VIVAMUS

Abundance of Diurnal Primates in Mwanihana Forest, Udzungwa Mountains, Tanzania: A Multi-Observer Comparison of Line-Transect Data

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Many individual researchers have used line transect counts to estimate forest primate abundance. They have devoted less attention to the interpretation of line transect data obtained by several observers, as is often the case in long-term monitoring programs. We present primate relative abundance data that 5 observers collected over 6 yr (not continuous) along 4 different transects each 4 km long in the Mwanihana Forest, Udzungwa Mountains National Park, Tanzania. Total distance walked during transect repetitions is ca. *700 km. The species we saw most frequently was the endemic Udzungwa red colobus* Procolobus gordonorum *(mean 0.59 groups/km walked), followed by the Angolan black-and-white colobus* Colobus angolensis *(0.43 groups/km) and Sykes's monkey* Cercopithecus mitis *(0.35 groups/km). We sighted the endemic Sanje mangabey* Cercocebus galeritus sanjei *and the yellow baboon* Papio cynocephalus *infrequently, the latter being confined to the deciduous forest parts of the transects.*

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We analyzed sighting frequency by gross habitat type, transect, season, and observer. Interobserver differences in the relative abundance of each species were moderate and the few cases of significant variations were due to discordance of only 1 observer from the others. Estimated distances of primate group sightings differ significantly among observers, thus preventing us from deriving estimates of absolute density. Frequency distributions of distance-class intervals are not significantly different among observers, which may indicate gross interobserver consistency in the width of the area sampled. We conclude that unless consistency in data collection is checked, as we did for 2 observers who collected data simultaneously, potential interobserver differences remain an underlying source of variance in the results that cannot be separated from other sources of variance.

INTRODUCTION

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

The Udzungwa Mountains of south-central Tanzania are one of the most important sites in East Africa for primate conservation, primarily because of the presence of the endemic, IUCN-Vulnerable Udzungwa red colobus (*Procolobus gordonorum*) and the endemic, IUCN-Endangered Sanje mangabey (*Cercocebus galeritus sanjei*, Ehardt, 2001; Homewood and Rodgers, 1981; IUCN 2003; Struhsaker and Leland, 1980). With an overall area of 10,000 km² (centered on 8°20′S, 35°50′E), the Udzungwa Mountains are the southernmost and largest block of the Eastern Arc Mountains,

which are part of a biodiversity hotspot of global importance for conservation (Burgess *et al.*, 1998; Myers *et al.*, 2000; Rodgers and Homewood, 1982). The Udzungwa Mountains, in particular, are characterized by a great altitudinal range of forest cover (300–2600 m a.s.l.) that includes habitats ranging from lowland deciduous forest to montane evergreen forest, as well as many areas of exploited and degraded forest and grassland (Dinesen *et al.*, 2001; Marshall *et al.*, 2005; Struhsaker *et al.*, 2004).

Information on population abundance of the Udzungwa primates is scant. Aside from several unsystematic zoological surveys (Butynski *et al.*, 1998; Dinesen *et al.*, 2001; Rodgers and Homewood, 1982), researchers have conducted detailed primatological studies primarily on polyspecific associations (Wasser, 1993), demographic variation in *Procolobus gordonorum* (Struhsaker *et al.*, 2004), and primate abundance and social structure in 2 high-elevation forests (Marshall *et al.*, 2005). Our study is the first to employ systematic line-transect censuses to estimate the abundance of diurnal primates in Mwanihana Forest, one of the largest forests in the Udzungwa Mountains. We also assessed differences in line transect data collection among several observers.

METHODS

Study Area and Subjects

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

The diurnal primates in Mwanihana Forest include Udzungwa red colobus, Sanje mangabey, Angolan black-and-white colobus (*Colobus angolensis*), Sykes's monkey (*Cercopithecus mitis*), and yellow baboon (*Papio cynocephalus*). Also present are 3 of the 4 species of galagos that occur in the Udzungwa Mountains (Butynski *et al.*, 1998). The main potential predators of all the diurnal primates are African crowned eagles (*Stephanoaetus coronatus*) and leopards (*Panthera pardus*).

Fig. 1. Map of the Udzungwa Mountains of south-central Tanzania highlighting the main forest blocks (in black) including Mwanihana Forest, and the Uduzngwa Mountains National Park (in gray). (From Marshall *et al.*, 2005).

Data Collection

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): 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 during firewood collection. Though the rising number of people using the 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 in Table I:

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).

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	350–800	Deciduous (0.8 km), semideciduous (0.6 km), open area (0.4 km), evergreen (2.2 km)
T2 (Mwanihana Trail)	4	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	330–600	Mixed deciduous and semideciduous (1 km), evergreen (3 km)

2. Semideciduous forest: moderate to old-growth forest, transitional between deciduous and evergreen. Common species are *Sorindeia madagascariensis* (Anacardiaceae), *Combretum* spp. (Combretaceae) *Ricinodendron heudelotii* (Euphorbiaceae), *Ficus* spp. (Moraceae), and *Trema orientalis* (Ulmaceae).

3. Evergreen forest: the primary habitat type on the second and higher altitude half of transects, mainly moderate to old-growth forest. Common species are *Parinari excelsa* (Chrysobalanaceae), *Macaranga* spp. (Euphorbiaceae), *Erythrophloeum suaveolens* (Leguminosae), *Synsepalum cerasiferum* (Sapotaceae), *Sorindeia madagascariensis* (Anacardiaceae), and *Parkia filicoidea* (Leguminosae).

4. Open areas: ex-logging area within T1, now occupied by regenerating vegetation, mainly shrubs and scattered trees. Common species are *Celtis gomphophylla* (Ulmaceae), *Albizia gummifera* (Leguminosae), and *Trema orientalis* (Ulmaceae).

Ulrik Pedersen (UBP), Castro Magwila (CAS), Andrew Marshall (ARM), Francesco Rovero (FR), and Arafat Mtui (ASM) collected data between 1998 and 2003, during periods that were noncontinuous among observers except for FR and ASM, as the latter began data collection soon after FR. Details of sampling effort by each observer are contained

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

		Transect			
Observer	Period	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

in Table II: ARM, FR, and ASM did not collect data along T4. The number of censuses conducted per transect per mo varied from 1 to 4. We walked census lines beginning at 0700–0730 h at an average speed of about 1 km h^{-1}, recording all sightings of primates. For each primate sighting we recorded time, species, estimated number of individuals (when possible), distance from the observer to the first individual seen, and position of the observer along the transect. The estimated number of individuals is the number of individuals counted during a maximum of 10–15 min observing each group. Struhsaker (TTS) trained observers before the beginning of data collection to standardize methods. TTS spent ≥ 2 d training each observer. We estimated position on the transect by referring to numbered tags placed every 50 m along the trails. We visually estimated distances, after training observers through calibration of estimation with actual measures obtained via a range finder or a tape measure. Because data collection did not overlap among observers, apart from FR and ASM, we could not test interobserver accuracy in estimated group distances.

Data Analysis

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

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

Following the standard approach on analysis of habitat use data (Neu *et al.*, 1974; *cf.* Thomas, 1991 and Wallace *et al.*, 1998), we used χ^2 tests to compare the distribution of primate group sightings among different habitat types with that expected assuming no selection, i.e., proportional to the availability of habitat types along the transect routes. We pooled data for all observers to meet sample size requirements for the χ^2 test (Sokal and Rohlf, 1995). We computed an index of habitat selection—selection ratio—as the ratio between number of groups observed and expected for each habitat type. We further investigated the differences between habitat use and availability by computing Bonferroni confidence intervals on the proportion of groups observed for each habitat type and then comparing them with expected values based on habitat availability (Byers *et al.*, 1984). The following is the formula for computing confidence intervals:

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

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

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

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

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

RESULTS

The rank order of species by mean sighting frequency when all observers were pooled is, from highest to lowest: red colobus, Angolan colobus, Sykes's monkey, baboon and mangabey (Table III). For any observer, differences in ER among species are highly significant (Kruskal-Wallis test, $p < 0.001$ both for each transect and pooling data for all transects; Table III). This pattern held for all observers except ARM when we repeated the comparison using only the 3 species most frequently seen ($\chi^2 = 31.57$, $p < 0.001$, $\chi^2 = 14.20$, $p < 0.05$, $\chi^2 = 0.55$, $p = 0.76$, $\chi^2 = 26.16$, $p < 0.001$, $\chi^2 = 19.53$, $p < 0.001$ for UBP, CAS, ARM, FR, and ASM, respectively). Sampling precision profiles for the 3 species most frequently seen are in Fig. 2. Data by CAS, FR, and ASM show asymptotic precision after 12–15 censuses. UBP reached comparable levels of high precision after only 6 censuses. UBP did not conduct further censuses; therefore, the validity of this trend cannot be assessed. A comparison of the curves for different species among observers reveals no consistent pattern except for
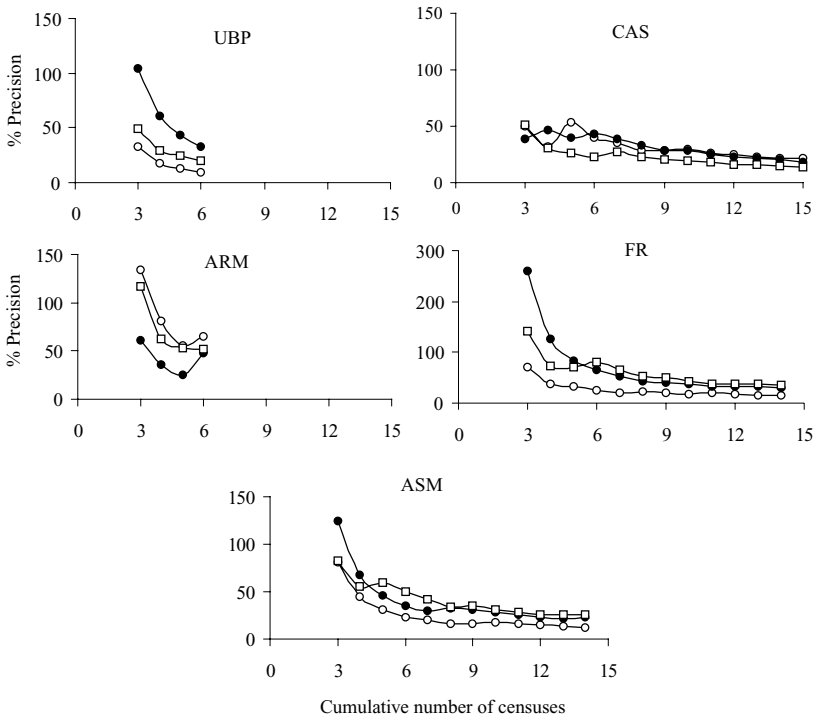
Fig. 2. Sampling precision of relative abundance data plotted against cumulative number of census repetitions for the 3 most frequently seen species (red colobus, open circles; Angolan colobus, closed circles; Sykes's monkey, open squares) during censuses conducted in Mwanihana Forest, Udzungwa Mountains 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.

data FR and ASM collected that show greater precision for the red colobus, i.e., the most frequently seen species.

Differences in ER among transects revealed no consistent pattern among observers (Table III and Appendix). In spite of differences recorded across transects by each observer, most of the interobserver variations in relative abundance of each species are not significant (Table IV). The few exceptions are related to single transects and discordance of one observer from the others (test outcome of post-hoc comparisons in Table IV), notably: ARM recorded significantly more Angolan colobus along T2 than other observers did, UBP recorded more red colobus along T2 than other observers did (weakly significant differences), and CAS 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 3 transects in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania

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

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 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 (χ^2 and *p* value) of differences in ER among species for each observer.
[a]Not significant when excluding T4 from comparisons, which only UBP and CAS walked for censuses.

Table IV. Test outcome (χ^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

	Transect							
	T1		T2		T3		T4	
Species	χ^2	p	χ^2	p	χ^2	p	U	p
Procolobus gordonorum	4.59	0.33	8.70	0.40	15.95	<0.01[d]	7	<0.01
Colobus angolensis	3.27	0.51	13.31	0.02[a]	6.23	0.18	22.5	0.23
Cercopithecus mitis	7.07	0.13	14.44	0.01[b]	0.85	0.93	25	0.35
Cercocebus galeritus sanjei	7.25	0.12	12.45	0.02[c]	6.28	0.18	22.5	0.24
Papio cynocephalus	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.
[a]Kruskal-Wallis test: $p = 0.13$ when ARM is excluded.
[b]Kruskal-Wallis test: $p = 0.42$ when CAS is excluded.
[c]Kruskal-Wallis test: $p = 0.10$ when CAS is excluded.
[d]Kruskal-Wallis test: $p = 0.07$ when ASM is excluded.

The distributions of primate sightings per gross habitat type are in Table V as selection ratios; data for the mangabeys are not shown because we did not see them frequently enough for the analysis. Analysis of the goodness-of-fit of observed vs expected use shows that most differences are for baboons (p significant for all the transects), followed by Sykes's, Angolan colobus (p significant for T1 and T3), and red colobus (p significant for T1 and marginally nonsignificant for T3). Conclusions on selection or avoidance for each habitat type indicate that baboons select deciduous forest and avoid the evergreen forest; Sykes's select semideciduous forest in T1 and T3 (no conclusion for T2) and avoid evergreen forest; Angolan colobus select evergreen forest and avoid deciduous forest in T1 and T2, while the occurrence of red colobus did not allow for conclusions apart from T1 where they select semideciduous forest and avoid open areas.

Estimated group distances varied considerably among observers (mean and standard deviation pooling all species and transects and excluding values >100 m: 45 ± 32; 28 ± 16; 34 ± 17; 37 ± 19; 36 ± 17 m for UBP, CAS, ARM, FR and ASM, respectively; $\chi^2 = 130.6$, $p < 0.001$). The maximum distance recorded varied from 90 to 400 m; however 90% of the values were within 100 m. Differences are also significant for distance values >100 m ($\chi^2 = 170.6$, $p < 0.001$ all species pooled). Most discordance resulted from distance estimate differences between UBP and CAS than from differences among the other 3 observers (ARM, FR, and ASM), for which differences are weakly significant ($\chi^2 = 3.70$, $p = 0.054$). In spite of these differences, in comparisons among frequency distributions of distance

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			
	P.g.[a]	C.a.[b]	C.m.[c]	P.c.[d]	P.g.	C.a.	C.m.	P.c.	P.g.	C.a.	C.m.	P.c.
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 (nc)	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 (nc)	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
P	<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, χ^2 and p values from goodness-of-fit tests of observed versus expected distributions of primate groups per habitat.
[a] *Procolobus gordonorum.*
[b] *Colobus angolensis.*
[c] *Cercopithecus mitis.*
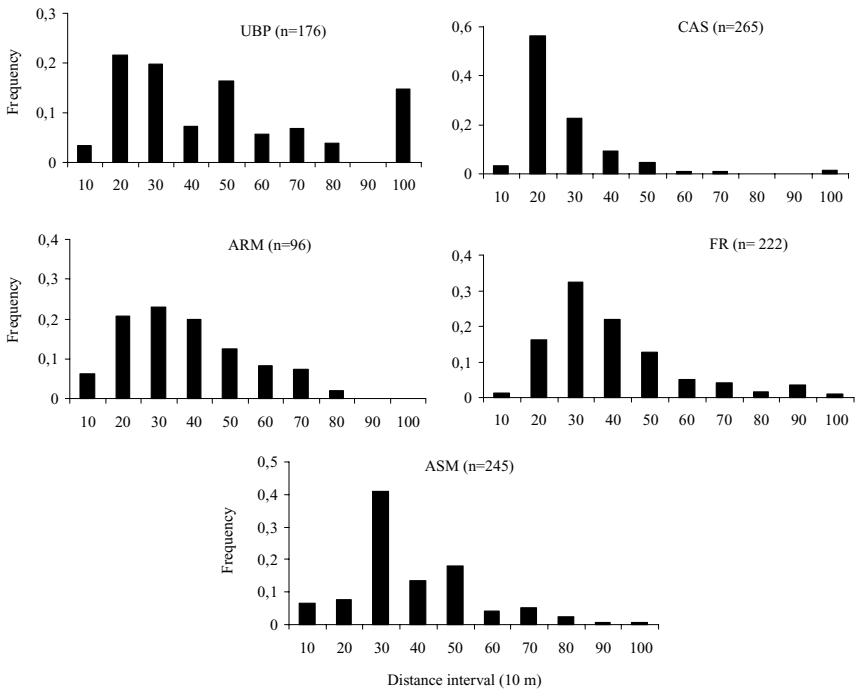[d] *Papio cynocephalus.*

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.

values in 10 m-classes (Fig. 3), there is no major variation (Kruskal-Wallis test: $\chi^2 = 2.57$, $p = 0.63$). This applies also to comparisons of the 3 most frequently seen species (Kruskal-Wallis tests: $\chi^2 = 0.82$, $p = 0.94$, $\chi^2 = 0.84$, $p = 0.93$, $\chi^2 = 0.41$, $p = 0.98$ for red colobus, Angolan colobus, and Sykes's monkey, respectively). In other words, within a variation of 10 m in estimated group distance among observers, the sighting curves are generally similar. Comparisons of distance values by species revealed that, for any observer, sighting distance was slightly higher for red colobus (mean and standard deviation pooling all observer 38 ± 3 m, excluding values >100 m) than Angolan colobus and Sykes's monkey (34 ± 3 and 33 ± 7 m, respectively; Krusal-Wallis test pooling all observer: $\chi^2 = 26.48$, $p < 0.001$), possibly because red colobus groups are larger and noiser.

Distance estimates that FR and ASM recorded during 7 censuses conducted simultaneously over 4 mo (we did not use data for the first 3 mo for this comparisons to account for potential differences in learning

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	
	n	Mean $\pm$ SD	n	Mean $\pm$ SD	n	Mean $\pm$ SD
Deciduous	23	41 ± 22	36	33 ± 13		
Semideciduous	28	37 ± 20	15	31 ± 15	50	29 ± 15^a
Open areas	15	57 ± 27	—	—	—	—
Evergreen	86	37 ± 19	89	37 ± 14	110	37 ± 16
Test outcome (p value)		$<0.05^b$		0.19		<0.05

Note. Test outcome of comparisons among habitat types is also shown (see text for details)
[a]Mixed deciduous and semideciduous.
[b]$p = 0.55$ when the category open areas is excluded.

between observers) are similar for red colobus and Angolan colobus (Wilcoxon Signed-Ranks test: $\chi^2 = -0.97$, $p = 0.33$, $\chi^2 = -0.67$, $p = 0.50$) while they differ for Sykes's ($\chi^2 = -2.39$, $p < 0.02$). We computed density only for *Procolobus gordonorum* because of adequate sample size, i.e., ≥ 20 group sightings recorded per transect and observer within the cutoff distance (Peres, 1999). The cutoff distance was 50 m for both FR and ASM, and mean density estimates per transect vary from 3.8 to 6.9 groups per km^2 (see Appendix for all values). Density estimates from data by FR and ASM are similar (Mann-Whitney U-test: $U = 756$, $p = 0.98$). Analysis of sighting distance values of primate groups by habitat type (data by FR and ASM only, Table VI) shows that while there was consistency across transects in sighting distance in evergreen forest (mean of 37 m for all transects), there was more variation for the other habitat types, e.g., mean of 41 m in the deciduous forest of T1 vs 33 m in T2 and 29 m in the mixed deciduous and semideciduous forest of T3. Overall, variations per habitat type are significant for T1 (Kruskall-Wallis test: $\chi^2 = 8.88$, $p < 0.05$, but $\chi^2 = 0.55$, $p = 0.76$ when the open areas habitat is excluded from analysis), nonsignificant for T2 ($\chi^2 = 3.31$, $p = 0.19$) and significant for T3 (Mann-Whitney U-test: $U = 1865$, $p < 0.05$).

DISCUSSION

Methodological Implications of Comparing Results Among Observers

One of the most important contributions of this study is that it improves our understanding of how variations among observers should be analyzed and interpreted to derive a reliable approximation of primate abundance. This in turn will be important to the design of future monitoring

programs. Census data that consist of several subsamples create a set of problems that apply to many monitoring programs (Mitani *et al.*, 2000; Struhsaker, 2002). Estimation of precision provides an indication of the reliability of the samples. Interestingly, the number of census repetitions necessary to obtain high levels of precision of abundance estimates is similar to that reported for Kibale National Park, Uganda (Mitani *et al.*, 2000), where precision reached its highest levels after 12–16 census walks for the most frequently seen species. A similar number of census walks were necessary to achieve nearly stable density estimates for the 3 most common species in a primate community in Kakamega Forest, Kenya (Fashing and Cords, 2000). Comparing census results among different observers indicates that variations are fairly moderate, because cases of significant differences were due to discordance of 1 data set from the other 4. Such cases of discordance are difficult to explain because they do not always involve the same observer, as we would expect if there were inconsistency in census methods by a particular observer. Moreover, we noted no temporal trend, with the partial exception of red colobus along T2 that was sighted relatively more by UBP in 1998 than by some of the subsequent observers, even though differences among all observers are not significant.

In agreement with Mitani *et al.* (2000), we found marked differences among observers in estimated distances of primate sightings. The great variation in the maximum distance at which we recorded primates is probably due to the uneven topography of the study area. On certain parts of transects, we recorded primate groups across valleys on distant slopes and ridges. Brugière and Fleury (2000) reported similar topographic effects on primate censuses in mountainous areas of Gabon. However, in contrast with Mitani *et al.* (2000) the frequency distribution of estimated distances in 10 m classes did not differ significantly among observers. This indicates that relative abundance data can be compared among observers with some degree of confidence. However, because most observers collected data in different time periods, there is the very unlikely chance that differences in mean estimated distances are due to differences in primate distances from the trail over time rather than to interobserver differences in accuracy/ability. Differences in estimated distance remain an underlying, potential source of variance in the results that cannot be separated from other sources of variance, e.g., interannual and intraannual, rendering problematic the recognition of real population trends. The data FR and ASM collected are a good example of interobserver consistency. Standardizing data collection methods, including simultaneous training and practice of census walks, is clearly important (Defler and Pintor, 1985).

Differences Among Species and Comparison
with Other Primate Communities

Researchers have reported greater relative abundance of colobines than of other primates for other communities in Africa (at Kibale, Uganda; Struhsaker, 1997). Fashing and Cords (2000) provided evidence that total colobine biomass explains the variation in total primate biomass at 10 Guineo-Congolian rainforest sites. Davies (1994) suggests that folivorous primates generally achieve higher abundances than frugivorous primates in tropical forests in Africa because of their ability to eat leaves, especially mature leaves, which allows them to sustain large populations even during periods of seasonal food scarcity.

Detailed comparisons of our census results with those for other primate communities are best made with geographically close communities for which comparable data are available (Table VII). Data from unlogged compartments in Kibale, Uganda (Chapman *et al.*, 2000; Mitani *et al.*, 2000 Struhsaker, 1975, 1997) indicate that the range of variations in relative abundance of red colobus overlap with Mwanihana Forest. Results for Sykes's monkey and mangabeys in Mwanihana Forest are well within the range of variation for their taxonomic counterparts in Kibale (*Cercopithecus mitis stuhlmanni* and *Lophocebus albigena*). In contrast, Angolan colobus and baboons seem more abundant in Mwanihana Forest than their taxonomic counterparts from unlogged forest in Kibale (*Colobus guereza* and *Papio anubis*). We stress, however, that comparisons might be biased by the fact that visibility in Mwanihana Forest is probably greater than

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)[d]	Kakamega Forest[e]
	UMNP[a]	WKS[b]	NDU[c]		
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	

[a]Present study (mean for all transects, range for different observers).
[b]West Kilombero Scarp Forest Reserve (Marshall *et al.*, 2005).
[c]New Dabaga-Ulangambi Forest Reserve (Marshall *et al.*, 2005).
[d]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).
[e]Fashing and Cords (2000).

at Kibale because of the mountainous terrain that allows long-distance viewing. Also, the extent of deciduous forest is greater in Mwanihana Forest. Data for Kakamega Forest (Fashing and Cords, 2000) indicate lower primate diversity, but greater abundance of *Colobus guereza* and *Cercopithecus mitis* compared to their taxonomic counterparts in Mwanihana Forest.

Our relatively low sighting rates of baboons is clearly related to their almost exclusive occurrence in the deciduous forest, which comprises only one fifth of the transect length. Conversely, we observed mangabeys in different habitat types and especially in evergreen forest, but very rarely in comparison to other species. As such, alternative methods such as range mapping of habituated groups might be required to determine their abundance (Ehardt *et al.*, 2005). The shyness of the species, often moving on the ground in dense vegetation, probably contributes to the infrequent sightings (T. Jones, pers. comm.). Differences in the ease of detection might also account for some of the variation among the 3 most sighted species. An important variable in this regard is group size: it is much larger for red colobus (mean of 40 individuals for Mwanihana Forest, Struhsaker *et al.*, 2004) than Angolan colobus (range 2–12, present study) and Sykes's monkey (range 2–14, present study). Our slightly different estimated sighting distances of groups among the 3 species may reflect group size differences. Generally, distances were greater for red colobus than for Angolan colobus and Sykes's monkeys. Similarly, the cutoff value in the frequency distribution of sighting distance was 50 m for red colobus and 30–40 m for Angolan colobus and Sykes's monkeys (data by FR and ASM).

Marshall *et al.* (2005) reported primate abundance data from other forests of the Udzungwa Mountains, in higher elevation forests on the northwestern side of the mountainous range that present various levels of habitat alteration due to past logging and current human encroachment. The relative abundances of Angolan colobus and Sykes's monkey for Ndundulu Forest, a large and relatively undisturbed forest block located outside the western border of UMNP, are broadly within the range observed in Mwanihana Forest, while the abundance of red colobus appears higher in Mwanihana Forest (Table VII). In contrast, primate abundance in Mwanihana Forest is much higher than in the highly encroached and degraded New Dabaga/Ulangambi, an isolated forest block. Numerous researchers have reported similar negative effects of habitat degradation, isolation, and hunting on primate populations (Cowlishaw and Dunbar, 2000; Skorupa, 1986, 1988; Struhsaker, 1975, 1997).

Patterns of Variation in Relative Abundance
Within and Among Transects

The habitat use pattern is clear for baboons and Sykes's monkeys because they prefer deciduous and semideciduous habitats, respectively. A distinct characteristic of the semideciduous habitat is its relatively high floristic diversity (F. Rovero, unpublished data). The habitat use pattern is less clear for the colobines, but they showed some habitat selection in T1 and T2, where there is more habitat variability than in T3. Habitat type does not seem to affect primate detection to a large extent, because mean values vary by ≤ 8 m among habitats, with the exception of the large open area in T1. Wallace *et al.* (1998) reported similar results from northeastern Bolivia: they found no significant difference for each species in sighting distances across diverse habitats spanning from semideciduous forest to gallery forest and mature forest.

The variations in primate abundance among transect lines are likely related to the differential occurrence of habitat types. That we generally recorded fewer baboons and more mangabeys at T3 than at T1 and T2 might reflect the small proportion of deciduous versus evergreen forest along T3. Moreover, an inverse relationship between abundance of the 2 species may reflect greater competition for food due to greater dietary overlap, as the 2 species belong to the same tribe (Cercocebini) and both spend time foraging on the ground. The variation in abundance among transects recorded for the other species is difficult to explain because there is no consistent pattern among observers. Longer, more continuous sampling would be required to properly assess variations in specific abundance among transects.

Similarly, more data are needed to understand patterns of seasonal variations in relative abundance. Early qualitative observations suggested seasonal use of deciduous areas by the colobines and mangabeys, possibly related to tree flushing at the beginning of the rainy season. Data FR collected show no statistical difference in relative abundance of any species when results from different periods are compared (July–August, September–October and November–January, corresponding to post-rain, dry, and rainy periods, respectively), but greater variation occurs at T1 and T2, which have a greater presence of deciduous forest. Similar evidence comes from comparing relative abundance across different seasons when the analysis is applied only to deciduous portions of T1 and T2, with sighting frequency generally lower during the dry season (July–August) than during the wet season (November–February). Thus, the mean ER of red colobus, pooling data for FR and ASM, is 0.33 vs 0.88 for T1 and 0.17 vs 0.25 for T2, during dry and wet season, respectively. Differences for T1 are weakly

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

Density Estimation of the Udzungwa Red Colobus

Pooling density estimations from data FR and ASM collected gives mean estimates that were similar for T1 and T2 (4.9 ± 2.8 and 4.4 ± 2.3 groups/km^2, respectively) and higher for T3 (6.0 ± 2.7 groups/km^2), with the differences among transects being significant (Kruskal-Wallis test: $\chi^2 = 12.24$, $p < 0.01$ and Mann-Whitney *U*-test between T1 and T2: $U = 302$, $p = 0.49$). We derived estimates in the range of 3–4 groups/km^2 from preliminary information on ranging patterns of red colobus groups from an area of mixed deciduous and evergreen, secondary forest at about 350 m a.s.l., between T1 and T2 (F. Rovero, unpublished data; K. Detwiler, pers. comm.). We used a mean group size of 40.7 individuals for Mwanihana Forest for red colobus (Struhsaker *et al.*, 2004) that yielded a crude density estimate of 180–245 red colobus per km^2 in the low to medium altitude forests of Mwanihana Forest. We cannot make direct comparisons with data from Marshall *et al.* (2005) because densities are not estimated in the latter study. However, both the lower relative abundance and smaller group size of red colobus (22.5 for Ndundulu and 11.8 for New Dabaga/Ulangambi) recorded at the 2 higher elevation forests (Marshall *et al.*, 2005) suggest that individual density is lower at higher elevations than in the low to medium altitude forests of Mwanihana Forest. This supports an earlier conclusion that the Udzungwa red colobus achieves highest densities in large blocks of mature, mixed evergreen, and semideciduous forests at low to medium altitudes and that densities are adversely affected by human-induced forest degradation (Struhsaker *et al.*, 2004).

CONCLUSIONS, RECOMMENDATIONS, AND FURTHER WORK

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

be a valid method to assess abundance of forest-dwelling primates. The method is usually less costly and time consuming than alternative methods such as long-term, focal-group studies of ranging patterns (Brockelman and Ali, 1987; Skorupa, 1987; Struhsaker, 1981; Whitesides *et al.*, 1988).

Sightings of Sanje mangabeys were too infrequent to give reliable estimates of abundance, and therefore we could not adequately assess their population. Moreover, the great habitat heterogeneity of Mwanihana Forest requires that a wider range of habitat types and altitudes be sampled to adequately extrapolate primate population abundances to the whole forest. Data from higher altitudes are particularly necessary, because data from other Udzungwa forests and preliminary surveys in Mwanihana indicate decreasing density of some species, particularly red colobus, at higher altitudes. Similarly, the qualitative evidence provided here of seasonal use of deciduous habitats by some species requires more study. Finally, continued monitoring is needed to assess the effect on primates of National Park management, primarily firewood collection in the lower 1–2 km of Mwanihana Forest. Firewood collection has continued since the establishment of the National Park in 1992 and human encroachment was probably heavier before (Rodgers and Homewood, 1982). The practice most likely has negative impacts on ground foraging primates such as Sanje mangabeys and baboons because they frequently forage for invertebrates in and under 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
Procolobus gordonorum	UBP	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	
		5.4 ± 3.4 (28)	*3.8 ± 2.7 (21)*	*4.8 ± 2.6 (25)*	
	ASM	0.5 ± 0.2	0.52 ± 0.23	0.79 ± 0.21	
		4.1 ± 2.3 (23)	*4.5 ± 2.2 (25)*	*6.9 ± 2.8 (33)*	
Colobus angolensis	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	

Table A1. Continued.

Species	Observer	T1	T2	T3	T4
Cercopithecusmitis	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	
Cercocebus galeritus sanjei	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	
Papio cynocephalus	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^2) 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).

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