



Demographic Variation Among Udzungwa Red Colobus in Relation to Gross Ecological and Sociological Parameters

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*We evaluated variation in group size and composition of Udzungwa red colobus (*Procolobus gordonorum*) in relation to gross-habitat and sociological parameters. The endangered species is endemic to the Udzungwa Mountains and nearby forests in the Kilombero Valley of south-central Tanzania. We counted 63 groups in 10 forests, ranging in altitude from 250 to 1,800 m. Group size ranged from 7 to 83 ($\bar{x} = 36.3$) individuals and adult sex ratios (females/male) ranged from 1.5 to 7.3 ($\bar{x} = 3.5$), excluding solitary individuals. Group size was influenced by several habitat parameters, including tree density, degree of deciduousness, and forest size. Groups were largest in large blocks of mature, moist, mixed evergreen and semideciduous forests, but group size is not correlated with altitude. Groups in a highly degraded forest appeared to have fission-fusion societies. The effect of habitat quality on age-sex composition of groups was most apparent in natality and less so in survivorship of adult females and juveniles. The number of adult males in groups accounted for 50% of the variance in group size and 34–39% of the variance in numbers of adult females in groups. Habitat quality affects natality more than demographic parameters do. Groups with a low proportion of*

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adult females had greater juvenile survivorship, perhaps because of lower food competition between these two classes. We proffer hypotheses based on our study and previous intertaxonal comparisons to explain cause and effect relationships between habitat quality and demography. Finally, our study demonstrates the importance of large blocks of old-growth forest to the conservation of *Udzungwa red colobus*, and we make recommendations for conservation and research.

KEY WORDS: colobus; demography; group size; sex ratio; natality; Udzungwa.

INTRODUCTION

The extent of intraspecific demographic variation is poorly understood for most primate species. The correlates of the variation are even less well known, often because sample sizes are small and from a single site. Nonetheless, much of theoretical primate behavioral ecology focuses on interspecific comparisons that assume the small samples are representative of the species being contrasted (Chapman and Chapman, 2000a; Clutton-Brock and Harvey, 1977; Isbell, 1994; Mitani *et al.*, 1996; Van Schaik, 1983; Van Schaik and Van Hooff, 1983; Wrangham, 1980; Wrangham *et al.*, 1993). The same assumption is often made when extrapolating population densities from line-transect censuses, which count groups rather than individuals (Chapman *et al.*, 2000; Struhsaker, 1975). This approach can be particularly misleading and even counterproductive when using small samples and before we fully understand the extent and basis of intraspecific variation in group size and composition (Chapman *et al.*, 2002; Chapman and Chapman, 2000b; Struhsaker, 2000a). Furthermore, comparisons within a superspecies and among taxa are unable to separate the possible influence of ecological and sociological variables from ones reflecting phylogenetic inertia, i.e. differences between taxa in evolutionary history.

Our study demonstrates the extreme variation in size and age-sex composition of social groups or foraging parties within one primate species, Udzungwa red colobus (*Procolobus gordonorum*). We made comparisons within populations and between populations separated by major breaks in habitat or ones joined only by marginal habitat strips that are unlikely to be used by red colobus for dispersal. Our sample of group size is one of the largest for any population of African monkeys and perhaps the largest for any population of nonhuman primate studied anywhere, excepting *Macaca mulatta* (Southwick *et al.*, 1965).

We compare gross ecological parameters—altitude, tree density and habitat disturbance, forest type, and forest patch size—with demographic variation and evaluate hypotheses on the sociological basis for variation in

group size and age-sex composition. Previous evaluations of red colobus demographic variation have relied primarily on intertaxonal comparisons (species and/or subspecies of red colobus: Struhsaker, 1975; Struhsaker, 2000a,b; Struhsaker and Leland, 1979). Notable exceptions are the intraspecific studies of Decker (1994a,b), Siex and Struhsaker (1999), Chapman and Chapman (2000b), Chapman *et al.* (2002) and Marshall *et al.* (in press).

Finally, our study demonstrates the importance of detailed demographic data in developing effective conservation management practices, especially in regard to habitat protection and restoration.

STUDY SITES (Fig. 1)

We counted groups in 7 isolated forests scattered throughout the Udzungwa Mountains (centered near 8° 20'S., 35° 50'E.) and in 3 small, isolated forest patches in the low and flat Kilombero Valley near the eastern side of the Udzungwas. Most of them were either in the Udzungwa Mountains National Park (UMNP) or in government forest reserves (FR). The greatest distance between any 2 sites was *ca.* 140 km. While it seems certain that the different forest blocks and fragments were contiguous at one time, it is not known how long they have been separated from one another. Some have probably been separated for ≥ 100 years, with anthropogenic

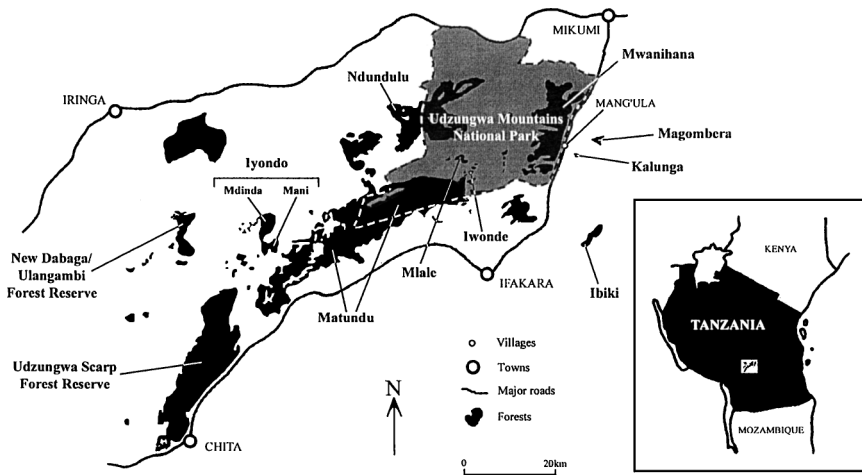


Fig. 1. Map of the Udzungwa Mountains and main study forests. Magombera, Kalunga, and Ibiki are in the Kilombero Valley, while all other forests are in the mountains.

fires maintaining the separations. The Udzungwa Mts. are estimated to be ca. 7–10 million years old (Griffiths, 1993), which may partially explain their high degree of biological endemism, including the 2 endemic primates (Udzungwa red colobus and Sanje mangabey: *Cercocebus galeritus sanjei*). The Udzungwa Mts. cover ca. 10,000 km² and contain the greatest amount of forest cover and the largest altitudinal range (300–2,600 m) in the Eastern Arc Mountain chain.

Mwanihana Forest

(300–2,080 m asl [asl = above sea level], 7°40'–7°57'S, 36°46'–36°56'E). Most of our data is from the Mwanihana forest, which is located entirely within UMNP. Annual rainfall is 2,000–2,500 mm. It is a mosaic of vegetation types, including lowland, submontane, montane and upper montane moist, mixed evergreen and semideciduous forests with canopy height ≤30–40 m in the older stands. Miombo woodland (dominated by *Brachystegia* spp.) occurs on the lower and drier areas, while bamboo and grassland occur at higher altitudes (Lovett, 1993; Lovett *et al.*, 1988; Lovett and Pocs, 1993).

Some extraction of timber occurred in Mwanihana in the 1960s and 1970s when it was a government forest reserve. The disturbance was primarily along the eastern side near the road between Kidatu and Kiberege. Logging adjacent to UMNP headquarters at Mang'ula was unusually heavy (Table I). Firewood can be legally collected in the area. There is also some illegal removal of building poles and timber, as well as snare trapping in Mwanihana. The forest is more intact further west and away from the road.

The amount of closed canopy forest in Mwanihana was estimated at 59 km² by Rodgers and Homewood (1982) and 177 km² by Dinesen *et al.*

Table I. Habitat differences between Mwanihana and Kalunga^a

Site	Tree density (no./ha)	Tree Stump Density (no./ha)	Tree Canopy Cover (%)	Ground cover (%)			
				Herbs	Shrubs	Trees	Rice
Mwanihana (500–550 m a.s.l.)	370.0a	24.0a	53.6a	52.5a	32.8a	14.7a	0.0a
Mwanihana (300–350 m a.s.l.)	447.5a	45.0a	40.1b	47.7a	38.7a	13.5b	0.0a
Kalunga (280 m a.s.l.)	68.0b	78.0b	10.0c	43.5a	35.3a	0.4c	20.8b

Note. For each column entries with same letter are not significantly different, whereas those with different letters are significantly different (Mann–Whitney *U*, $p \leq 0.05$, 1-tailed). Trees were >20 cm. dbh.

(2001). It is not known how much of the discrepancy is due to the fact that the latter estimate includes bamboo, a habitat not generally used by the primates. Regardless which estimate is most accurate, Mwanihana represents one of the largest examples of relatively mature, moist, mixed evergreen and semideciduous forest in our sample.

All of us collected data in Mwanihana.

Kalunga Forest

(280 m asl, 7°53'S, 36°56'E). Kalunga is the second most important site in our study in terms of numbers of red colobus groups counted. This small forest is located in the Kilombero valley 5 kms southeast of Mang'ula and UMNP. It was at one time a government forest reserve, but around 1980 it was sold to General Tyre. In 1981 planting of rubber trees (*Hevea* sp.) began and ca. 1.72 km² of the natural forest was eventually clear cut and replaced with rubber plantation. Based on Landsat images from October 1999, we estimated that the remaining natural forest covered only 2.65 km², while ca. 1.36 km² was under rubber. The natural forest was completely surrounded by agriculture.

When we first visited Kalunga in 1997 it was being severely exploited by villagers for timber, charcoal, and firewood. Most of the products were transported to the main road for commercial sale. In addition, some areas within the Kalunga forest were planted with rice during the rainy season. After 1997, exploitation of the forest increased dramatically. Although sometimes referred to as a village government forest reserve, its legal status was disputed throughout our study and at no time was there any attempt to regulate its exploitation. The remaining forest was semideciduous with the tallest trees ca. 25 m high. The entire area was prone to seasonal flooding, probably due to an underlying hard pan. In 2000, the density of trees ≥ 20 cms dbh was significantly lower in Kalunga than in Mwanihana (Table I), reflecting the highly fragmented and disturbed character of the forest.

All of us except Marshall collected data in Kalunga.

Magombera (Magombero Forest)

(270 m asl, 7°49'S, 36°58'E). We collected data on red colobus groups from Magombera Forest during 2 periods: 1977 (Struhsaker and Leland, 1980) and 1992 (Decker, 1994b). It is a small forest in the Kilombero Valley near the village of Katulukila ca. 6.5 km. NNE. of Kalunga and 6.5 km. east of Mwanihana. Magombera has a high water table that supports

ground-water forest and is less deciduous than Kalunga Forest. In the 1960s, it was a government reserve that was bisected by the TAZARA railway. When the railway was constructed, many of the larger trees were cut for timber. Then, the forest was further degraded by villagers, who illegally encroached for agriculture, illegally harvested timber, charcoal, and building poles, and poached wildlife. The area of the reserve was *ca.* 11 km². In 1980, the government excised the part of Magombera lying north of the railway. It was soon clear-cut and replaced with agriculture, thereby reducing the forest to *ca.* 6 km² (Decker, 1994b). The remaining forest was intended for annexation to the Selous Game Reserve, but it is unclear if this actually happened. Based on Landsat images taken in October 1999, we estimated that the remaining area of the Magombera Forest adjacent to the Selous Game Reserve was between 9.4 and 11 km². This discrepancy in estimates of forest size may be due to a combination of factors, including forest regeneration since the original estimates were made and differences in habitat classification between aerial photography and Landsat images. In any event, Magombera represents the second smallest forest in our study. Although significantly disturbed in the past, Decker's (1994b) survey indicated that forest disturbance and encroachment had been greatly reduced. This also appeared to be so during a one-day visit in July 2002 (Struhsaker). Magombera differs from Kalunga in being larger, wetter, more evergreen, less disturbed, and less isolated by agriculture.

Iyondo (Lyondo) Forest

(1,000 to 1,850 m asl, 8°00'–8°16'S, 36°06'–36°22'E). Iyondo Forest is part of the central government West Kilombero Scarp Forest Reserve (WKS). It is essentially divided into 2 forest blocks that are locally known as Mani and Mbinda, which are connected by a narrow strip of forest along the Mngeta River. They are dominated by tall, moist evergreen forest (Lovett and Pocs, 1993). Total forest area is *ca.* 51 km² (Dinesen *et al.*, 2001). Marshall counted red colobus groups in relatively intact parts of the forests at elevations of *ca.* 1,600–1,800 m during 2 short visits in 2001.

Udzungwa Scarp Forest Reserve

(300–2,068 m asl, 8°14'–8°32'S, 35°51'–36°02'E). Udzungwa Scarp is a government forest reserve of 512 km². It contains lowland, submontane, and montane forests (Lovett and Pocs, 1993). Marshall counted 2 groups of red colobus in 2001 *ca.* 3 kms from Chita village at *ca.* 1,100 m asl in

tall evergreen forest, where low to high levels of pitsawing had occurred Dinesen *et al.* (2001) estimated forest cover to be 230 km², including bamboo.

Ndundulu (Luhombero)

Part of Ndundulu forest is in WKS and part in UMNP. One count of a red colobus group was made by Struhsaker and Marshall in June 2001 at Nyati Camp (ca. 1,400 m asl, 7°48.5'S, 36°28.5'E) in tall, moist, evergreen forest. There was no sign of timber cutting, but we heard hunters and saw their foot prints. Dinesen *et al.* (2001) estimated forest cover of Ndundulu to be 250 km², including bamboo.

Matundu Forest

(300–ca. 680 m asl, 7°55'–8°9'S, 36°18'–36°36'E). The majority of Matundu Forest is administered as a government forest reserve (FR). The remainder is within the UMNP. The southern half of Matundu is covered with miombo and dry forest, whereas the northern half is a large tract of lowland forest with a canopy <50 m high (Lovett and Pocs, 1993). Total forest cover is ca. 522 km² (Dinesen *et al.*, 2001). In 2001, Marshall counted 3 groups of red colobus in the dry, deciduous forest of the southern part of Matundu FR (ca. 400 m asl, 8°3.4'S, 36°19.9'E) and outside UMNP, where it had experienced moderately high levels of selective logging.

Iwonde

Iwonde contains 3 isolated patches of forest that are surrounded by grassland and miombo within UMNP. One group of red colobus was counted in a tall, mature, evergreen forest patch ca. 5 km² at 1,128 m asl and 7°55.9'S, 36°38'E. Iwonde is one of the most remote forests in the Udzungwas, and Ehardt, and Butynski noted no evidence of human activity.

Mlale

(1,158 m asl, 7°51.6'S, 36°37'E). Mlale is a small strip of forest <2 km² within UMNP. It is an evergreen, moist, closed-canopy forest with a well-developed understory and midstory surrounded by grassland and miombo. Like Iwonde, Mlale is very remote, and Ehardt and Butynski saw no sign of human activity there. Ehardt counted one group of red colobus there.

Ibiki

(250 m asl, 8°01'–8°06'S, 36°55'–37°00'E). Ibiki lies in the Kilombero Valley along the right bank (west side) of the Msolwa River and it is flooded during rainy seasons. It is ca. 22 km² based on a map printed in 1983 (1:50,000, Lukamanga, sheet 235/2). Ibiki is a dry, deciduous, and low stature forest, with most trees <10 m high, but some reach 15–20 m. Ibiki had no conservation status and was being degraded throughout by extensive pitsawing. Some of the forest edge had been cleared for agriculture. Approximately half of Ibiki is bordered by the Selous Game Reserve and the remainder by public land dominated by seasonal agriculture. Struhsaker and Dahl Lisbjerg counted one group of red colobus near the center of Ibiki.

In summary: the 10 forest sites in this study represent:

1. 4 large blocks of relatively intact, mature, moist, mixed evergreen and semideciduous forest—Mwanihana, Iyondo/Lyondo, Udzungwa Scarp, and Ndundulu—covering a wide range of elevations;
2. 2 small patches of intact, old-growth, moist, mixed evergreen and semi-deciduous forest at high elevations: Iwonde and Mlale;
3. one large block of low altitude, dry and deciduous forest degraded by moderately high levels of pit sawing: Matundu;
4. one small patch of recently and severely degraded low altitude, semideciduous forest with some seasonal flooding: Kalunga;
5. one small patch of low altitude, semideciduous forest with high water table, seasonal flooding, and past history of moderate degradation by humans: Magombera;
6. one small to moderate-sized patch of low altitude, dry, deciduous forest with seasonal flooding and widespread, recent degradation by humans: Ibiki.

Predation

We found no evidence at any site that Udzungwa red colobus were hunted by humans using guns, but Marshall *et al.* (in press) thought that primates were being hunted at low levels in the Ndundulu and New Dabaga/Ulangambi Forests. Although we found a few snare traps, they were on the ground and in areas where red colobus groups were large. Certainly, they caught mangabeys (Marshall) and black-and-white colobus (*Colobus angolensis*, photo from H. Dule seen by Struhsaker), but there is no evidence that they had any impact on red colobus numbers, group size or group composition at our sites.

Crowned eagles (*Stephanoaetus coronatus*) were very common at all of our study sites, and we consider predation pressure by them on red colobus to be constant in our comparisons among sites.

METHODS

We collected demographic data from 1997 through 2001 during field trips lasting from a few weeks to several months. We counted groups during broad biological surveys and while studying specific groups to collect detailed information on group size, behavior and ecology. We plotted locations of groups on 1:50,000 maps via a combination of landmarks and GPS readings. We tried to avoid including the same group more than once in the analysis via a combination of information on group size, composition, and location.

Although counts were of cohesive groups of colobus that were spread over ≤ 50 m, observations at our smallest and most disturbed site (Kalunga) indicated that groups sometimes split into smaller units and then reunited later in the day: fission-fusion society. This might have also occurred on at least one occasion in the much larger Mwanihana site. Consequently, though most of our counts are probably of entire social groups, some may be counts of foraging parties.

In an attempt to minimize differences among observers in counting and distinguishing age-sex classes, Struhsaker, who has >30 years experience with red colobus, spent several days training each of the other observers. We made interobserver reliability checks throughout the training periods to ensure standardization and consistency among observers. This was particularly important for consistency in classifying the various size classes and distinguishing males from females. Sexual dimorphism is weakly developed in this species and distinguishing adult males from adult females in the field requires training and practice.

We determined the density of trees and stumps ≥ 20 cm dbh along 5-m wide transects. We tallied only trees and stumps whose centers were ≤ 2.5 m of the transect center. We estimated tree canopy and ground cover in circular plots with a 2.5 m radius (19.6 m²) at 20 m intervals along the transects. We estimated tree canopy cover as the percentage of sky covered by trees ≥ 20 m tall over the plots. Five transects each 200 m long were enumerated in the Kalunga forest (280 m asl) in July and August 2000 by Detwiler and R. Mwangulango. The Mwanihana forest within UMNP was sampled along 5 transects by Mwangulango in June 2001; 4 were 200 m long (ca. 300–350 m asl) and 1 was one km long (ca. 500–550 m asl on the trail between Mkula ranger post and Sanje Falls). The Mwanihana transects were

distributed over a linear distance of about 7.5 km from a point about half way between the Mkula ranger post and the Sanje Falls to a point about 0.5 km south of the UMNP headquarters near Mang'ula. The Mwanihana forest sampled at lower elevations had been partially influenced by selective logging in the 1960s–1970s, while that at higher elevations was relatively undisturbed.

We used Mann-Whitney U tests (1-tailed because predictions were directional) to compare group size and composition among sites and over time. We made no Bonferroni adjustments because we had made predictions a priori and because such adjustments increase the probability of type II errors (Perneger, 1998). When examining relationships between variables, we square root transformed data to stabilize the variance and to meet the assumptions of linear regression models.

RESULTS

Group Size and Observer

Group size ranged from 7–83 ($n = 60$, $\bar{x} = 36.3$, ± 15.14 , coefficient of variation [$cv = \text{standard deviation}/\text{mean} \times 100$] = 41.8%), excluding 3 counts from Iwonde, Mlale, and Ibiki because of uncertainty in accuracy, Appendix). Interobserver consistency is high and there is no significant difference in the group counts made by Struhsaker and Detwiler ($U = 45$, $p = 0.50$) or between their combined counts and those of Marshall ($U = 55.5$, $p = 0.18$) in the Udzungwa Mts. (Appendix) from 1997 to 2001.

We noted ≥ 8 solitary adult and subadult males. Twice we saw single adult females each with a clinging infant and we saw a medium juvenile once. Solitaries are excluded from the analysis of group size and composition.

Group Size and Altitude

In spite of differences in temperature and specific composition of trees, there is no significant difference in the size of red colobus groups at different altitudes within the mixed evergreen and semideciduous forests of the Udzungwa Mts. We compared group sizes at elevations of 300–700 m (Mwanihana, $\bar{x} = 40$) to those at 900–1,800 m (Mwanihana, Iyondo, Udzungwa Scarp, and Ndundulu, $\bar{x} = 45$, $U = 205.5$, $p = 0.14$, Appendix and Fig. 2). It may be, however, that red colobus groups were smaller in the high altitude ($>1,100$ m), moist, evergreen forests, e.g., Ndundulu, of the western Udzungwas than elsewhere in the mountains.

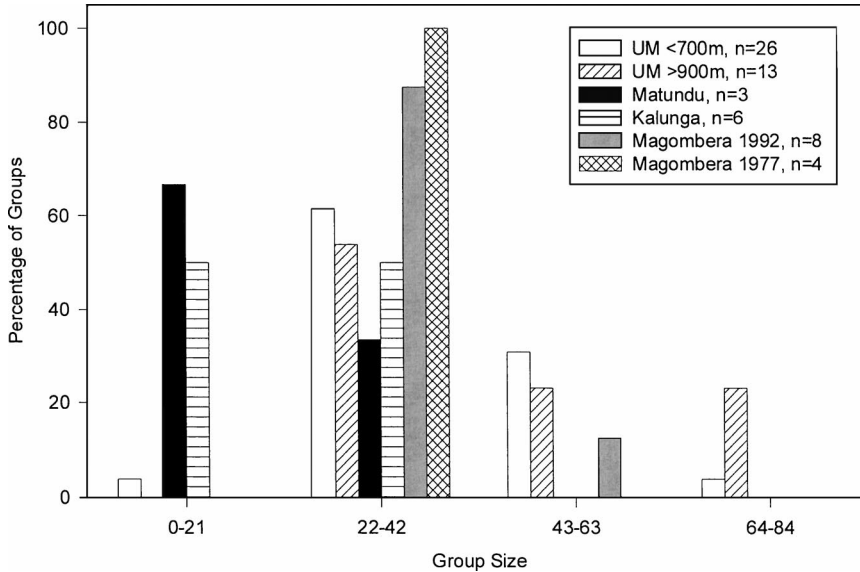


Fig. 2. Distribution of Udzungwa red colobus group size by forest and altitude. UM < 700 m elevation includes only groups in the Mwanihana forest. UM > 900 m elevation includes groups from the following forests: Mwanihana, Mani, Mdinda, Udzungwa Scarp Forest, and Ndundulu (appendix).

Group Size and Habitat Quality (Appendix and Fig. 2)

Based on earlier research (Struhsaker, 2000a; Struhsaker and Leland, 1979) we expected that forest quality would influence group size. The highly disturbed Kalunga Forest differed greatly from the Mwanihana forest. It had a lower density of trees, a higher density of cut tree stumps, a more open canopy, a different kind of understory (Table I), and was much smaller. Furthermore, Kalunga appeared to contain a higher proportion of deciduous tree species than did the Udzungwa forests, except for Matundu. Consequently, in Kalunga, the density of potential food sources for red colobus was lower and the canopy was much more broken than in the Udzungwa moist, evergreen forest. As expected, red colobus groups/parties were smaller in Kalunga ($\bar{x} = 18.6$) than in the Udzungwa moist, mixed evergreen and semideciduous forests ($\bar{x} = 41.6$, $U = 11.5$, $p < 0.001$, Matundu excluded).

During our brief study of the Kalunga population, we saw parties of red colobus joining together without any aggression or other unusual behavior, which suggests that the social groups were dividing into smaller foraging

parties and then reuniting (fission-fusion). This finding is consistent with the hypothesis that lower densities of food result in smaller party and/or social group size.

Although larger than Kalunga, the Magombera Forest is also small. However, because Magombera is a ground-water forest and has a relatively low proportion of deciduous trees, one might not expect to find smaller groups of red colobus there. In fact, the results are somewhat ambiguous (Appendix). The small sample of group counts from Magombera in 1977 ($\bar{x} = 26.4$, $n = 4$) indicates that the groups were slightly larger than those in Kalunga ($\bar{x} = 18.6$, $U = 5$, $p = 0.086$), and by 1992, the Magombera groups ($\bar{x} = 34.3$) were even larger ($U = 2$, $p = 0.004$). The 1977 Magombera study groups are significantly smaller than those from the moist, mixed evergreen and semideciduous forests of the Udzungwas ($\bar{x} = 41.6$, $U = 18.5$, $p = 0.0065$), whereas the Magombera counts made in 1992 are not ($\bar{x} = 34.3$, $U = 108.5$, $p = 0.089$). As expected, the 1977 and 1992 Magombera counts are significantly different from one another ($U = 4$, $p = 0.024$). Group size at Magombera seems to have increased between 1977 and 1992 (Decker, 1994b). During this interval the entire forested area of Magombera was reduced by *ca.* 45% (Decker, 1994b). Relevant here is a count of one group in Magombera made by Struhsaker in July 2002. He counted 17 or 18 monkeys and estimated the group to have ≤ 20 individuals, which is smaller than in 1992 ($\bar{x} = 34.3$).

The small sample of group counts from the Matundu Forest is from a low-lying (*ca.* 400 m asl) part of the forest that was dry, deciduous, and impacted by logging. The groups were small ($\bar{x} = 20.7$, $n = 3$) like those in Kalunga ($U = 8$, $p = 0.45$) and significantly smaller than the groups in the moist, mixed evergreen and semideciduous forests elsewhere in the Udzungwas ($U = 4.5$, $p = 0.0065$). Compared to Magombera, the Matundu groups are not smaller than the 1977 sample ($U = 3$, $p = 0.20$), but are smaller than the 1992 sample ($U = 1$, $p = 0.012$). Accordingly, though Matundu is a large forest, the combination of being dry, deciduous, and disturbed by logging may have resulted in smaller groups of red colobus than those in other large forests of the Udzungwas. Anecdotal evidence from the relatively large (*ca.* 22 km²), dry, and deciduous Ibiki Forest is consistent with the conclusion that the influence of forest size is outweighed by the degree of deciduousness. A single group of ≥ 19 (*ca.* <25) red colobus was there in 2001 (Appendix).

Forest size may also affect red colobus group size even when the forest appears to be of high quality for colobus, *i.e.* moist, evergreen and mature. We have 2 more or less complete counts of red colobus groups in small high quality forests. Both counts were small: 12 in Iwonde (about 5 km²) and 15 in Mlale (less than 2 km²) (Appendix).

Our results indicate that red colobus group size is influenced by several gross habitat parameters, including tree density, degree of deciduousness, and forest size. Within large areas of moist, evergreen, mature forests, where red colobus groups are largest, group size is not correlated with altitude. Red colobus group size and composition are also affected by human-induced disturbance.

Age-sex Composition of Groups and Inter-Observer Reliability

We used the data of Struhsaker and Detwiler in the analysis of group composition because only they had complete data on group composition. We made statistical comparisons of age (size) classes, adult sex ratios (females per male); infants per adult female, and juveniles per adult female. We restricted analyses involving adults to groups in which we could determine the sex of $\geq 89\%$ of the adults (Table II). This restriction was necessary because external signs of sexual dimorphism are subtle in Udzungwa red colobus. It is easier to recognize adult females than adult males because females often carry infants or have prominent nipples or perineal swellings or both. In contrast, adult males are difficult to distinguish from subadult males and females, because their scrotums are hard to see and they are not strikingly larger or more robust than females. Consequently, unless most of the adults are clearly seen, there is likely to be a bias toward adult females over males, which we confirmed by comparing adult sex ratios recorded by Struhsaker from Mwanihana and Kalunga. The sex ratio is significantly lower when the sex was determined for $>89\%$ of the adults ($\bar{x} = 3.86$, $n = 10$) than when determined for $<89\%$ of the adults ($\bar{x} = 8.73$, $n = 5$) ($U = 11$, $p = 0.05$).

There is no statistically significant difference in composition or age and sex ratios between the 2 observers when comparing Mwanihana groups (Table II). We obtained similar results when the 2 observers counted the same group together.

In contrast, a comparison of data collected in the Magombera Forest in 1977 by Struhsaker and Leland (1980) with those collected by Decker in 1992 (1994b) revealed significant differences. We restricted analysis to group counts where the sex was determined for $\geq 89\%$ of the adults ($n_1 = 2$, $n_2 = 4$), except when evaluating percentage representation of infants ($n_1 = 4$, $n_2 = 6$) and juveniles ($n_1 = 3$, $n_2 = 6$) (Table III). Then we analyzed all complete group counts because the infant and juvenile classes are relatively easy to recognize. The most pronounced difference was in the ratio of adult females per adult males, but it is only weakly significant because of the small samples (1977 $\bar{x} = 2.36$ vs 1992 $\bar{x} = 9.17$, $U = 0$, $p = 0.067$, Decker, 1994b). There were more adult males and they represented a greater percentage of the group in 1977 ($\bar{x} = 14\%$) and than in 1992 ($\bar{x} = 6.4\%$) ($U = 0$,

Table II. Age-sex composition of *Procolobus gordonorum* groups in Mwanihana and Kalunga^{a,b}

Location ^b	Counter ^c	Date	Age-sex categories ^d													Total				
			AM	SAM	AF	SAF	SA	~A	LJ	MJ	SJ	LJ	MI	SI	?					
Mwanihana	TTS	Aug 98	1	0	4	0	0	0	0	0	0	1	0	0	0	0	1	0	0	7
Mwanihana	TTS	Aug 98	4	1	29	3	0	0	0	0	4	0	4	0	2	8	4	0	0	55
Mwanihana	TTS	Oct 01	6	0	15	2	0	1	3	4	4	4	1	3	0	1	3	0	1	40
Mwanihana	TTS	Oct 01	3	0	9	0	1	1	1	1	3	1	1	1	1	2	0	0	0	23
Mwanihana	TTS	Oct 01	4.5	0	28	1	4	4	2	1	4	5	4	0	5	4	0	0	0	61.5
Mwanihana	KD	Jun 00	4	1	11	2	0	1	3	3	0	0	1	2	0	1	2	0	0	28
Mwanihana	KD	Jul 00	5	1	17	2	0	1	3	3	3	1	3	1	3	1	0	0	0	38
Mwanihana	KD	Jul 00	3	2	20	1	0	2	3	3	3	2	3	5	0	4	0	0	0	47
Mwanihana	KD	Jul 00	5	0	15	2	0	1	4	4	1	0	5	3	0	4	0	0	0	40
Mwanihana	KD	Aug 00	4	1	14	2	0	1	0	0	1	0	1	1	1	1	1	1	1	26
Mwanihana	KD	Aug 00	6	2	16	1	0	0	2	3	2	2	5	1	0	4	0	0	0	40
Mwanihana	KD	Aug 00	3	1	11	1	0	0	2	1	2	1	2	5	2	0	0	0	0	28
Mean			4.04	0.75	15.75	1.42	0.42	1.00	1.75	2.42	1.67	1.25	3.33	2.17	0.17	36.13				
Std. Dev.			1.42	0.75	7.25	0.90	1.16	1.13	1.60	1.44	1.30	1.22	2.35	1.53	0.39	14.84				
Kalunga	TTS	Jul 98	2	0	3	2	0	0	2	0	0	0	0	0	0	0	0	0	0	9
Kalunga	TTS	Jul 98	8	0	13	1	0	0	1.5	1	1	1	1	0	0	0	0	0	0	27.5
Kalunga	TTS	Aug 98	3	0	11	0	0	0	2	4	3	1	0	0	0	0	0	0	0	24
Kalunga	TTS	Aug 98	2	0	9.5	1.5	0	1	0	0	1	0	1	3	0	1	3	0	0	19
Kalunga	TTS	July 99	1	0	4	1	1	0	0	0	1	0	0	0	0	0	0	0	0	8
Mean			3.2	0.00	8.1	1.1	0.2	0.2	0.7	0.6	1.4	0.8	0.6	0.6	0.00	18.6				
Std. Dev.			2.48	0.00	3.93	0.66	0.4	0.4	0.87	0.8	1.36	1.17	0.49	1.2	0.00	7.55				

^a Only considers groups where sex was determined for $\geq 89\%$ of adults.^b All Mwanihana counts were made near UMNPN headquarters at Mang'ula and between there and Sanje River, including Sonjo River and Mwaya River valleys, Bokela and Sole areas.^c TTS = T. Struhsaker, KD = K. Detwiler.^d AM = adult male, SAM = subadult male, AF = adult female, SAF = subadult female, SA = subadult of unidentified sex, ~A = adult of unidentified sex, LJ = large juvenile, MJ = medium juvenile, SJ = small juvenile, LI = large infant, MI = medium infant, SI = small infant, ? = unidentified individual, as per Struhsaker (1975).

Table III. Age-sex composition of *Procolobus gordonorum* groups in Magombera^a

Location	Counter ^b	Date	Age-sex categories ^c														Total
			AM	SAM	AF	SAF	SA	~A	LJ	MJ ^d	SJ	LI	MI ^d	SI	?		
Magombera	TTS/LL	1977	3	0	9	1	0	1	1	1	3	0	1	2	2	0	23
Magombera	TTS/LL	1977	5	0	11	0	0	2	2	5	3	3	1	2	2	0	33
Mean			4.00	0.00	10.00	0.50	0.00	1.50	1.50	4.00	1.50	1.00	2.00	2.00	2.00	0.00	28.00
Std. Dev.			1.41	0.00	1.41	0.71	0.71	0.71	1.41	1.41	2.12	0.00	0.00	0.00	0.00	0.00	7.07
Magombera	BD	1992	1	0	13	0	3	0	5	2	2	0	0	9	1	1	34
Magombera	BD	1992	2	0	14	0	2	0	3	0	0	0	0	10	0	0	31
Magombera	BD	1992	3	0	11	0	2	0	1	1	1	1	1	6	1	1	26
Magombera	BD	1992	2	0	26	0	2	0	5	4	4	0	0	3	0	0	42
Mean			2.00	0.00	16.00	0.00	2.25	0.00	3.50	1.75	0.25	0.25	0.25	7.00	0.50	0.50	33.25
Std. Dev.			0.82	0.00	6.78	0.00	0.50	0.00	1.91	1.71	0.50	0.50	0.50	3.16	0.58	0.58	6.70

^aOnly considers groups where sex was determined for ≥89% of adults.

^bTTS/LL = T. Struhsaker & L. Leland (Struhsaker and Leland, 1980), BD = B. Decker (Decker, 1994a,b).

^cAM = adult male, SAM = subadult male, AF = adult female, SAF = subadult female, SA = subadult of unidentified sex, ~A = adult of unidentified sex, LJ = large juvenile, MJ = medium juvenile, SJ = small juvenile, LI = large infant, MI = medium infant, SI = small infant, ? = unidentified individual.

^dBD did not use categories of MJ and MI.

$p = 0.067$). The differences can be explained in at least 3 ways. They might be artifacts of small samples, especially for 1977; there was a real decline in the numbers of adult males in the Magombera groups (either fewer in the total population or just fewer living in social groups); and/or the differences reflect interobserver differences in identifying adult males. Relevant here is a count of a single Magombera group made by Struhsaker in July 2002. It gave an adult sex ratio of between 1.5 and 2.5, which is consistent with the 1977 data from Magombera, but differs appreciably from the 1992 estimates.

Although Decker (1994b) concluded that there were more clinging infants in the 1992 counts versus those made in 1977, our analysis comparing the ratio of infants per adult female revealed no significant difference ($U = 2$, $p = 0.267$). However, the percentage of infants in the Magombera groups was greater in 1992 ($\bar{x} = 23.9\%$, $n = 6$) than in 1977 ($\bar{x} = 16.4\%$, $n = 4$) ($U = 4$, $p = 0.057$).

Even though the small sample suggests that more juveniles were present in the Magombera population in 1977 than in 1992, the ratio of all juveniles (regardless of size) per adult female is not significantly different (1977 $\bar{x} = 0.68$, $n = 2$ vs 1992 $\bar{x} = 0.32$, $n = 4$) ($U = 1$, $p = 0.133$). If the number of adult females was artificially inflated in the 1992 sample because some adult males were misidentified as adult females, then the difference in juvenile per adult female ratio between the 2 sample periods would be even less. Furthermore, the difference in proportional representation of juveniles in the group is only weakly significant (1977 $\bar{x} = 25\%$, $n = 3$, vs 1992 $\bar{x} = 15.3\%$, $n = 6$; $U = 3$, $p = 0.083$; Decker, 1994b). Although far from conclusive, the results suggest a slight decline in juvenile survivorship with a possible increase in natality between 1977 and 1992.

Age-Sex Composition of Groups and Habitat Quality

Habitat quality is expected to affect group composition through differential mortality and altered fecundity (Struhsaker, 2000a). For example, groups living in degraded forests are predicted to have lower adult sex ratios, i.e. greater female mortality, and lower fecundity and juvenile survivorship than those of groups living in more intact and mature forests. Comparisons between groups in the large, relatively mature and intact forest of Mwanihana with those in the small and heavily disturbed Kalunga Forest, as well as with those in the small, but less disturbed Magombera Forest lend partial support to these ideas.

Adult Sex Ratios in Groups and Habitat Quality (Tables II and III)

Although the average adult sex ratio (females per male) appeared to be higher in the 12 Mwanihana groups ($\bar{x} = 4.05$) than in the 5 Kalunga groups

($\bar{x} = 3.11$), the differences are not significant ($U = 24$, $p > 0.10$). In addition to the possible effect of the small sample size from Kalunga, we suggest that insufficient time had elapsed since the major habitat perturbations occurred in Kalunga for there to be a significant increase in female mortality and a concomitant change in adult sex ratio.

In contrast, both of the Magombera samples differed in adult sex ratios from that of Mwanihana, but in opposite ways. The ratio is higher in the Mwanihana groups than in those of the 1977 Magombera sample ($\bar{x} = 2.36$, $n = 2$, $U = 2$, $p = 0.034$), as is the proportion of group members that were adult females ($U = 2.5$, $p = 0.04$). Although the 1977 sample was small, the lower sex ratio and lower proportional representation of adult females in these groups are consistent with the idea that groups in small and degraded forests have higher rates of female mortality than groups living in larger, intact and more mature forests have.

The adult sex ratios in the 1992 Magombera group counts are more difficult to understand. In this comparison, the Mwanihana groups had lower adult sex ratios than those in the 1992 Magombera sample ($\bar{x} = 9.17$, $n = 4$) ($U = 5.5$, $p = 0.0125$). A similar contrast between the 1977 and 1992 Magombera sex ratios appears when they are compared to the Kalunga data. While the adult sex ratios in the Kalunga groups do not differ from those in the 1977 Magombera sample ($U = 4$, $p = 0.43$), they are significantly lower than those in the 1992 Magombera groups ($U = 2$, $p = 0.032$). The adult sex ratio also differs between the two Magombera samples, being higher in 1992 than in 1977. The 1992 Magombera data clearly differ from all others in adult sex ratios. These contrasts can be interpreted like those for interobserver reliability, wherein interobserver differences are significant and are likely the most important explanatory variable.

Our data on adult sex ratios support the hypothesis that groups of red colobus in small and degraded forests are likely to suffer greater female mortality rates than those in large, mature and intact forests will.

Natality

We used the ratio of infants per adult females as an index of natality, i.e. birth rate or fecundity. The weakness of this assumption is that our data were only collected during 4 mo of the year (June-August and October). Consequently, they may not reflect the infant/female ratios over the entire year. However, this bias applies equally to all populations being compared. Given this limitation, our data indicate that natality is lower in small and degraded forests than in large, intact forests.

Data for groups in which sex was determined for $\geq 89\%$ of the adults indicates that females in the small and heavily degraded Kalunga Forest had lower birth rates than those of groups in the large and more intact

Mwanihana Forest. This is reflected by the Kalunga groups having lower ratios of infants (all 3 size classes) per adult females and a greater cv (Kalunga $\bar{x} = 0.19, \pm 0.18, cv = 94.6\%, n = 5$ vs Mwanihana $\bar{x} = 0.41, \pm 0.17, cv = 41.9\%, n = 12, U = 13, p = 0.05$), lower proportional representation in the groups of all 3 infant size classes ($U = 13, p = 0.05$), small infants only ($U = 13.5, p = 0.05$), and medium-sized infants ($U = 9.5, p = 0.025$) than in the Mwanihana groups (Table II).

Although the Magombera Forest was only slightly larger than Kalunga, it was less degraded. The better habitat may account for the higher ratio of infants per adult females there than in Kalunga (1977 and 1992 Magombera groups combined $\bar{x} = 0.53, \pm 0.20, n = 6$ vs Kalunga, $\bar{x} = 0.19, \pm 0.18, n = 5, U = 2, p = 0.009$).

In contrast, overall natality—infants per adult females—did not differ between the Mwanihana groups and either of the Magombera samples (1977 vs Mwanihana, $U = 17, p = 0.18$; 1992 vs Mwanihana $U = 15, p = 0.135$). The results suggest that, although Magombera is small, the quality of the forest is sufficiently good for red colobus so as to support levels of natality equivalent to a large and more intact forest. However, in a count of a Magombera group made by Struhsaker in July 2002, there were no infants even though the group contained ≥ 6 and perhaps as many as 9 to 10 adult females. Perhaps natality in Magombera declined between 1992 and 2002.

Juvenile Survivorship/Recruitment

There are few differences between the Mwanihana and Kalunga samples in the proportional representation of juveniles (all 3 sizes) or in the ratios of all juveniles per adult female ($U = 23, p = 0.45$) in social groups (Table II). Medium-sized juveniles were somewhat more abundant in the Mwanihana groups than in those at Kalunga (proportional representation in groups: $U = 14, p = 0.11$; number per adult female $U = 12, p = 0.05$).

Likewise the proportional representation of subadult males in groups is significantly higher in Mwanihana than in the Kalunga sample ($U = 10, p = 0.03$). Although far from conclusive, the latter two results suggest that survivorship of young may have begun to decline in Kalunga.

A comparison of the Mwanihana sample with the 2 from Magombera shows no difference in the ratio of juveniles (all size classes) per adult females (1977 data $U = 5.5, p = 0.12$; 1992 data $U = 17, p = 0.20$). The percentage representation of medium juveniles in groups is significantly higher in the 1977 Magombera sample than in that of Mwanihana ($U = 2, p = 0.014$) and so is the ratio of medium juveniles to adult females ($U = 0, p = 0.014$). A similar comparison cannot be made for the 1992 data because Decker (1994b) did not distinguish medium juveniles. However, the 1977 data indicate that

in terms of juvenile survivorship, the Magombera groups were at least as successful as the Mwanihana groups, if not more so.

Consistent with the preceding results is the comparison of the Magombera (1977 and 1992 combined, $n = 6$) data with those from Kalunga ($n = 5$). There is no significant difference in juvenile survival when expressed either as the number of juveniles (all classes) per adult female ($U = 12$, $p = 0.55$) or the proportional representation of juveniles in the group ($U = 12$, $p = 0.55$).

The preceding results from 3 different forest types indicate that the effect of habitat quality—size, extent of degradation, and degree of deciduousness—on age-sex composition of groups is most apparent in natality and less so in adult sex ratios and juvenile survivorship. The results are partially consistent with the idea that the Magombera Forest represents for red colobus a habitat of intermediate quality between that of the large and relatively intact Mwanihana Forest and the small and heavily degraded Kalunga Forest. This is similar to our findings on group size. We predict that in the near future greater demographic differences will emerge, particularly for the Kalunga population, because of time-lag effects.

Sociological Variables and Age-Sex Composition of Groups

In this analysis, we assumed that Udzungwa red colobus have a social system similar to that of red colobus in Uganda (*Procolobus badius tephrosceles*), in which females disperse and males tend to remain in their natal groups (Struhsaker, 1975, 2000b; Struhsaker and Leland, 1987). If the core of social groups is a coalition of adult males, then one expects both group size and the number of adult females to be affected by the size of the male coalition, i.e. the number of adult males in the group, because the size of the male coalition will influence a female's mating options. The size of a male coalition will also likely influence priority of access to food trees for all group members where home ranges overlap with other red colobus groups. Adult male red colobus appear not to constitute an effective deterrent to predation by the crowned eagle and, Struhsaker (2000b) found no correlation between the number of adult males or adult sex ratios in social groups and the relative abundance of eagles. So, the hypothesis is that the size of the male coalition influences the attractiveness of a group to immigrating females because of mating and foraging advantages, which, in turn, influences group size. The predictions are that group size is directly related to the number of adult males in the group and that the number of adult females in a group is directly related to the number of adult males. Correspondingly, group size and the number of adult females should covary.

Group Size and Numbers of Adult Males

We analyzed 3 sets of data that included only groups for which sex was determined for $\geq 89\%$ of the adults: all groups combined from Mwanihana, Kalunga, and Magombera (1977 data, excluding the 1992 data) ($n = 19$); only the Mwanihana data ($n = 12$); and only the Magombera 1992 data ($n = 5$). In regression analysis group size is the dependent variable and the number of adult males is the independent variable.

For all the groups from Mwanihana, Kalunga and Magombera (1977) there is a significant regression between group size and the number of adult males in the group (Fig. 3, $r^2 = 0.50$, $p = 0.0005$). The same relationship

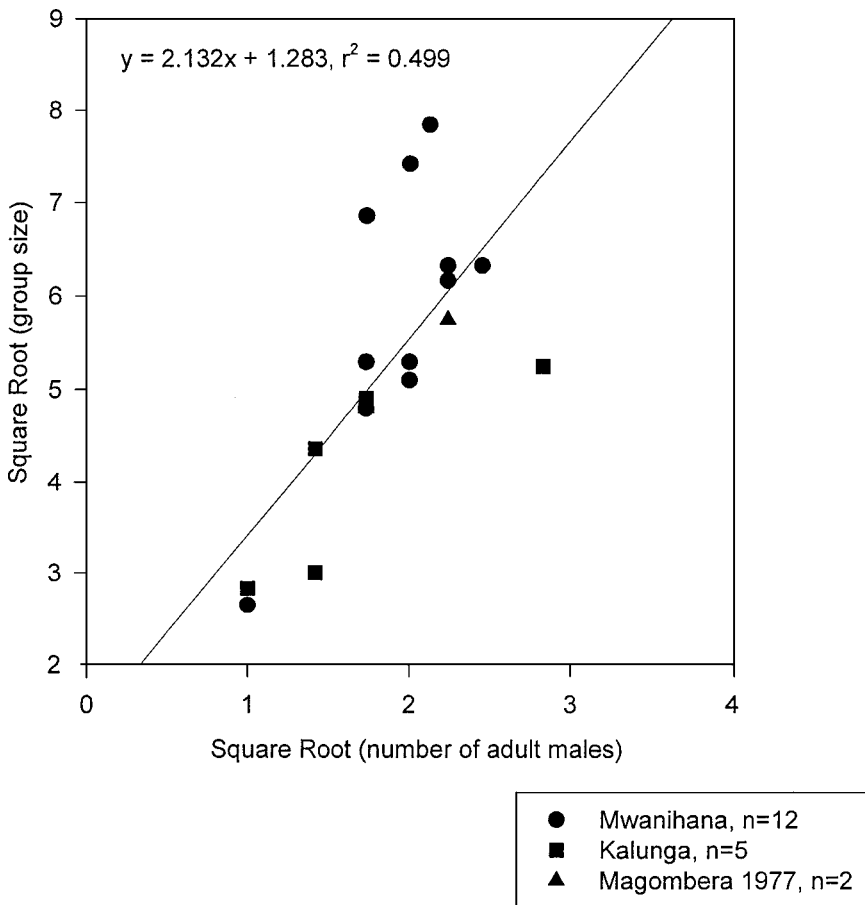


Fig. 3. The number of adult males in Udzungwa red colobus social groups can account for 50% of the variance in group size ($p = 0.0005$). See text and tables II and III for details.

also held when only the 12 groups from Mwanihana were considered ($r^2 = 0.50$, $p = 0.006$). This is particularly important because it was shown earlier that group size is affected by habitat quality. Further, the number of adult males accounted for 50% of the variance in group size even though adult males represented only a small percentage of the entire group membership (Tables II and III).

In contrast, the Magombera 1992 sample ($n = 4$) shows no significant regression between group size and the number of adult males ($r^2 = 0.22$, $p = 0.25$). Although this result may be due to a small sample, the proportion of adult males in this sample was lower than in the 1977 sample of Magombera and lower than in the other 2 study sites.

Numbers of Adult Females and Adult Males

In the same three data sets the number of females (dependent variable) was influenced by the number of adult males (independent) in all cases (Mwanihana, Kalunga and Magombera 1977, Fig. 4, $n = 19$, $r^2 = 0.39$, $p = 0.002$) and also for the Mwanihana data alone ($n = 12$, $r^2 = 0.34$, $p = 0.024$), but not at all for the Magombera 1992 data ($n = 4$, $r^2 = 0.007$, $p = 0.45$). Although the number of adult males significantly predicted the number of adult females in 2 of the comparisons, they only accounted for 34–39% of the variance in the number of adult females.

Group Size and Numbers of Adult Females

These 2 variables were highly correlated for the analyses of all data combined ($r = 0.97$, $p < 0.0009$, Fig. 5), for the Mwanihana data alone (Fig. 5, $r = 0.95$, $p < 0.0009$), and for the Magombera 1992 data alone ($r = 0.9$, $p = 0.038$). This pronounced covariance is not surprising given the fact that adult females are 32–62% of the groups analyzed (Table II). These results support the hypothesis that the size of male coalitions influences both group size and the number of adult females in groups.

Variables Influencing Reproductive Success

Given the results supporting the hypothesis that large coalitions of adult males attract adult females because of potential benefits—increased mating options and priority to food—which leads to larger groups, it is essential to test whether these variables correlate with greater natality and juvenile survivorship.

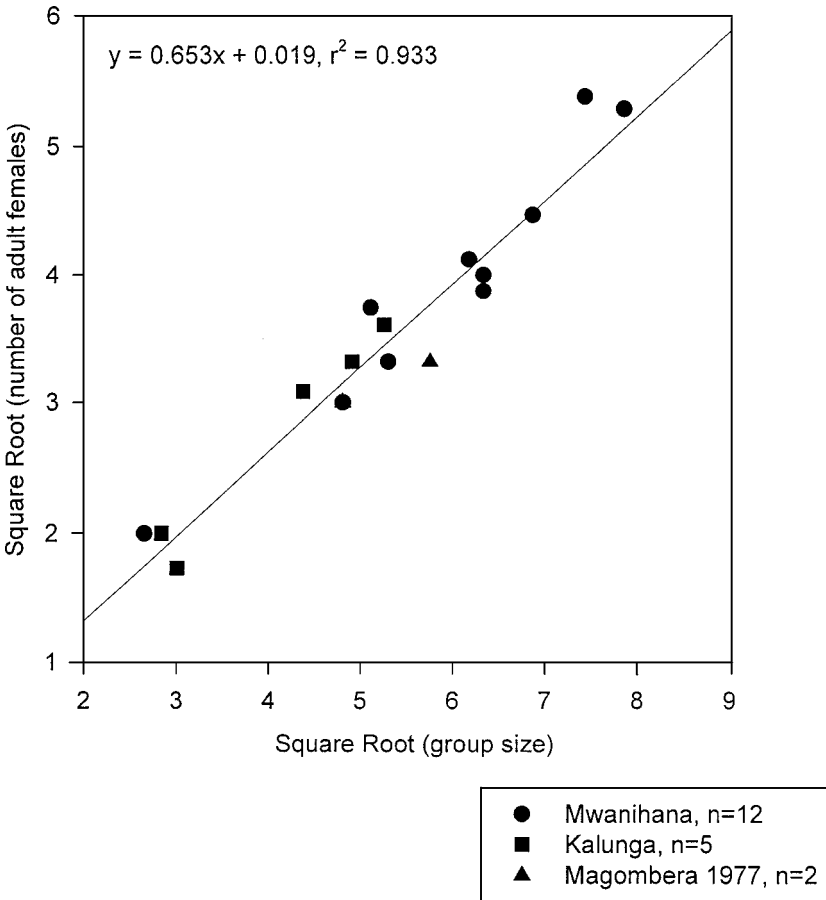


Fig. 5. Udzungwa red colobus groups size and the number of adult females in the group are significantly correlated ($p = 0.0009$). See text and tables II and III for details.

number of adult females in the group ($r^2 = 0.31$, $p = 0.0065$) and 38% by group size ($r^2 = 0.38$, $p = 0.0025$). Only 11% of the variance in the number of infants per adult female is accounted for by the adult sex ratio (adult females per adult male) ($r^2 = 0.11$, $p = 0.08$). Because the relative number of adult males decreases as the sex ratio increases, the number of adult males in a group also accounted for little of the variance in the ratio of infants per adult female ($r^2 = 0.10$, $p = 0.089$). The latter relationship is even weaker when the 12 Mwanihana groups are considered alone ($r^2 = 0.001$, $p = 0.46$).

Our results suggest that natality is higher in larger groups with greater numbers of females and a relatively high adult sex ratio. Accordingly,

although the number of adult males may attract females and lead to larger groups and higher sex ratios, the number of adult males on its own has little direct effect on natality. However, this may be misleading because both group size and natality are influenced by habitat quality, being greater in the Mwanihana groups and usually so in those from Magombera than in Kalunga. Because of this apparent effect of habitat, we excluded the 5 Kalunga groups from the analysis. As expected, this had a profound influence on the results. Considering only the 12 Mwanihana and 2 Magombera 1977 groups, there is no significant relationship between natality (infants per adult female) and any of the preceding demographic variables, i.e. the number of adult females in the group ($r^2 = 0.023$, $p = 0.30$), group size ($r^2 = 0.079$, $p = 0.17$), adult sex ratio ($r^2 = 0.14$, $p = 0.31$) or the number of adult males in the group ($r^2 = 0.000$, $p = 0.50$). The results indicate that habitat quality had a much greater effect on natality than any of the demographic parameters.

For all groups combined (Mwanihana, Kalunga and Magombera 1977, $n = 19$), our data revealed no significant regression between the number of juveniles (*ca.* 1–3 years old) per adult female (dependent variable) and any of the following variables: the total number of adult females in the group ($r^2 = 0.033$, $p = 0.23$); adult sex ratio in the group ($r^2 = 0.000$, $p = 0.47$); group size ($r^2 = 0.09$, $p = 0.11$), or the number of adult males in the group ($r^2 = 0.061$, $p = 0.15$). Correcting for habitat quality by excluding the 5 groups from Kalunga and considering only the Mwanihana ($n = 12$) and the Magombera 1977 ($n = 2$) groups gave similar results, i.e. number of juveniles per adult female versus: total number of adult females in the group ($r^2 = 0.086$, $p = 0.15$), group size ($r^2 = 0.002$, $p = 0.44$), and total number of adult males in the group ($r^2 = 0.053$, $p = 0.21$).

The only exception was the adult sex ratio. Amongst the latter 14 groups, adult sex ratio accounted for 29.6% of the variance in the number of juveniles per adult female ($r^2 = 0.296$, $p = 0.022$). This was a negative relationship and indicates that groups with a low ratio of adult females per adult male had greater juvenile survivorship. This was further verified by a highly significant negative regression between the proportion of the group made up of adult females (independent variable) and the ratio of juveniles per adult female (dependent variable) ($r^2 = 0.595$, $p = 0.0005$, Fig. 6). In other words, groups with a low proportion of adult females had higher juvenile survivorship. Conversely, given the negative relationship, one might expect the proportion of the group composed of adult males to be positively correlated with the ratio of juveniles per adult female, but this is not the case ($r^2 = 0.04$, $p > 0.10$).

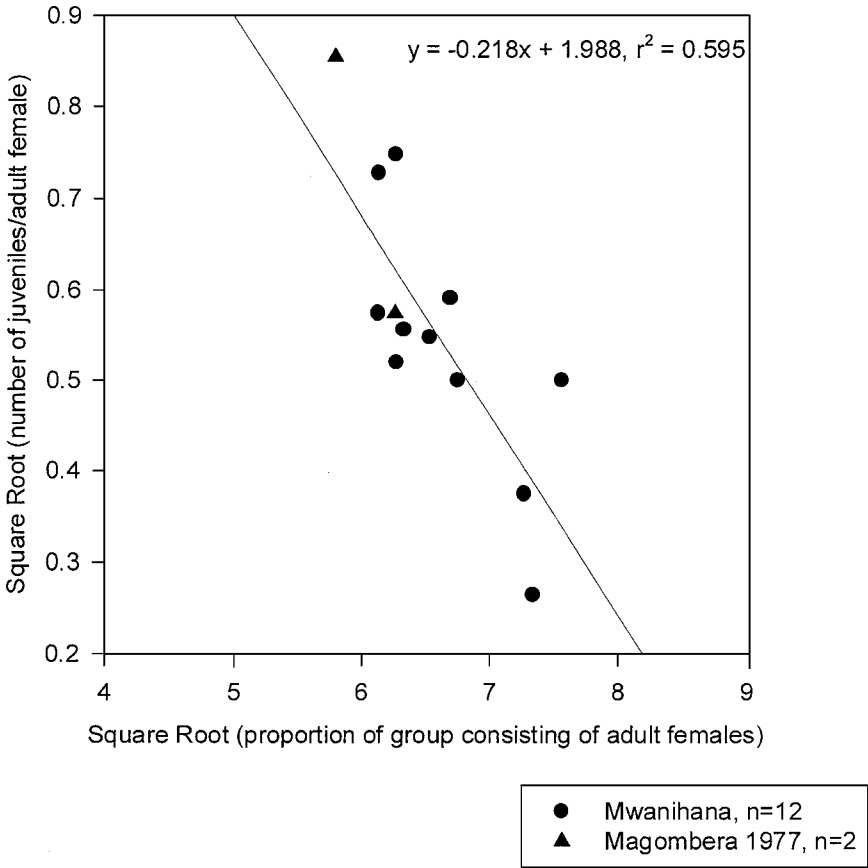


Fig. 6. Udzungwa red colobus groups with a low proportion of adult females had higher juvenile survivorship. The proportion of the group made up of adult females can account for 60% of the variance in the ratio of juveniles to adult females ($p = 0.0005$). This is a negative relationship. See text and tables II and III for details.

CONCLUSIONS AND DISCUSSION

Variation in Group Size

Our sample of group size is one of the largest ever collected for a taxon of monkey ($n = 63$) and it covers a relatively wide geographical area and variety of forest habitats. Group size (7–83), excluding solitary individuals, is highly variable. Mean group size is 36.3 and similar to the results of Decker

(1994b) ($\bar{x} = 34.3$) from Magombera Forest, but larger than an earlier study in Magombera (Struhsaker and Leland, 1980, $\bar{x} = 26.6$). Wasser (1993) also reports a smaller mean group size ($\bar{x} = 23.3$, range 1–75) from Mwanihana Forest in 1984 and 1986. The difference in mean group size between his study and ours may be due to real changes over the intervening 11–17 years and/or because he may have included solitary monkeys in his estimate. Rodgers and Homewood (1982) report a mean group size for Udzungwa red colobus of 25, but it is unclear how it was derived.

Dinesen *et al.* (2001) report an even smaller mean group size for red colobus in 3 high-altitude forests in the western Udzungwas (Nyumbanitu $\bar{x} = 18$, Ndundulu $\bar{x} = 18$, and Ukami $\bar{x} = 17$; range 1–50), which may be due, in part, to the inclusion of solitary monkeys in their estimates. Although red colobus groups might be smaller at higher altitudes in the western Udzungwa, it may be that Dinesen *et al.* (2001) undercounted the red colobus groups because it was not the main objective of their research. It is also likely that they counted some of the same groups more than once and included the repeat counts as if they were different groups. For example, they report counts for 46 groups in the Ndundulu Forest. The systematic censuses of Marshall *et al.* (in press) indicate low densities of red colobus in Ndundulu (0.48 groups/km censused) versus Mwanihana (0.7–0.88 groups/km., from Pedersen and Kishe, p. 31 in Ehardt *et al.*, 1999). Given the low densities, we think it would have been extremely difficult to obtain accurate counts of 46 different groups of red colobus as an incidental component to an ornithological study.

In spite of these doubts, a more recent study in Ndundulu by Marshall *et al.* (in press) that focused on primates also shows smaller groups of red colobus ($\bar{x} = 22.5, \pm 3.6$ SE, range 12–40, $n = 8$, including our single count of 25 (estimate 25–30)). The mean is significantly smaller than those for groups elsewhere in the Udzungwa Mts., excluding the 3 groups from Matundu and the 2 counts of uncertain accuracy from Iwonde and Mlale ($z = 3.21, p = 0.0007$). The differences may be due to altitudinal or human impacts on forest quality or both. To address the issue we segregated our data and compared them to the Ndundulu sample of Marshall *et al.* (in press). The Ndundulu groups remained significantly smaller regardless of altitude: 1) Mwanihana (>900 m asl) ($U = 4, p < 0.009$), 2) Mwanihana (<700 m asl) ($z = 2.84, p = 0.0023$), 3) Mani and Mdinda (1,000–1,800 m asl) ($U = 3, p = 0.005$), 4) Udzungwa Scarp Forest Reserve (1,100 m asl) ($U = 0, p = 0.022$), and 5) Magombera 1977 and 1992 (270 m asl) ($U = 25, p = 0.05$). Furthermore, the Ndundulu groups are not significantly different in size from those we counted in Kalunga (280 m asl) and Matundu (400 m asl) ($U = 16, p = 0.17$ and $U = 11, p = 0.46$, respectively). In other words, the Ndundulu red colobus groups

were smaller than those in all other forests except for those that were either small and heavily degraded (Kalunga) or that were subjected to moderately high levels of logging and were dry and deciduous (Matundu). Except for two counts at Ndundulu, all other Ndundulu groups in this comparison lived in an area that had been commercially logged and was characterized as having a broken canopy and some open areas with regenerating trees (Marshall *et al.*, in press). The Ndundulu results appear consistent with the general hypothesis that forest degradation results in smaller party or group size in red colobus.

As Marshall *et al.* (in press) emphasize, altitudinal effects are most likely to influence group size through their impact on nutritional demands of thermoregulation and on vegetation. However, our data indicate that within large blocks of relatively mature, evergreen rain forests in the Udzungwa Mountains there is no altitudinal effect on the size of red colobus groups. The differences in group size between the Ndundulu sample and those elsewhere in the Udzungwas are more likely due to differences in habitat and vegetation as the result of recent human activities than to altitude.

The mean group size (36.3) in our study is within the range of other red colobus taxa, but somewhat smaller than those in large blocks of mature, evergreen rain forest, such as Kibale, Uganda (>44); Taï, Côte d'Ivoire (~40); and Korup, Cameroun (>47) (Struhsaker, 2000a,b), probably because our sample of the Udzungwa red colobus included not only this forest type, but also small blocks of degraded and semideciduous forest where groups are typically smaller, e.g. the forests of Mbisi, Tanzania; Tana, Kenya; Senegal; and Gambia (Struhsaker, 2000a,b). When only the Udzungwa red colobus groups in the large, mature, mixed evergreen and semideciduous forests are considered ($n = 39$), mean group size is larger (41.6) and closer to that of other red colobus taxa living in this forest type.

Group Size and Gross Habitat and Disturbance Effects

Our results indicate that among the Udzungwa red colobus, groups are smaller in forests that are small (<5 km²), dominated by deciduous trees, and/or are heavily degraded by human activities than are groups living in large, intact, and relatively mature blocks of moist, mixed evergreen and semideciduous forest. This is consistent with comparisons of group size between taxa of red colobus when predation pressure is similar (Struhsaker, 2000a,b). Chapman *et al.* (2002) also showed that within the Kibale Forest, Uganda, average party size of red colobus in areas that were heavily logged about 30–35 years earlier were less than half the size of those in 3 other parts

of the forest that were more mature and intact ($\bar{x} = 14.2$ vs $\bar{x} = 30.5, 34,$ and 40). Group size of red colobus in Kibale appears to be directly correlated with density of food trees (Chapman and Chapman, 2000b). Another study in Kibale indicated no apparent difference in red colobus social group size between heavily logged and unlogged forest. Instead, the main study group in the logged forest achieved a similar result by fragmenting into smaller foraging parties 33% of the time, unlike the groups in adjacent unlogged forest (Skorupa, 1988; Struhsaker, 1997). A similar phenomenon may be occurring in Kalunga red colobus groups.

Marshall *et al.* (in press) also concluded that extensive habitat disturbance and overall reduction of forest patch size accounted for the unusually small red colobus groups ($\bar{x} = 11.75$) in the New Dabaga/Ulangambi Forest Reserve (37 km²), which are significantly smaller than are those in any other population studied in the Udzungwas. In addition, they suggested that the absence of leopards and crowned eagles (likely predators) from this forest may have also reduced the advantages of larger groups.

Even with fairly dramatic reductions in food supplies it may take several years before monkey populations and group size are reduced. For example, among the vervets of Amboseli, Kenya it was nearly 7 years after a 90% decline in their major food resources that their group size was significantly reduced (Struhsaker, 1976). Similarly, it may have been 14–19 years after the Tana River red colobus (*Procolobus rufomitatus*) populations were compressed into small forest patches as a result of habitat destruction by humans before their group size and population densities were significantly reduced (Decker, 1994a). The Tana population continued to decline during the 1990s with a 32% reduction in group size, but no apparent reduction in the number of groups. This was coincident with major reductions in forest area (Mboru, 2003; Wiczowski and Mboru, 1999–2000). Skorupa (1988) estimated that it requires ≥ 7 years before there is a statistically significant decline in the density of primate social groups following moderate to heavy logging in Kibale, Uganda.

Furthermore, not all species or groups respond in the same way to habitat loss or degradation. For example, while group size of blue monkeys (*Cercopithecus mitis*), black-and-white colobus (*Colobus guereza*) (Struhsaker, 1997), and some groups of red colobus (Chapman *et al.*, 2002) apparently declined after heavy logging in Kibale, other groups of red colobus remained large and regularly divided into smaller foraging parties (Skorupa, 1988).

Given these trends, we expected that with a 45% reduction in the size of the Magombera Forest (circa 1980), there would be a reduction in red colobus group size over the following 12 years, but this appears not to be

the case. Surprisingly, the groups were larger in 1992 (post-habitat loss) than in 1977 (pre-habitat loss). Several factors may have contributed to the apparent change. Firstly, the 1977 sample is small ($n = 4$) and may not be representative. Secondly, during the 1977 study there was illegal agricultural encroachment into Magombera (Struhsaker and Leland, 1980), which may have adversely affected group size. Thirdly, based on area estimates from 1999 Landsat images, there appears to have been forest regeneration equivalent to that which was destroyed, i.e. no net loss of colobus habitat. Accordingly, we suggest that when the Magombera red colobus population was compressed in the 1980s due to habitat loss, groups underwent fusion and/or a reduction in emigration. Subsequently, with greater legal protection for the remaining 55% of Magombera, disturbance from humans decreased, forest regeneration increased, thereby improving the colobus habitat. These conditions allowed the persistence of larger groups. It must be emphasized, however, that group size in Magombera may have undergone a reduction since 1992, as suggested by a single group count in July 2002 (17–18, estimated <20 vs $\bar{x} = 34.3$ for 1992). Small groups may now prevail and there is an obvious need for more current data from Magombera.

Fission-fusion and Habitat Quality

The effects of gross habitat quality on red colobus grouping tendencies is also reflected by the tendency of groups living in forests that have been recently degraded or severely reduced in size to split up into smaller, temporary foraging parties (fission-fusion). This was most evident in the Kalunga Forest and resembled the pattern described for a group of *Procolobus badius tephrosceles* in heavily logged forest of Kibale, Uganda (Skorupa, 1988; Struhsaker, 1997, 2000a,b); one group of *P. b. tephrosceles* in a degraded part of Gombe, Tanzania (Kamenya, 1997); the Zanzibar red colobus (*kirkii*) in the Jozani forest (Siex and Struhsaker, 1999); and for colobines and macaques in degraded forests of Malaysia (Johns, 1983) and E. Kalimantan (Berenstain, 1986).

Fission-fusion appeared to be rare, if not absent, in the degraded forest near UMNP headquarters at Mang'ula (Mwanihana). This may have been because the degradation near Mang'ula was due to commercial logging in the 1960s and 1970s (>20 – 30 years before our studies), versus Kalunga where cutting was more recent (≤ 5 – 6 years) and ongoing during the course of our studies. The cutting at Kalunga was also more intense because it was not only for timber, but also for charcoal, firewood, and cultivation. Consequently, the understory vegetation in Kalunga was younger, less woody, and less

able to support colobus climbing through it. In contrast, the understory of the young secondary forest at Mang'ula was dominated by saplings, poles, and woody tangle that could support colobus and provide them with food. Furthermore, Kalunga was a small habitat island of $\leq 2 \text{ km}^2$, whereas the degraded forest near Mang'ula was contiguous with a very large area of older, intact forest. These structural differences in habitat along with the more fragmented and patchy distributions of foods for the red colobus may have resulted in a greater frequency of fissioning among the red colobus social groups in Kalunga than at Mang'ula.

All these examples of fission-fusion can be related to situations in which food occurs in low densities, in a highly clumped pattern, and/or is widely dispersed. In other words, intragroup spacing is directly affected by the abundance and distribution of food, presumably to minimize competition and to increase foraging efficiency. This is consistent with conclusions reached from earlier intertaxonal comparisons (Struhsaker, 1997, 2000a,b; Struhsaker and Leland, 1979).

Sociological Effects on Group Size

We showed that the size of the adult male coalition influenced both the number of adult females and group size, supporting the idea that adult males are the stable component of the group, attracting subadult and adult females, who are the primary dispersers. We suggest this is because the size of the adult male coalition will influence mating options for the females, as well as improve priority of access to food where ranges overlap extensively between groups (Struhsaker, 1975). Group size and the number of adult females are strongly correlated because adult females constitute 32-62% of the group. All of these results are consistent with intertaxonal comparisons of red colobus (Struhsaker, 2000b).

Variation in Adult Sex Ratio of Groups

The ratio of adult females per adult males among the 12 groups sampled in the Mwanihana Forest is highly variable ($\bar{x} = 4.05$, $cv = 39.5\%$, range 2.5–7.25). This remained the case when we included the 5 groups from Kalunga and the 2 from the 1977 Magombera sample ($n = 19$, $\bar{x} = 3.65$, $cv. = 42.3\%$, range 1.5–7.25). The only other taxa of red colobus for which there are comparable samples are those from Senegal, the Tana River in Kenya, and Zanzibar. The Senegal sample showed relatively little variance in adult sex ratio ($\bar{x} = 1.98$, $cv = 22.6\%$, range 1 to 2.7, $n = 13$, Gatnot, 1975), whereas

those from the Tana River (1973–1974: $\bar{x} = 7.27$, $cv = 44.6\%$, range 3–15, $n = 13$, Marsh, 1979; 1987–1992: $\bar{x} = 5.11$, $cv = 48.4\%$, range 2–11.3, $n = 17$, Decker, 1994a) and Zanzibar ($\bar{x} = 6.67$, $cv = 45\%$, range 2.85–13.5, $n = 7$, for groups where in the sex was determined for $\geq 89\%$ of adults, table VII in Siex and Struhsaker, 1999) exhibited high variance like the Udzungwa red colobus did. However, the average ratio of adult females per males is greater for both the Tana River ($\bar{x} = 7.3$, Marsh, 1979 and $\bar{x} = 5.1$, Decker, 1994a) and Zanzibar colobus ($\bar{x} = 6.7$) than for the Udzungwa and Senegal red colobus. These intertaxonal differences may be due to higher mortality rates and/or greater exclusion of adult males from the Tana and Zanzibar groups than in those of Senegal and Udzungwa. However, the relative importance of the 2 variables cannot be evaluated without accurate data on the adult sex ratio in the total population, i.e. including extragroup adults.

Adult sex ratios within social groups are not necessarily stable. For example, the ratio declined significantly among the Tana River groups sometime during the 13-yr interval between studies, as did the number of adult females per group. This change was coincident with an overall population decline, probably due to population compression as the result of habitat loss, and suggests greater mortality among adult females than among adult males (Struhsaker, 2000a). The proportion of adult females in the Tana groups continued to decline in the 1990s and was apparently related to major losses of forest habitat (Mbona, 2003). A similar significant reduction in adult sex ratio occurred during a 7–8 year interval in groups of the Zanzibar red colobus living in agricultural areas, including perennial tree-crop gardens, young secondary forest, and fallow bush (from 9.8 in 1992–1993 to 3.8 in 1999, Siex, 2003). This decline in adult sex ratio of groups was also associated with population compression due to habitat loss and was apparently due in part to increased immigration of adult males to the study population (Siex, 2003). These males probably came from areas where habitat was destroyed or severely degraded. It is not known what became of the adult females and other age classes in these source areas. If they died or simply replaced similar age-sex classes in the study population that died, then this is another case supporting the hypothesis that, with habitat loss, adult females and immatures suffer greater mortality than adult males do.

The Magombera adult sex ratios from our study differ from those of Decker's (1994b, Struhsaker, 2000a,b) 1992 study. The differences between them are thought to be largely due to interobserver differences in identifying adult males. Other contributing factors might include a decline in group-living adult males and the effect of small samples.

The new data, larger sample, and more conservative analyses (including only groups in which the sex was determined for $\geq 89\%$ of the adults) used in our study result in a lower adult sex ratio for social groups of the Udzungwa

red colobus than was reported by Decker (1994b) and Struhsaker (2000b). They are much more consistent with those reported for other red colobus taxa and are rather intermediate between the extreme means of all other red colobus taxa for which data are available (1.8–7.3; Table 15.9 in Struhsaker, 2000a). Nonetheless, our revision does not alter earlier conclusions, namely that predation pressure by crowned eagles does not represent a strong enough selective force to significantly influence adult sex ratios of group-living red colobus (Struhsaker, 2000a,b).

Habitat Quality and Adult Sex Ratio in Groups

Although the adult sex ratio in groups was 40% greater in the large, relatively intact, mixed evergreen and semideciduous forest of Mwanihana than those in the small patch of severely degraded, semideciduous forest of Kalunga, the differences are not statistically significant, perhaps because not enough time had elapsed since the habitat at Kalunga was disturbed. In other words, there is likely a long temporal lag in demographic response, particularly so in terms of adult female mortality. For example, on the Tana River, Kenya, it may have taken 13–19 years after population compression and an appreciable loss of habitat before there was a significant decline in the adult sex ratio (Decker, 1994a; Struhsaker, 2000a). However, there was a lapse of 13 years between the Tana studies so the decline in sex ratio may have occurred earlier. Likewise on Zanzibar, *ca.* 6–7 years elapsed before there was a significant decline in adult sex ratio due to habitat loss and population compression (Siex, 2003). If this is a general response to habitat degradation, then we should expect a similar decline in adult sex ratios over the next few years at Kalunga because of an increase in adult female mortality. Although some of the Magombera data support the hypothesis that adult sex ratios in social groups are lower in small and poor-quality habitats, the situation there may be more complex and needs further study to determine if the differences in adult sex ratios between the two study periods reflect trends, instability, or interobserver differences.

The Effect of Adult Male Numbers on Adult Female Numbers

An intertaxonal comparison of red colobus (Struhsaker, 2000b) showed that, with the exception of the Udzungwa red colobus, the number of adult males in a social group is strongly correlated with the number of adult females. The number of adult males in a group accounted for 50–84% of the

variance in the number of adult females in the same groups (Struhsaker, 2000b). The new data and more conservative analysis show that, in contrast to the earlier report, the Udzungwa red colobus have a similar pattern to that of other red colobus taxa. However, the relationship is not as strong and, at best, the number of adult males only accounts for 34% of the variance in the number of adult females in a group. The 1992 data from Magombera remain an outstanding exception, with no correlation between the number of adult males and females in groups.

Natality and Juvenile Survivorship in Relation to Habitat Quality

Habitat quality is generally thought to influence natality and juvenile survivorship. Our data lend some support to this concept because the red colobus groups living in the small, semideciduous, and heavily degraded Kalunga Forest had lower percentages of infants and appeared to have lower and more variable ratios of infants per adult female ($\bar{x} = 0.19$, $cv = 94.6\%$, range 0–0.42, $n = 5$ groups) than those in the more intact, larger, mixed evergreen and semideciduous Mwanihana Forest ($\bar{x} = 0.41$, $cv = 41.9\%$, range: 0.14–0.82, $n = 12$ groups). The relationship is even stronger when the samples for Mwanihana and Magombera ($\bar{x} = 0.53$, $cv = 39\%$, range: 0.12–0.71, $n = 6$ groups) are combined and contrasted with Kalunga.

The infant/adult female ratios in the Kalunga groups are generally lower and often more variable than those of other taxa of red colobus. We compared the results with 4 other taxa of red colobus. Although not all of the data for these taxa are based on slice-in-time samples, i.e., each group counted only 1–3 times within 1 or 2 days), as in the Udzungwa study, they provide indices for comparison. Demographic data collected during a 12-mo period from 15 groups of the *temmincki* red colobus in Senegal gave a mean ratio of clinging infants per adult female of 0.43 ($cv = 54.9\%$, range: 0–1.0; tab. XXIV in Gatnot, 1975).

The long-term studies on 16 recognizable adult females of the Uganda red colobus (*tephrosceles*) in Kibale yielded a mean interbirth interval (IBI) of 24.4 mo (all IBIs, equivalent to an annual birth rate of 0.49 infants/adult female, $cv = 25.8\%$, range: 0.29–0.76, $n = 56$ births) or 27.5 mo when we excluded cases of neonatal mortality (Struhsaker and Pope, 1991). An average of the 2 figures (26 mo) is equivalent to an infant to adult female ratio of 0.46. A similar ratio can be derived from single counts of 14 groups, excluding the 3 main study groups, over an 18-mo period for the same population: 0.47 [infants per adult female plus 60% (proportion of adult population that are females) of approximate adults in Table VI, Struhsaker, 1975].

Two studies of the Tana River red colobus found different infant/female ratios. They were separated by 14–19 years during which time the population declined significantly. Marsh (1979) reported lower and extremely variable ratios of infants/females based on single counts of 10 groups ($\bar{x} = 0.26$, $cv = 85.9\%$, range: 0–0.67). Marsh (1979) collected the data within a few years after large-scale forest clearance led to compression of the colobus population (Decker, 1994a). Fourteen to 19 years later, Decker (1994a) found much higher and somewhat less variable ratios ($\bar{x} = 0.51$, $cv = 66.1\%$, range 0–1.2, $n = 18$) based primarily on single counts of groups in the same population. The differences are statistically significant ($z = 2.214$, $p = 0.0136$). However, both Marsh (1979) and Decker (1994a) reported similar birth rates in groups they studied in detail over a period of more than 1 yr, i.e. 0.54 (Marsh $n = 1$ group), 0.5 and 0.58 (Decker $n = 2$) per female-yr.

Siex and Struhsaker (1999) collected data on the Zanzibar red colobus intermittently over a 5-yr period (1992–1996 inclusive) and counted the groups multiple times. Two contiguous subpopulations at Jozani on Zanzibar had significantly different ratios of infants per adult females: 0.27 ($n = 5$ forest groups) versus 0.43 ($n = 8$ agricultural groups) (Table VIII in Siex and Struhsaker, 1999), reflecting both differences in habitat quality and juvenile survivorship. However, if one selects from the sample single counts of specific groups made during the same month and year, the methods are more comparable to those of the Udzungwa study and the subpopulation differences are not significant. For example, comparison of the July 1993 counts on Zanzibar indicates that the 2 subpopulations did not differ then in ratios of infants/adult female (4 forest groups: $\bar{x} = 0.15$, $cv = 73.6\%$, range: 0–0.27 vs 4 agricultural groups $\bar{x} = 0.32$, $cv = 36.8\%$, range: 0.18–0.45; $U = 4$, $p = 0.171$). Likewise, the July 1994 counts indicate no difference between the 2 subpopulations in infant/adult female ratios (forest: $\bar{x} = 0.28$, $cv = 40.9\%$, range: 0.2–0.5, $n = 5$ vs agricultural: $\bar{x} = 0.34$, $cv = 52.8\%$, range: 0.08–0.55, $n = 6$; $U = 12$, $p = 0.331$).

These comparisons establish two important points. Firstly infant/female ratios based on single counts of groups during a restricted time of year must be interpreted with caution. For example, they will, be strongly influenced by any tendency toward birth peaks or seasonality. Slice-in-time samples are unlikely to represent a specific group's annual birth rate. So, for this approach to be reliable, a representative sample of groups must be collected for each population. The sample size will, in turn, depend on the degree of intergroup variation.

Secondly, the ratios are dynamic and vary over time within and between years, just as most other demographic parameters do. Furthermore, high ratios of infants/adult female do not necessarily reflect either a stable or

growing population because they can be increased by high neonatal and juvenile mortality rates.

In spite of the limitations of samples collected during single counts of groups, our intertaxonal comparisons suggest a bimodal distribution in infant/adult female ratios. Populations with relatively high ratios (0.41–0.53) include Mwanihana, Magombera, Senegal, Kibale, Tana 1987–1992, and the Jozani agricultural groups on Zanzibar. Populations with relatively low ratios (0.23–0.27) include Kalunga, Tana 1973–4, and the Jozani Forest groups on Zanzibar. Interpretation of these ratios is more complex. Similar ratios do not necessarily reflect similar cause and effect relationships. For example, the high ratios of infants/females in the Kibale groups reflect a relatively healthy and stable population (Struhsaker and Pope, 1991). In contrast, the high ratios in the groups of the Jozani agricultural areas on Zanzibar and the Tana River 1987–1992 sample, may be the consequence of high mortality among semi-independent infants and young juveniles, which would shorten interbirth intervals and lead to higher infant/adult female ratios. Indeed, a comparison of the 2 Tana River studies shows that there were significantly fewer juveniles per adult female during Decker's (1994a) 1987–1992 study than during Marsh's (1979) 1973–1974 study ($n = 10$, $n = 18$, $z = 2.417$, $p = 0.008$). In other words, higher juvenile mortality 2–3 years before and during the 1987–1992 study may have resulted in higher ratios of infants/adult female. So, contrary to indicating a healthy and recovering population (Decker, 1994a), it may well be that the population was continuing to decline. Indeed, Mborá (2003) found that in 1999–2001, red colobus groups ($n = 55$) along the Tana were significantly smaller than during Decker's study and nearly 50% smaller than in any of the previous studies dating back to 1973.

The comparison of the agricultural and forest populations on Zanzibar suggest a similar conclusion. Juvenile recruitment was lower in the agricultural groups than in groups of the Jozani Forest. Siex and Struhsaker (1999) estimated that only 21% of the infants in the agricultural groups survived the first 26 mo of life, while in the forest 66% of the infants survived that long. Accordingly, the high ratios of infants/adult females in the agricultural groups may have been a consequence of higher juvenile mortality (Siex and Struhsaker, 1999).

In Kalunga, the low infant/female ratios were not accompanied by higher ratios of juveniles/adult females versus groups in the larger, evergreen, and more intact forests of Mwanihana. There were few differences between groups in these 2 habitats in terms of juveniles (percentage of group or ratio to adult females): there were somewhat fewer medium-sized juveniles and significantly fewer subadult males in the degraded Kalunga Forest.

The lack of stronger differences in juvenile survivorship between Kalunga and Mwanihana may be due in part to the small sample from Kalunga ($n = 4$). It is also possible that insufficient time had passed since the major habitat perturbations occurred for there to be a significant change in juvenile numbers in Kalunga. Much of the degradation of Kalunga through tree cutting occurred in the mid to late 1990s and, if our hypothesis is correct, we expect even greater differences to develop between the 2 populations in the near future because of the temporal lag in demographic response to the degradation. Recall the example of the Amboseli vervet monkeys in which there was no significant decline in young juveniles until nearly 7 yr after a 90% loss of their major food trees, and even then fecundity remained extremely high (Struhsaker, 1973, 1976). Although there is need for larger samples and more current information on the Kalunga red colobus groups, our results indicate that they have lower fecundity without increased juvenile survivorship. Consequently, we predict that the Kalunga population will crash in the near future.

Even though Magombera was a small forest, fecundity was better there than in the smaller and heavily degraded Kalunga Forest. The data from the Magombera Forest also suggest a slight decline in juveniles and perhaps an increase in infants between 1977 and 1992.

Natality and Juvenile Survivorship in Relation to Group Size and Adult Sex Ratio

The effect of group size on birth rate and juvenile survivorship will depend on the cost to benefit ratio of group size to the individual. Benefits of larger groups can include competitive advantages over other groups (Wrangham, 1980) and improved detection of and/or defense against predators (Isbell, 1994; Struhsaker, 2000a; Van Schaik, 1983). The costs of larger groups are assumed to lie in the extent of food competition among members of the group (Van Schaik, 1983). In all of our study populations there was extensive overlap in home ranges between groups and crowned eagles were common, i.e. we saw them daily. Consequently, both intergroup competition and predation pressure were potentially high.

Natality in our study is positively correlated with group size, total number of adult females in the group, and adult sex ratio. However, none of these demographic variables were strong predictors of natality and generally accounted for <26% of the variance in ratios of infants per adult female. The number of adult males in the group had no significant effect on natality. Sociological variables were apparently less important determinants of natality

than habitat quality was. Indeed, both natality and group size were affected by habitat quality. When habitat quality is considered, none of the preceding demographic variables correlate with natality (infants per adult female). Habitat quality appears to be the dominant variable affecting natality.

The ratio of juveniles per adult female—an index of juvenile survivorship—is not strongly correlated with gross habitat differences or with any of the demographic variables that we considered. When we restricted the analysis of demographic variables to groups in higher quality habitats—Mwanihana and Magombera—only one correlated with juvenile survivorship. Juvenile survivorship is negatively correlated with adult sex ratios. Correspondingly, groups with large proportions of adult females had low ratios of juveniles per adult female. The proportional representation of adult females in groups accounted for 60% of the variance in the ratio of juveniles per adult female (a negative relationship). A possible explanation for this relationship is that adult females constitute the single most important age-sex class in terms of potential food competitors with juveniles. Adult males represent a small proportion of the group and all 3 infant classes rely on their mothers' milk. Consequently, none of them is likely to represent major competitors with juveniles for food. In contrast, adult females represented 43% of the membership of the 14 groups and their nutritional requirements were likely high because of lactation and pregnancy. The nutritional requirements of juveniles are also expected to be high because of rapid growth. Accordingly, assuming that there is competition for food, adult females are likely to be the most important conspecific competitors for juveniles within their social groups because of their high nutritional requirements and larger body size. Furthermore, if females among Udzungwa red colobus are the primary dispersing sex, as they are in Kibale (a different taxon of red colobus), then they are less likely to be close relatives of other group members and competition with unrelated juveniles will be less likely to have negative consequences for their own inclusive fitness.

An alternative explanation for the relationship between juvenile survivorship (juveniles/adult female) and the adult sex ratio is that number and proportional representation of adult males in a group have a positive influence on juvenile survivorship. This does not appear to be the case at Udzungwa because there is no significant correlation between either measure of adult male abundance in groups and juvenile survivorship.

Although habitat quality is likely to be an important determinant of juvenile survivorship, perhaps more so than most demographic variables, we cannot examine this hypothesis in our study area without larger and longer-term samples from the poor quality habitats.

Determinants of Group Size

In previous comparisons between taxa of red colobus and *Cercopithecus* species Struhsaker (2000a,b) concluded that habitat quality, predation pressure, and male competition for mates influenced group size and the frequency of fission-fusion groups. In some taxa and populations of red colobus, prolonged and intense predation by chimpanzees may reduce group size (Stanford, 1998) and group density (Mitani *et al.*, 2000), while hunting by humans has driven others to extinction (Struhsaker, 1997, 1999). In contrast, comparisons between taxa of red colobus failed to show any difference or consistent pattern in adult sex ratios as a function of potential predation pressure from crowned eagles (Struhsaker, 2000a,b).

Our data suggest that group size for the Udzungwa red colobus is determined by a complex interplay of habitat quality, size of adult male coalitions, and intragroup competition for food, especially between adult females and juveniles. Assuming constant predation pressure, we hypothesize that high quality habitats allow the formation of larger male coalitions, which attract more subadult and adult females. Large male coalitions attract more females because of potential benefits to the females, including more options for mate choice and competitive advantages over other groups for food. This results in larger groups in optimal than in suboptimal habitats. Natality

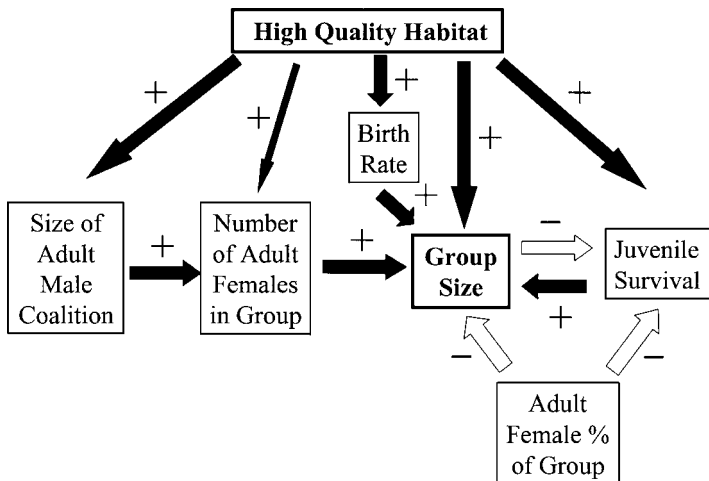


Fig. 7. Schematic diagram summarizing results and speculation (indicated by open arrows) on determinants of group size and composition in Udzungwa red colobus. Predation pressure is assumed to be constant. Width of arrow indicates strength of relationship.

and probably juvenile survivorship are both dependent on habitat quality. We speculate that, when habitat quality is held constant, as the sex ratio and the proportional representation of adult females in groups increase, juvenile survivorship decreases because of competition from these females. Group size is thereby limited (Fig. 7). Furthermore, in some habitats direct or interference competition for food within social groups can also be reduced by fission-fusion.

Implications for Conservation

Our data show the importance of protecting large blocks of old-growth, mixed evergreen and semideciduous forest for the conservation of the endemic Udzungwa red colobus. This habitat has the largest groups of red colobus with the highest natality. Population densities also appear to be highest in this habitat, but this must be verified with more systematic data. Our results also indicate the importance of establishing habitat corridors between patches of this forest type to increase the effective size of the forest and to increase the effective population size and natality of red colobus. Forest restoration will depend largely on fire prevention because within UMNP and the forest reserves anthropogenic fires appear to be the major deterrents to forest regeneration. Protecting and expanding the old-growth, evergreen forests is also important for conserving numerous other forest species endemic to the Udzungwas and the Eastern Arc Mountains (Dinesen *et al.*, 2001; Marshall *et al.*, in press).

It is equally clear, that cutting trees in the Kalunga Forest has disastrous effects on the red colobus living there. If this isolated population is to be saved, then Kalunga must be given full protection immediately. The Magombera and Ibiki Forests must also be legally annexed to the Selous Game Reserve in order to secure their long-term conservation. The other forest reserves, which are near, but currently outside the UMNP boundaries—Matundu, Udzungwa Scarp Forest, Iyondo, Ukami, Ndundulu, Nyumbanitu, Nyanganje—must be added to the park in order to protect the red colobus and other forest endemics from suffering the same fate as those in Kalunga. Park status is recommended for these reserves because at present they are unprotected and are being degraded by illegal human activities, such as logging, pole cutting, firewood collection, poaching, and agricultural encroachment (Dinesen *et al.*, 2001; Marshall *et al.*, in press; Pedersen and Topp-Jorgensen 2000, personal observations). All of these forests are vitally important for the conservation of biodiversity and the maintenance of water catchments that serve a major agricultural area—Kilombero Valley—fisheries, especially the Rufiji Delta, domestic water needs of many thousands of people, and two of Tanzania's most important hydroelectric

installations, that provide two-thirds of Tanzania's electricity (Struhsaker, 2001).

Recommendations for Future Research

Although our data represent the best demographic sample there is for the Udzungwa red colobus, there is much more to be done. Specifically, we recommend studies that will provide the following information:

1. better estimates of red colobus population densities from a variety of forest types. The published accounts are simply inadequate. Density estimates must be integrated with data on group size and composition in order to fully understand the relationship between habitat quality and demography.
2. detailed studies of habitat to better understand the vegetative correlates and ecological requirements of red colobus and other forest endemics.
3. more data on group size and composition especially from forests other than Mwanihana, such as Matundu, Udzungwa Scarp Forest, Ndundulu, and Nyumbanitu. Topics 1–3 will assist in prioritizing conservation areas for the colobus.
4. more studies in Kalunga to better understand the demographic responses of red colobus to major habitat perturbation.
5. more studies in Magombera to determine the current status and demographic trends of this important population of red colobus and to evaluate the status of its habitat. This is probably the most important population of red colobus remaining in the Kilombero Valley, as others have been virtually eliminated by habitat destruction, e.g. Lukoga (Ehardt *et al.*, 1999). The relationship of the Magombera population to the very small populations along the Msolwa riverine forest (Decker, 1994b) and in the Ibiki Forest should be determined, i.e. is there dispersal among them?
6. more sampling of group composition and density based on recognizable individuals and groups throughout the year and over multiple years to distinguish between real demographic trends within populations, real differences between sites (habitats), and differences due to intra- and interannual variation in reproduction. This is particularly important for the study of birth rates and juvenile survivorship. Long-term monitoring of animal and plant populations and their interactions is crucial to understanding the relative success of conservation management strategies and to anticipate conservation problems.

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