

Diurnal Primate Densities and Biomass in the Kakamega Forest: An Evaluation of Census Methods and a Comparison with Other Forests

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Line-transect surveys were conducted at the Isecheno study site in the Kakamega Forest, western Kenya to estimate diurnal primate densities. The estimates from several different methods of analysis of census data were compared to “true” density values based on home range size and overlap for two species. The Whitesides method [Whitesides et al., 1988], which incorporates species-specific mean group spread into its formula for estimating transect width, provided the most accurate density estimates. The importance of including as many groups as possible when calculating density from home range size and overlap is demonstrated with long-term data from *Colobus guereza* and *Cercopithecus mitis*. *Colobus guereza* group density at Isecheno was much lower than that published from a recent brief study [von Hippel, 1996]. *Cercopithecus mitis* group density has fallen while overall population biomass appears to have remained stable over 20 years of study. Isecheno has the second highest diurnal primate biomass of the ten Guineo-Congolian rainforest sites for which biomass data are available, despite having the lowest primate species richness. Within the Guineo-Congolian rainforest system, primate biomass appears to vary to some extent between ecogeographic regions: two of three mid-elevation East African sites have high biomasses, two of two lowland West African sites have intermediate biomasses, and four of five lowland Central African sites have low biomasses. There is a strong positive correlation between total colobine biomass and total primate biomass at the ten Guineo-Congolian rainforest sites. Am. J. Primatol. 50:139–152, 2000. © 2000 Wiley-Liss, Inc.

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INTRODUCTION

Census surveys of non-human primate populations are an integral part of primate field studies for two reasons. First, population density estimates are important variables to consider when determining conservation priorities and creating management plans for primate populations [Ganzhorn et al., 1996/1997]. Second, these estimates are valuable to researchers trying to understand socioecological differences between primate populations [Butynski, 1990].

The most common method of censusing non-human primate populations is to conduct line transect surveys [e.g., Cant, 1978; Green, 1978; Freese et al., 1982; Peres, 1990; Glenn, 1998; Gonzalez-Kirchner, 1998; Wallace et al., 1998]. These surveys have the advantage of providing information on primate distribution and abundance in a relatively short period [Struhsaker, 1981]. A more accurate, though time-intensive, means of assessing primate densities is through long-term monitoring of home range size and overlap in a population [Struhsaker, 1975, 1981; Defler and Pintor, 1985; Brockelman and Ali, 1987; Chapman et al., 1988; Whitesides et al., 1988]. This paper will evaluate four different density estimating techniques and determine which technique provides group densities most similar to those derived from long-term monitoring of home range use patterns for the primates inhabiting the Isecheno study site in the Kakamega Forest, the easternmost remnant of Guineo-Congolian rainforest.

The Guineo-Congolian rainforest belt stretches across much of equatorial Africa and is home to most of Africa's primate species. Surveys have been conducted to determine the densities and biomasses of primates in numerous rainforests in the region [e.g., Struhsaker, 1975; Bourliere, 1985; Whitesides et al., 1988; Thomas, 1991; McGraw, 1994; White, 1994]. The results of the present study at Isecheno are compared to those from other Guineo-Congolian rainforests.

METHODS

Study Site

The Kakamega Forest (0°19'N 34°52'E; Elev. 1,580 m) reportedly covers 43 km² and is the only remaining area of Guineo-Congolian rainforest in Kenya [Wass, 1995]. It is home to five diurnal primate species, *Colobus guereza*, *Cercopithecus ascanius*, *C. mitis*, *C. neglectus*, and *Papio anubis*, though only the first three species reside permanently within the area surveyed for this study. Further details about the Isecheno study site can be found in Cords [1987].

Data Collection

Line transect surveys. Twenty-four line transect surveys were conducted by Fashing from 23 December 1997 to 24 March 1998 and 24–28 August 1998 along a 2.88 km census route at Isecheno. In compliance with the local forester's policy against cutting new trails, censuses followed a nonlinear route along existing linear trails through the study area. Because most groups in the censused area were at least partially habituated to humans, there is little reason to assume that monkeys of any species were avoiding existing trails.

Census walks began between 9:30 and 11:00 A.M. and lasted 110–194 min (mean = 150 min; S.D. = 20.9; n=24). Once a monkey was spotted, it was observed from the transect path for up to 10 min to determine whether it belonged to a bisexual group, or whether it was a solitary individual or a member of an all-male band. The following data were recorded for monkeys observed along the

transect: 1) time of sighting, 2) initial cue of detection (auditory or visual; those infrequent occasions when monkeys were heard but not eventually seen were not recorded), 3) location along census route, 4) species sighted, 5) number of monkeys present, 6) perpendicular transect to animal distance, and 7) observer to animal distance. The estimation of distances was facilitated by Fashing's prior experience in mapping colobus monkey movements and vegetation transects. Sightings of solitary monkeys were excluded from all analyses of line transect data following Whitesides et al. [1988], as were the infrequent sightings of all-male bands.

Home range size and overlap. Data on home range size and overlap were also used to determine population density for two species, *Colobus guereza* and *Cercopithecus mitis*. Ranging data on colobus monkeys were collected by Fashing during long-term monitoring of five groups between March 1997 and February 1998. Home ranges are based on 60 all-day follows for O Group, 59 all-day follows and 2 half-day follows for T Group, 23 all-day follows for GC Group, 22 all-day follows for BS Group, and 21 all-day follows for ML Group. Additional data on the ranges of other groups, which overlapped those of the five main study groups, were collected opportunistically during the study, most often during encounters with one of the main study groups.

The blue monkey data on home range size and overlap used in this paper were collected by Cords during a 21 month study between 1979 and 1981 and during yearly 2–3 month visits to Isecheno from 1994 to 1998. Between 1979 and 1981, Cords intensively mapped ranging patterns of one group and made ad libitum observations on ranging patterns of three other groups. Between 1994 and 1998, Cords collected ranging data for four groups of blue monkeys, two of which were focal groups monitored on a daily basis. Detailed descriptions of area used were noted ad libitum, and home range areas were later mapped with reference to these notes.

The use of home range size and overlap data to compute the “true” density is justified because most of the quadrats along the census route are included in the home ranges of the study groups of both species. Of the 61 quarter-hectare quadrats through which the census route passed, 44 (72%) quadrats were included within the home ranges of at least one of the five colobus monkey study groups and 49 (80%) quadrats were included within the home ranges of at least one of the four blue monkey study groups.

Data Analysis

Line transect surveys. Data from the line transect surveys were analyzed by using several techniques that varied according to how transect width was estimated and the formula used to calculate population density (see Table I). The transect width estimators used were a) maximum reliable distance from observer to animal [reliable distance to animal method: Struhsaker, 1981; Defler and Pintor, 1985; Chapman et al., 1988]; b) maximum reliable perpendicular distance from transect to animal [reliable perpendicular distance method: Struhsaker, 1981; Chapman et al., 1988]; and c) maximum reliable perpendicular distance from transect to animal, taking into account the species-specific mean group spread [Whitesides method: Whitesides et al., 1988; White, 1994]. Mean group spread for *Colobus guereza* (22 m) was calculated from data collected by Fashing during approximately 50 hr of scan sampling during August 1993, while group spreads for the two *Cercopithecus* species (*C. ascanius*: 56 m, *C. mitis*: 109 m) were taken from Cords [1987].

TABLE I. Formulae for Calculating Group Density Used in This Paper

Name	Group density formula	Reference
Whitesides method ^a	Group density = $\frac{N_i}{2(S/2+D) L_t}$	Whitesides et al., 1988
Max. reliable observer to animal distance method	Group density = $\frac{\text{Sum of group sightings}^b}{2(\text{length} \times \text{width of 1 side of transect in km})}$	Struhsaker, 1981
Max. reliable transect to animal distance method	Group density = $\frac{\text{Sum of group sightings}^c}{2(\text{length} \times \text{width of 1 side of transect in km})}$	Struhsaker, 1981
TRANSAN	Group density is computed by a PC program using a non-parametric, shape restricted estimator	Johnson and Routledge, 1985

^aN_i, total number of groups seen for each species; S, estimate of species-specific mean group spread in km; D, estimate of species-specific effective distance in km [effective distance = (FD) (N_i/N_t), where FD, fall-off distance or the largest number in the first 10 m interval (e.g., 39 in the interval 30–39 m) in transect to animal distances before which a 50% or greater drop in group sightings is recorded in the subsequent 10 m interval (e.g., from 12 group sightings in the 30–39 m interval to 6 or fewer group sightings in the 40–49 m interval); N_t, species-specific number of sightings of groups at distances less than the fall-off distance]; L_t, sum length in km of all censuses combined.

^bSum of group sightings refers to the total number of groups sighted at distances equal to or smaller than the fall-off distance. The fall-off distance is here defined as under footnote ^a except that observer to animal distances are used instead of transect to animal distances.

^cSum of group sightings refers to the total number of groups sighted at distances equal to or smaller than the fall-off distance. The fall-off distance is here defined as under footnote ^a.

Data for transect width estimators a) and b) were entered into the National Research Council (NRC) formula for calculating population density [Table I; Struhsaker, 1981]. Data for transect width estimator b) were also entered into the PC program TRANSAN, which uses a non-parametric, shape-restricted estimator to calculate density [Johnson and Routledge, 1985]. Data for transect width estimator c) were entered into the Whitesides et al. [1988] formula for calculating population density based on single-observer censuses [Table I].

Home range size and overlap. Density estimates based on home range size and overlap were computed using the “block method” outlined in Struhsaker [1981], Chapman et al. [1988], and Whitesides et al. [1988]. A grid of 0.25 ha quadrats was superimposed over a map of the home ranges of the study groups of each species. Quadrats of range overlap with non-study groups were identified and divided into categories based on the number of non-study groups which shared each quadrat with at least one study group. The total number of quadrats used only by study groups was divided by one, the total number of quadrats used by study groups and only one non-study group was divided by two, the total number of quadrats used by study groups and only two non-study groups was divided by three, and so forth. The values for each category of quadrat were then summed to produce an adjusted home range size for the five colobus monkey study groups combined and the four blue monkey study groups combined. We then divided the adjusted home range size for colobus monkeys by 5 and for blue monkeys by 4 to produce an average adjusted home range size for each species. Finally, we divided 1 by the average adjusted home range size for each species (in square kilometers) to provide a density value of groups per km². This density value was considered to be the best approximation of the “true” density for each species in the study area.

The above analysis was also conducted for each study group individually to compare group density estimates based on home range size and overlap data from different single study groups. This analysis provided five different density estimates for colobus monkeys and four different density estimates for blue monkeys. A current home range-based population density estimate could not be obtained for redtail monkeys because no quantitative data have been collected on their ranging patterns in recent years.

Biomass. Biomass for each species was calculated by multiplying the number of groups per km² by the mass of an average sized group. Group composition was known from repeated counts of focal study groups. Adult body weight values from Harvey et al. [1987] and density values from the home range size and overlap method were used to calculate biomass for colobus and blue monkeys. Adult body weight values from Harvey et al. [1987] and density values from the Whitesides method were used to calculate biomass for redtails. Following Oates et al. [1990], subadult male body weight was estimated to equal that of adult females, and juvenile body weight was estimated to equal one-half of adult female weight. However, we estimated infant body weight by adding the neonate weight provided in Harvey et al. [1987] to juvenile body weight and dividing by 2.

RESULTS

The mean rate at which monkeys were encountered per kilometer walked varied from 1.20 (S.D.±0.52) groups of colobus monkeys to 0.74 (S.D.±0.33) groups of blue monkeys to 0.46 (S.D.±0.30) groups of redtail monkeys across the 24 censuses. Table II compares the number of times each monkey species was initially detected by auditory cues versus the number of times each monkey species was

TABLE II. Mode of Initial Detection of Primate Species During Census Walks at Isecheno

Species	Mode of detection ^a	
	Sight	Sound
<i>Colobus guereza</i>	26	29
<i>Cercothecus mitis</i>	11	26
<i>Cercopithecus ascanius</i>	6	14

^aTable includes only those cases in which a single mode of detection was unambiguous and in which a group was eventually sighted.

initially detected by visual cues. Colobus monkeys were initially detected by visual cues about twice as often as the two guenon species grouped together, though the difference is not significant (G-test $P=0.06$).

Of the four methods employed to analyze line transect data, the Whitesides method yielded densities most similar to those derived from combined adjusted home range sizes for both colobus monkeys and blue monkeys (Table III). The Whitesides method underestimated colobus monkey density by only 3% and blue monkey density by only 16%. The maximum reliable observer-animal distance transect estimator applied to the NRC-recommended population density formula was somewhat less accurate, underestimating colobus monkey density by 8% and overestimating blue monkey density by 36%. The maximum reliable transect-animal distance-based estimates using the NRC-recommended population density formula was even less consistent with estimates from home range use, overestimating colobus monkey densities by 21% and blue monkey densities by 114%. The TRANSAN program produced the least accurate density values of all, overestimating colobus densities by 47% and blue monkey densities by 164%.

Figure 1 shows the changes over time in density estimates calculated by the Whitesides method for each species. Blue monkey and redtail monkey density estimates varied little over time, while colobus monkey density estimates had possibly reached an asymptote during the final 12 censuses. These patterns suggest that had census work continued, population density values for the guenon species would likely have remained stable, while colobus monkey densities would likely have remained stable or increased only slightly. With the reliable distance to animal method, blue and redtail monkey density estimates similarly varied little over time. However, colobus monkey density estimates appeared to be still increasing as of the 24th census, suggesting that estimates of colobus monkey density would have been higher had more censuses been completed.

TABLE III. Population Density (grps/km²) Estimates (mean±S.E.) Computed With Five Different Methods for Isecheno Diurnal Primates*

Species	Range use ("true" density) ^a	Whitesides method	Reliable observer- animal distance	Reliable transect- animal distance	TRANSAN program
<i>Colobus guereza</i>	11.5	11.1 ± .37	10.6 ± .32	13.9 ± .62	16.9
<i>Cercopithecus mitis</i>	5.0	4.2 ± .06	6.8 ± .07	10.7 ± .25	13.2
<i>C. ascanius</i>	—	4.0 ± .25	4.5 ± .65	7.6 ± 1.40	6.8

*Standard error was calculated using density estimates that incorporated the fall-off distance after each census rather than using the final (after 24 censuses) fall-off distance throughout.

^aBased on adjusted home range sizes for all five colobus monkey study groups combined and all four blue monkey study groups combined.

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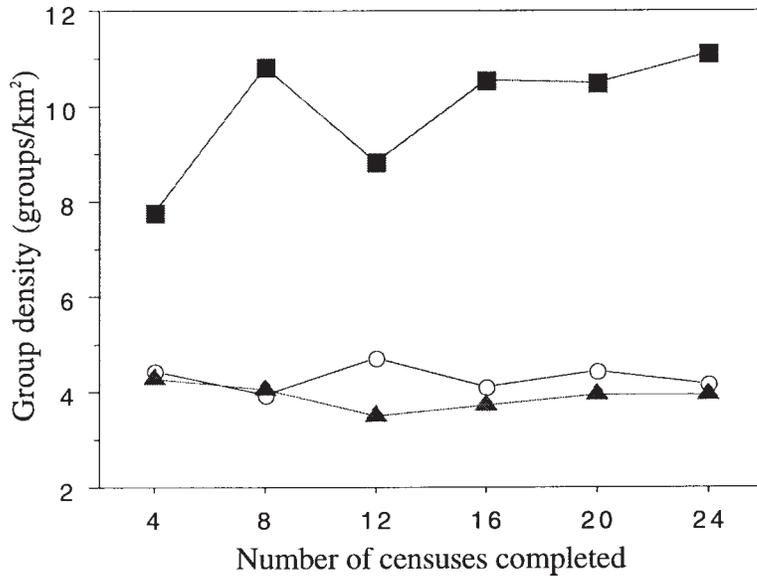


Fig. 1. Changes in Whitesides-method group density (groups/Km²) estimates over time in Isecheno primate species. Squares, *Colobus guereza*; circles, *Cercopithecus mitis*; triangles, *Cercopithecus ascanius*.

Population density estimates based on the adjusted home range sizes of each of the five study groups of colobus monkeys and four study groups of blue monkeys were quite variable (Table IV). Estimates ranged from 9.5 to 13.6 (mean = 11.5; SD±1.9) groups/km² for colobus monkeys and from 4.3 to 6.0 (mean = 5.0; SD±0.7) groups/km² for blue monkeys.

Based on comparisons of home range use in 1979–1981 [Cords, 1987] and 1994–1998, blue monkey group density at Isecheno is 17% lower today than it was 20 years ago (Table V). It appears that groups have increased in average size over the same period, however, so that blue monkey population density has increased by 11% and population biomass has remained nearly stable (3% increase). We are cautious in this conclusion, however, because of the limited sample of groups for which group counts are available for 1994–1998 (n=2).

Table VI presents biomass estimates from the ten Guineo-Congolian rainforests for which data are available. This comparison yields interesting re-

TABLE IV. *Colobus guereza* and *Cercopithecus mitis* Population Density Values Based on Calculations for Each Group Individually

<i>Colobus guereza</i>			<i>Cercopithecus mitis</i>		
Group	Density (grps/km ²)	Difference from "true" density*	Group	Density (grps/km ²)	Difference from "true" density*
BS	9.5	-17%	G	4.3	-14%
T	9.8	-15%	SE	4.6	-8%
ML	11.0	-4%	TW	5.0	0%
GC	13.5	+17%	F	6.0	+20%
O	13.6	+18%			

*Based on adjusted home range sizes for all five colobus monkey study groups combined and all four blue monkey study groups combined.

TABLE V. Long-Term Changes in Blue Monkey Density and Biomass at Isecheno Calculated by the Home Range Size and Overlap Method

Time period	Density (grps/km ²)	Mean group size	Density (ind/km ²)	Mean group biomass (kg/km ²)	Biomass (kg/km ²)
1979–1981	6.0	33 ^a	198	104	624
1994–1998	5.0	44 ^b	220	129	645

^an=5.^bn=2.

sults though it should be noted that levels of human disturbance and hunting pressure vary among sites. Also, census methods were not the same for all sites, and inter-observer reliability cannot be tested. The Isecheno/Kakamega site has the second highest primate biomass despite having the lowest primate species-richness of any site. If the ten sites are subdivided into ecogeographical regions, two of the three mid-elevation Congolian rainforests in East Africa have extremely high primate biomasses, both lowland Upper Guinean rainforests in West Africa have intermediate primate biomasses, and four of the five lowland Congolian rainforests in Central Africa have low primate biomasses.

DISCUSSION

Primate Detectability

The fact that colobus monkeys were more likely than the two guenon species to be initially detected by visual cues is probably related to the less active lifestyle of the colobus. Because colobus monkeys spend much of their time silent and motionless, they can easily go undetected unless the observer relies on a visual search image. With the more active guenons, the observer is most often alerted to their presence by the sounds of their movements or vocalizations. A similar pattern occurred at El Tuparro in Colombia where Defler and Pintor [1985] found that the least active primates, *Alouatta seniculus*, were far more likely to be detected by visual cues than were the other more active primate species.

Since guenons are more active and vocalize more often than colobus monkeys at Isecheno, they are probably less likely to be missed during census walks. This difference in detectability might explain why reasonably stable density estimates were achieved faster for the guenons. Nonetheless, reasonably stable density estimates were obtained after a rather small number of censuses for all three species at Isecheno (n=4 for both guenons; n=16 for colobus monkeys). This rapid attainment of stable density estimates may be related to the good visibility of primates at Isecheno.

Techniques for Estimating Density

The analysis of home range size and overlap data from Isecheno reveals an important methodological point: if population density is determined based on the adjusted home range size of only one group, the density value may be very inaccurate. For example, if ranging patterns of only one group had been studied at Isecheno, the population density value for colobus monkeys would have ranged from 9.5 groups/km² to 13.6 groups/km², depending on the group chosen for study. A wide range of density estimates (4.3 groups/km²– 6.0 groups/km²) would have been produced for blue monkeys as well. Attempts to “test” the accuracy of different census methods against the colobus monkey population density estimate of

TABLE VI. Comparison of Diurnal Primate Biomass at Ten Guineo-Congolian Rainforest Sites

Site	Forest size (km ²)	No. of diurnal primate spp.	Colobine biomass		Total		Region of Africa	Source ^a
			(kg/km ²)	% of total	diurnal primate biomass (kg/km ²)	biomass (kg/km ²)		
Kibale, Uganda	460	8 (7) ^b	2,386	82	2898	East	1	
Kakamega, Kenya	43	5 (3)	1,035	54	1,900 ^c	East	2,3	
Tiwai, Sierra Leone	12	8 (8)	786	57	1,379	West	4	
Lomako, D.R.C.	—	7 (5)	57	6	1,034	Central	5	
Tai, Cote d'Ivoire	3,030	9 (8)	704	70	1,010	West	6,7	
Ituri, D.R.C.	70,000	12 (12)	308	43	710	Central	8	
Budongo, Uganda	428	5 (5)	275	43	639 ^d	East	9	
M'Passa, Cabon	—	7 (7)	0	0	627	Central	6	
Douala-Edea, Cameroon	1,300	7 (7)	198	48	409	Central	10	
Lope, Gabon	5,000	8 (8)	91	29	319	Central	11	

^a1, Stuhsaker [1975, 1997]; 2, this study; 3, Wass [1995]; 4, Oates et al. [1990]; 5, McGraw [1994]; 6, Bourliere [1985]; 7, McGraw [1996]; 8, Thomas [1991]; 9, Plumtre and Reynolds [1994]; 10, McKey in Oates et al. [1990]; 11, White [1994].

^b(). Number of species surveyed for biomass estimate.

^cMean body weight data from Harvey et al. [1987]. Juvenile body weight was estimated to be one half of adult female body weight. Infant body weight estimated to be: (juvenile weight + neonate weight)/2.

^dBiomass estimated by authors of this study based on group density data in Plumtre and Reynolds [1994].

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13.6 groups/km² and the blue monkey estimate of 6.0 groups/km² would have led to an incorrect conclusion about which census method was most accurate. It is therefore recommended that primate density based on adjusted home range size be calculated for as many groups of a species as possible, and that the density value calculated from the combined adjusted home range size for each species in the study area be regarded as the most representative estimate of “true” density. This density value is equivalent to that obtained by calculating the mean of the density values for each group individually.

The Whitesides method proved to be the most accurate technique for estimating population densities from line transect data at Isecheno. The reliable distance to animal method was the second most accurate technique at Isecheno and has provided relatively accurate results at three other sites for which “true” primate density values are also available for comparison: Kibale, Uganda [Struhsaker, 1981], El Tuparro, Colombia [Defler and Pintor, 1985], and Santa Rosa, Costa Rica [Chapman et al., 1988]. Either of these two techniques appears to be a good choice for estimating primate group densities, though the latter technique risks overestimating densities in species with large mean group spreads. If two different species exist at the same group density, the species with the largest group spread is more likely to be encountered along transect walks because it is spread over a larger area. The risk of overestimating densities therefore occurs in the reliable distance to animal method because it does not take into account mean species-specific group spread.

Struhsaker [1997] has questioned the validity of the Whitesides method which sets the species-specific mean group spread equal to the diameter of a circle when estimating transect width. Because primate groups do not in fact spread out in a perfect circle, Struhsaker feels the Whitesides method should not be used. While it is true that primate groups are unlikely to adopt a perfectly circular group spread, two of the three species surveyed at Isecheno (blue and redtail monkeys) commonly spread out in irregular amoeboid shapes that are usually more circular than linear (Cords, personal observation). Even for species without a typically circular spread, after many random sightings of groups in a variety of formations, the best two-dimensional approximation of group spread may be a circle. For species such as blue monkeys with large mean group spreads, even an inexact method of accounting for group spread substantially increases transect width, thereby decreasing the probability that group density will be overestimated.

The reliable perpendicular distance method greatly overestimated population density at Isecheno just as it did at Kibale [Struhsaker, 1981]. The TRANSAN program using perpendicular transect to animal distance data provided the greatest overestimates of any of the four methods considered here for line transect census analysis at Isecheno. These techniques both fail to take into account mean species-specific group spread and neither can be recommended for future use in primate censuses because of their tendency to greatly overestimate group densities.

Overall, for a researcher interested in estimating primate densities in forested environments, we recommend that the home range size and overlap method be used for as many groups as possible assuming time and money are not constraints. If long-term research is not possible, but mean group spread can be determined for the species surveyed, we recommend the Whitesides method. If mean group spread cannot be reliably determined, the reliable distance to animal method provides a reasonable alternative as long as researchers are aware that this method is prone to providing overestimates of density for species whose groups spread out over large areas. There is, of course, no harm in collecting data on both animal-transect distance and animal-observer distance when group

sightings are made during censuses since densities can then be estimated using both the Whitesides method and the reliable distance to animal method.

When using line transect methods, however, researchers should consider the possibility that short-term census data may yield inaccurate density estimates for those species showing strong seasonality in the use of different parts of their home ranges [Struhsaker, 1981]. This consideration did not prove to be a problem for *Colobus guereza* and *Cercopithecus mitis* at Isecheno because neither species showed strong seasonality in range use (Fashing, unpublished data; Cords, unpublished data), thus making it possible to achieve relatively accurate density estimates from censuses conducted mostly during a 3-month period. For those species showing strong seasonality in range use, however, it is probably necessary to conduct censuses throughout the year to achieve accurate density estimates.

Finally, the line transect methods recommended in this paper may not be useful for censusing all forest-living primates. For example, nocturnal primates, heavily-hunted primates, and primates living at extremely low densities or in mountainous areas may be very difficult to census using traditional line transect methods [Duckworth 1998; E. Sterling, personal communication]. For these primates, basic data on their presence or absence and frequency of sightings may be the only information that can be collected related to their distribution and abundance.

Density Changes Over Time at Isecheno

Based on the home range size and overlap method, blue monkey group density has decreased from the 1979–1981 to 1994–1998 study periods. An increase in mean group size over the same period, however, means that the population density today is actually 11% higher and the overall population biomass is 3% higher than it was 20 years ago. We acknowledge some uncertainty associated with these estimates, because of the limited sample of groups for which group counts are available for 1994–1998 (n=2). Nevertheless, they demonstrate how changes in group density, size and composition all contribute to changes in biomass.

Colobus monkey density is much lower at Isecheno than was recently reported by von Hippel [1996] who used a similar home range size and overlap method to calculate density during a 2-month study in 1992. While our estimate of 11.5 groups/km² is a high density for black and white colobus monkeys at a rainforest site [Oates 1974; Suzuki 1979; Bocian 1997], it is 45% lower than von Hippel's [1996, p 195] estimate of 20.8 groups/km². If the population crashed, it went undetected by us during annual 2–3 month visits to Isecheno between 1992 and 1996. During Fashing's long-term study (November 1996 to March 1998), colobus groups averaged 13 individuals per group, only slightly more than the mean of 12 reported by von Hippel [1996, p 195]. Assuming von Hippel's population density estimate was correct, at least seven average-sized groups would have had to become extinct or have left the study area in the years between von Hippel's and Fashing's studies for the population density to have dropped so precipitously. While this scenario cannot be ruled out, it seems more likely that von Hippel's density value represents an overestimate due to the short duration of his study.

Biomass in Guineo-Congolian Rainforests

The diurnal primate biomass at Isecheno is the second highest yet recorded for a Guineo-Congolian rainforest. This high biomass fits the pattern of high primate biomass in most East African forests, intermediate biomass in West Af-

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rican forests, and low biomass in most Central African forests. This ecogeographic variation in biomass may be related to some extent to differences in the sizes of the forests surveyed in each region. The second and third highest biomass sites, Kakamega and Tiwai, are of very small size, 43 km² and 12 km², respectively. The compression of primate populations into small areas may have led to the relatively high biomasses at these two sites. The same explanation, however, is not likely to account for the unusually high primate biomass at Kibale which includes approximately 460 km² of forest.

Oates et al. [1990] noted that much of the primate biomass at four different African sites appeared to be accounted for by red colobus monkeys. With data from six additional sites now available, the correlation between red colobus monkey biomass and total primate biomass still exists ($r=0.82$; $r^2=0.67$; $P<.01$), though it is due primarily to the extraordinarily high values for red colobus monkey biomass and total primate biomass at Kibale. Total colobine biomass ($r=0.95$; $r^2=0.90$; $P<.0001$) better explains the variation in total primate biomass at the ten Guineo-Congolian rainforest sites than does red colobus monkey biomass alone. This point becomes even more convincing if Kibale is regarded as an outlier and removed from the analysis. In the nine remaining sites, there is no correlation between red colobus monkey biomass and total primate biomass ($r=0.27$; $r^2=0.07$; n.s.), while a correlation still exists between total colobine biomass and total primate biomass ($r=0.84$; $r^2=0.71$; $P<.01$). To better understand the ecogeographic variation in colobine biomass, and primate biomass in general, more quantitative data are necessary on the many factors listed by Oates et al. [1990, p 339–340] as influencing primate biomass in tropical forests including soil quality, phytochemistry, habitat disturbance, tree-species composition, climate, historical and zoogeographical forces, competition, predation, and disease.

CONCLUSIONS

1. Several methods of analysis were applied to line transect data to estimate population densities of diurnal Kakamega Forest primates at the Isecheno study site.

2. The Whitesides method provided population density estimates most similar to known densities calculated with long-term data on home range size and overlap.

3. The results of the analysis of home range size and overlap at Isecheno reveal the importance of including data from as many groups as possible when calculating population density using this method.

4. Group density of *Cercopithecus mitis* has fallen by 17% while overall population biomass appears to have remained relatively stable over the past 20 years at Isecheno.

5. Colobus guereza density is high for a rainforest site, though much lower than was reported several years ago in a brief study at Isecheno by von Hippel [1996].

6. Isecheno has the second highest primate biomass of the ten Guineo-Congolian rainforest sites for which biomass values exist despite the fact that it is inhabited by the smallest number of primate species.

7. Primate biomass appears to be related to ecogeographic region within the Guineo-Congolian rainforest system: most mid-elevation East African sites have high biomasses, lowland West African sites have intermediate biomasses, and most lowland Central African sites have low biomasses.

8. Total colobine biomass exhibits a strong correlation with total primate biomass at the ten Guineo-Congolian rainforest sites.

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