throughout the range of Apollo's group. The context of encounters was not always clear, although many encounters with other groups occurred at or near fruit trees. Fifty-five percent of non- co-nesting encounters (n = 9) occurred at a fruiting large tree (*Gambeya*) or in a small area where fruiting trees of *Santiria* species were clustered. None of the co-nesting events occurred at a feeding tree. Encounters with lone males were not related to fruit trees.

The focal group silverback's response to lone males usually consisted of aggressive vocal displays (50%) or avoidance (50%). The focal group silverback's response to other groups (n = 14) included tolerance in 64% of cases, avoidance (14%), and aggression, with (7%) or without (14%) physical contact. Apollo's group exhibited an unusual form of tolerant behavior toward some other groups, by occasionally forming ''nesting supergroups'' (the two groups nested together overnight at distances of 30–50 m).

TABLE III. Response of Apollo During Intergroup (AR, PO, and Unknown) Encounters and Encounters With Lone Males

Response	AR (n = 8)	PO (n = 4)	Unknown (n = 2)	Total group (n = 14)	Lone males (n = 8)
Tolerance	50%			29%	
Tolerance-co-nesting	37.5%	50%		36%	
Avoid	12.5%	25%		14%	50%
Aggression-vocal display		25%	50%	14%	50%
Aggression-physical			50%	07%	

The AP group silverback's response to other groups varied depending upon the identity of the extragroup male (Table III). The primary response to AR was tolerance, to the unknown group it was aggression, and to PO it was more varied (Table III).

Apollo's group was not always cohesive. Subgroups of Apollo's group formed three times in which a smaller party (one or two adult females, one blackback male, and one juvenile) foraged separately from and nested >1 km from the rest of the group. Foraging subgroups of females were formed eight times, with females at distances of up to 500 m from the silverback. Additionally, foraging parties of females formed on 14 other occasions, when an adult female and her 12-year-old son and 8-year-old daughter foraged separately from the group on bark, roots, and wood.

DISCUSSION

Home-Range Use

Apollo's group home range was 11 km^2, based on 579 days of ranging behavior. This finding is similar to or slightly smaller than those reported in two other studies of western gorilla home-range size that were based on follows of largely habituated groups (11.4 km^2, n = 361 days [Cipolletta , 2003]; 15.75 km^2, n = 453 days (Doran et al., this issue)). Although home-range continued to increase over time during the study, subsequent data collected in 1995–2002 by the trackers during the researchers' absence did not indicate that home-range size continued to increase with time.

Although the home range of the focal group overlapped with three other groups and several lone males, the majority of its home range was unused by other groups. This is not the case for mountain gorillas [Watts, 1998], eastern lowland gorillas [Yamagiwa et al., 1996], or several western gorilla populations [Kuroda et al., 1996; Olejnuczak, 1994; Tutin, 1996]. The gorillas interacted with each other primarily on the periphery of their home range, suggesting that western gorillas configure their use of space and movements in response to neighboring groups. High home-range overlap and limited site fidelity are characteristic of many primates in which female transfer occurs [Isbell & Van Vuren, 1996]. Intergroup encounters may facilitate the transfer of migrants into nearby groups [Harcourt, 1978; Watts, 1990]. However, although western gorillas also exhibit female transfer [Stokes et al., 2003], they appear to use space differently and remain in a more circumscribed area at Lossi. This may be beneficial if it allows them to become familiar with the distribution and

phenological cycles of food plants and the shortest routes between resource patches [Dunbar, 1988]. On occasion, the Apollo group traveled outside its core area on a daily basis for periods of 1–2 weeks. However, the group usually returned to the core area to nest in the evening, which suggests that they use space in such a way as to minimize the risk of confrontations.

Intergroup Encounters

Mountain gorilla intergroup encounters, which are typically aggressive, are generally related to the acquisition of females, rather than the defense of home ranges or food resources [Sicotte, 1993; Watts, 1996; Yamagiwa, 1987]. The aggressive or fearful response of the AP group silverback to solitary males was also consistent with male–male competition. However, aggression was not the typical response of western gorilla groups during encounters with other groups at Lossi. These encounters, which were most frequently related to access to food, as reported earlier at another western gorilla site [Tutin, 1996], were generally peaceful. Although vocal displays were an important component of some intergroup encounters, contact aggression was notably less frequent than previously reported for mountain gorillas [Harcourt, 1978; Sicotte, 1993]. The focal group silverback's response to different group males varied according to the identity of the other male. It showed primarily aggression in some cases, and tolerance (including co-nesting) in others. This suggests that some males are highly tolerant of each other, consistent with earlier reports [Tutin, 1996] (Doran et al., this issue), and may be explained by high male relatedness across western gorilla groups within a study site, as previously suggested [Bradley et al., 2004]. Data are not currently available to test male relatedness at Lossi.

Sub- and supergrouping both occurred at Lossi, although both were relatively rare. The pattern of subgrouping differed slightly from that described previously by Remis [1997a], because a silverback was not necessarily present in the nesting subgroups. The contexts of these events are not completely clear. Supergroups did not form at food sources, as might be expected, whereas subgrouping appeared to occur when foraging behavior was distinct from the rest of the group. As more data become available on gorilla social organization, we are seeing increasingly more variation among populations. I stress the need for intraspecific comparisons and more complete data sets on western gorilla social organization. Identifying mechanisms whereby western gorillas reduce within- and between-group competition will be a profitable avenue for future research.

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