



## 1 **Abundance of Diurnal Primates in Mwanihana** 2 **Forest, Udzungwa Mountains, Tanzania**

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7 *Many studies have used line transect counts to estimate forest primate abun-*  
8 *dance. Researchers have devoted less attention to the interpretation of line*  
9 *transect data obtained by several observers, as is often the case in long-term*  
10 *monitoring programs. We present primate relative abundance data that 5 ob-*  
11 *servers collected over 6 yr (not continuous) along 4 different transects each*  
12 *4 km long in the Mwanihana Forest, Udzungwa Mountains National Park,*  
13 *Tanzania. Total distance walked during transect repetitions was ca. 700 km.*  
14 *The species we saw most frequently was the endemic Udzungwa red colobus*  
15 *Procolobus gordonorum (mean 0.59 groups/km walked), followed by the*  
16 *Angolan black and white colobus Colobus angolensis (0.43 groups/km) and*  
17 *Sykes's monkey Cercopithecus mitis (0.35 groups/km). We sighted the en-*  
18 *demic Sanje mangabey Cercocebus galeritus sanjei and the yellow baboon*  
19 *Papio cynocephalus infrequently, the latter being confined to the deciduous*  
20 *forest parts of the transects. We analyzed sighting frequency by gross habitat*  
21 *type, transect, season, and observer. Interobserver differences in the relative*  
22 *abundance of each species were moderate and the few cases of significant*

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23 variations were due to discordance of only 1 observer from the others. Esti-  
 24 mated distances of primate group sightings differed significantly among ob-  
 25 servers, thus preventing us from deriving estimates of absolute density. Fre-  
 26 quency distributions of distance-class intervals were not significantly differ-  
 27 ent among observers, which may indicate gross interobserver consistency in  
 28 the width of the area sampled. We conclude that unless consistency in data  
 29 collection is checked, as we did for 2 observers who collected data simul-  
 30 taneously, potential interobserver differences remain an underlying source  
 31 of variance in the results that cannot be separated from other sources of  
 32 variance.

34 **KEY WORDS:** census methods; Eastern Arc; line transect; monkeys; primate monitoring;  
 Udzungwa.

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## INTRODUCTION

36 Censusing nonhuman primates over time is necessary for monitoring  
 37 population trends, which is important for designing and evaluating man-  
 38 agement practices (Gibbs *et al.*, 1998; Kremen *et al.*, 1994). Census data also  
 39 provide the baseline for more detailed socioecological and behavioral stud-  
 40 ies (Butynski, 1990; Struhsaker, 1975). Line transect census is the most com-  
 41 monly used method in forest primate abundance studies (Chapman *et al.*,  
 42 2000; Defler and Pintor, 1985; Fashing and Cords, 2000; Struhsaker, 1975;  
 43 Whitesides *et al.*, 1988). Researchers have proposed several techniques to  
 44 convert raw data into density estimates (Buckland *et al.*, 2001; Plumptre,  
 45 2000; Skorupa, 1987; Struhsaker, 1981, 2002; Whitesides *et al.*, 1988). How-  
 46 ever, scientists have rarely considered compatibility of data collected by  
 47 multiple observers over different periods at the same site, though it must  
 48 be addressed if long-term monitoring programs are to produce meaningful  
 49 results. Mitani *et al.* (2000) showed that different observers may vary signif-  
 50 icantly in estimates of primate sighting distances, rendering computation of  
 51 absolute densities problematic. Lack of consistency among observers might  
 52 ultimately prevent adequate assessment of population changes.

53 The Udzungwa Mountains of south-central Tanzania are one of the  
 54 most important sites in East Africa for primate conservation, primarily be-  
 55 cause of the presence of the endemic, IUCN-Vulnerable Udzungwa red  
 56 colobus (*Procolobus gordonorum*) and the endemic, IUCN-Endangered  
 57 Sanje mangabey (*Cercocebus galeritus sanjei*, Ehardt, 2001; Homewood and  
 58 Rodgers, 1981; IUCN 2003; Struhsaker and Leland, 1980). With an overall  
 59 area of 10,000 km<sup>2</sup> (centered on 8°20'S, 35°50'E), the Udzungwa Moun-  
 60 tains are the southernmost and largest block of the Eastern Arc Mountains,  
 61 which are part of a biodiversity hotspot of global importance for conser-  
 62 vation (Burgess *et al.*, 1998; Myers *et al.*, 2000; Rodgers and Homewood,

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63 1982). The Udzungwa Mountains, in particular, are characterized by a great  
64 altitudinal range of forest cover (300–2600 m a.s.l.) that includes habi-  
65 tats ranging from lowland deciduous forest to montane evergreen for-  
66 est, as well as many areas of exploited and degraded forest and grass-  
67 land (Dinesen *et al.*, 2001; Marshall *et al.*, ~~in press~~; Struhsaker *et al.*,  
68 2004).

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69 Information on population abundance of the Udzungwa primates is  
70 scant. Aside from several unsystematic zoological surveys (Butynski *et al.*,  
71 1998; Dinesen *et al.*, 2001; Rodgers and Homewood, 1982), researchers have  
72 conducted detailed primatological studies primarily on polyspecific associ-  
73 ations (Wasser, 1993), demographic variation in *Procolobus gordonorum*  
74 (Struhsaker *et al.*, 2004), and primate abundance and social structure in  
75 2 high-elevation forests (Marshall *et al.*, ~~in press~~). Our study is the first  
76 to employ systematic line-transect censuses to estimate the abundance of  
77 diurnal primates in Mwanihana Forest, one of the largest forests in the  
78 Udzungwa Mountains. We also assessed differences in line transect data  
collection among several observers.

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**METHODS**

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**Study Area and Subjects**

82 We conducted the study in the Mwanihana Forest (177 km<sup>2</sup>, Dinesen  
83 *et al.*, 2001) of the Udzungwa Mountains National Park (UMNP, 1990 km<sup>2</sup>,  
84 centered on 7°46'S, 36°43'E). UMNP covers the northeastern portion of  
85 the Udzungwa Mountains (Fig. 1). Mwanihana Forest is situated on the  
86 slope of the east-facing escarpment, which has continuous forest from 300 m  
87 to 2100 m a.s.l. Mean annual rainfall is *ca.* 2000 mm, occurring mainly in  
88 November–January and March–May. Average monthly temperature, mea-  
89 sured at 300 m a.s.l., ranges from 24°C in June–July to 28°C in November–  
90 December (UMNP data for 1998, ~~Abel~~ Mtui, pers. comm.). Details of  
91 vegetation zones and plant species composition of Mwanihana Forest are  
92 reported below (see also Lovett *et al.*, 1988).

93 The diurnal primates in Mwanihana Forest include Udzungwa red  
94 colobus, Sanje mangabey, Angolan black and white colobus (*Colobus*  
95 *angolensis*), Sykes’s monkey (*Cercopithecus mitis*), and yellow baboon  
96 (*Papio cynocephalus*). Also present are 3 of the 4 species of galagos  
97 known in the Udzungwa Mountains ~~are~~ (Butynski *et al.*, 1998). The  
98 main potential predators of all the diurnal primates are the African  
99 crowned eagle (*Stephanoaetus coronatus*) and the leopard (*Panthera*  
100 *pardus*).



**Fig. 1.** Map of the Udzungwa Mountains of south-central Tanzania highlighting the main forest blocks (in black) including Mwanihana Forest, and the Udzungwa Mountains National Park (in gray). (From Marshall *et al.*, [in press](#)).

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## Data Collection

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We obtained census data via line transect methods (Struhsaker, 1981; Whitesides *et al.*, 1988). We placed 4 line transects (T1–T4), each 4 km long and positioned *ca.* 6 km apart, along existing pathways that run mainly from east to west (Table I), known as Camp Site 3, Mwanihana Trail, Sanje Falls, and Msolwa, for T1–T4, respectively. A rapidly increasing number of tourists use the first 3 trails, especially the Sanje Falls trail (*ca.* 1800 during 2003/2004; Udzungwa Mountains National Park data, G. Kimaro, pers. comm.). In addition, local people use the lower 1–2 km of the trails on 2 d/wk ~~by~~ for firewood collection. Though the rising number of people using these trails might have induced habituation and caused disturbance to the primates, most tourists walk along another trail to the Sanje Falls that is not used for primate censusing. We assumed that the likelihood of sighting primates was not altered by using the tourist trails.

The vegetation of our transects was heterogeneous and patchy. For our analysis, we recognized the following 4 habitat types; their relative occurrence along transect routes is reported in Table I:

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1. Deciduous forest: mainly mature miombo forest. Common species are *Brachystegia* spp. (Leguminosae), *Dalbergia* spp. (Papilionoideae), *Diplorhincus condylocarpon* (Apocynaceae), *Uapaca mitida* (Euphorbiaceae), and *Combretum* spp. (Combretaceae).

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**Table I.** Characteristics of four transects used for primate censuses in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania

Transect	Length of transect (km)	Altitude (m a.s.l.)	Gross forest type and portion along the line (km)
T1 (Camp Site 3)	4.0	350–800	Deciduous (0.8 km), semideciduous (0.6 km), open area (0.4 km), evergreen (2.2 km)
T2 (Mwanihana Trail)	4.0	320–590	Deciduous (1.4 km), semideciduous (0.4 km), evergreen (2.2 km)
T3 (Sanje Falls)	3.7	330–700	Mixed deciduous and semideciduous (0.8 km), evergreen (2.9 km)
T4 (Msolwa)	4.0	330–600	Mixed deciduous and semideciduous (1 km), evergreen (3 km)

- 122 2. Semideciduous forest: moderate to old-growth forest, transitional  
 123 between deciduous and evergreen. Common species are *Sorindeia*  
 124 *madagascariensis* (Anacardiaceae), *Combretum* spp. (Combretaceae)  
 125 *Ricinodendron heudelotii* (Euphorbiaceae), *Ficus* spp. (Moraceae),  
 126 and *Trema orientalis* (Ulmaceae).  
 127 3. Evergreen forest: the primary habitat type on the second and  
 128 higher altitude half of transects, mainly moderate to old-growth  
 129 forest. Common species are *Parinari excelsa* (Chrysobalanaceae),  
 130 *Macaranga* spp. (Euphorbiaceae), *Erythrophloeum suaveolens*  
 131 (Leguminosae), *Synsepalum cerasiferum* (Sapotaceae), *Sorindeia*  
 132 *madagascariensis* (Anacardiaceae), and *Parkia filicoidea* (Leguminosae).  
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 134 4. Open areas: ex-logging area within T1, now occupied by regenerat-  
 135 ing vegetation, mainly shrubs and scattered trees. Common species  
 136 are *Celtis gomphophylla* (Ulmaceae), *Albizia gummifera* (Leguminosae),  
 137 and *Trema orientalis* (Ulmaceae).

138 Ulrik Pedersen (UBP), Castro Magwila (CAS), Andrew Marshall  
 139 (ARM), Francesco Rovero (FR), and Arafat Mtui (ASM) collected data  
 140 between 1998 and 2003, during periods that were noncontinuous among  
 141 observers except for FR and ASM, who began data collection soon after  
 142 ASM. Details of sampling effort by each observer are contained in Table II:

**Table II.** Number of primate censuses conducted by each observer in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania

Observer	Period	Transect			
		T1	T2	T3	T4
UBP	August–October 1998	6	6	8	6
CAS	October 1999–February 2000	15	15	14	11
ARM	May–September 2001	5	5	6	—
FR	July 2002–January 2003	13	14	14	—
ASM	February–August 2003	14	14	13	—
All observers		53	54	55	17

143 ARM, FR, and ASM did not collect data along T4. The number of censuses  
 144 conducted per transect per mo varied from 1 to 4. We walked census lines  
 145 beginning at 0700–0730 h at an average speed of about 1 km h<sup>-1</sup>, record-  
 146 ing all sightings of primates. For each primate sighting we recorded time,  
 147 species, estimated number of individuals (when possible), distance from  
 148 the observer to the first individual seen, and position of the observer along  
 149 the transect. The estimated number of individuals is the number of indi-  
 150 viduals counted during a maximum of 10–15 min of observing each group.  
 151 TTS trained observers before the beginning of data collection to standard-  
 152 ize methods. TTS spent at least 2 d training each observer. We estimated  
 153 position on the transect by referring to numbered tags placed every 50 m  
 154 along the trails. We visually estimated distances, after training of observers  
 155 through calibration of estimation with actual measures obtained via a range  
 156 finder or a tape measure. Because data collection did not overlap among  
 157 observers, apart from FR and ASM, we could not test interobserver accu-  
 158 racy in estimated group distances. As further discussed later, interobserver  
 159 range and differences in estimated group distances should be tested in  
 future studies.

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### Data Analysis

162 We used the primate social group as the basic unit for data analy-  
 163 sis, and thus excluded counts of known or suspected solitary individuals  
 164 (Whitesides *et al.*, 1988). We computed sampling precision for each ob-  
 165 server and species as the 95% confidence limits of the mean number of  
 166 groups seen per km walked expressed as the percentage of the mean  
 167 (Struhsaker, 1981). We converted census data into encounter rate (ER:  
 168 number of groups seen per km walked), generally considered an index  
 169 of relative abundance (Seber, 1982). We tested differences in encounter  
 170 rates among transects (for each observer) and among observers (for each

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171 transect) for each species via Kruskal-Wallis tests and post hoc Mann-  
172 Whitney  $U$ -tests (Siegel and Castellan, 1989). We also used Kruskal-Wallis  
173 tests to compare ER among different species for each observer. We did not  
174 use parametric statistical tests because the data did not meet the assump-  
175 tions of normality and of equality of variances. Probability of all tests was  
176 2-tailed.

177 Following the standard approach on analysis of habitat use data (Neu  
178 *et al.*, 1974; see also Thomas, 1991 and Wallace *et al.*, 1998 for examples of  
179 application of this method to primates), we used  $\chi^2$  tests to compare the  
180 distribution of primate group sightings among different habitat types with  
181 that expected assuming no selection (i.e., proportional to the availability of  
182 habitat types along the transect routes). We pooled data for all observers to  
183 meet sample size requirements for the  $\chi^2$  test (Sokal and Rohlf, 1995). We  
184 computed an index of habitat selection (referred to as selection ratio) as  
185 the ratio between number of groups observed and expected for each habi-  
186 tat type. We further investigated the differences between habitat use and  
187 availability by computing Bonferroni confidence intervals on the propor-  
188 tion of groups observed for each habitat type and then comparing them  
189 with expected values based on habitat availability (Byers *et al.*, 1984). The  
190 following is the formula for computing confidence intervals:

$$p_i - z_{\alpha/2k}[p_i(1 - p_i)/n]^{1/2} < p_i < p_i + z_{\alpha/2k}[p_i(1 - p_i)/n]^{1/2}$$

191 where  $p_i$  is the proportion of locations in habitat type  $i$ ,  $z_{\alpha/2k}$  is the upper  
192 standard normal variate corresponding to the probability tail of  $\alpha/2k$ ,  $k$  is  
193 the number of habitat types, and  $n$  is the number of locations. This allows  
194 one to draw conclusions on primate habitat selectivity: when the interval  
195 of values of observed habitat use does not overlap with the expected use  
196 value a conclusion of selection or avoidance can be drawn (interval greater  
197 or smaller than the observed value, respectively). When the interval of ex-  
198 pected values overlaps with the observed use value, one cannot draw a con-  
199 clusion on selection or avoidance.

200 Interobserver consistency in estimated group distance could be  
201 checked only between FR and ASM, because the latter served as an as-  
202 sistant to FR (they walked census trails together but collected data inde-  
203 pendently during July–December 2002), and then censused primates alone  
204 during February–August 2003. We used Wilcoxon Signed Ranks test for  
205 related samples (Siegel and Castellan, 1989) to compare estimated group  
206 distances when censuses were walked simultaneously. We then used the  
207 2 data sets to estimate absolute density (groups/km<sup>2</sup>) by applying an em-  
208 pirical method that estimates the area sampled on the basis of maximum  
209 reliable observer to animal distance (Struhsaker, 1981), selected from the  
210 frequency distribution of sighting distances in 10 m classes via the 50%

211 rule (Chapman *et al.*, 2000), i.e., the distance estimate beyond which val-  
 212 ues decrease to half or more, or the cutoff distance. We preferred to  
 213 use the observer to animal distance rather than the perpendicular dis-  
 214 tance method (Struhsaker, 1981) because several studies comparing them  
 215 have shown that the former provides closer estimates to true densities of  
 216 forest-dwelling primates as derived from range-mapping studies (Chapman  
 217 *et al.*, 1988; DeFler and Pintor, 1985; Fashing and Cords, 2000; Struhsaker,  
 218 1981). Density is given by the ratio between number of sightings scored  
 219 within the truncated distance divided by the area censused (Struhsaker,  
 220 1981).

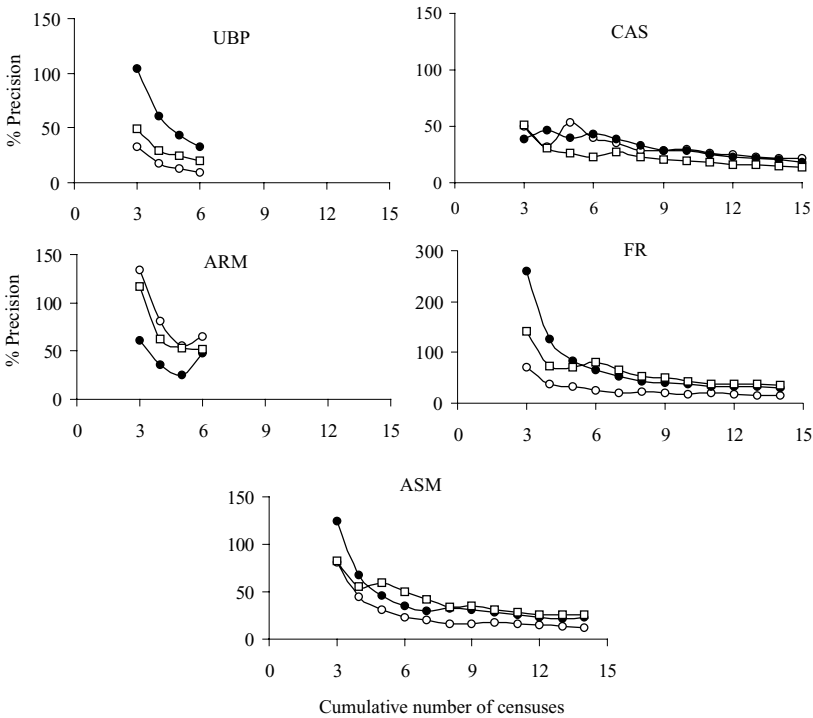
221 To evaluate the amplitude of interobserver variations in distance es-  
 222 timation, which reflects the width of the area sampled, we also tested dif-  
 223 ferences in estimated group distance among all observers (see Mitani *et al.*,  
 224 2000). We compared estimated group distances among observers via the  
 225 Kruskal-Wallis tests on both values and frequency distribution of values in  
 226 10 m-classes. Finally, we compared the primate sighting distances among  
 227 different habitat types to test the hypothesis that differential visibility could  
 228 exist in different forest types because of the density of vegetation. We used  
 229 the pooled data of FR and ASM, both because of the above-described con-  
 230 sistency in distance estimation and because their sampling covered 14 mo  
 231 and should, therefore, account for seasonal differences in visibility due to  
 232 leaf cover. We pooled all species in the comparison because of sample size  
 requirements.

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## RESULTS

235 The rank order of species by mean sighting frequency when all ob-  
 236 servers were pooled was, from highest to lowest: red colobus, Angolan  
 237 colobus, Sykes's monkey, baboon and mangabey (Table III). For any ob-  
 238 server, differences in ER among species were highly significant (Kruskal-  
 239 Wallis test,  $p < 0.001$  both for each transect and pooling data for all tran-  
 240 sects; see Table III). This pattern held for all observers except ARM when  
 241 we repeated the comparison using only the 3 species most frequently seen  
 242 ( $\chi^2 = 31.57$ ,  $p < 0.001$ ,  $\chi^2 = 14.20$ ,  $p < 0.05$ ,  $\chi^2 = 0.55$ ,  $p = 0.76$ ,  $\chi^2 = 26.16$ ,  
 243  $p < 0.001$ ,  $\chi^2 = 19.53$ ,  $p < 0.001$  for UBP, CAS, ARM, FR, and ASM,  
 244 respectively). Sampling precision profiles for the 3 species most fre-  
 245 quently seen are in Fig. 2. Data by CAS, FR, and ASM show asymp-  
 246 totic precision after 12–15 censuses. UBP reached comparable levels of  
 247 high precision after only 6 censuses. UBP did not conduct further cen-  
 248 suses; therefore, the validity of this trend cannot be assessed. A com-  
 249 parison of the curves for different species among observers reveals no  
 250 consistent pattern except for data FR and ASM collected that show

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**Fig. 2.** Sampling precision of relative abundance data plotted against cumulative number of census repetitions for the 3 most frequently seen species (red colobus, open circles; Angolan colobus, closed circles; Sykes’s monkey, open squares) during censuses conducted in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania. Precision is indicated by 95% confidence limits of the mean number of groups seen per km walked and expressed as the percentage of the mean. The lower this ratio, the higher the precision of the sample.

251 greater precision for the red colobus, i.e., the most frequently seen  
 252 species.

253 Differences in ER among transects did not reveal a consistent pattern  
 254 among observers (see details in Table III and Appendix 1). In spite of dif-  
 255 ferences recorded across transects by each observer, most of the interob-  
 256 server variations in relative abundance of each species were not significant  
 257 (Table IV). The few exceptions are related to single transects and discor-  
 258 dance of one observer from the others (see test outcome of post-hoc com-  
 259 parisons in Table IV), notably: ARM recorded significantly more Angolan  
 260 colobus along T2 than other observers, UB recorded more red colobus  
 261 along T2 than other observers (weakly significant differences), and CAS  
 262 recorded significantly more Sykes’s monkeys along T2.

**Table III.** Mean encounter rate (ER, groups/km walked) and standard deviation per each primate species and observer from censuses conducted along three transects in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania

Species	Observer					
	UBP	CAS	ARM	FR	ASM	ALL
<i>Procolobus gordonorum</i>	0.74 ± 0.25 (0.93) <sup>a</sup>	0.49 ± 0.22 (0.17) <sup>a</sup>	0.51 ± 0.37 (0.86)	0.61 ± 0.29 (≤ 0.05)	0.60 ± 0.21 (≤ 0.01)	0.59 ± 0.27
<i>Colobus angolensis</i>	0.4 ± 0.23 (0.87) <sup>a</sup>	0.33 ± 0.21 (0.74) <sup>a</sup>	0.54 ± 0.25 (0.06)	0.41 ± 0.34 (0.81)	0.44 ± 0.27 (≤ 0.03)	0.43 ± 0.26
<i>Cercopithecus mitis</i>	0.2 ± 0.25 (0.97) <sup>a</sup>	0.40 ± 0.22 (≤ 0.05) <sup>a</sup>	0.40 ± 0.34 (0.65)	0.27 ± 0.21 (≤ 0.05)	0.33 ± 0.23 (0.77)	0.35 ± 0.25
<i>Cercocebus galeritus sanjei</i>	0.7 ± 0.08 (0.09) <sup>a</sup>	0.17 ± 0.16 (≤ 0.01)	0.03 ± 0.04 (0.17)	0.03 ± 0.11 (0.51)	0.10 ± 0.15 (0.80)	0.08 ± 0.11
<i>Papio cynocephalus</i>	0.3 ± 0.19 (0.16) <sup>a</sup>	0.14 ± 0.14 (0.13) <sup>a</sup>	0.08 ± 0.12 (0.27)	0.10 ± 0.16 (0.19)	0.08 ± 0.11 (0.15)	0.12 ± 0.14
Among-species comparison	67.56 <0.001	81.27 <0.001	40.31 <0.001	100.32 <0.001	104.6 <0.001	
$\chi^2$						
<i>p</i>						

*Note.* In parentheses, Kruskal-Wallis test outcome (*p* value) for differences among transects in ER recorded by each observer. Statistically significant results (*p* < 0.05) are underlined (see Appendix 1 for ER values of each transect). In the last column, mean ER values and standard deviation for all observers are shown. In the last row, Kruskal-Wallis test outcome ( $\chi^2$  and *p* value) of differences in ER among species for each observer.

<sup>a</sup>Not significant when excluding T4 from comparisons, which only UBPP and CAS walked for censuses.

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**Table IV.** Test outcome ( $\chi^2$  and  $p$  values) from Kruskal-Wallis tests on differences in encounter rate (groups/km walked), per each transect and species, among five observers that conducted primate censuses in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania

Species	Transect							
	T1		T2		T3		T4	
	$\chi^2$	$p$	$\chi^2$	$p$	$\chi^2$	$p$	$U$	$p$
<i>Procolobus gordonorum</i>	4.59	0.33	8.70	0.40	15.95	<0.01 <sup>d</sup>	7	<0.01
<i>Colobus angolensis</i>	3.27	0.51	13.31	0.02 <sup>a</sup>	6.23	0.18	22.5	0.23
<i>Cercopithecus mitis</i>	7.07	0.13	14.44	0.01 <sup>b</sup>	0.85	0.93	25	0.35
<i>Cercocebus galeritus sanjei</i>	7.25	0.12	12.45	0.02 <sup>c</sup>	6.28	0.18	22.5	0.24
<i>Papio cynocephalus</i>	9.16	0.06	8.96	0.06	6.93	0.14	29	0.65

Note. Comparisons for T4 are made by using Mann-Whitney  $U$ -tests between two observers.

<sup>a</sup>Kruskal-Wallis test:  $p = 0.13$  when ARM is excluded.

<sup>b</sup>Kruskal-Wallis test:  $p = 0.42$  when CAS is excluded.

<sup>c</sup>Kruskal-Wallis test:  $p = 0.10$  when CAS is excluded.

<sup>d</sup>Kruskal-Wallis test:  $p = 0.07$  when ASM is excluded.

263 The distributions of primate sightings per gross habitat type are in  
 264 Table V as selection ratios; data for the mangabeys are not shown, be-  
 265 cause we did not see mangabeys frequently enough for this analysis. Anal-  
 266 ysis of the goodness-of-fit of observed vs expected use shows that most dif-  
 267 ferences were for baboons ( $p$  significant for all the transects), followed by  
 268 Sykes’s, Angolan colobus ( $p$  significant for T1 and T3), and red colobus  
 269 ( $p$  significant for T1 and marginally nonsignificant for T3). Conclusions on  
 270 selection or avoidance for each habitat type indicate that baboons select  
 271 deciduous forest and avoid the evergreen forest; Sykes’s select semidecid-  
 272 uous forest in T1 and T3 (no conclusion for T2) and avoid evergreen for-  
 273 est; Angolan colobus select evergreen forest and avoid deciduous forest in  
 274 T1 and T2, while the occurrence of red colobus did not allow for conclu-  
 275 sions apart from T1 where they select semideciduous forest and avoid open  
 276 areas.

277 Estimated group distances varied considerably among observers (mean  
 278 and standard deviation pooling all species and transects and excluding val-  
 279 ues greater than 100 m:  $45 \pm 32$ ;  $28 \pm 16$ ;  $34 \pm 17$ ;  $37 \pm 19$ ;  $36 \pm 17$  m for  
 280 UBP, CAS, ARM, FR and ASM, respectively;  $\chi^2 = 130.6$ ,  $p < 0.001$ ). The  
 281 maximum distance recorded varied from 90 to 400 m; however 90% of  
 282 the values were within 100 m. Differences were also significant for dis-  
 283 tance values  $>100$  m ( $\chi^2 = 170.6$ ,  $p < 0.001$  all species pooled). Most discor-  
 284 dance resulted from distance estimate differences between UBP and CAS  
 285 than from differences among the other three observers (ARM, FR, and  
 286 ASM), for which differences were weakly significant ( $\chi^2 = 3.70$ ,  $p = 0.054$ ).  
 287 In spite of these differences, when comparisons are made among frequency

**Table V.** Habitat selection ratios (number of observed groups/expected per habitat type) for each transect and primate species (indicated with initials of Latin name) from census data collected in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania ~~type~~

Habitat type	Transect 1			Transect 2			Transect 3					
	<i>P.g.<sup>a</sup></i>	<i>C.a.<sup>b</sup></i>	<i>C.m.<sup>c</sup></i>	<i>P.c.<sup>d</sup></i>	<i>P.g.</i>	<i>C.a.</i>	<i>C.m.</i>	<i>P.c.</i>	<i>P.g.</i>	<i>C.a.</i>	<i>C.m.</i>	<i>P.c.</i>
Deciduous	0.83 (nc)	0.42 (avoid)	1.08 (nc)	4.52 (pref.)	0.89 (nc)	0.48 (avoid)	1.17 (nc)	2.59 (pref.)				
Semi-deciduous	1.86 (pref.)	1.29 (nc)	2.15 (pref.)	0.65 (avoid)	1.04 (nc)	0.89 (nc)	1.96 (nc)	0.47 (nc)	1.42 (nc)	1	2.57 (pref.)	4.35 (pref.)
Evergreen	1.48 (nc)	2.05 (pref.)	1.69 (nc)	0 (—)	1.06 (nc)	1.35 (pref.)	0.71 (avoid)	0.08 (avoid)	0.88 (nc)	1	0.57 (avoid)	0.08 (avoid)
Open areas	0.74 (avoid)	0.94 (nc)	0.53 (avoid)	0 (—)								
Chi-squared	8.16	8.08	10.08	34.76	0.33	8.67	3.20	29.9	3.24	0	16.83	17.48
<i>P</i>	<0.05	<0.05	<0.02	<0.001	0.85	<0.02	0.20	<0.001	0.07	1	<0.001	<0.001

Note. In parentheses, conclusion on preference (pref.), avoidance (avoid) or no conclusion (nc) from Bonferroni analysis of observed use (see text). In the last row,  $\chi^2$  and *p* values from goodness-of-fit tests of observed versus expected distributions of primate groups per habitat.

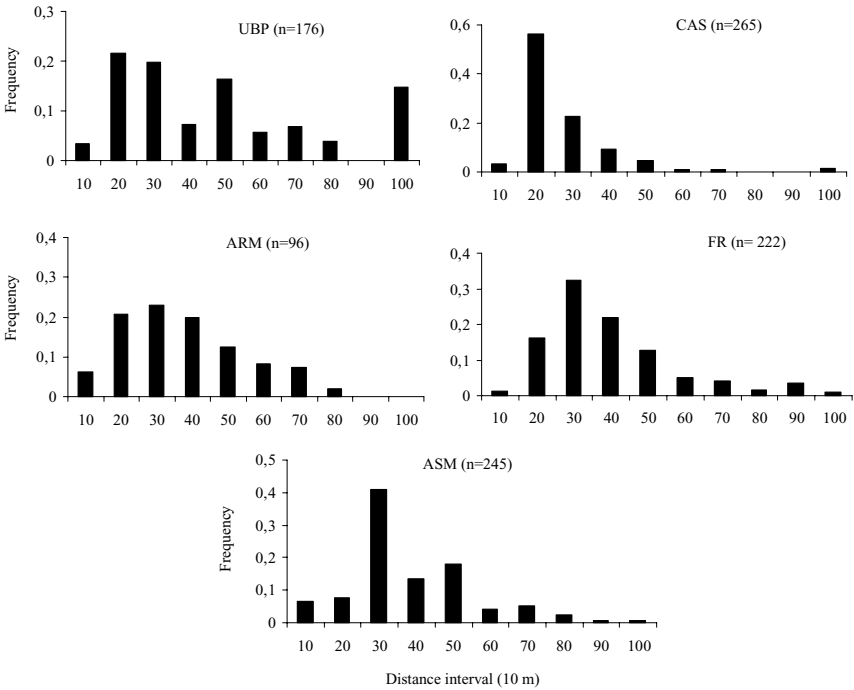
<sup>a</sup> *Procolobus gordonorum*.

<sup>b</sup> *Colobus angolensis*.

<sup>c</sup> *Cercopithecus mitis*.

<sup>d</sup> *Papio cynocephalus*.

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**Fig. 3.** Frequency distribution of primate group sighting distances (10-m intervals), pooling data for all primate species, from line transect censuses conducted in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania.

288 distributions of distance values in 10 m-classes (Fig. 3), there are no ma-  
 289 jor variations (Kruskal-Wallis test:  $\chi^2 = 2.57, p = 0.63$ ). This applies also  
 290 to comparisons made on the 3 most frequently seen species (Kruskal-  
 291 Wallis tests:  $\chi^2 = 0.82, p = 0.94, \chi^2 = 0.84, p = 0.93, \chi^2 = 0.41, p = 0.98$  for  
 292 red colobus, Angolan colobus, and Sykes’s monkey, respectively). In other  
 293 words, within a variation of 10 m in estimated group distance among ob-  
 294 servers, the sighting curves were generally similar. Comparisons of distance  
 295 values by species revealed that, for any observer, sighting distance was  
 296 slightly higher for red colobus (mean and standard deviation pooling all  
 297 observer  $38 \pm 3$  m, excluding values  $>100$  m) than Angolan colobus and  
 298 Sykes’s monkey ( $34 \pm 3$  and  $33 \pm 7$  m, respectively; Krusal-Wallis test pooling  
 299 all observer:  $\chi^2 = 26.48, p < 0.001$ ), possibly because red colobus groups  
 300 are larger and noiser.

301 Distance estimates that FR and ASM recorded during 7 censuses con-  
 302 ducted simultaneously over 4 mo (we did not use data for the first 3 mo for

**Table VI.** Mean and standard deviation (sd) of distance estimates of primate group sightings (all species pooled) by habitat type (FR and ASM data only) from censuses conducted in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania

Habitat type	T1		T2		T3	
	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD
Deciduous	23	41 ± 22	36	33 ± 13		
Semideciduous	28	37 ± 20	15	31 ± 15	50	29 ± 15 <sup>a</sup>
Open areas	15	57 ± 27	—	—	—	—
Evergreen	86	37 ± 19	89	37 ± 14	110	37 ± 16
Test outcome ( <i>p</i> value)		<0.05 <sup>b</sup>		0.19		<0.05

Note. Test outcome of comparisons among habitat types is also shown (see text for details)

<sup>a</sup>Mixed deciduous and semideciduous.

<sup>b</sup>*p* = 0.55 when the category open areas is excluded.

303 this comparisons to account for potential differences in learning between  
 304 observers) were similar for red colobus and Angolan colobus (Wilcoxon  
 305 Signed-Ranks test:  $\chi^2 = -0.97, p = 0.33, \chi^2 = -0.67, p = 0.50$ ) while they  
 306 differed for Sykes's ( $\chi^2 = -2.39, p < 0.02$ ). We computed density ~~computed~~  
 307 only for *Procolobus gordonorum* because of adequate sample size, i.e., at  
 308 least 20 group sightings recorded per each transect and observer within the  
 309 cutoff distance (Peres, 1999). The cutoff distance was 50 m for both FR and  
 310 ASM, and mean density estimates per transect vary from 3.8 to 6.9 groups  
 311 per km<sup>2</sup> (see Appendix 1 for all values). Density estimates from data by FR  
 312 and ASM were similar (Mann-Whitney *U*-test:  $U = 756, p = 0.98$ ). Analysis  
 313 of sighting distance values of primate groups by habitat type (data by FR  
 314 and ASM only, Table VI) shows that while there was consistency across  
 315 transects in sighting distance in evergreen forest (mean of 37 m for all tran-  
 316 sects), there was more variation for the other habitat types (e.g., mean of  
 317 41 m in the deciduous forest of T1 vs 33 m in T2 and 29 m in the mixed  
 318 deciduous and semideciduous forest of T3). Overall, variations per habi-  
 319 tat type were significant for T1 (Kruskall-Wallis test:  $\chi^2 = 8.88, p < 0.05$ ,  
 320 but  $\chi^2 = 0.55, p = 0.76$  when the open areas habitat is excluded from analy-  
 321 sis), nonsignificant for T2 ( $\chi^2 = 3.31, p = 0.19$ ) and significant for T3 (Mann-  
 322 Whitney *U*-test:  $U = 1865, p < 0.05$ ).

323

## DISCUSSION

### 324 Methodological Implications of Comparing Results Among Observers

325 One of the most important contributions of this study is that it im-  
 326 proves our understanding of how variations among observers should be

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327 analyzed and interpreted to derive a reliable approximation of primate  
328 abundance. This in turn will be important to the design of future moni-  
329 toring programs. Census data that consist of several subsamples create a set  
330 of problems that apply to many monitoring programs (Mitani *et al.*, 2000;  
331 Struhsaker, 2002). Estimation of precision provides an indication of the  
332 reliability of the samples. Interestingly, the number of census repetitions  
333 necessary to obtain high levels of precision of abundance estimates is  
334 similar to that reported for Kibale National Park, Uganda (Mitani *et al.*,  
335 2000), where precision reached its highest levels after 12–16 census walks  
336 for the most frequently seen species. A similar number of census walks  
337 were necessary to achieve nearly stable density estimates for the 3 most  
338 common species in a primate community in Kakamega Forest, Kenya  
339 (Fashing and Cords, 2000). Comparing census results among different ob-  
340 servers indicates that variations are fairly moderate, as cases of signifi-  
341 cant differences were due to discordance of 1 data set from the other 4.  
342 Such cases of discordance are difficult to explain because they do not al-  
343 ways involve the same observer, as we would expect if there was incon-  
344 sistency in census methods by a particular observer. Moreover, we saw no  
345 temporal trends, with the partial exception of red colobus along T2 that  
346 was sighted relatively more by UBP in 1998 than by some of the subse-  
347 quent observers, even though differences among all observers were not  
348 significant.

349 In agreement with Mitani *et al.* (2000), we found marked differences  
350 among observers in estimated distances of primate sightings. The great vari-  
351 ation in the maximum distance at which we recorded primates is proba-  
352 bly due to the uneven topography of the study area. On certain parts of  
353 transects, we recorded primate groups across valleys on distant slopes and  
354 ridges. Brugière and Fleury (2000) reported similar topographic effects on  
355 primate censuses in mountainous areas of Gabon. It is notable, however, and  
356 in contrast with Mitani *et al.* (2000), that the frequency distribution of esti-  
357 mated distances in 10 m classes did not differ significantly among observers.  
358 This indicates that relative abundance data can be compared among ob-  
359 servers with some degree of confidence. However, because most observers  
360 collected data in different time periods, there is the very unlikely chance  
361 that differences in mean estimated distances are due to differences in pri-  
362 mate distances from the trail over time rather than to interobserver dif-  
363 ferences in accuracy/ability. Differences in estimated distance remain an  
364 underlying, potential source of variance in the results that cannot be sep-  
365 arated from other sources of variance (e.g. interannual and intraannual),  
366 rendering problematic the recognition of real population trends. The data  
367 FR and ASM collected are a good example of interobserver consistency.  
368 Standardizing data collection methods, including simultaneous training

370  
369 and practice of census walks, is clearly important (Defler and Pintor,  
1985).

371 **Differences Among Species and Comparison**  
372 **with Other Primate Communities**

373 Researchers have reported greater relative abundance of colobines  
374 than of other primates for other communities in Africa (e.g., at Kibale,  
375 Uganda; Struhsaker, 1997 and see later). Fashing and Cords (2000) pro-  
376 vide evidence that total colobine biomass explains the variation in to-  
377 tal primate biomass at 10 Guineo-Congolian rainforest sites. Davies  
378 (1994) suggests that folivorous primates generally achieve higher abun-  
379 dances than frugivorous primates in tropical forests in Africa because  
380 of their ability to eat leaves, especially mature leaves, which allows  
381 them to sustain large populations even during periods of seasonal food  
382 scarcity.

383 Detailed comparisons of our census results with those for other pri-  
384 mate communities are best made with geographically close communities  
385 for which comparable data are available (Table VII). Data from unlogged  
386 compartments in Kibale, Uganda (Chapman *et al.*, 2000; Mitani *et al.*,  
387 2000; Struhsaker, 1975, 1997) indicate that the range of variations in re-  
388 lative abundance of red colobus overlap with Mwanihana Forest. Results  
389 for Sykes’s monkey and mangabeys in Mwanihana Forest are well within  
390 the range of variation for their taxonomic counterparts in Kibale (*Cerco-*  
391 *pithecus mitis stuhlmanni* and *Lophocebus albigena*). In contrast, Angolan  
392 colobus and baboons seem more abundant in Mwanihana Forest than their  
393 taxonomic counterparts from unlogged forest in Kibale (*Colobus guereza*

**Table VII.** Relative abundance data (number of groups seen per km walked) from different forests in the Udzungwa Mountains of Tanzania and elsewhere in Africa

	Udzungwa Mountains			Kibale (unlogged forest) <sup>d</sup>	Kakamega Forest <sup>e</sup>
	UMNP <sup>a</sup>	WKS <sup>b</sup>	NDU <sup>c</sup>		
Red colobus	0.49–0.74	0.45	0.24	0.3–1.06	
Black and white colobus	0.33–0.54	0.52	0.16	0.03–0.23	1.20
Sykes’s and blue monkey	0.27–0.40	0.33	0.15	0.01–0.44	0.74
Mangabey	0.03–0.17			0.03–0.23	
Baboon	0.08–0.23			0.08–0.09	

<sup>a</sup>Present study (mean for all transects, range for different observers).

<sup>b</sup>West Kilombero Scarp Forest Reserve (Marshall *et al.*, *in press*).

<sup>c</sup>New Dabaga-Ulangambi Forest Reserve (Marshall *et al.*, *in press*).

<sup>d</sup>Means of data from 1970–1972, 1974–1976, 1980–1981, 1996–1997, and 1997–1998 (Struhsaker *et al.*, 1997; Chapman *et al.*, 2000; Mitani *et al.*, 2000).

<sup>e</sup>Fashing and Cords (2000).

A6

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394 and *Papio anubis*). We stress, however, that comparisons might be biased  
395 by the fact that visibility in Mwanihana Forest is probably greater than at  
396 Kibale because of the mountainous terrain that allows long-distance view-  
397 ing. Also, the extent of deciduous forest is greater in Mwanihana For-  
398 est. Data for Kakamega Forest (Fashing and Cords, 2000) indicate lower  
399 primate diversity, but greater abundance of *Colobus guereza* and *Cerco-*  
400 *pithecus mitis* compared to their taxonomic counterparts in Mwanihana  
401 Forest.

402 Our relatively low sighting rates of baboons is clearly related to their  
403 almost exclusive occurrence in the deciduous forest, which comprises only  
404 one fifth of the transect length. Conversely, we observed mangabeys in dif-  
405 ferent habitat types and especially in evergreen forest, but very rarely in  
406 comparison to other species. As such, alternative methods such as range  
407 mapping of habituated groups might be required to determine their abun-  
408 dance (see also Ehardt *et al.*, [in press](#)). The shyness of this species, often A7  
409 moving on the ground in dense vegetation, probably contributes to the in-  
410 frequent sightings (T. Jones, pers. comm.). Differences in the ease of de-  
411 tection might also account for some of the variation among the 3 most  
412 sighted species. An important variable in this regard is group size: it is  
413 much larger for red colobus (mean of 40 individuals for Mwanihana For-  
414 est, Struhsaker *et al.*, 2004) than Angolan colobus (range 2–12, present  
415 study) and Sykes’s monkey (range 2–14, present study). Our slightly differ-  
416 ent estimated sighting distances of groups among the 3 species may reflect  
417 group size differences. Generally, distances were greater for red colobus  
418 than for Angolan colobus and Sykes’s monkeys. Similarly, the cutoff value  
419 in the frequency distribution of sighting distance was 50 m for red colobus  
420 and 30–40 m for Angolan colobus and Sykes’s monkeys (data by FR and  
421 ASM).

422 Marshall *et al.* ([in press](#)) reported primate abundance data from other A8  
423 forests of the Udzungwa Mountains, in higher elevation forests on the  
424 northwestern side of the mountainous range that present various levels  
425 of habitat alteration due to past logging and current human encroach-  
426 ment. The relative abundances of Angolan colobus and Sykes’s monkey for  
427 Ndundulu Forest, a large and relatively undisturbed forest block located  
428 outside the western border of UMNP, are broadly within the range ob-  
429 served in Mwanihana Forest, while the abundance of red colobus appears  
430 higher in Mwanihana Forest (Table VII). In contrast, primate abundance  
431 in Mwanihana Forest is much higher than in the highly encroached and  
432 degraded New Dabaga/Ulangambi, an isolated forest block. Numerous re-  
433 searchers have reported similar negative effects of habitat degradation, iso-  
434 lation, and hunting on primate populations (Cowlshaw and Dunbar, 2000;  
435 Skorupa, 1986, 1988; Struhsaker, 1975, 1997).

436  
437**Patterns of Variation in Relative Abundance  
Within and Among Transects**

438 The habitat use pattern is clear for baboons and Sykes's monkeys, as  
439 they prefer deciduous and semideciduous habitats, respectively. A distinct  
440 characteristic of the semideciduous habitat is its relatively high floristic di-  
441 versity (F. Rovero, unpublished data). The habitat use pattern is less clear  
442 for the colobines, but the species showed some habitat selection in T1 and  
443 T2, where there is more habitat variability than in T3. Habitat type does  
444 not seem to affect primate detection to a large extent, because mean values  
445 vary by  $\leq 8$  m among habitats, with the exception of the large open area  
446 in T1. Wallace *et al.* (1998) reported similar results from northeastern Bo-  
447 livia: the authors found no significant differences for each species in sighting  
448 distances across a variety of diverse habitats spanning from semideciduous  
449 forest to gallery forest and mature forest.

450 The variations in primate abundance among transect lines are likely  
451 related to the differential occurrence of habitat types. That we generally  
452 recorded fewer baboons and more mangabeys at T3 than at T1 and T2  
453 might reflect the small proportion of deciduous versus evergreen forest  
454 along T3. Moreover, an inverse relationship between abundance of the 2  
455 species may reflect greater competition for food due to greater dietary over-  
456 lap, as the 2 species belong to the same tribe (Cercopithecini) and both spend  
457 time foraging on the ground. The variation in abundance among transects  
458 recorded for the other species is difficult to explain because there is no con-  
459 sistent pattern among observers. Longer, more continuous sampling would  
460 be required to properly assess variations in species' abundance among  
461 transects.

462 Similarly, more data are needed to understand patterns of seasonal  
463 variations in relative abundance. Early qualitative observations suggested  
464 seasonal use of deciduous areas by the colobines and mangabeys, possi-  
465 bly related to tree flushing at the beginning of the rainy season. Data  
466 FR collected show no statistical differences in relative abundance of any  
467 species when results from different periods are compared (July–August,  
468 September–October and November–January, corresponding to post-rain,  
469 dry, and rainy periods, respectively), but greater variation is found at T1  
470 and T2, which have a greater presence of deciduous forest. Similar evidence  
471 comes from comparing relative abundance across different seasons when  
472 the analysis is applied only to deciduous portions of T1 and T2, with sight-  
473 ing frequency generally lower during the dry season (July–August) than  
474 during the wet season (November–February), which indicates the need for  
475 further, more intensive sampling. Thus, the mean ER of red colobus, pool-  
476 ing data for FR and ASM, was 0.33 vs 0.88 for T1 and 0.17 vs 0.25 for T2,

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477 during dry and wet season, respectively. Differences for T1 are weakly sig-  
478 nificant (Mann-Whitney *U*-test:  $U = 2, p = 0.12$ ). No evident trend emerged  
479 for Angolan colobus, mean ER being 0.13 vs 0.38 for T1 and 0.25 vs 0.17 for  
480 T2, during the dry and wet season, respectively.

**Density Estimation of the Udzungwa Red Colobus**

482 Pooling density estimations from data FR and ASM collected  
483 gives mean estimates that were similar for T1 and T2 ( $4.9 \pm 2.8$  and  
484  $4.4 \pm 2.3$  groups/km<sup>2</sup>, respectively) and higher for T3 ( $6.0 \pm 2.7$  groups/  
485 km<sup>2</sup>), with the differences among transects being significant (Kruskal-  
486 Wallis test:  $\chi^2 = 12.24, p < 0.01$  and Mann-Whitney *U*-test between T1 and  
487 T2:  $U = 302, p = 0.49$ ). We derived estimates in the range of 3–4 groups/km<sup>2</sup>  
488 from preliminary information on ranging patterns of red colobus groups  
489 from an area of mixed deciduous and evergreen, secondary forest at  
490 about 350 m a.s.l., between T1 and T2 (F. Rovero, unpublished data; K.  
491 Detwiler, pers. comm.). We used a mean group size of 40.7 individuals for  
492 Mwanihana Forest for red colobus (Struhsaker *et al.*, 2004) that yielded  
493 a crude density estimate of 180–245 red colobus per km<sup>2</sup> in the low to  
494 medium altitude forests of Mwanihana Forest. We cannot make direct com-  
495 parisons with data from Marshall *et al.* (~~in press~~) because densities are A9  
496 not estimated in the latter study. However, both the lower relative abun-  
497 dance and smaller group size of red colobus (22.5 for Ndundulu and 11.8  
498 for New Dabaga/Ulangambi) recorded at the 2 higher elevation forests  
499 (Marshall *et al.*, ~~in press~~) suggest that individual density is lower at higher A10  
500 elevations than in the low to medium altitude forests of Mwanihana Forest.  
501 This supports an earlier conclusion that the Udzungwa red colobus achieves  
502 highest densities in large blocks of mature, mixed evergreen, and semide-  
503 ciduous forests at low to medium altitudes and that densities are adversely  
504 affected by human-induced forest degradation (Struhsaker *et al.*, 2004).

**CONCLUSIONS, RECOMMENDATIONS,  
AND FURTHER WORK**

505  
506  
507 Our data from medium-term censuses of diurnal primates in one of  
508 the largest forest blocks of the Udzungwa Mountains provide reliable  
509 approximations of relative abundance, thus allowing for comparisons of  
510 results among species and sites. Field training of local assistants in cen-  
511 sus techniques (Ehardt *et al.*, 1999), coupled with simultaneous practice of  
512 census walks, are essential to the collection of reliable data for long-term  
513 monitoring of populations. With adequate training and frequent evalua-  
514 tions of interobserver consistency, the line transect census appears to be

515 a valid method for assessing abundance of forest-dwelling primates. The  
 516 method is usually less costly and time consuming than alternative meth-  
 517 ods such as long-term, focal-group studies of ranging patterns (Brockelman  
 518 and Ali, 1987; Skorupa, 1987; Struhsaker, 1981; Whitesides *et al.*, 1988).

519 Sightings of Sanje mangabeys were too infrequent to give reliable es-  
 520 timates of abundance, and therefore we could not adequately assess their  
 521 population. Moreover, the great habitat heterogeneity of Mwanihana For-  
 522 est requires that a wider range of habitat types and altitudes be sampled to  
 523 adequately extrapolate primate population abundances to the whole forest.  
 524 Data from higher altitudes are particularly necessary, because data from  
 525 other Udzungwa forests and preliminary surveys in Mwanihana indicate  
 526 decreasing density of some species, particularly the red colobus, at higher  
 527 altitudes. Similarly, the qualitative evidence provided here of seasonal use  
 528 of deciduous habitats by some species requires more study. Finally, con-  
 529 tinued monitoring is needed to assess the effect on primates of National  
 530 Park management, primarily the firewood collection in the lower 1–2 km of  
 531 Mwanihana Forest. Firewood collection has continued since the establish-  
 532 ment of the National Park in 1992 and human encroachment was probably  
 533 heavier before (Rodgers and Homewood, 1982). The practice most likely  
 534 has negative impacts on ground foraging primates such as Sanje mangabeys  
 535 and baboons because they frequently forage for invertebrates in and under  
 536 fallen tree branches and trunks.

APPENDIX

**Table A1.** Encounter rate (ER) values (mean and standard deviation primate group sightings per km walked) for each observer and transect (T1–T4) from censuses conducted in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania.

Species	Observer	T1	T2	T3	T4	
<i>Procolobus gordonorum</i>	UBP	0.71 ± 0.10	0.75 ± 0.45	0.75 ± 0.23	0.75 ± 0.22	
	CAS	0.53 ± 0.30	0.48 ± 0.22	0.55 ± 0.13	0.39 ± 0.17	
	ARM	0.50 ± 0.35	0.45 ± 0.37	0.58 ± 0.38		
	FR	0.68 ± 0.39	0.46 ± 0.22	0.68 ± 0.25		
	ASM		5.4 ± 3.4 (28)	3.8 ± 2.7 (21)	4.8 ± 2.6 (25)	
			0.5 ± 0.2	0.52 ± 0.23	0.79 ± 0.21	
<i>Colobus angolensis</i>		4.1 ± 2.3 (23)	4.5 ± 2.2 (25)	6.9 ± 2.8 (33)		
	UBP	0.46 ± 0.43	0.42 ± 0.13	0.47 ± 0.16	0.42 ± 0.20	
	CAS	0.35 ± 0.21	0.27 ± 0.22	0.36 ± 0.21	0.32 ± 0.20	
	ARM	0.30 ± 0.21	0.85 ± 0.34	0.46 ± 0.19		
	FR	0.39 ± 0.42	0.50 ± 0.35	0.35 ± 0.25		
	ASM	0.50 ± 0.22	0.27 ± 0.23	0.54 ± 0.35		

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**Table A1.** Continued.

Species	Observer	T1	T2	T3	T4
<i>Cercopithecus mitis</i>	UBP	0.33 ± 0.26	0.29 ± 0.29	0.34 ± 0.3	0.33 ± 0.13
	CAS	0.38 ± 0.19	0.57 ± 0.31	0.38 ± 0.16	0.27 ± 0.21
	ARM	0.45 ± 0.27	0.30 ± 0.41	0.46 ± 0.33	
	FR	0.24 ± 0.27	0.18 ± 0.01	0.39 ± 0.35	
	ASM	0.38 ± 0.24	0.3 ± 0.17	0.31 ± 0.29	
<i>Cercocebus galeritus sanjei</i>	UBP	0	0	0.13 ± 0.19	0.13 ± 0.14
	CAS	0.03 ± 0.09	0.22 ± 0.23	0.23 ± 0.21	0.23 ± 0.18
	ARM	0	0	0.08 ± 0.13	
	FR	0.03 ± 0.10	0.01 ± 0.11	0.06 ± 0.12	
	ASM	0.11 ± 0.16	0.11 ± 0.13	0.08 ± 0.17	
<i>Papio cynocephalus</i>	UBP	0.29 ± 0.1	0.33 ± 0.26	0.13 ± 0.19	0.17 ± 0.2
	CAS	0.10 ± 0.13	0.22 ± 0.16	0.11 ± 0.13	0.11 ± 0.13
	ARM	0.15 ± 0.14	0.05 ± 0.11	0.04 ± 0.1	
	FR	0.14 ± 0.19	0.13 ± 0.21	0.02 ± 0.07	
	ASM	0.09 ± 0.12	0.13 ± 0.13	0.02 ± 0.07	

Note. Density estimates (groups/km<sup>2</sup>) for *Procolobus gordonorum* are computed using data by FR and ASM only and are given in *Italic* (in parenthesis is the number of groups used for computing the estimate).

538

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