

Activity and Ranging Patterns of *Colobus angolensis ruwenzorii* in Nyungwe Forest, Rwanda: Possible Costs of Large Group Size

Peter J. Fashing,^{1,2,3,8} Felix Mulindahabi,⁴ Jean-Baptiste Gakima,⁴ Michel Masozera,⁴ Ian Mununura,⁴ Andrew J. Plumptre,⁵ and Nga Nguyen^{6,7}

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*With group sizes sometimes >300 individuals, the Angolan black-and-white colobus (*Colobus angolensis ruwenzorii*) population in Nyungwe Forest, Rwanda is an intriguing exception to the tendency for folivores to live in smaller groups than expected relative to body size. Researchers have hypothesized that the unusually high quality of foliage at Nyungwe allows colobus there to avoid intragroup feeding competition, releasing constraints on the formation of large groups (Fimbel et al., 2001). We collected data on the activity and ranging patterns of a >300-member Nyungwe colobus group and compared our results to those from smaller groups in other black-and-white colobus (*Colobus spp.*) populations. Colobus at Nyungwe spent far more time feeding and moving (62%) and far less time resting (32%) than black-and-white colobus at any other site. The annual home range of the Nyungwe*

¹Department of Science and Conservation, Pittsburgh Zoo and PPG Aquarium, One Wild Place, Pittsburgh, Pennsylvania 15206.

²Department of Biological Sciences, Carnegie Mellon University, Pittsburgh, Pennsylvania 15206.

³Department of Anthropology, University of Pittsburgh, Pittsburgh, Pennsylvania 15206.

⁴Projet Conservation de la Forêt de Nyungwe, Wildlife Conservation Society, Gisakura, Rwanda.

⁵Albertine Rift Programme, Wildlife Conservation Society, P.O. Box 7487, Kampala, Uganda.

⁶Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544.

⁷Department of Conservation and Science, Cleveland Metroparks Zoo, 3900 Wildlife Way, Cleveland, Ohio 44109.

⁸To whom correspondence should be addressed; e-mail: peterfashing@gmail.com.

colobus was also many times larger (95% minimum convex polygon: 20.7 km²; 95% fixed kernel: 24.4 km²) than those for other populations. We terminated our research after the group engaged in an unprecedented migration among black-and-white colobus by moving 13 km south of their former range. Our results suggest that intragroup scramble competition may be more intense than originally believed within the large colobus groups at Nyungwe and that long periods of resource renewal may be necessary after a large colobus group passes through an area, thereby potentially helping to explain their wide ranging patterns. We discuss the socioecological convergence between the Nyungwe colobus and Chinese snub-nosed monkeys (*Rhinopithecus* spp.) and suggest directions for future research on the unique black-and-white colobus population at Nyungwe.

KEY WORDS: Colobine; Fixed kernel; Folivore paradox; Minimum convex polygon; *Rhinopithecus*; Scramble competition.

INTRODUCTION

The availability and spatial patterning of food resources affect the activity and ranging patterns of many primates (Bennett, 1986; Boinski, 1987; Clutton-Brock, 1975; Kinnaird and O'Brien, 2000; Milton, 1980; Olupot *et al.*, 1997; Watts, 1998; Zhang, 1995). Because leaves are more abundant and evenly distributed than fruits and insects, folivores generally spend less time feeding and moving, more time resting, travel shorter distances per day, and occupy smaller home ranges than frugivores and insectivores (Clutton-Brock and Harvey, 1977b). These behavioral patterns are associated with a strategy of energy conservation typical of many folivores (Dasilva, 1992, 1993; Milton, 1998; Oates, 1977a; Stanford, 1991). The group sizes of folivores also tend to be smaller than those of other primates of similar body size (Clutton-Brock and Harvey, 1977a), a phenomenon labeled the folivore paradox because the relative ubiquity of their foods suggests folivores ought to be able to form large groups (Steenbeek and van Schaik, 2001). Few empirical studies have attempted to explain the folivore paradox, though researchers have suggested that social factors such as infanticide risk may limit group size for some populations (Chapman and Pavelka, 2005; Crockett and Janson, 2000; Steenbeek and van Schaik, 2001), while food competition may limit group size for others (Fashing, 2001; Gillespie and Chapman, 2001; Teichroeb *et al.*, 2003).

The Angolan black-and-white colobus (*Colobus angolensis*) population in Nyungwe Forest, Rwanda is an intriguing exception to the tendency of folivores to live in relatively small groups. Though other populations

of black-and-white colobus¹ typically feature groups ranging in size from 2 to 20 (Fashing, 2006; Oates, 1994), colobus group sizes at Nyungwe sometimes exceed 300 individuals (Fimbel *et al.*, 2001; Plumptre *et al.*, 2002). Fimbel *et al.* (2001) provided intriguing evidence that the unusually high quality of the leaf forage at Nyungwe facilitates the formation of exceptionally large colobus groups at this site. They argued that the superabundance of leaves with high protein/fiber ratios at Nyungwe ensures that the colobus there experience essentially no intragroup feeding competition. Though researchers have intensively investigated the diet of the large colobus groups at Nyungwe (Fimbel *et al.*, 2001; Vedder and Fashing, 2002), few data are available on other aspects of the colobus' behavior and ecology. To address this deficiency, we studied the activity and ranging patterns of a >300-member Nyungwe colobus group. Here, we report our results and compare them to those from other field studies of black-and-white colobus living in smaller groups. Based on these comparisons, we assess the extent to which there may be costs to large group size for Angolan black-and-white colobus at Nyungwe. We also discuss the curious socioecological convergence between the Nyungwe colobus and the snub-nosed monkeys (*Rhinopithecus* spp.) inhabiting the temperate and subtropical forests of China. Lastly, we suggest future directions for research on the unique colobus population at Nyungwe.

METHODS

Study Site

The Nyungwe Forest (2°17'–2°50'S and 29°07'–29°26'E; elevation 1600–2950 m) is one of the largest and most important montane forests remaining in Africa. Recently gazetted as a National Park to protect its extensive floral and faunal diversity (Anonymous, 2004), Nyungwe covers 970 km² in southwest Rwanda (Plumptre *et al.*, 2002; Weber, 1989). It is home to ≥13 nonhuman primate species, including Angolan black-and-white colobus (*Colobus angolensis*), chimpanzees (*Pan troglodytes*), and the Albertine Rift-endemic owl-faced guenon (*Cercopithecus hamlyni*) (Plumptre *et al.*, 2002).

Nyungwe consists of a mixture of primary and secondary forest interspersed with several large marshes. Though ≥100 large tree [≥30 cm diameter at breast height (DBH)] species occur at Nyungwe, 5 of them—

¹The term black-and-white colobus as used here refers to all 5 *Colobus* spp. collectively as in Groves (2001).

Syzygium guineense (Myrtaceae), *Macaranga kilimandscharica* (Euphorbiaceae), *Carapa grandiflora* (Meliaceae), *Strombosia schefferi* (Oleaceae), and *Hagenia abyssinica* (Rosaceae)—account for 51% of the large stems (Plumptre *et al.*, 2002, *unpub. data*). Further, 52% of the large stems at Nyungwe belong to just 3 families: Euphorbiaceae, Myrtaceae, and Meliaceae (Table I; Plumptre *et al.*, 2002). In addition to trees and shrubs, an unusually dense layer of terrestrial herbaceous vegetation blankets the steep slopes at Nyungwe (Fimbel *et al.*, 2001; Maisels *et al.*, 2001). Many forms of human disturbance occur in the forest, including fires, tree cutting, gold mining, honey collection, trapping, and poaching (Fimbel and Kristensen, 1994; Plumptre *et al.*, 2002). Rainfall averages 1744 mm/yr, with July and August the only months when rainfall drops well below 100 mm (Sun *et al.*, 1996). Temperature ranges from a mean daily maximum of 19.6°C to a mean daily minimum of 10.9°C (Sun *et al.*, 1996).

We carried out most of our research on *Colobus angolensis* at Uwinka study site, in the northwest portion of the park. However, by the end of our study, the group had relocated to Bweyeye, 13 km south of Uwinka.

Study Species

Colobus angolensis is 1 of 5 species of black-and-white colobus that live in the forests of tropical Africa (Groves, 2001). The range of *Colobus angolensis* extends from eastern Kenya to western D. R. Congo and they live in a wide variety of habitats, including lowland, coastal, gallery, and montane forests (Fashing, 2006). The ecological flexibility of *Colobus angolensis* is also apparent in the diversity of their diet both within and between sites. Though leaves comprised a substantial part of the diet in all 5 long-term studies to date (Diani, Kenya: Moreno-Black and Maples, 1977; Salonga, D. R. Congo: Maisels *et al.*, 1994; Ituri, D. R. Congo: Bocian, 1997; Nyungwe: Fimbel *et al.*, 2001 and Vedder and Fashing, 2002), *Colobus angolensis* at Salonga, Ituri, and Nyungwe frequently ate seeds (Bocian, 1997; Maisels *et al.*, 1994; Vedder and Fashing, 2002), and in 1 study at Nyungwe often ate lichen and seeds (Vedder and Fashing, 2002).

Groups of *Colobus angolensis* typically include 2–20 individuals, with ≥ 1 adult males, several adult females, and their dependent offspring (Bocian, 1997; Groves, 1973; Kanga, 2001; Kanga and Heidi, 1999/2000; Maisels *et al.*, 1994). However, *Colobus angolensis* at Nyungwe are unusual in that some groups consist of permanent associations of > 300 individuals (Fimbel *et al.*, 2001). Social organization within these large groups remains unknown beyond that many males, females, and immatures are clearly present (Fashing, *pers. obs.*). Researchers have occasionally spotted small

Table 1. The 5 most abundant tree families and their relative densities, i.e., percentage contribution to the total number of stems, at 7 *Colobus* spp. study sites

Rank	Nyungwe, Rwanda ^{a,e,j}	Doula-Edea, Cameroon ^{b,f,k}	Salonga, D.R. Congo ^{g,i,l}	Kakamega, Kenya ^{c,g,m}	Tai, Ivory Coast ^{d,h,n}	Forêt des Abeilles, Gabon ^{b,i,o}	Kibale, Uganda ^{c,j,p}
1	<i>Euphorbiaceae</i> (26%)	<i>Euphorbiaceae</i> (49%)	<i>Caesalpinaceae</i> (39%)	Moraceae (31%)	Ebenaceae (29%)	<i>Caesalpinaceae</i> (24%)	Ulmaceae (24%)
2	<i>Myrtaceae</i> (18%)	Fabaceae (11%)	Annonaceae (7%)	Ulmaceae (13%)	<i>Euphorbiaceae</i> (8%)	Burseraceae (14%)	Bignoniaceae (19%)
3	<i>Meliaceae</i> (8%)	<i>Clusiaceae</i> (5%)	<i>Euphorbiaceae</i> (7%)	<i>Euphorbiaceae</i> (11%)	Annonaceae (6%)	Ebenaceae (8%)	Ebenaceae (11%)
4	<i>Olacaceae</i> (5%)	Anacardiaceae (5%)	Burseraceae (7%)	Apocynaceae (9%)	Mimosaceae (6%)	Mimosaceae (5%)	Moraceae (6%)
5	<i>Clusiaceae</i> (5%)	<i>Olacaceae</i> (5%)	<i>Olacaceae</i> (6%)	Sapotaceae (6%)	Melastomaceae (6%)	<i>Olacaceae</i> (5%)	Rutaceae (5%)

Italics denote the top 5 families at Nyungwe as well as instances where the same families are among the top 5 at other sites.

^a*Colobus angolensis* present; ^b*C. satanas* present; ^c*C. guereza* present; ^d*C. polykomos* present.

^etrees ≥30 cm DBH; ^ftrees ≥50 cm GBH; ^gtrees ≥15 cm DBH; ^htrees >20 cm GBH; ⁱtrees ≥10 cm DBH.

^jPlumptre *et al.* (2002); ^kMcKey (1979); ^lMaisels *et al.* (1994); ^mFashing and Gathua (2004); ⁿKorsijens (2001); ^oBrugiere *et al.* (2002); ^pOates (1974).

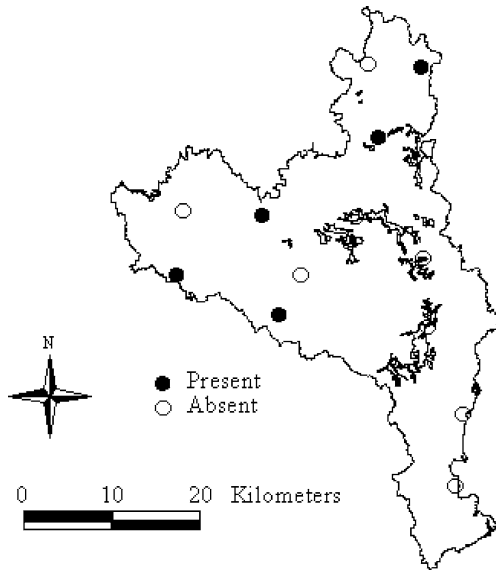


Fig. 1. Distribution of *Colobus angolensis* across Nyungwe Forest based on surveys at 13 sites in 1999. (Modified with permission from Plumtre *et al.*, 2002.)

(<50 members) groups during surveys, though these groups have not yet been studied (Fimbel *et al.*, 2001; Mulindahabi, *pers. obs.*). Surveys also suggest that colobus are distributed unevenly across the forest (Fig. 1) and that their density is low, though researchers have not yet conducted line-transect censuses to estimate colobus abundance at Nyungwe (Plumtre *et al.*, 2002).

We chose to study the same group (Rose group) of *Colobus angolensis* that Fimbel *et al.* (2001) previously investigated in 1993. Rose group comprised >300 individuals, though we did not obtain an exact count, and occupied elevations of 1985–2415 m (mean = 2278 m). The presence of 1 marker individual, an easily identifiable adult female missing part of her tail, as well as the fact that she and her group mates were the only colobus we encountered that did not flee from observers, helped ensure we were following Rose group.

Data Collection and Analysis

Plumtre designed and implemented most of the data collection protocols for the first phase of this study (1998–99), for which, after a training

period, Gakima and Mulindahabi collected most of the data. Fashing and Nguyen spent 5 wk at Nyungwe in April–May, 2000 during which they initiated the second phase of the study (2000–01), for which Gakima and Mulindahabi again collected most of the data. Because Rose group occupied such a large home range and spent much time several h hike away from the research station at Uwinka, we typically began observations at *ca.* 10:00 h and ended at *ca.* 15:00 h.

Activity Budgets

We collected activity budget data on 38 d from November 1998 to October 1999. We selected a focal adult individual opportunistically when we reached the group and recorded its behavior via scan sampling at 30-min intervals throughout the remainder of the day. If we lost the focal individual before the end of the day, we located another adult in the area and followed it for as long as possible. We conducted an average of 9.9 ± 0.4 scan samples ($n = 378$) per d. We recorded the subject's behavior instantaneously at the time of the scan and categorized it as rest, move, feed, groom, aggression, or other. Rest includes all instances in which the subject was inactive. Move includes any locomotor behavior resulting in a change in spatial position. Feed includes the acts of plucking, masticating, or swallowing food. Groom includes instances when the subject was either cleaning or exploring the fur of another individual or having its own fur cleaned or explored by another individual. Aggression includes instances in which the subject was either the actor or recipient in an attack or chase.

Ranging Patterns

We obtained GPS (Global Positioning System) readings of Rose group's location via a portable Garmin GPS unit on 89 d from November 1998 to October 1999 and on 32 d from May 2000 to February 2001. On 51 d during the first period, we recorded only a single reading (*ca.* 10:00 h.) at a location estimated to be the center of Rose group. We conducted longer follows of Rose group on 38 additional days during the first period, during which we obtained GPS readings every 30 min at the location of the same focal adult individual on which we were also conducting activity scans. During the second study period, we obtained GPS readings at irregular intervals beginning *ca.* 10:00 h at locations near the center of the group immediately after each major movement by the group. If we could not pick up a clear satellite signal in the immediate vicinity of the individual(s) owing to heavy canopy cover (Dominy and Duncan, 2001), we moved to a more open

location nearby to obtain the GPS reading. We did not record readings unless the estimated positional error displayed on the GPS unit was <30 m.

We analyzed ranging data via ArcView 3.2 in conjunction with the Animal Movement Analysis Extension (AMAE) to produce estimates of hourly movement rate and home range size (Breslin *et al.*, 1999; Hooge *et al.*, 1999). We estimated hourly movement rate based on data from the 26 d in 1998–99 during which we conducted follows of ≥ 4 consecutive h. We used the AMAE to determine the distances between GPS locations for consecutive 30-min intervals, from which we calculated a mean distance moved per h.

For analyses of home range size, we used only the first locational data point collected at or after 10:00 h. on each study day to minimize autocorrelation of data (Kernohan *et al.*, 2001). Before we could calculate home range size, however, we had to determine whether Rose group exhibited site fidelity (Hooge *et al.*, 1999). We subjected our data to the Monte Carlo random walk-based test for site fidelity provided by the AMAE. We generated 100 random movement paths from our data points and compared the results with the actual patterns of movement to ensure that group movements were site-faithful (Hooge *et al.*, 1999). Per Hooge *et al.* (1999), we considered site fidelity to exist only when the proportion (p) of random movement paths that exceeded actual movement paths in terms of mean squared distances from the center of activity were $>.95$.

We then estimated home range size via a simple technique [minimum convex polygon (MCP)] often used in primate studies (Kaplin, 2001; Sterling *et al.*, 2000; Vie *et al.*, 2001) and a complex technique (fixed kernel) generally regarded as the best home range estimator currently available (Kernohan *et al.*, 2001; Seaman *et al.*, 1999; Worton, 1989). MCP analysis involves creating the smallest possible polygon consisting of internal angles $\leq 180^\circ$ that encompasses all the locations at which one has recorded a study individual or group. The technique has 2 major weaknesses: 1) estimates often include large areas the study individual(s) never entered and 2) estimates are often strongly dependent on sample size (Hooge *et al.*, 1999; Worton, 1987). To reduce the influence of the first weakness, we constructed 95% instead of 100% MCPs, which eliminate the 5% of locations furthest from the mean x - and y -coordinates before constructing the polygon. To address the second weakness, we reported our sample size so that future researchers will be aware of the number of locational data points necessary to produce comparable home range estimates (Seaman *et al.*, 1999). In addition, we assessed whether we had collected a sufficient number of data points to achieve a complete measure of home range area by plotting cumulative range area against number of study

days grouped into intervals of 5. We regarded range area as fully estimated if the cumulative range area curve reached an asymptote (Robbins and McNeilage, 2003).

Fixed kernel analysis is a nonparametric technique for estimating the utilization distribution—the spatial distribution of an individual's movement along a plane—of an individual or group based on a random sample of locational data points (Worton, 1989). Home range estimates computed with kernel analysis are presented as the smallest area that incorporates a set percentage—most commonly 95% or 50% or both—of the utilization distribution (Kernohan *et al.*, 2001). Locations within the 95% contour represent “the area the animal actually uses” and those within the 50% contour represent “the core area of activity” (Hooge *et al.*, 1999, p. 7). Because the choice of smoothing parameter (H) is the most crucial variable influencing estimates of kernel density, it is critical to report the smoothing parameter chosen for a fixed kernel analysis (Kernohan *et al.*, 2001). We allowed the AMAE to choose the most appropriate smoothing factor using least-squares cross-validation (Seaman and Powell, 1996).

RESULTS

Activity Budgets

Adults in Rose group devoted 62% of their time to feeding and moving (Fig. 2). They spent an additional 32% of their time resting and 5% of their time grooming. Aggression accounted for <1% of activity records though scan sampling regimens are probably prone to underestimating time spent engaged in ephemeral events such as aggression.

Females and males devoted similar amounts of time to feeding (Fig. 3). However, females spent more time moving and grooming than males did and considerably less time resting. The only instance of aggression we recorded during a scan involved a male.

Home Range Area

From November 1998–October 1999, the actual movement paths of Rose group diverged significantly from random walks, providing evidence of site fidelity (AMAE Site Fidelity Test, $p > .99$). The 2 methods we used to estimate home range area for this period yielded similar results (Fig. 4). According to 95% MCP analysis ($n = 89$), Rose group occupied a home range of 20.7 km². Fixed kernel analysis ($n = 89$) with $H = 542.6$ estimated

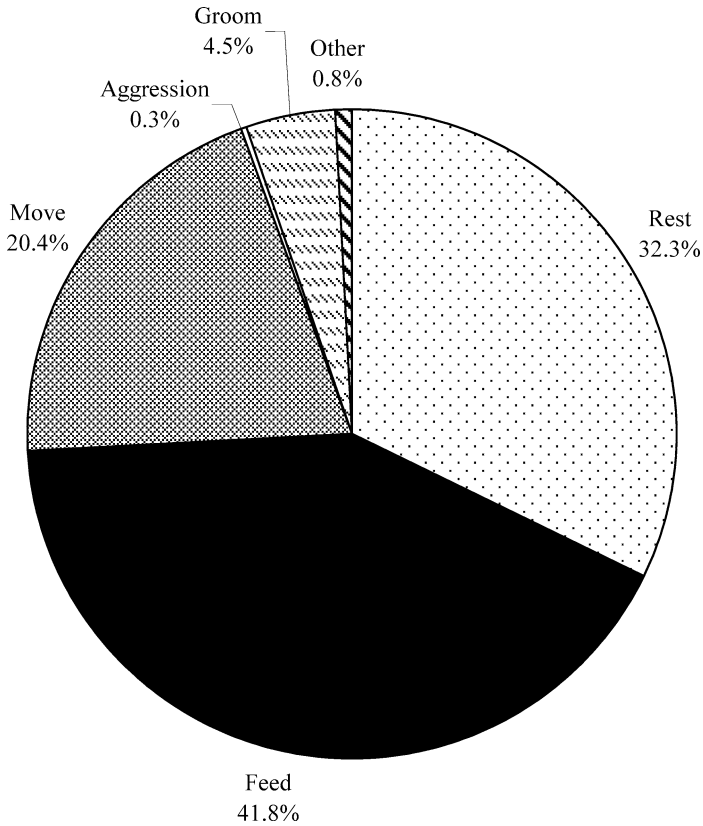


Fig. 2. Activity budget ($n = 378$ scans on 38 d) for adult *Colobus angolensis* at Nyungwe.

the 95% utilization distribution to be 24.4 km² and the 50% utilization distribution to be 3.2 km². These annual range size estimates are relatively complete because our plot of home range area against cumulative number of study days revealed an initial inflection after only 20 d and became clearly asymptotic after 75 d (Fig. 5).

Ranging data from May 2000–February 2001 proved more problematic to analyze. After 24 d of study, Rose group suddenly disappeared in October 2000. Repeated searches of their usual home range over the next 2 mo were unsuccessful and we finally relocated the group in January 2001 near the site of Bweyeye, based on the presence of the marker individual and well habituated nature of the group, 13 km south of the nearest point in their previous home range. We then followed them around Bweyeye for

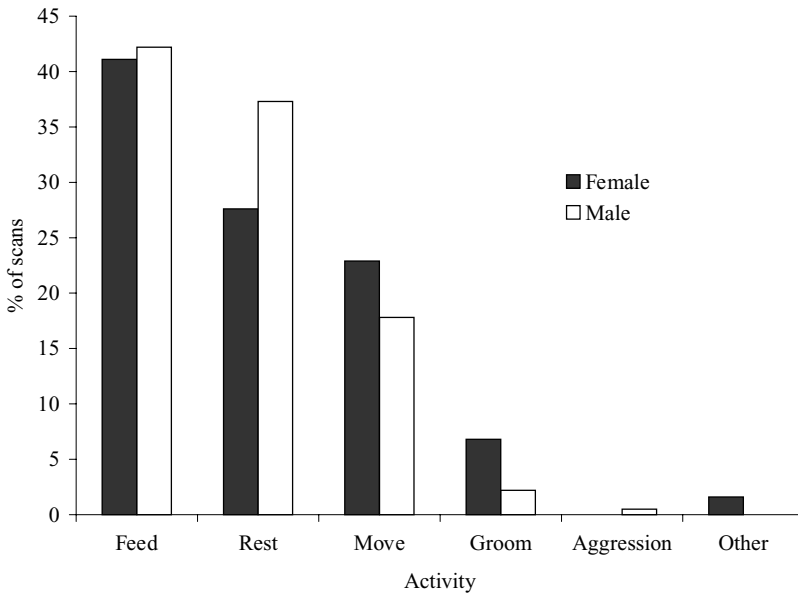


Fig. 3. Comparison of activity budgets between adult females ($n = 192$) and males ($n = 185$). [We conducted 1 additional scan on an adult of undetermined sex that is not included in the figure.]

3 d in both January and February before we abandoned the study owing to logistical difficulties associated with monitoring the group at their new location. Not surprisingly, ranging data for the 2000–01 study period fail the site fidelity test ($p > .31$). However, even if we analyze only the data from before the migration to Bweyeye, Rose group still did not exhibit site fidelity ($p > .83$), though owing primarily to small sample size ($n = 24$).

Because the ranging data from 2000–01 failed the site fidelity test, we could not determine the extent to which home ranges overlapped between the 1998–99 and 2000–01 study periods. However, when we added the 24 points from 2000, i.e., before the migration to Bweyeye, to the 89 points from 1998–99, the site fidelity test remained strong ($p > .99$) and allowed an estimate of Rose group's increase in home range size during the second study period, at least before the migration to Bweyeye. After we added the ranging data from 2000, the 95% MCP increased by 12% to 23.2 km². Similarly, the 95% and 50% utilization distributions derived from fixed kernel analysis ($H = 541.5$) both increased by 9% to 26.5 km² and 3.5 km², respectively, after we added data from 2000.

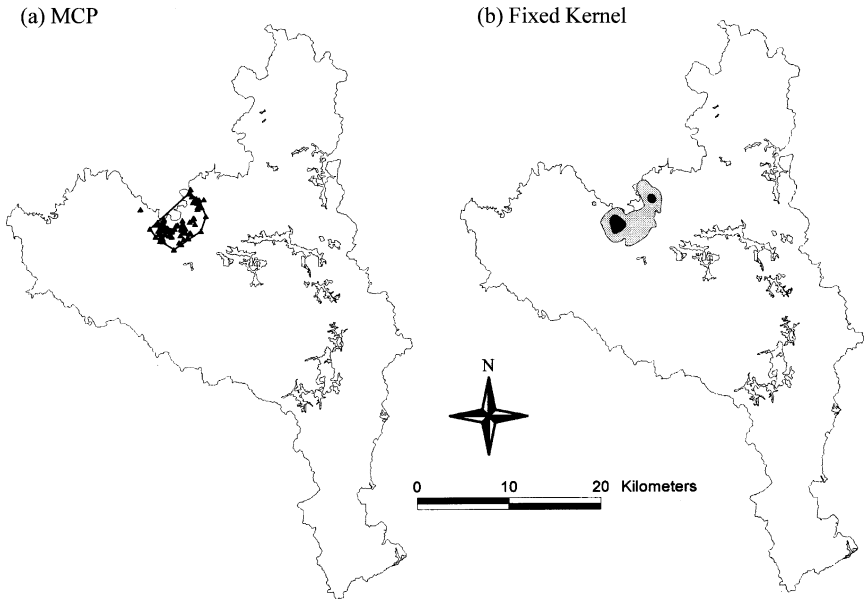


Fig. 4. Annual home range area ($n = 89$ daily data points) for *Colobus angolensis* at Nyungwe estimated as (a) 95% minimum convex polygon (20.7 km^2) and (b) 95% fixed kernel (24.4 km^2). Black areas within the gray 95% fixed kernel represent the 50% fixed kernel (3.2 km^2), or core area.

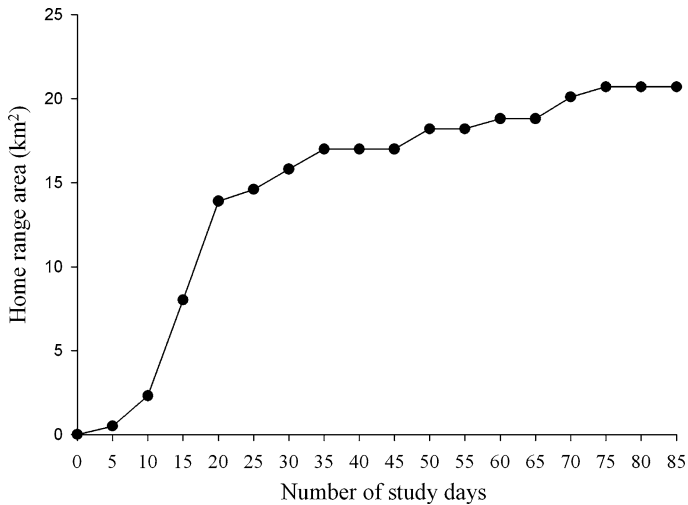


Fig. 5. Cumulative home range area vs. number of study days based on 95% MCP analysis.

Rates of Movement

We calculated rates of movement using data from the 26 d during 1998–99 when we recorded GPS locations for an individual every 30 min over a ≥ 4 h period. Focal individuals traveled a mean distance of 720 m (SD = 409; range = 0–1508 m; $n = 26$) during these observation periods, which averaged 5.12 h/d (SD = .67; range = 4.0–7.0 h; $n = 26$). If we assume the travel rate of 141 m/h is representative of the rate of movement over an entire 12-h day, it can be used to extrapolate to a rough estimated daily path length of *ca.* 1700 m.

DISCUSSION

Comparisons with Other Populations of *Colobus* and Possible Costs of Large Group Size

Our results suggest that *Colobus angolensis* at Nyungwe spend markedly less time resting, spend more time feeding and moving, and travel much longer distances per h than black-and-white colobus in other forests (Table II). This evidence for increased foraging effort and decreased inactivity among the Nyungwe colobus relative to other populations is surprising in light of earlier research demonstrating that leaves are abundant and of unusually high quality at Nyungwe (Fimbel *et al.*, 2001). Our activity budget and movement rate results suggest that, contrary to the impression of previous researchers (Fimbel *et al.*, 2001), there may be substantial energetic costs to living in large groups at Nyungwe. Foraging amidst several hundred conspecifics, even under near optimal ecological conditions, may result in levels of intragroup scramble competition (van Schaik, 1989) sufficient to prevent *Colobus angolensis* at Nyungwe from adopting the energy conservation strategy typical of other black-and-white colobus (Dasilva, 1992, 1993; Oates, 1977a). In addition, energetic strategies of *Colobus angolensis* in general may differ from those of other well-studied *Colobus* such as *C. guereza* and *C. polykomos* (Dasilva, 1992, 1993; Oates, 1977a). Though they still spent 11% more time per day resting and traveled 42% fewer m/h than the Nyungwe colobus, conspecifics in Ituri Forest, D. R. Congo are the only other black-and-white colobus population known to devote <50% of their time to resting and to travel at >75 m/h (Table II; Bocian, 1997).

Despite the possibility our study raised that scramble competition may be intense within the large colobus groups at Nyungwe, our comparisons of black-and-white colobus activity budgets and movement rates across

Table II. Activity budgets, home range sizes, and hourly movement rates of black and white colobus at 13 study sites

Species	Study site	Group size (mean) ^a	Rest (%)	Feed (%)	Move (%)	Social (%)	Other (%)	Home range (ha)	Movement rate (m/h)	References
<i>Colobus angolensis</i> ^b	Nyungwe, Rwanda	> 300	32	42	20	5	1	2440 ^c	141	This study
<i>C. angolensis</i> ^d	Ituri, D.R. Congo	14	43	27	24	5	1	371	82	Bocian (1997)
<i>C. guereza</i>	Kibale, Uganda	11	57	20	5	11	7	28	45	Oates (1977a,b)
<i>C. guereza</i> ^d	Ituri, D.R. Congo	8	52	19	22	5	2	100	51	Bocian (1997)
<i>C. guereza</i> ^{d,e}	Kakamega, Kenya	13	63	26	2	7	2	18	49	Fashing (2001)
<i>C. guereza</i> ^{d,g}	Entebbe, Uganda	7	58	20	12	10	1	8	32	Grimes (2000)
<i>C. guereza</i>	Budongo, Uganda	7	—	—	—	—	—	14	—	Suzuki (1979)
<i>C. polykomos</i> ^h	Tiwai, Sierra Leone	11	61	28	9	1	1	24	69	Dasilva (1989, 1992)
<i>C. polykomos</i>	Tai, Ivory Coast	16	—	—	—	—	—	77	51	Korsijens (2001)
<i>C. satanas</i>	Douala-Edea, Cameroon	15	60 ⁱ	23	4	14 ^j	0	60	38	McKey and Waterman (1982)
<i>C. satanas</i>	Lopé, Gabon	9	—	—	—	—	—	184	43	Harrison (1986); Oates (1994)
<i>C. satanas</i>	Forêt des Abeilles, Gabon	17	—	—	—	—	—	573	71	Fleury and Gautier-Hion (1999)
<i>C. vellerosus</i>	Boabeng-Fiema, Ghana	14	59	24	15	3	0	—	—	Teichroeb <i>et al.</i> (2003)
<i>C. vellerosus</i>	Bia, Ghana	16	—	—	—	—	—	48	26	Olson (1986); Oates (1994)

The table includes only those activity budget studies of ≥ 4 mo and ranging studies of ≥ 6 mo. Activity budgets are based on scan sampling of the first behavior performed for > 5 s continuously unless otherwise noted. Home range areas are calculated via the grid cell method unless otherwise noted.

^aFrom Fashing (2006).

^bRecorded first behavior performed regardless of duration during scan samples.

^cFixed kernel 95% utilization distribution over a 1-year period.

^dRecorded first behavior performed for > 3 s continuously during scan samples.

^eMean of activity budgets of 2 groups.

^fMean of activity budgets for 3 groups studied for 6 mo each. Values were recalculated after discarding 18.6% of 5790 total scans which were out of sight.

^gConducted instantaneous scan samples.

^hRecorded first behavior performed 5 s after spotting an individual.

ⁱTotal of time spent sitting, lying, and clinging.

^jAuthors included time spent self-cleaning and grooming as 1 category so time spent social (playing and grooming) is overestimated here.

sites must be regarded with caution due to differences in methodology and forest composition across studies. For example, methods of sampling activity were inconsistent across studies (Table II), though fortunately previous researchers have shown that the different methods used to study colobine activity patterns typically produce similar results (Clutton-Brock, 1977). A more critical methodological difference between our study and previous black-and-white colobus studies is that we collected both activity and ranging data primarily between 10:00–15:00 h whereas authors of most previous studies collected data during dawn-to-dusk samples. While we cannot unequivocally rule out time of day as a confounding factor in our comparisons, there is no evidence from other black-and-white colobus populations that the 10:00–15:00 h-period is typified by widely divergent activity or travel rates relative to other times of day (Bocian, 1997; Dasilva, 1989; Fashing, 1999; McKey, 1979; Oates, 1974; Teichroeb *et al.* 2003). Lastly, forests at black-and-white colobus study sites across Africa vary widely in vegetation structure and composition, making it impossible to control for habitat differences that might contribute to intersite variation in activity and movement patterns. Of the 3 most common tree families at Nyungwe, which combine to account for 52% of total trees, only Euphorbiaceae are also common at some of the other black-and-white colobus sites (Table I). Nyungwe is also unusual among black-and-white colobus sites in its high elevation, steep slopes, relatively open canopy, and thick layer of terrestrial herbaceous vegetation, which Fimbel *et al.* (2001) suggested contribute to the high nutritional quality of the vegetation at Nyungwe which in turn may permit the formation of the unusually large colobus groups there.

Another unusual feature of Rose group is that it occupied a home range far larger than any previously recorded for black-and-white colobus (Table II). They exhibited strong site fidelity while ranging widely over a 26.5-km² area during a *ca.* 2-yr period before suddenly migrating 13 km south of their former range where it ceased being practical for observers to follow them. Fleury and Gautier-Hion (1999) previously described semi-nomadic ranging patterns for *Colobus satanas* in the Forêt des Abeilles, Gabon, though a relocation of the magnitude we observed among the Nyungwe colobus is unprecedented. As with their high activity levels and movement rates, the wide-ranging habits of the colobus are difficult to reconcile with the abundance and high quality of foliage at Nyungwe. Occupying large home ranges and migrating into unfamiliar areas are likely to entail significant costs. For example, as range size increases, familiarity with key resource patches and the phenological patterns that determine resource availability at different locations within the range are likely to decrease. Further, expanding into unfamiliar areas increases predation risk for other

primates such as vervets (Isbell *et al.*, 1990), though the large group sizes of colobus at Nyungwe may help counteract this effect.

A possible explanation for the wide ranging habits of the Nyungwe colobus is that the food sources they exploit may have long resource renewal times, particularly when the potential destruction resulting from simultaneous visits by >300 individuals is considered. Though they live in far smaller groups than Nyungwe colobus, mountain gorillas in similar montane forest habitat in northern Rwanda do so much trampling damage to their terrestrial food patches that plants in the patches require 6–8 mo to return to their original stem heights and biomasses (Plumptre, 1993; Watts, 1987). Angolan colobus at Nyungwe also feed heavily on terrestrial vegetation, particularly *Sericostachys scandens* (Amaranthaceae), the mature leaves of which were among the top food items in both studies of colobus diets at Nyungwe (Fimbel *et al.*, 2001; Vedder and Fashing, 2002, *unpub. data*). In our study, wide areas of terrestrial vegetation left behind after Rose group passed through them exhibited evidence of severe trampling damage, and seemed to require considerable amounts of time for recovery (Fig. 6; Fashing, *pers. obs.*). Lichen is another food source that could require colobus groups to range over large areas at Nyungwe. Though



Fig. 6. Damage to terrestrial vegetation by *Colobus angolensis* at Nyungwe. The photo shows only a small portion of the area typically damaged by colobus trampling when large groups descend to the ground to forage.

infrequently consumed during Fimbel *et al.*'s (2002) study, lichen was a major food source for the Nyungwe colobus in a study Amy Vedder conducted at a nearby location 5 yr earlier, when it accounted for 32% of the annual diet and up to 57% of the monthly diet (Vedder and Fashing, 2002). Lichen has an extraordinarily long recovery time, requiring up to 20 yr for regrowth after harvesting in the temperate montane forests of China (Kirkpatrick, 1996; Li, 2004). Thus, with the destruction caused by >300 individuals foraging simultaneously, the need to allow sufficient regeneration time for food sources such as lichen and terrestrial vegetation in exploited areas might help explain the large home range and migratory tendencies of Angolan colobus at Nyungwe, though a simultaneous study of feeding ecology and ranging patterns will be necessary to test this hypothesis properly.

Socioecological Convergence with Chinese Snub-nosed Monkeys

Though their combination of large group size, wide ranging patterns, and extensive consumption of lichen and terrestrial vegetation is unique among the African colobines, Angolan colobus at Nyungwe exhibit a fascinating socioecological convergence with the snub-nosed monkeys (*Rhinopithecus* spp.) inhabiting the forests of China. All 3 Chinese snub-nosed monkey species [Yunnan snub-nosed langur (*Rhinopithecus bieti*), Guizhou snub-nosed langur (*R. brelichi*), and Sichuan snub-nosed langur (*R. roxellana*)] occupy extensive (>20 km²) home ranges and form large (100–600 member) bands, though only in *R. bieti* are these groupings essentially permanent as in Nyungwe *Colobus angolensis* (Kirkpatrick, 1998). Groups of *Rhinopithecus brelichi* and *R. roxellana* frequently fission and fuse, presumably in response to temporal changes in food abundance and distribution (Bleisch *et al.*, 1993; Bleisch and Xie, 1998; Kirkpatrick, 1998). The 3 Chinese snub-nosed species also exhibit a multitiered social organization in which the large bands consist of many 1-male units as in gelada and hamadryas baboons (Kirkpatrick, 1998). Unfortunately, researchers have not yet investigated whether the large groups of *Colobus angolensis* at Nyungwe represent similar aggregations of many 1-male units.

Like *Colobus angolensis* at Nyungwe, 2 of the 3 Chinese snub-nosed species, *Rhinopithecus bieti* and *R. roxellana*, feed on lichen (Kirkpatrick, 1996; Li *et al.*, 2002; Schaller, 1985; Su *et al.*, 1998). In fact, Kirkpatrick *et al.* (1998) suggested that formation of permanent large groups by *Rhinopithecus bieti* is a response to feeding almost exclusively on lichen, an ubiquitous but slowly replenishing food source in the harsh temperate montane forests where they live. They argue that when all the individuals in an

area forage together on lichen over a large home range, they are able to avoid wasting energy encountering patches previously depleted by others where lichen regrowth may not be completed for another 20 yr (Kirkpatrick *et al.*, 1998). Heavy consumption of lichen is probably too irregular among *Colobus angolensis* at Nyungwe to be the selective force causing them to form large groups. However, the widespread availability of lichen may play a role, along with the abundance of high-quality mature leaves that Fimbel *et al.* (2001) noted, in facilitating the formation of large colobus groups at Nyungwe.

Future Research Directions on *Colobus angolensis* at Nyungwe

To achieve a fuller understanding of the socioecology of the unique colobus population at Nyungwe, future studies must acquire more detailed data on the spatiotemporal characteristics of colobus food sources, the social organization within groups, and the nature and intensity of the predation pressure exerted on these groups. Our hypothesis that the wide-ranging patterns of colobus at Nyungwe can be explained by the need to allow food sources long periods to recover from trampling or browsing damage requires testing through long-term monitoring of resource renewal rates after exploitation as well as examination of the rates of colobus food patch revisitation. Further study is also essential to determine whether the large colobus groups at Nyungwe consist of many discrete 1-male units banding together as in Chinese snub-nosed monkeys (Kirkpatrick, 1998) or whether they are simply enormous multimale, multifemale groups. Lastly, the possibility we raised that there are significant costs to life in large groups for the Nyungwe colobus suggests that a relatively strong selective pressure exists, or has existed in the past, to promote large group size. One such selective pressure might be predation risk: a concurrent study of chimpanzee feeding ecology employing scatological analysis found black or brown-and-white primate hairs (colobus or L'Hoest's monkeys) in 7 chimpanzee fecal samples (Masozera, Gakima, and Mulindahabi, *pers. obs.*). With the recent successful habituation of a chimpanzee community at Nyungwe, a possible link between chimpanzee predation risk and large group size in Angolan colobus deserves investigation, particularly because red colobus, the prey favored by chimpanzees in other African forests (Boesch and Boesch, 1989; Stanford, 1998; Watts and Mitani, 2002), are not found at Nyungwe.

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