Monkey Abundance and Social Structure in Two High-Elevation Forest Reserves in the Udzungwa Mountains of Tanzania

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The effects of human activity on population and social structure are a pantropical concern for primate conservation. We compare census data and social group counts from two forests in the Udzungwa Mountains, Tanzania. The main aim is to relate differences within and between the forests to current theory on the effect of human disturbance on primate abundance and group size. The survey reveals the presence of the restricted-range red colobus, Procolobus gordonorum, *in New Dabaga/Ulangambi Forest Reserve (NDUFR). The primate community of NDUFR is impoverished compared to that in Ndundulu forest. Red colobus and black-and-white colobus (*Colobus angolensis palliatus*) abundance and group size are lowest in NDUFR. Fission-fusion of red colobus social groups may be occurring in previously logged areas of both forests. Our observations are consistent with current theory on the effect of habitat degradation and hunting on primates, but the relative effects of the 2 factors could not be differentiated. We pooled the results with previous data to show that abundance of red colobus in the Udzungwa Mountains is lowest at high elevations. Low red colobus group sizes appear to be related to human activity rather than elevation. Black-and-white colobus and Sykes monkeys (*Cercopithecus mitis*) show no relationship with elevation. Future studies will require more detailed information on vegetation, diet and ranging*

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*patterns to interpret fully intraspecific variation in population demography
and social structure in the Udzungwa Mountains.*

KEY WORDS: altitude; transect; logging; bushmeat; Eastern Arc.

INTRODUCTION

Most primate species live in tropical forests, where 2 major threats are
habitat destruction and hunting by humans (Mittermeier, 1987). Most pri-
mate species evidence reduced abundance in areas where they are heav-
ily hunted, and hunting has caused local extinctions (Mittermeier, 1986;
Struhsaker, 1999; Oates *et al.*, 2000). With few exceptions, primate popu-
lations in forests sufficiently degraded by human activity, such as logging,
show similar responses (Struhsaker, 1997; Cowlishaw and Dunbar, 2000).
Habitat degradation and hunting can also elicit changes in social structure.
Variation in social group size is largely determined through a compromise
between foraging and predation avoidance (Aldrich-Blake, 1970; Crook,
1970; Goss-Custard *et al.*, 1972; Terborgh and Janson, 1986; Struhsaker,
2000). Significant decreases in resources cause increased intragroup com-
petition and potentially decreased social group cohesion (Terborgh and
Janson, 1986; Gillespie and Chapman, 2001). The demographic and socio-
logical responses to forest degradation will depend on the degree of depen-
dence on forest habitat. The impact of hunting by humans on social group
size is less clear due to confounding factors and limited data. Small groups
tend to be more common in hunted areas, through increased mortality or
behavioural responses (Cowlishaw and Dunbar, 2000).

The Udzungwa Mountains of south-central Tanzania (Fig. 1) have
a wide range of forest habitats with different levels of human activity,
which is ideal for investigating anthropogenic influences on primate abun-
dance and socio-ecology. The Udzungwas are found in the south of the
ancient Eastern Arc mountain chain that runs from southern Kenya to
southern Tanzania. Within the chain are several fragmented forests im-
portant as centers of biodiversity and water catchments. Together with
nearby coastal forests, the Eastern Arc contains highest number of en-
demic species per unit area in the world (Myers *et al.*, 2000). The Udzungwa
Mountains probably contain the biologically most important area of for-
est in East Africa and the most important site for primates in Tanzania
(Butynski *et al.*, 1998). Among the 10 primate species are 2 restricted-
range monkeys of conservation concern. The Udzungwa red colobus (*Pro-
colobus gordonorum*; IUCN vulnerable, Hilton-Taylor, 2000), lives only in
forests of the Udzungwa Mountains, plus some lowland forest fragments
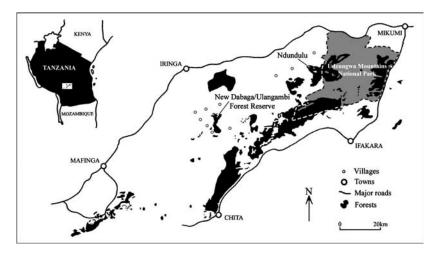to the east of the Udzungwa Mountains National Park (UMNP). Even

Fig. 1. Approximate distribution of forest-dominated areas in and around the Udzungwa Mountains, showing forests surveyed in the current study and their nearest villages. Adapted from Moyer (1992) using Landsat imagery.

less abundant is the IUCN endangered endemic Sanje mangabey (*Cercocebus galeritus sanjei*), discovered in 1979 (Homewood and Rodgers, 1981) and occuring in only 3 forests of the Udzungwa Mountains (Rodgers and Homewood, 1982; Dinesen *et al.*, 2001). Two further species in the Udzungwa Mountains forests are the Angolan black-and-white colobus (*Colobus angolensis palliatus*; IUCN data deficient) and Sykes monkey (*Cercopithecus mitis* ssp.).

Despite the diversity and restricted range of the Udzungwa Mountains primate fauna, much of the area remains unsurveyed. Rodgers and Homewood (1982) and Dinesen *et al.* (2001) showed that the range of the endemic primates is restricted by habitat fragmentation. A preliminary comparison between 2 forest reserves further suggested that human activity has led to a decline in primate group abundance and social group size (Pedersen and Topp-Jørgensen, 2000). Further studies in UMNP have begun to acquire more detailed information on demography, distribution and relative abundance (Ehardt, 1999–2000; Ehardt *et al.*, 2000, 2001; Struhsaker *et al.*, 2004). Most publications on primate communities in the area are focussed on lowland forests. Two short surveys showed an unusually high level of interspecific association between *Pocolobus gordonorum* and *Colobus argolensis palliatus* (Struhsaker and Leland, 1980; Wasser, 1993). Studies in Magombera, a former forest reserve in the lowlands of the Udzungwa catchment area highlight the vulnerability of Udzungwa primates. Magombera is 5 km east of UMNP and was reduced in size by

railroad construction and subsequent clearance, seriously harming the primate populations (Rodgers *et al.*, 1980; Rodgers and Homewood, 1982; Decker, 1994, 1996). The protected status of the forest was later removed and in 2003 conservationists had to persuade the Tanzanian government not to destroy the forest for settlement (Dinesen, Rovero and Struhsaker, pers. comm.).

The aims of our study are (1) to provide basic information on the monkey communities of 2 poorly known high elevation forest areas in the Udzungwa Mountains; (2) to assess habitat dependence and sensitivity of different species to human forest use, based on variation in abundance and social structure; and (3) to discuss deviations from previous studies elsewhere in the Udzungwa Mountains.

METHODS

Study Sites

We surveyed primates in 2 forest fragments. New Dabaga/Ulangambi Forest Reserve (NDUFR; 35°54′–35°57′ E; 08°01′–08°06′ S), is an isolated forest fragment of 3,728 ha surrounded on all sides by cultivation and in close proximity to several villages (Fig. 1). Past commercial timber extraction, which ceased in the early 1990s, is evident from old logging roads in the north of the reserve and cut stumps throughout. The Forest Reserve designation means that natural resource extraction is not permitted without official permission. Despite this, human forest use in NDUFR is high (Table I). Commercial logging and pitsawing have reduced the canopy and scrubby vegetation predominates. Pioneer tree species are also common in NDUFR, including *Macaranga kilimandscharica* (Euphorbiaceae), which accounts for 20% of mature trees (Munyuku, 1993; Marshall *et al.*, 2001a).

In contrast to NDUFR, West Kilombero Scarp Forest Reserve (WKSFR; 36°05′–36°33′ E, 07°38′–08°17′ S) is relative wilderness. In the north are 3 forest fragments: Ndundulu, Nyumbanitu and Ukami (Fig. 1). They are separated by a mosaic of fire-maintained wooded grassland, on slopes and ridges, and riverine forest in the valleys. We focused on Ndundulu (a.k.a. Luhombero), a 250 km² forest fragment partially within WKSFR and partially within the Udzungwa Mountains National Park (Fig. 1; Dinesen *et al.*, 2001). In Ndundulu, habitat diversity and forest area is far greater than NDUFR, with ≥4 distinct tree communities (Hall, 1988; Marshall *et al.*, 2001b). Some commercial logging occurred in the north of Ndundulu forest in 1993–94, in the area around one study site (WKS1; Dinesen and Lehmberg, 1996), whereas human activity is low in the remainder of Ndundulu, including our southern study site (WKS3; Table I).

Table I. Description of census transect routes in Ndundulu forest in West Kilombero Scarp Forest Reserve and New Dabaga/Ulangambi Forest Reserve, Tanzania Habitat data taken from Marshall et al. (2001a,b).

	Ndundulu forest in WKSFR		New Dabaga/Ulangambi Forest Reserve	
	WKS1	WKS3	NDU2	NDU3
Length[a]	3,164 m (2,646 m)	3,116 m (2,520 m)	3,109 m	3,134 m (2,619 m)
Repetitions[a]	10 (1)	7 (2)	10	8 (3)
Elevation range	1940–2089 m a.s.l.	1372–1625 m a.s.l.	1877–2055 m a.s.l.	1784–1992 m a.s.l.
Forest type	Montane; open areas with gap habitat	Mature montane; some young forest	Montane; several gaps; high tree diversity	Mostly regenerating montane forest
Dominant trees	Podocarpus milanjensis Neoboutonia macrocalyx Bridelia micrantha Cassipourea gummiflua Hagenia abyssinica	C. gummiflua Cola schefferi Macaranga sp. Teclea sp. Parinari excelsa	M. kilimandscarica Garcinia volkensii Aphloia theiformis C. gummiflua Albizia gummifera	A. theiformis C. gummiflua Nuxia floribunda M. kilimandscharica P. excelsa
Human activity	Past logging; fire	Minimal	Past logging (and some present); pole cutting; ground traps; paths; honey collecting; hunting[b]	
Canopy	Broken canopy 10–20 m	Closed canopy >20 m	Broken canopy 5–20 m	Broken canopy 5–20 m
Predators	Crowned eagles and leopards throughout Ndundulu		Absent throughout NDUFR	

[a]Figures in parentheses indicate shorter walks made on a few occasions.

Surveys of Ndundulu by Dinesen *et al.* (2001) sparked interest in WKSFR primates, through discovery of the Sanje mangabey. They also found that red colobus, Sykes monkeys and black-and-white colobus were also common in Ndundulu. Before their study, no primate census work had been conducted in NDUFR. Rodgers (1981) mentioned 2 previous short expeditions to NDUFR, which noted the presence of black and white colobus and Sykes monkeys in the reserve in 1950 and 1972. The second survey failed to note the presence of red colobus during 4 days of observation. Subsequently, Rodgers and Homewood (1982) listed the red colobus as certainly absent from the reserve and at the time of survey, the species had not been recorded from NDUFR for 50 years. The Sanje mangabey has never been documented from NDUFR.

In NDUFR and surrounding farmland, many mammals are hunted for meat or to prevent crop damage. Bush pigs, hyrax, duikers and ground-living monkeys are particularly targeted via snares, pitfall traps, iron leg traps, falling log traps and dogs. There is no large mammal in this area. Despite finding an iron leg trap in a tree and a discarded shotgun cartridge, villagers did not acknowledge that colobus monkeys were hunted in NDUFR. However, subsequent researchers found further traps and gained co-operation from 135 hunters, many of whom claimed to hunt colobus monkeys (Nielsen, 2002 and pers. comm.). In Ndundulu, our observations and comments from local people suggest that antelope, bush pig, buffalo, hyrax and elephant are hunted. Villagers in Udekwa and Ifuwa have also admitted to hunting colobus monkeys (Nielsen, pers. comm.). However, due to the large size of Ndundulu, distance from settlements and the use of nails as bullets, hunting intensity is probably lower than in NDUFR (pers. obs.; Nielsen, pers. comm.).

Data Collection and Analysis

We collected data as part of biodiversity surveys during 5 mo in NDUFR and 10 mo in WKSFR. We cut 2 census transect routes each in NDUFR and Ndundulu (Fig. 2) and marked them with plastic tags at 50-m intervals. Transects were 2,520–3,192 m long and sampled montane forest habitats (Table I). Marshall conducted all census walks during January–December 2000. Census walks began at 0700 h and were repeated between 9 and 11 times at a pace of around 1 km h^{-1}. We recorded all monkey groups and spent *ca.* 10 min with each group to record species identification, observer location and distance of first individual observed from each group. Distant observations made across valleys are not included in the analysis. For analysis of census data, we used sighting frequencies per km transect in
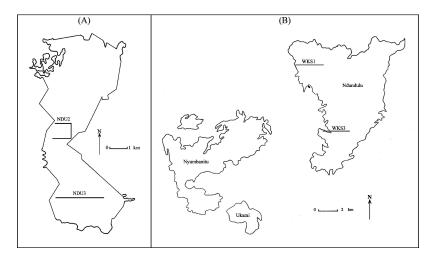
Fig. 2. Location of transects in New Dabaga/Ulangambi Forest Reserve (A) and Ndundulu forest in West Kilombero Scarp Forest Reserve (B).

preference to density estimation, which complies with the data of Skorupa, (1986, 1988), Struhsaker, (1997) and Mitani *et al.* (2000). Low group density in the study areas means that the total number of observations falls far short of the minimum requirement for reliable density estimation (60–80). We did not use a rangefinder so distances to groups are unlikely to be exact.

Marshall made counts of social groups during the same fieldwork period as census walks. Concurrently, Topp-Jørgensen counted another group, Marshall and Struhsaker counted a group in July 2001. Social groups were counted both during and outside of census walks. We defined an individual as associating in a group if it was the same or immediately adjacent trees as other group members. Group counts made during census walks were only possible on rare occasions when groups fled quickly in single file, which required more than the stipulated 10 min to record basic census data (Plumptre and Reynolds, 1994). We used only complete or near-complete counts of all individuals in association at the time of counting. Data were only obtained for the 2 colobus species. Given that some groups were not watched for >30 min, it is possible that some counts are incomplete. In a few cases where counts are nearly complete, we used the mean of the actual count and the estimated group size (per Struhsaker *et al.*, 2004).

To determine the relationship between census data and human activity, all signs of human forest use within 5 m of each transect line were enumerated. This included animal traps, pit-sawing sites and timber piles. Cut tree stumps were counted and categorised as either *poles* (trees 5–15 cm

diameters at cut height) or *timber* (trees >15 cm diameter at cut height). All forest use data were collected in 1999 and 2000.

We used 2-tailed nonparametric tests throughout unless otherwise stated. We compared group sizes via Mann-Whitney U-tests (after Sokal and Rohlf, 1995), which are 1-tailed based on previous evidence that primate group size is lower in poor quality habitat (Struhsaker *et al.*, 2004). We performed Kruskal-Wallis tests via *post hoc* Mann-Whitney U-tests (Day and Quinn, 1989). We present data as mean ± standard error to allow comparison with other primate studies.

RESULTS

Social Group Size and Abundance

We obtained 24 counts of social groups with ≥2 individuals (Table II). Red colobus showed the most variation, with mean $11.8 ± 3.8$ S.E. individuals per group in NDUFR (range 5–24; $n = 6$) and $22.5 ± 3.6$ in Ndundulu (range 12–33.5; $n = 8$). Groups in Ndundulu were larger than those in NDUFR, though the difference is only weakly significant (one-tailed Mann-Whitney U-test, $p = 0.071$, $U = 36.0$, $n = 14$). Groups of larger size also occurred but were not accurately counted in Ndundulu and the other 2 WKSFR fragments of Nyumbanitu and Ukami. Larger groups tend to be harder to count because they are more spread out and are thus more likely to be obscured by vegetation or terrain. Furthermore, large groups have a higher chance of detecting an observer. This has a strong influence in areas such as Ndundulu where monkeys are not habituated and tend to flee.

Table II. Monkey social group counts. In five cases the mean of the estimate and actual count was used to calculate mean group size

Red colobus		Black and white colobus	
NDUFR	WKSFR	NDUFR	WKSFR
3	12	2	9
3	12	6	9.5
5	13	7	11[a]
17	16	7	12
18.5	27.5[b]	8	
24	33[a]	8	
	33		
	33.5		

[a] JETJ.
[b] ARM and T. Struhsaker.

Black-and-white colobus groups are significantly larger in Ndundulu (mean 10.4 ± 0.7; range 9–12; $n = 4$) than in NDUFR (mean 6.3 ± 0.9; range 2–8; $n = 6$; 1-tailed Mann-Whitney U-test, $p = 0.005$, $U = 24.0$, $n = 10$).

Solitary colobus monkeys occur infrequently in both forests. There were solitary monkeys in NDUFR than in Ndundulu, for both colobus species. One adult female red colobus with an infant was in NDUFR together with 2 medium-sized black-and-white colobus. Also in NDUFR, a single red colobus was in a group of 7 black-and-white colobus. No solitary red colobus was in Ndundulu. There were 4 solitary black-and-white colobus in NDUFR and 2 in Ndundulu. One of them in Ndundulu was a mother with an infant.

We obtained a total of 37 and 86 visual records of monkey social groups during census walks in NDUFR and Ndundulu respectively. There are 15 records of red colobus groups in NDUFR and 29 in Ndundulu. Totals for black-and-white colobus are 10 and 34 and for Sykes monkeys 11 and 20 in the 2 areas (Table III) We used estimates of mean social group sizes to convert group abundance to individual abundance for Table III. Kruskal-Wallis tests show that social group and individual abundance of the 2 colobus species tend to be significantly highest along WKS1 and lowest along NDU3. Transects WKS3 and NDU2 had equivalent social group abundance for all species. The abundance of Sykes monkey social

Table III. Mean $\pm$ standard error of the number of social groups and individuals per km transect. Observations sharing the same letters in superscript showed significant difference ($p < 0.05$) from Kruskal-Wallis tests within species (underlined letters indicate $p < 0.067$)

Species	Transect	Groups	Individuals
Red colobus	WKS1	0.70 ± 0.11^{ab}	15.64 ± 2.46^{ab}
	WKS3	0.20 ± 0.08^{a}	4.39 ± 1.85^{a}
	NDU2	0.39 ± 0.09^{c}	4.54 ± 0.92^{bc}
	NDU3	0.09 ± 0.04^{bc}	1.02 ± 1.05^{bc}
Black and white colobus	WKS1	0.79 ± 0.16^{ab}	8.17 ± 1.67^{ab}
	WKS3	0.26 ± 0.07^{a}	2.68 ± 0.76^{a}
	NDU2	0.26 ± 0.08^{b}	1.63 ± 0.51^{bc}
	NDU3	0.06 ± 0.04^{a}	0.40 ± 0.27^{ac}
Sykes monkey	WKS1	0.29 ± 0.08	no data
	WKS3	0.37 ± 0.06	no data
	NDU2	0.19 ± 0.07	no data
	NDU3	0.15 ± 0.05	no data
All species	WKS1	1.83 ± 0.19^{ab}	23.81 ± 4.13^{ab}
	WKS3	0.86 ± 0.11^{a}	7.07 ± 2.61^{a}
	NDU2	0.87 ± 0.15^{bc}	6.16 ± 1.42^{bc}
	NDU3	0.30 ± 0.07^{ac}	1.43 ± 1.32^{ac}

groups is not statistically different between all transects. We neither saw nor heard Sanje mangabeys during the entire 15 mo of fieldwork in either reserve.

To illustrate the overall differences in abundance between Ndundulu and NDUFR, we combined observations using means of pairs of transect walks. There is a significantly higher number of groups per km transect from Ndundulu transects ($n = 9$) versus NDUFR ($n = 10$), for both colobus species, and for all species combined (Mann-Whitney U-test: red colobus, $p = 0.033$, $U = 71.0$; black-and-white colobus, $p = 0.002$, $U = 81.0$; all species combined, $p = 0.028$, $U = 85.0$), but not for Sykes monkeys (Mann-Whitney U-test: $p = 0.095$, $U = 66.0$). Results similar are for individuals (Mann-Whitney U-test: red colobus, $p = 0.001$, $U = 84.0$; black-and-white colobus, $p = 0.001$, $U = 87.0$; both colobus combined, $p < 0.001$, $U = 89.0$).

Human Forest Use

Human forest use in NDUFR is greater than in Ndundulu, with 47.2 versus 4.0 observations per ha. Within the 2 forests, there was little variation in human forest use between the 2 pairs of transects (Fig. 3). Commercial logging that took place in the north of Ndundulu in 1993–94 was evident from cut timber tree stumps and pitsaw sites near to WKS1. In addition (not shown by Fig. 4), there were signs of old bushfires along transect WKS1 through an undetermined area of forest. Nos evidence of human presence
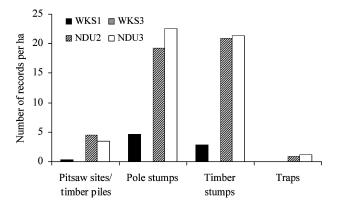

Fig. 3. Signs of human forest use per ha along transects in NDUFR and Ndundulu forest in WKSFR. Data collected 5 m either side of all transects.
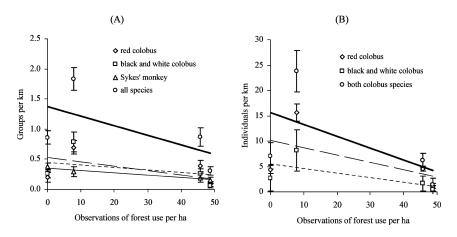
Fig. 4. Correlations of (A) group abundance, and (B) individual abundance, versus observations of human forest-use along the 4 census transects. Spearman's rank correlation tests are only significant for Sykes monkey groups ($r_s = -1.0, p < 0.001$).

was along transect WKS3, though human footprints and an old hunters' camp were nearby. Tests for Spearman's rank correlation show that Sykes monkey group abundance is negatively correlated with the number of traces of human forest use (Fig. 4; $n = 4, r_s = -1.0, p < 0.001$). Similar tests using group and individual abundance for the colobus species and for all species combined show a negative yet non-significant relationship with forest use (Fig. 4; $n = 4; r_s \leq -0.4; p \geq 0.2$).

DISCUSSION

Social Group Size and Abundance

Our results show differences in the abundance and group size of primates between Ndundulu and NDUFR. The 2 colobus species are less abundant, have smaller group size, and more solitary individuals in NDUFR than in Ndundulu. Furthermore, we suspect that the areas sampled in NDUFR contain the highest density of red colobus in the reserve. During *ca.* 5 mo in NDUFR, only 5 red colobus groups occurred outside of the areas around transects NDU2 and NDU3. Conversely, we saw or heard monkeys of all 3 species regularly throughout Ndundulu forest. Factors related to elevation are unlikely to be responsible for the contrasting abundance and group size of NDUFR and Ndundulu, because the elevational ranges of 3 of the transects overlap considerably (Table I). The

smaller size of NDUFR is also unlikely to be responsible because there are much smaller forests in the Kilombero Valley and elsewhere that have higher monkey densities and larger groups (Decker, 1994; Struhsaker *et al.*, 2004; Ehardt *et al.*, 2000).

It is not possible to determine the relative effects of hunting and habitat degradation. The relationship between habitat disturbance, abundance, group size and the number of solitary individuals is consistent with previous studies (Skorupa, 1986, 1988; Struhsaker, 1997; Cowlishaw and Dunbar, 2000). Reduced abundance and group size also occurs in areas with a high level of hunting (Cowlishaw and Dunbar, 2000). In addition, the isolation of NDUFR prevents natural population reinforcement from elsewhere following loss, e.g. through human activity or natural mechanisms such as disease. The extremely low size of some red colobus groups in NDUFR is noteworthy (3, 3 and 5; Table II). Previous researchers found that groups of *Procolobus badius* rarely have <10 individuals (Struhsaker, 1975; Struhsaker *et al.*, 2004), which suggests that the NDUFR monkey social structure has been seriously affected. It is likely that the small groups are a result of the high hunting levels and degraded habitat. Furthermore, given the lack of nonhuman predators in NDUFR, there is little benefit in maintaining large groups.

We rarely followed groups beyond making group counts, so their temporal stability is not known. In degraded areas of both NDUFR and Ndundulu, a high variability of group size occurred at certain locations, which was not noted in areas of tall closed-canopy forest. Colobine populations can have a wide range of group sizes (Groves, 1973; Struhsaker, 1975, 1997; Siex and Struhsaker, 1999; Struhsaker *et al.*, 2004). Alternatively, some of the smaller groups may represent foraging parties that have split from larger groups. Such fission-fusion social dynamics occurs in the Udzungwa Mountains and elsewhere in response to habitat degradation and limited, clumped or widely spaced resources (Klein and Klein, 1977; Waser, 1977; Struhsaker and Leland, 1979; Skorupa, 1988; Siex and Struhsaker, 1999; Struhsaker, 1997, 2000; Struhsaker *et al.*, 2004). This would explain why red colobus abundance along WKS1 was unexpectedly greater than along WKS3 (Table III). If groups periodically split, there would have been a higher chance that one of the resulting parties would be detected. However, the WKS1 monkeys may also have benefited from the emergence of a high diversity of pioneer tree species. Folivorous primates sometimes increase following low-level disturbance in response to growth of high quality food (Oates, 1996). The observation of increased black-and-white colobus abundance in the logged area is less surprising as they are less dependent on mature forest than of red colobus are.

Sanje Mangabey

The IUCN endangered Sanje mangabey is limited to the 3 biggest fragments of evergreen forest in the Udzungwa Mountains, including Ndundulu/Luhombero (Rodgers and Homewood, 1982; Dinesen *et al.*, 2001). We did record them during our fieldwork, nor have other survey in Ndundulu between 1998–2000 (Pedersen and Topp-Jørgensen, 2000; Ehardt *et al.*, 2000, 2001). If mangabeys still exist in Ndundulu, they are probably restricted to an area between transects WKS1 and WKS3 (Dinesen, pers. comm.). Their ecology is poorly known and the reason for their restricted range is uncertain. From preliminary observations in Mwanihana Forest, it is likely that mangabeys have larger home ranges than those of red colobus (Struhsaker, pers. comm.). Therefore, small patch size would be more likely to lead to extinction of mangabeys than of red colobus.

Elevational Effects

Red colobus abundances in Ndundulu (0.48 ± 0.06 groups km^{-1}) and NDUFR (0.24 ± 0.06) are similar to other high elevation data from the Udzungwa Mountains. Pedersen and Topp-Jørgensen (2000) noted mean 0.44 red colobus groups km^{-1} above 1540 m elevation in west-central Ndundulu and 0.20 groups km^{-1} above 1540 m in Udzungwa Scarp Forest Reserve (USFR). Via census walks along 4 transects $\leq$700 m in Mwanihana forest Pedersen and Kishe recorded 0.70–0.88 groups km^{-1} (Ehardt *et al.*, 2000). This is significantly greater than abundances from Pedersen and Topp-Jørgensen (2000) and our study (Mann-Whitney U-test: $U = 16.0$, $p = 0.021$). Other Udzungwa monkeys show no such differentiation in abundance between low and high elevation transects (black-and-white colobus: $U = 11.5, p = 0.309$; Sykes: $U = 12.0, p = 0.248$).

Studies of *Procolobus gordonorum* by Struhsaker and Leland (1980) and Decker (1994) in the lowland Magombera forest (270 m elevation) found larger mean group sizes than that for our study (mean 34.4 and 26.6). Further, counts of 48 social groups in 5 forest/woodland areas $\leq$700 m elevation produce a mean group size of 33.7 ± 2.1 (calculated from appendix in Struhsaker *et al.*, 2004), which is significantly larger than our observed group sizes (Kruskal-Wallis: NDUFR, $U = 555.0$, $p < 0.001$; Ndundulu, $U = 453.0$, $p = 0.002$). However, large red colobus social groups (31–69.5; $n = 5$) in the less disturbed Iyondo forest (1600–1800 m a.s.l.) suggest that human activity is responsible rather than elevation (Struhsaker *et al.*, 2004). Black-and-white colobus social group size is not related

to elevation in the Udzungwa Mountains. Twelve counts of black-and-white colobus social groups in Mwanihana and Kalunga Forests (7.5 ± 0.8; Struhsaker and Marshall, unpublished data) are not significantly different to our counts (Kruskal-Wallis: $\chi^2 = 5.64, p > 0.05$). Studies on *Colobus angolensis* groups elsewhere in East Africa, have shown positive relationships between group size and elevation (Groves, 1973; Fimbel *et al.*, 2001).

The reason for low abundance of red colobus at high elevations is uncertain. Data on dietary quality of vegetation from the Udzungwa Mountains is not currently available, but it could be useful in assessing it. Data from Rwanda and Cameroon suggest that mature leaves from high elevation sites are more digestible than those from low elevation sites due to low fiber content (Fimbel *et al.*, 2001; Beeson and Lea, 1994). Fimbel *et al.*, (2001) suggested this as a reason for the occurrence of supergroups of *Colobus angolensis* at high elevation. However, evidence from elsewhere suggests that the relationship is not universal. Caldecott (1980) suggested that the ratio between energy expenditure and nutrient intake becomes unfavourable for Malayan gibbons at high elevation, which is attributed to the increased costs of thermoregulation and locomotion in cool and tangled habitats. Elevational range of primates can be further constrained by reduced food density at high elevations (Durham, 1975; Caldecott, 1980). Diversity, basal area and proportion of food trees, are all correlated with lar gibbon biomass (Caldecott, 1980). The same study indicated a switch to less favorable food species at high elevation. Red colobus in the Udzungwa Mountains also select different food species at high elevation. Notably, only one of the top 8 food items in Mwanihana Forest (*Albizia gummifera*: Wasser, 1993) is present in the high elevation forests of NDUFR and Ndundulu. Decreased food tree quantity also leads to decreased quality, as seen from reduced fruit production of trees eaten by Japanese macaques (Hanya *et al.*, 2003). Similarly, plants from resource-poor habitats have a slower turnover of leaves and are less able to replace lost or damaged leaves due to energy limitations (Bryant *et al.*, 1983). Energy costs and exposure to sunlight at high elevation also result in less digestible leaves with increased tannins and phenolic defences (Bryant *et al.*, 1983; Dudt and Shure, 1994).

Habitat Dependence

The reduced group size and abundance of both species of colobus in NDUFR suggests that they are dependent on low levels of human disturbance. However the high level of hunting in NDUFR precludes conclusions regarding habitat dependence *per se*. The lack of elevational difference in abundance or group size for black-and-white colobus may be due

to their flexible diet. Studies in Gombe and Kibale suggest that *Colobus guereza* are better able to survive on mature leaves than *Procolobus badiusis*, and they are less dependent on closed-canopy forest (Clutton-Brock, 1972; Struhsaker, 1975; Struhsaker and Oates, 1975; Chapman *et al.*, 2000). The diet of *Colobus angolensis* also includes a high proportion of mature leaves, whereas that of *Procolobus gordonorum* largely comprises young leaves and petioles (Groves, 1973; Wasser, 1993). Contrary data for *Procolobus badius* in the Kibale forest, Uganda, indicate a high degree of dietary flexibility across sites (Chapman *et al.*, 2002). The relative habitat dependence of the 2 Udzungwa colobines therefore remains uncertain. Sykes monkeys show no difference in abundance between high and low elevation forests or between NDUFR and Ndundulu. They are highly opportunistic and utilize food and shelter in arable land surrounding NDUFR. Accordingly, the significant negative correlation between Sykes group abundance and density of stumps is surprising (Fig. 4). However, without group size data this is hard to interpret, and given the low variation in abundance between the four transects, it is probably an artefact of low sample size.

Conservation Implications and Further Work

Udzungwa red colobus have not been eliminated from NDUFR as once feared. However, it is clear that the monkey population and social structure have been affected by human activity. Our results and recommendations are now being used to develop management plans with villages and local authorities. The priority for management in Ndundulu is the cessation of bushfires in the surrounding grassland, which are preventing forest expansion and connectivity (Marshall *et al.*, 2001c). In both forests there is also a need to monitor and to curb hunting levels.

We attempted to explain differences in abundance and group size of 2 populations and to make comparisons with other locations. However, our counts and abundance estimates are only a snapshot of a dynamic system for which years of observation may be required to fully understand. Also, it is hard to make conclusions without detailed historical information (Butynski, 1990). Further work is needed to determine which factors have influenced the current distribution, demography and social structure of Udzungwa primates. This will require data from a variety of habitats, including density/abundance, group composition, ranging patterns, diet, human forest use and vegetation structure/diversity. Differentiating the relative impact of habitat degradation versus hunting will require surveys of areas where either hunting or habitat degradation are negligible.

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