Chapter 6

Biomass of rain forest mammals, and the effects of logging.

Introduction.

Tropical rain forest vertebrate communities are diverse and are dominated by frugivores (Emmons *ai al.,* 1983; Fleming *et al.,* 1987; Gautier-Hion *et ut.,* 1980; Terborgh, 1983, 1986; Willis, 1980). There are complex interactions between species, and wide scope for competition (Gautier-Hion *ai al.,* 1980). In order to understand these interactions detailed studies of feeding ecology and community structure are necessary. However, few studies have involved simultaneous investigations of the biology of more than one group of species (e.g., primates), and few estimates of community biomass, arguably the best means of making comparisons between areas, are available.

In African lowland rain forests there are many estimates of population densities of individual species or groups, but no estimates are available of mammalian community biomass based an systematic, long-term data. In this study, population densities and biomasses were estimated simultaneously for diurnal primates, ruminants, pigs, elephants and squirrels using a combination of direct and indirect census techniques. Results from different census methods and the changes in animal density due to logging are discussed, and biomass estimates are compared between sites and with comparable data from Africa and elsewhere.

Methods.

Census methods

Line-transect methods (c.f., Burnham *et al.,* 1981) were used to estimate mammal densities. Two types of census were undertaken, one recording sighting frequencies, and the second recording signs of mammal presence (dung and nests) as well as sightings.

Animal sighting censuses

Censuses to record animal sightings were commenced between *06:30* and 09:30 hrs. If rain fell continuously for more than 15 minutes the census was abandoned. In Site 1 (see Chapter 2) successive censuses were conducted in opposite directions, but in the other sites this was not possible for logistical reasons. Censuses in each site were generally about a month or more apart, and never within less than three days of one another.

Otherwise, methodology and data collection were as described in Whitesides *etal* (1988): the observer moved slowly and quietly along the transect at a rate of 1-1.5 km h^{-1}, never leaving the line, stopping periodically to watch and listen for animals. Upon detecting a group or individual animal, up to 10 minutes were spent *in situ* recording data, and occasionally the observer moved up to 25m in reverse to obtain a better view. For the first individual of each species seen detection method, time, height, behaviour, distance along transect, distance from the observer, sighting angle and perpendicular distance from the transect were recorded. Distances were estimated by eye. The number of individuals seen and estimated to be present were also recorded. When more than one species was present data were recorded for the first individual of each species seen, and any species detected (e.g., by vocalisation) but not seen were also noted. Primates were corisidered to be in polyspecific associations if they were sighted within 50m of one another, and individuals considered to be solitary were at least 50m from any other individual. Vocalisations of species not sighted were recorded whenever heard, and loud vocalisations of those species seen were also recorded. Data were recorded on a checksheet adapted from that used by Whitesides *Pl* al. (1988) IG. H. Whitesides, personal communication).

Data were collected for *Gorilla g. gorilla* (western lowland gorilla), *Pan t. troglodytes* (chimpanzee), *Mandrillus sphinx* (mandrill), *Colobus satanus* (black' colobus), **Cercocebus** *albigena* (grey cheeked mangabey) *Cercopithecus nictitans* (greater spot-nosed monkey) *Cercopithecus pogonias* (crowned guenon), ***Cercopithecus** cephus* (moustached monkey), *Loxodonta africana* (elephant), *Syncerus* caffer (buffalo), *Cephalophus monticola* (blue duiker), *Cephalophus leucogaster* (Gaboon duiker), ***Cephalophus*** callipygus (Peter's duiker) ***Cephalophus** d'salis* (bay duiker), *Cephalophus* *sylvicultor* (yellow-backed duiker) , Hyemoschus aquaticua (water chevrotain), Potamochoerus porcus (red - river hog), Protoxerus stangeri (giant forest squirrel), Epixerus wilsoni (Wilson's splendid-tailed squirrel), Heliosciurus rufobrachium (red - legged sun - squirrel) , Funisciurus lemniscatus (LeConte‘s four-striped tree squirrel) and Nyosciurus pumilio (pygmy squirrel).

Dung and nest counts.

Standard dung (cf., Barnes and Jensen, 1987) and nest counts (cf. Tutin and Fernandez, 1983) were undertaken simultaneously. During censuses average rate of travel was 0.5-0.75 km hr-1 and two days were often required to complete data collection. Censuses were conducted once monthly in each site. For each dung deposit the species, distance along the transect and perpendicular distance from the centre of the transect to the centre of the dung deposit (measured to the nearest 5cm using a tape measure) were recorded. Any deposit present in more than one month was only included in the sample for the month in which it was deposited . Dung of Loxodonta africana , Syncerus caffer, Gorilla g gorilla, Pan t, troglodytes, Cephalophus monticola, red duikers (Cephalophus leucogaster, Cephalophus callipygus and Cephalophus dorsalis) , Cephalophus sylvicultor and Potamochoerus porcus were recorded.

For gorilla and chimpanzee nest sites (Plate 6.1) the distance to the first nest sighted was estimated visually and by pacing. Maps of the nest sites were made and detailed data taken for all nests (height, tree species it was in, construction materials for ground nests, age class of occupant if fresh dung was present, c.f., Williamson, 1988). The distance to the nest group centre was determined by calculating the average distance of all nests from the transect, scoring one side positive and the other side negative if nests occurred on both sides. During dung and nest counts data on species sightings and calls were recorded as for animal sighting censuses. Table 6.1 gives the number of censuses conducted in each study site.

Plate 6.1.

An adult female western lowland gorilla (*Gorilla g. gorilla*) climbs a *Cola lizae* tree.

A human ape (the author's mother) in a gorilla nest, constructed from leaves and stems of *Haumania liebrechtsiana* and *Megaphrynium gabonense*.

Table 6.1: The number of censuses conducted in each site.

Site	**Number of Censuses**		
	Animal sighting	Dung/nest	Total
1	18	25	43
2	13	22	35
3	11	10	21
3a (after logging)	7	12	19
4	11	20	31
5	9	17	26

Dung and nest decay rates.

Fresh elephant dung piles seen from transects each month were observed *in situ* from the transect (i.e., no attempt was made to approach them) at two week intervals in the first year of the study, and at monthly intervals in the second year, until they were no longer visible. Similarly, samples of 28 and 30 fresh gorilla dung piles were observed weekly in the dry and wet seasons respectively until they disappeared, and 15 piles of fresh red duiker pellets were checked daily in the wet season until none remained. All fresh ape nest sites were monitored at two-weekly intervals until no longer visible from the transect.

Statistical tests

Non-parametric statistical tests were used to test whether census data were affected by season, time of day, direction of travel or the type of census used (Siegel & Castellan 1988). Encounter rates (sightings) for each species and nest encounter frequencies did not differ significantly from the Poisson distribution, but dung was distributed patchily in space and time and did not conform to the Poisson distribution. Parametric tests (following Sokal & Rohlf,

1981) were carried out on square-root transformed data where appropriate, to confirm results obtained using non-parametric procedures. The criterion for statistical significance was $P < 0.05$ in all cases, and tests were two-tailed.

Estimates of **density** and *biomass* from *animal* census ***data***

Animal sighting censuses.

Many of the species studied live in social groups, and it was therefore these groups that were detected by the observer and for which data were recorded. It was not possible to estimate reliably the position of the group centre, since groups were often spread over a large area and only a few individuals were visible. When group spread could be reliably determined it was noted, and using these data, and experience of other workers at SEGC, species specific group spreads were estimated. Individual measures of perpendicular distance to the transect were converted to estimates for groups following the protocol of Whitesides *et al.,* (1988): It was assumed that the first individual sighted was at the group's periphery nearest the observer. The perpendicular distance, X, of the group centre from the first individual was given by:

$$X = r \cos \varnothing \qquad (6.1)$$

where r = half the species specific group spread, and $\varnothing$ is the sighting angle. This correction factor was added to the perpendicular distance of the first sighted individual for species living in groups. Fourier series analysis (Burnham *et al.,* 1981 - using a programme written by White, 1988), and the hazard-rate model (Buckland, 1985; Hayes & Buckland, 1983 - using a programme provided by S. T.' Buckland), were used to calculate group densities from perpendicular sighting distance data for groups and solitary animals, when the sample size was 25 or more (cf. Koster and Hart, 1988). Duikers were often "flushed", and detected by alarm vocalisation and the sound of movement as they left cover. It was generally possible to estimate the location from which they were flushed, but not always possible to identify the species, so census data for duiker sighting (and flushing) were lumped and an overall figure calculated.

The hazard-rate model is a two-parameter model, which uses sighting angle and distance to the individuals or geometric centre of groups sighted, to calculate the perpendicular transect to individual or group centre distance. It assumes that changes in distance and sighting angle alter the probability of sighting a group as the observer advances along the transect. The Fourier series is a non-parametric model which uses data for the perpendicular distance of each individual or group centre from the transect to calculate a 'probability density function', which is the probability of seeing a dropping at a given distance from the transect. Both models make use of all data collected, rather than restricting data collection to a strip of fixed width in which it is assumed that all individuals or groups are detected (cf. Wilson & Wilson, 1975), but both are mathematically complex and make several assumptions that may not always apply to field data (see Buckland, 1985; Burnham *et al.,* 1981; Hayes & Buckland, 1983; Whitesides *et al.,* 1988).

Small sample sizes precluded the use of these density estimation techniques in one or more of the sites for all species. For this reason, densities were also estimated using a method modified from Whitesides *et* al., (1988): The 'effective distance' for each species was calculated by plotting the cumulative percentage of total sightings for each species as a function of the perpendicular distance from the transect to the first individual sighted. *As* there was no statistically significant difference in species detection distances between sites (see below), data for all sites were combined to increase sample sizes for this analysis. Two straight lines that best fit the cumulative percentage sighting points so as to minimise the error sum-of-squares were then plotted, and the distance from the transect that corresponded to the point of intersection of these two lines was taken to be the effective distance. The width sampled on either side of the transect was equivalent to this distance plus one-half the estimated species group spread. The sample width was double this, as observations were made on both sides of the transect.

In addition, histograms of the perpendicular distance to the first individual sighted (grouped into 10m categories) were plotted. The distance at which the number of observations missed was compensated for by observations beyond was estimated. Again, the width sampled to either side of the transect was equivalent to this distance plus one-half the estimated species group spread. The average of these two estimates was taken to be the strip width sampled.

Average encounter rates were calculated for each species in each site. Due to small sample sizes and low encounter rates it was not possible to calculate 95% confidence limits reliably for all species in all sites. Instead, the cumulative average encounter rate was calculated after each census:

$$C_n = E_n / n \qquad (6.2)$$

where, C_n = cumulative average after n censuses, E_n = total number of encounters after n censuses, n = number of censuses.

The variation about the mean should decrease with the number of repeat censuses, and the range for the average encounter rate was assumed to be between the highest and lowest values for cumulative average number of encounters / census for the last 10 censuses. Estimates for group spread were assumed to be within 10m of the actual value, except for *Mandrillus sphinx* (50m) and *Potamochoerus porcus* (25m), both of which travel in large, diffuse groups. Effective distances were assumed to be within 10m of the actual figure except for ungulates (5m) and squirrels (2.5m), for which sighting distances were low. Group density was calculated using the equation:

$$G_d = E_r / A \qquad (6.3)$$

where G_d = group density (Groups km-^{2}), E_r = average encounter rate per census, A = area censused. The total area censused is given **by:**

$$A = L \times 2(D_e + S/2) \qquad (6.4)$$

where L = transect length (km), D_e = species specific effective distance (km), S = species group spread **(km).**

Group density was calculated as a range by putting minimum and maximum estimated values of E_r, D_e and S into equations *(6.3)* and **(6.4).**

Dung and nest count censuses

Hazard-rate, Fourier and Whitesides' methods of analysis described above were used to calculate dung densities with the exception that where fewer than 20 repeat dung counts had been undertaken on a transect, the range of the average encounter rate was calculated from the cumulative average of the second half of the sample. Effective distances for nests and dung were assumed to be accurate to within 10m and 0.5m respectively.

To calculate animal density from dung (and nest) densities it was necessary to know the defecation rate (calculated from values in the literature), that apes build one nest each night / independent individual (Tutin and Fernandez, 1983), and the % of dung piles (or nests), if any, that would not survive for at least one month, and hence might be missed on monthly censuses (see below). Density was given **by:**

$$D = Dd / F \times T \qquad (6.5)$$

where D = animal density (individuals km^{-2}), Dd = dung or nest density (deposits km^{-2}), F = defecations day-1 (=1 for nests), T = time between censuses in days.

Biomass calculation

To calculate the densities of individuals of species living in groups, and then biomass, average group sizes and the mass of an average individual must be known. Group counts for monkeys were rarely possible, so data collected during this study were combined with group counts obtained in the SEGC main study area by other workers (R. Ham & C. E. G. Tutin, unpublished data). Group counts included in the analysis were those where the observer was confident that all individuals had been detected, and where the location was sufficiently far away from groups that had been counted previously, to be sure that the same group was not represented more than once. For apes group size was assumed to be equal to the average nest group size. This would lead to individuals that were too young to build nests and which slept with their mothers being overlooked (cf. Tutin and Fernandez, 1983), but these individuals would only account for a minor part of the biomass. For elephants good data on group sizes were available for Lope (Chapter 5). For duikers and squirrels encounters were generally with only one individual (occasionally two), and data from censuses were used to calculate the average number encountered at any one time. For buffalo the average for a limited number of encounters in the forest was used.

Body masses were taken from the literature. The weight of an average individual was calculated as follows: for Cercopithecus spp. and Cercacebus ***albigena*** an average individual was assumed to be 75% the mass of an adult female (cf. Oates **et *al.,*** 1990). For Colobus satanus group composition was assumed to be as for Colobus polykomos reported in Oates **et *al.*** (1990) and the weight of the average individual was calculated following their protocol. For *Mandrillus sphinx* group composition was assumed to be as reported by Hoshino ***et al.*** (1984) in Cameroun, sub-adult males were assumed to be the weight of an adult female, and juveniles were assumed to be half the female weight (cf. Oates *et al.,* 1990). For apes it was assumed that there were two juveniles half the female weight for each male and female. For elephants the ratio was assumed to be one male, one female and two and a half juveniles of half the female weight (Chapter **5).** For ungulates the ratio was assumed to be one juvenile half the adult weight to two adults. For **Potamochoerus porcus** and for squirrels the ratio was assumed to be two juveniles to two adults. Average weights of males and females were used where available, and for ranges the mid-point was assumed to be representative.

it was not possible to calculate 95% confidence limits for the weight of an average individual, nor for group densities using the method adapted from Whitesides *et al.* (these authors gave 95% confidence limits for their method, but it is not clear how this was done). Therefore, the density of individuals using the Whitesides' method was calculated as a single figure using the average encounter rate to obtain group density. Where hazard-rate and Fourier analyses were possible, 95% confidence limits were calculated. Biomasses were the product of the individual densities and the weight of an average individual. Where individual densities could be calculated using the hazard-rate method this figure was used to calculate biomass (see below). Where individual density had been calculated using more than one method the average figure was used. For duikers, overall density calculated for sighting and flushing frequency data was converted to species densities by assuming that the ratio of C. *monticola:* Red duikers: **C.** *sylvicultor* H. ***aquaticus*** was equivalent to that for the individuals that were reliably identified.

Statistical tests of differences in animal densities between sites

For group, individual and nest sighting data, crude encounter rates per census were used in tests for statistical differences between sites, since there were no statistical differences in sighting distances between sites (see below). For dung counts, statistical tests were performed on densities estimated by the modified Whitesides' method (see below) for each census, correcting for differences in dung decay rates between wet and dry seasons where appropriate (see below).

Encounter rates (sightings) for each species conformed to the Poisson distribution, as did nest encounter frequency, so parametric tests were carried out on square-root transformed data. Dung was distributed patchily in space and time and did not conform to the Poisson distribution, so only non-parametric tests were used for dung data.

Sampling resolution was determined using a parametric formula (cf. Skorupa, 1987):

$$D = 4 (C.V.) / (N)^{0.5} \qquad \text{(Eq. 6.6)}$$

where,

D= minimum % difference in sample mean that indicates a statistical difference.
C. V. = coefficient of variation.
N = number of replicate samples.

Using this formula the difference in the mean encounter rate that indicated a statistical difference was calculated for each species in each site. In addition, differences in encounter rates for each species between sites were tested using the Kruskal-Wallis one-way ANOVA, testing for differences between specific pairs of sites by multiple comparisons as described in Siegel & Castellan (1988), and a one-way ANOVA with Tukey HSD multiple comparisons. $P < 0.05$ was the criterion for statistical significance in all cases, and tests were two-tailed. For details of statistical tests see Siegel & Castellan (1988) and Sokal & Rohlf (1981).

Results.

Pooling of data.

In Site 1 animal sighting data were recorded during both types of census, in both directions on the transect. Since censuses were conducted throughout the year, the effect of sampling date was tested (holding census type and direction constant) for all species sighted, and for primates alone (Friedman two-way ANOVAS: for animal sighting census data heading west considering all species $P < 0.05$; $P > 0.05$ in all other cases). Data for each census type and direction taken on different dates were pooled and directions were tested within survey types for any effects of time of day and sightings by species (for sighting times, Kolmogorov-Smirnov two-sample test, $P < 0.001$ in both cases; for sightings by species, Wilcoxon matched-pairs signed-ranks test, $P > 0.05$ in both cases). Therefore, there was a significant effect of time of day on sightings in opposite census directions. It was considered that this effect was due to actual differences in density along the transect, because for east-west censuses more sightings than were expected were recorded in the late morning and early afternoon, whereas on west-east censuses there were more sightings than expected in the early morning. Data for different directions were combined for the two census types.

Data for the two census types on all transects (for transect 3 the periods before and after logging were treated separately) were tested for differences in sightings by species and any effects of time of day. The expected distribution of sightings was generated assuming the number of sightings per hourly interval was directly proportional to the total time sampled in that interval (for sightings by species: Wilcoxon matched-pairs signed-ranks test, $P > 0.05$ in all cases; for sighting time: Kolmogorov-Smirnov one-sample test, $P < 0.05$ for all species on animal sighting censuses in Site 2 and for primates only on animal sighting censuses in Site 4, all other $P > 0.05$). Detection distances to the first individual' sighted during animal sighting censuses and dung/nest censuses were compared for species for which there was sufficient data, to check that observer efficiency was constant (Kruskal-Wallis one-way ANOVAS, $P > 0.05$ in all cases). Therefore data from the two types of census were lumped.

Detection distances to the first individual sighted, and to the centre of ape nest groups, were compared between sites where sample size permitted. The

Kruskal-Wallis one-way ANOVAS showed $P > 0.05$ in all cases, therefore sightings for all transects were combined to calculate species-specific effective distances. To check for differences in animal behaviour before arid after logging the frequency of primate male loud calls (number heard per hour of observation in hourly intervals) in Site 3 before and after exploitation were compared and found not to differ (Wilcoxon matched-pairs signed-ranks test, $P > 0.05$). No differences in behaviour were seen during casual observations whilst not censusing.

Density estimates

Table 6.2 summarises the estimated effective distances and group spreads for animals sighted in groups, and their derived sample widths. For species sighted singly, and for dung deposits and nest groups the sample width was double the effective distance. Since ground vegetation differed between sites, effective distances of dung deposits were calculated separately for each site (Table *6.2).*

Dung distribution data indicated that all species used the transect lines as a path to some extent, as sightings became skewed towards the first 0.5m from the mid-line after the first few months of data collection. This was especially so in Sites 1 and 5, where dense ground vegetation hampered movement off paths. Transects did not come to resemble game trails, suggesting that they only affected localised movements, so effective distances were calculated using data for dung deposited at least 50cm from the mid-line (the transect was about 1m wide).

Table 6.2: Estimates of average group spread and detection distance in metres.

Species	Group Spread	Detection Distance					
		Indivs.	Groups	Nests	Dung Site Number		
					1&5	2	3&4
Cercopithecus nictitans	60	40	85				
Cercopithecus pogonias	30		75				
Cercopithecus cephus	30		50				
Cercocebus albigena	60		85				
Colobus satanus	30		75				
Gorilla gorilla	50		60	20	2.5	3.5	3.5
Pan troglodytes	10		45	35	2	2.75	2.75
Mandrillus sphinx	250	25	200				
Loxodonta africana	20		50		4	5	5
Potamochaerus porcus	60		100		2.5	3.5	3.5
Red Duikers		20			2.25	2.75	3
Cephalophus monticola		20			1.50	2.00	2.00
Cephalophus sylvicultor		20			2.5	4	4
Syncerus caffer		20			3	4.5	4.5
Squirrels		10					

Of 1164 elephant dung piles monitored every two weeks until they disappeared, 1151 (99%) survived to three weeks, and 1025 *(88%)* to five weeks. Therefore, it was assumed that all elephant dung piles deposited each month survived to be counted, as the number that disappeared was small. For gorilla dung the average duration of fresh deposits monitored weekly was 23.5 (N=28) and 16.3 (N=30) days in dry and wet seasons respectively, {maximum duration was assumed to be four weeks as dung piles were counted only once if present in successive months). Dung counts were therefore assumed to be representative of the previous 23.5 and 16.3 days in dry (June, July and August) and wet months respectively, and counts during the dry season were scaled down accordingly by a factor of 16.3/23.5. Of 15 piles of red duiker pellets monitored daily in the wet season the average survival time was 4.3 days, so each census was considered to represent this time period. Dry season dung counts were not included in the analysis because many deposits survived through two or three censuses and it was not possible to determine reliably which had been counted previously because encounter rates increased to more than 100 dung piles per transect. Dung decay experiments were not undertaken for other species and mean dung survival was estimated. Of 57 and 84 fresh gorilla and chimpanzee nest sites monitored from transects, three and two respectively disappeared within one month. Any fresh nest sites encountered on transects between monthly censuses were noted and mapped; one chimpanzee nest site seen on a primate census in Site 1 had disappeared by the time the monthly nest count was undertaken, but this was exceptional, and it was assumed that all visible nest sites constructed in the previous month were detected on censuses.

Table 6.3 lists defecation rates from the literature (and estimates where none was available). Animal densities were calculated using formula (6.5), but for ungulates and ape dung it was modified to:

$$D = Dd/\ F \times S \qquad (6.7)$$

Where, S is the survival time in days (for elephant dung and ape nests S □ 30, the time in days between successive censuses).

Table 6.4 gives data on average group sizes of the species studied, the weights of adult males and females and the weight of an 'average individual' used for calculation of biomass.

Table 6.3: Defecation rates of species censused on dung counts.

Species	**Defecation Rate** (±95% confidence limit)	**Source**
Loxodonta africana	17.0	Wing & Buss (1970)
	18.0	Merz (1986b)
	17.4 ± 11.2	Coe (1972)
	16.2	Plumptre (1991)
Syncerus caffer	5.1 ± 0.5	Plumptre (1991)
Cephalophus monticola	4.9 ± 1.3	Koster & Hart (1988)
Red duikers	4.4 ± 1.3	Koster & Hart (1988)
[1] *Gorilla gorilla*	≥5	Schaller (1963)
	4-5	C.E.G. Tutin, (pers. comm.)
[1] *Pan troglodytes*	4-5	Assumed to be as *G. gorilla*
Potamochaerus porcus	5	Estimate

[1] = upper value used for density and biomass calculations.

Table 6.5 gives the group and individual densities calculated from sighting frequencies using hazard-rate, Fourier and modified Whitesides' methods for species for which there were at least 25 sightings. Densities calculated from animal sighting data by hazard-rate, Fourier and Whitesides' methods were comparable, although the Fourier model was particularly sensitive to sightings that occurred unusually far from the transect, hence the discrepancy in estimates for ***C nictitans*** Table 6.6 gives dung densities estimated by the three methods, and figures for the Whitesides' method adjusted for differences in defecation and dung decay rates in wet and dry seasons. Hazard-rate and Fourier model estimations were affected **by** the skewed dung distribution that resulted from animals' use of transects. individual densities were calculated using the Whitesides' method.

Table 6.4: Average group sizes and individual weights.

Species	**Group Size**	**Weight (kg)** Ad. Male	 Ad. Female	 Average
Cercopithecus nictitans	13.5 ± 2.1	6.3	4.3	3.2
Cercopithecus pogonias	12.6 ± 2.0	4.4	2.9	2.2
Cercopithecus cephus	9.6 ± 2.2	4.1	2.7	2.0
Cercocebus albigena	18.9 ± 2.3	6-11	4-7	4.1
Colobus satanus	12.1 ± 1.2	10-12	8-11	8.4
Gorilla gorilla	5.3 ± 0.8	140-200	70-110	85.0
Pan troglodytes	2.4 ± 0.4	40-55	30-50	31.9
Mandrillus sphinx	150[1]-400e	20-30	10-15	10.2
Loxodonta africana	2.8 ± 0.4	2800-3200	1800-2500	1741.7
Potamochoerus porcus	25-80	45-120	4-120	61.9
Cephalophus leucogaster	1.1 ± 0.1	16.7	16.7	13.9
Cephalophus dorsalis	1.1 ± 0.1	21.1	21.1	17.9
Cephalophus callipygus	1.1 ± 0.1	17.7	17.7	14.8
C. monticola	1.25 ± 0.4	4.7	4.7	3.9
C. sylvicultor	1.0	68	68	56.7
Hyemoschus aquaticus		10-15	10-15	10.4
Neotragus batesi		4-5	4-5	3.8
Syncerus caffer	2.5	250-320	250-320	237.5
Squirrels:	1.1 ± 0.1			
Protoxerus stangeri		0.54-1.00	0.54-1.00	0.6
Epixerus wilsoni				[2]0.4
Heliosciurus rufobrachium		0.25-0.40	0.25-0.40	0.3
Funisciurus lemniscatus		0.10-0.15	0.10-0.15	0.1
Myosciurus pumilio				

Group sizes calculated from Lopé data or estimated (e).

[1]= lower value used for biomass calculations. [2]= estimate as no figure available.

Weights from: Gautier-Hion & Gautier (1974); Haltenorth & Diller (1977); Harrison (1988b); Koster & Hart (1988). See text for protocol for calculation of average weight.

Table 6.5: Densities calculated using hazard-rate, Fourier and Whiteside's methods.

Species	**Site**	**Group Density (km^{-2})**			**Individual Density (Km^{-2})**		
		[1]Hazard	[1]Fourier	[2]Whitesides'	[1]Hazard	[1]Fourier	Whitesides'
Cercopithecus nictitans	1	1.2-2.0	0.7-2.2	1.4-2.2	23.9 ± 6.3	19.4 ± 10.0	22.9
	3	0.7-2.2	0-1.6	0.8-1.7	15.9 ± 9.7	7.8 ± 13.2	15.9
	4	1.4-2.6	0.0-1.7	1.5-2.5	25.7 ± 9.2	9.4 ± 13.6	25.2
	5	0.9-2.0	0.4-1.5	1.0-1.8	18.2 ± 7.7	5.8 ± 39.6	17.5
Cercocebus albigena	1	0.2-1.1	0.2-0.8	0.4-0.7	10.0 ± 7.7	10.2 ± 8.1	10.1
Colobus satanus	1	0.6-1.9	0.7 - 1.7	1.0-1.7	12.7 ± 7.4	14.7 ± 6.2	15.1
	2	0.7-2.2	0.7-2.0	0.9-1.6	15.3 ± 8.9	16.4 ± 7.6	14.0
Gorilla gorilla (n)	1	2.2-8.2	0.8-8.1	3.9-8.1	0.8 ± 0.5	0.8 ± 0.6	1.0
Pan troglodytes (n)	1	7.1-16.6	6.2-12.3	4.2-10.5	0.9 ±1.3	0.7 ± 1.1	0.7
	3	7.9-24.4	0.8-22.0	11.7-21.6	1.1 ± 0.6	0.8 ± 1.9	1.3
	4	4.1-10.4	3.8-9.9	4.8-7.8	0.5 ± 1.3	0.5 ± 1.0	0.5
	5	2.6-9.2	1.9-8.6	2.0-6.0	0.2 ± 1.1	0.4 ± 0.3	0.3
Loxodonta africana	1	0.5-1.7	0.4-1.7	0.8-1.7	2.7 ± 1.6	2.9 ± 1.9	3.1
Cephalophus spp.	1	2.0-10.6	2.3-8.4	2.3-4.7	5.1 ± 4.3	5.4 ± 4.1	3.5
	2	3.4-5.8	1.6-8.2	3.8-7.5	4.9 ± 1.4	5.4 ± 3.5	5.7
	4	6.6-21.3	5.5-12.5	5.2-9.7	13.1 ± 7.7	9.9 ± 3.8	7.6
	5	3.7-12.6	3.5-10.2	3.6-7.1	6.7 ± 4.6	7.5 ± 3.6	5.4
Squirrels	1	3.3-17.8	3.4-11.8	6.9-12.9	8.4 ± 7.2	8.4 ± 3.6	10.0

(n) = nest groups km^{-2} month^{-1}; [1] - with 95% confidence intervals. [2] - with range (see text for details).

Table 6.6: Dung densities calculated using hazard-rate, Fourier and Whitesides' methods.

Species	**Site**	**Dung Density (km^{-2})**			
		[1]Hazard	[1]Fourier	[2]Whitesides'	[2]Whitesides' adjusted.
Gorilla gorilla (d)	1	227-773	170-380	133-233	117-199
	5	185-753	123-658	125-306	106-250
Pan troglodytes (d)	1	41-314	37-220	43-86	34-64
Loxodonta africana (d)	1	1170-1980	1098-1746	751-1010	751-1010
	2	297-911	211-716	227-316	227-316
	3	40-232	12-201	109-213	109-213
	3a	177-1661	33-311	83-131	83-131
	4	259-492	275-542	189-269	189-269
	5	704-1506	570-980	329-454	329-454
Cephalophus monticola (d)	1	252-305	53-424	46-102	4-38
	2	267-2746	84-364	54-109	15-51
Red duiker (d)	1	702-2171	620-2202	531-1060	232-398
	2	469-2110	600-963	202-413	69-126
	3	505-4683	0-1139	311-620	63-113
	3a	167-773	71-678	174-286	51-125
	4	*	184-1621	303-632	41-87
	5	1648-10370	132-4996	771-2040	140-286
Cephalophus sylvicultor (d)	1	299-963	218-525	110-196	62-118
Potamochoerus porcus (d)	4	98-565	58-311	66-127	28-56

* - programme overload; [1] - with 95% confidence intervals. [2] - with range (see text for details).

Table 6.7 summarises the census data for the five sites, giving average encounter rates / census for groups and individual animals sighted, dung deposits, and nest sites.

Table 6.7: Average sighting frequencies / census.

Species	**Average encounter rate (sightings / census)**					
	Site 1	Site 2	Site 3	Site 3a	Site 4	Site 5
C. nictitans	1.54 $^{\underline{1}}$	0.46 $^{\underline{1}23\underline{45}}$	1.15 $^{(2)}$	0.89 $^{(3)}$	1.67 $^{\underline{4}}$	1.19 $^{(\underline{5})}$
C. nictitans (s)	0.19	0.17	0.05	0.00	0.10	0.08
C. pogonias	0.35	0.14 ^{1}	0.40	0.28	0.30	0.46 $^{(1)}$
C. cephus	0.33 $^{(1)}$	0.09 $^{1\underline{2}}$	0.20	0.22	0.50 $^{(\underline{2})}$	0.23
C. cephus (s)	0.02	0.00	0.00	0.06	0.00	0.00
C. albigena	0.49 $^{(1)}$	0.14 $^{1,2\underline{3}}$	0.40	0.33	0.53 $^{(2)}$	0.69 $^{(\underline{3})}$
C. albigena (s)	0.00	0.06	0.00	0.00	0.07	0.00
C. satanus	0.98 ^{1,2}	0.91	0.30 ^{1}	0.28 ^{2}	0.77	0.85
G. gorilla	0.21	0.11	0.20	0.17	0.13	0.31
G. gorilla (n)	1.04 $^{1,(2)}$	0.58	0.44	0.25 ^{1}	0.35 ^{2}	0.71
G. gorilla (d)	139.90 $^{\underline{1234}}$	23.71 $^{\underline{1}}$	5.71 $^{\underline{25}}$	23.43 $^{\underline{3}}$	18.57 $^{\underline{46}}$	127.20 $^{\underline{56}}$
P. troglodytes	0.14 ^{1}	0.00 $^{\underline{2}}$	0.45 $^{(1\underline{23})}$	0.17	0.03 $^{\underline{3}}$	0.19
P. troglodytes (d)	44.44	4.73	18.18	3.27	3.64	38.00
P. troglodytes (n)	2.81 $^{\underline{1,2}}$	0.75 $^{\underline{1,3,4}}$	4.56 $^{\underline{35}\ (\underline{6})}$	1.00 $^{\underline{2,5}}$	1.90 $^{\underline{4}}$	1.71 $^{(\underline{6})}$
M. sphinx	0.02	0.06	0.10	0.17	0.07	0.00
M. sphinx (s)	0.00	0.03	0.05	0.06	0.13	0.08
L. africana	0.54 $^{1\underline{23}4}$	0.20 ^{1}	0.00 $^{\underline{2}5}$	0.06 $^{\underline{3}6}$	0.17 ^{4}	0.31 ^{5,6}
L. africana (d)	852.6 $^{\underline{1234}}$	254.0 $^{\underline{1}}$	102.2 $^{\underline{2,5}}$	105.0 $^{\underline{3,6}}$	212.0 $^{\underline{4}}$	397.5 $^{\underline{5,6}}$
P. porcus	0.05	0.17	0.05	0.17	0.10	0.04
P. porcus (d)	19.32	23.14	4.86	21.43	42.86	0.00
Cephalophus spp.	0.70	1.11 $^{(\underline{1})}$	0.80	0.64 $^{(\underline{1})}$	1.40	1.04
C. monticola (d)	25.12	34.50	16.50	12.50	21.00	22.00
Red duiker (d)	283.84 $^{\underline{12}}$	86.55 $^{\underline{1}}$	94.33	104.33	72.33 $^{\underline{2}}$	174.22
C. sylvicultor (d)	88.80 $^{\underline{1234}}$	0.00 $^{\underline{1}}$	0.00 $^{\underline{2}}$	3.25 $^{\underline{3}}$	8.25 $^{\underline{4}}$	16.80
Squirrels	0.97	0.96	1.64	0.94	0.96	1.00
S. caffer	12.24	2.89	0.00	0.00	6.67	6.00
S. caffer (d)	0.42	0.13	0.00	0.00	0.30	0.18
Monkeys	3.79 $^{\underline{1}2,\underline{3}}$	1.77 $^{\underline{1,4,5}}$	2.45 $^{(2,7)}$	2.00 $^{\underline{3}6}$	3.77 $^{\underline{4}6,7}$	3.42 $^{\underline{5}}$

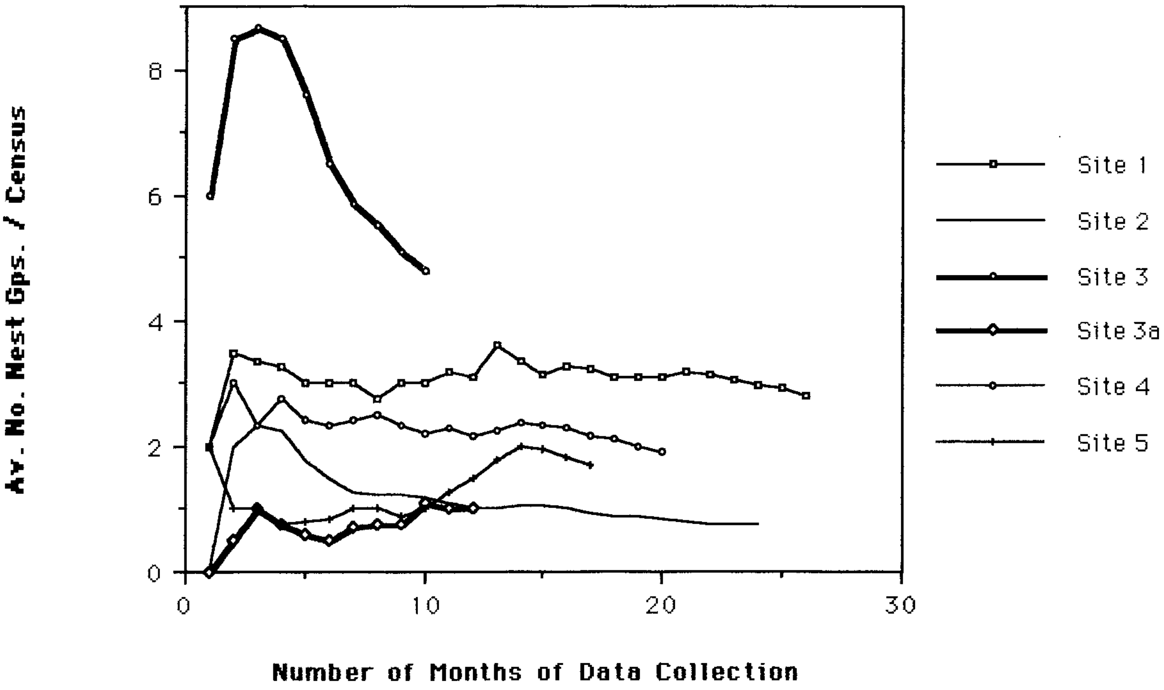
s = solitary, d = dung count (dung deposits km^{-2}), n = nest count (nest groups/census).
See text for explanation of superscripts and underlined species or groups.

Those species (or groups) for which statistical differences in encounter rate were detected are underlined. Pairs of sites where the mean encounter rate was greater than the minimum indicating a statistical difference (Eq. 6.6) are marked with a number (superscript). Resolution differed with the number of censuses conducted, and the encounter rate, so on occasion one site indicated a statistical difference whilst the other (superscript bracketed) did not. Underlined superscripts were also shown to be statistically different by both the Kruskal-Wallis one-way ANOVA and parametric one-way ANOVA (only the former for dung). There was a high degree of concordance between the statistical methods, and where there was sufficient difference in the means but no statistical difference indicated by the ANOVAS, $0.1 > P > 0.05$, suggesting a meaningful biological trend did exist. Statistical differences were detected in at least two sites for most species, and where more than one census method was used for the same species results were similar. Encounter rates were generally high in Sites 1 and 5, high for monkeys in Site 4, and generally low in Sites 2, and 3 before and after logging.

Nest counts showed a statistically significant difference in chimpanzee density in Site 3 after logging, when all three indices of abundance decreased. When the study began chimpanzees were seen regularly, and prolonged bouts of pant-hooting, drumming and excited screaming were heard at least once on most days. At this stage logging was underway about 5km to the north and the noise of chain saws and heavy machinery was audible. Several large excited groups were encountered in the forest. As logging advanced towards the transect vocalisations became less frequent, and only small, quiet groups were seen.

Figure 6.2 shows cumulative plots of average chimp nest encounter rates / census in all sites, with Site 3 divided into two data sets: before and after logging. After initial noise due to small sample sizes, data for Sites 1, 2, 4 and 5 settled close to their final overall averages, as does the data for Site 3 after logging. However, Site 3 had high nest group encounter rates in the first few months of the study, with six, 11, nine and eight fresh nest groups in the first four months respectively, concentrated in the last 2km of the transect, in the area later exploited and closest to logging activities at the time. In all the other sites only one census with 10 fresh nest groups occurred and otherwise counts did not exceed five, and were rarely above three. After the fifth month of the study logging was underway about 1km from the transect and the number of nests (and individuals seen arid heard) decreased. After logging (Site 3a in Figure 6.1) nest encounter rate was stable but low, and comparable to Site 2, where logging had taken place three to four years previously.

Figure 6.1: cumulative average chimp nest group encounter rates.



Tables 6.8 and 6.5 respectively give the density of individuals calculated by the various census techniques and the total estimated biomass, calculated for each species in each site. It was not possible to calculate 95% confidence limits so point estimates are given. Where more than one census method was applied to a species results were generally comparable. For apes, and especially elephants, densities calculated from sighting frequencies tended to be higher than for dung and nests, whilst for duikers densities from sightings were lower than for dung in Sites 1 and 5 but higher in Site 4. There was a great deal of variation between Sites, both in terms of the biomass attained by any given species, and the total biomass. Elephants dominated the biomass, accounting for *82, 72, 25,* 50, *62* and *76%* of total biomass in Sites 1 to 5 respectively. Primates accounted for 9, 13, 35, *26,* 16 and 14% of the total in the five sites.

Table 6.8: Density of individuals calculated by different census techniques.

Species	**Density (Individuals km^{-2})**					
	Site 1	Site 2	Site 3	Site 3a	Site 4	Site 5
Cercopithecus nictitans	23.9	7.0	15.9	15.1	25.7	18.2
* *C. nictitans*	0.5	0.4	0.1		0.3	0.3
Cercopithecus pogonias	5.4	2.3	6.0	4.4	5.8	8.1
Cercopithecus cephus	6.4	1.9	2.8	3.6	9.1	4.4
* *C. cephus*	0.1			0.1		
Cercocebus albigena	10.0	2.8	9.1	6.6	9.2	17.1
* *C. albigena*		0.1			0.1	
Colobus satanus	12.7	15.3	5.9	4.7	13.2	13.1
Gorilla gorilla	1.4	0.9	1.8	1.4	0.8	2.7
Gorilla gorilla (n)	0.8	0.6	0.3	0.3	0.1	0.8
Gorilla gorilla (d)	1.8	0.4	0.1	0.4	0.2	2.0
Pan troglodytes	0.5		2.9	1.5	0.3	1.3
Pan troglodytes (n)	0.9	0.1	1.1	0.2	0.5	0.2
Pan troglodytes (d)	1.3	0.1	0.4	0.2	0.1	1.1
Mandrillus sphinx	1.8	3.8	10.5	12.0	5.3	
* *M. sphinx*		P	0.1	0.4	0.5	0.2
Loxodonta africana	2.7	1.0		0.6	1.1	2.0
Loxodonta africana (d)	1.7	0.5	0.2	0.2	0.4	0.8
Potamochoerus porcus	1.5	5.4	2.5	7.9	3.3	1.8
P. porcus (d)	0.5	0.5	0.1	0.3	0.8	
Cephalophus spp.	5.1	4.9	4.5	3.7	13.1	6.7
Cephalophus monticola (d)	0.9	1.6	1.1	0.8	0.9	1.0
Red duiker (d)	15.7	4.9	4.4	4.7	3.5	10.4
Cephalophus sylvicultor (d)	4.5	0.0	P	0.1	0.3	0.8
Syncerus caffer	0.1				1.1	0.3
Syncerus caffer (d)	0.2	P			0.2	0.1
Squirrels	8.4	10.0	19.1	15.1	12.4	10.0

* = solitaries; (d) = dung counts; (n) = nest counts. P = present at < 0.05 individuals km^{-2}.

Table 6.9: Estimated species biomass for the study sites.

Species	**Estimated Biomass (kg km^{-2})**					
	Site 1	Site 2	Site 3	Site 3a	Site 4	Site 5
Cercopithecus nictitans	79.6	24.9	51.5	45.8	84.3	59.8
Cercopithecus pogonias	11.9	5.1	13.2	8.1	12.8	17.9
Cercopithecus cephus	13.0	3.8	5.6	6.4	18.2	8.8
Cercocebus albigena	41.0	12.3	37.3	25.0	38.6	70.1
Colobus satanus	106.7	128.5	47.8	34.8	106.9	106.5
Mandrillus sphinx	18.4	30.8	110.1	141.1	66.6	4.0
Gorilla gorilla	119.0	52.4	62.3	52.1	29.5	155.8
Pan troglodytes	29.1	3.2	48.9	17.0	9.4	28.4
Sub-total - (diurnal primates)	**418.7**	**238.6**	**376.7**	**330.3**	**366.3**	**451.3**
Loxodonta africana	3831.7	1304.6	174.2	627.0	1319.9	2443.6
Potamochoerus porcus	63.1	183.8	77.4	236.8	125.3	54.2
Cephalophus monticola	3.9	4.8	4.0	4.2	4.6	2.0
Red duikers	132.9	68.1	59.7	43.7	89.5	102.5
Cephalophus sylvicultor	205.8	P	9.4	16.2	76.5	108.7
Hyemochus aquaticus	P				1.8	1.4
Neotragus batesi	P	P	P	P		
Syncerus caffer	33.8	3.9		P	154.4	43.3
Sub-total - (ungulates)	**4271.2**	**1565.2**	**324.7**	**927.9**	**1772.0**	**2755.7**
Squirrels	2.7	3.5	6.9	4.6	3.8	3.9
TOTAL	**4692.6**	**1807.3**	**708.3**	**1262.8**	**2142.1**	**3210.9**

P = present but not recorded on censuses.

Discussion.

Reliability *of biomass estimates*

Line-transect census methods used in this study have been shown to give reasonable density estimates for primates (Whitesides et *al.,* 1988) and ungulates (Koster and Hart, 1988) in tropical rain forests. However, some studies have shown that this is not always the case and have demonstrated consistent over- or under-estimation for some species or groups (e.g., Anon, 1981; Butynski, 1990; Defler and Pintor, 1984). Failure of the technique can result when a study species does not conform to various assumptions (cf., Burnham *et al.,* 1981) fundamental to line transect censusing (e.g., Defler & Pintor, 1984) or because the area censused is wrongly estimated (e.g., Whitesides *et al.,* 1988). Whitesides et al. (1988) discussed the applicability of line-transect sampling for estimation of primate density in rain-forest in West Africa and compared various methods for calculating the area sampled (see also Brockelman & Ali, 1987; Buckland, 1985; Burnham *etal.,* 1981; Heyes & Buckland, 1983; Janson & Terborgh, 1980).

Line-transect censusing is a sampling technique, and like any sample, there will be a certain amount of error in the results. The accuracy, and hence resolution, of the sample will be dependent upon the sampling intensity and the degree of variability between censuses (e.g., Anon, 1981; Janson & Terborgh, 1980; Skorupa, 1988). When censuses rely upon estimation of traces left by an animal to calculate density, rather than sightings of the animals themselves, further sources of error are introduced. For example, to calculate elephant density from the abundance of their droppings one has to estimate the number of droppings produced per day (no easy matter in a tropical rain forest environment where visibility is poor and extended periods of good observation rare) and the length of time for which dung remains detectable (Barnes & Jansen, 1987). Defecation rate can vary with diet and season (e.g., Barnes, 1982; Koster & Hart, 1988), so it is difficult to justify the use of defecation rates obtained in one area to calculate densities in another. Similarly, dung decay rates vary between seasons in response to weather conditions and other factors, such as dung-beetle activity (e.g., Short, 1981; Wiles, 1980). It is preferable to undertake long-term studies which allow actual densities to be determined (c.f., Anon, 1981; Butynski, 1990; Johns, 1985), but where this is not possible line-transect censuses are the best alternative in the tropical rain forest environment, provided their limitations are borne in mind.

In this study three methods of density estimation from census data were used where sample size allowed, and more than one census technique was employed where possible. For monkeys standard primate census techniques were used, and data analyses using hazard-rate, Fourier and modified Whitesides' methods gave similar group densities where sample sizes were sufficiently large to use all three methods (see Table 6.5). Buckland (1985) found that the hazard-rate model was the most versatile of several methods of density estimation from line-transect data, and Whitesides et *al.*, **(1988)** confirmed that it was more reliable than the Fourier model for primate census data. Fourier analysis was found by Whitesides et *al.* to give widely differing results depending on the number of terms used, and the cut-off points chosen, as was the case in this study. The number of individuals was calculated for the hazard-rate, Fourier and Whitesides' methods and results did not differ significantly.

No evidence of differential visibility between sites was found, so lumping sighting data for each species in all sites enabled densities to be calculated using the Whitesides' method for species/sites where sample size was insufficient for hazard-rate analysis. Sampling intensity was sufficient to show statistical differences between two or more sites in abundance of Cercopithecus spp. and C. ***albigena*** but encounter rates for G *gorilla* P. troglodytes and ***M.*** *sphinx* were low, so densities for these species should be regarded as preliminary (but for apes dung and nest data were also available). The same sighting frequency method was used for terrestrial species, and results of the different methods of analysis again corresponded well.

Ape nest sites were detected more often than the animals themselves and sufficient data were obtained for chimpanzee nests in four sites to use hazard-rate and Fourier model analyses. Since censuses were conducted monthly few, if any, nest sites would have disappeared before detection and hence the decay rate was not required in order to calculate densities (cf., Tutin & Fernandez, 1983). Whilst transects did influence the movement of apes (see below) there was no evidence that the location of nest sites was affected. Since sample size for nest counts tended to be larger than animal sighting frequency, they were less prone to sampling error and are likely to have given more accurate ape densities, although in Sites 2, 3 and **4** sample sizes for gorilla nests were also low.

As noted above, after the first few censuses (months) distribution of dung of all species became skewed towards the transect, suggesting that animals defecated more often than expected on the line. This introduced a bias into dung counts (cf. Barnes & Jensen, 1987) which resulted in an over-estimate of dung (and hence animal) density. This skewed distribution resulted in implausibly large estimates from the Hazard-Rate and Fourier models. Transects did not come to resemble well-used game trails, and a transect cut in Site 1 five years before (Williamson, 1988) had no greater proportion of its length as game trails than the new line cut for this study (unpublished datal. Observations of several species suggested that they sometimes deviated somewhat from their line of travel to follow the transect, but would then continue in the original direction. This was particularly so in dense vegetation. There was no evidence of a steady increase in dung counts throughout the study, as would be expected if transects resulted in increased amounts of dung being deposited, so it seems safe to assume that it was the distribution, not the quantity of dung that was altered.

In order to calculate animal densities from dung counts defecation and decay rates must be known. Decay rates were studied *in situ* for most *of* the study species, and were estimated after almost three years field experience for the others. Defecation rates were taken from the literature and may not applicable to animals at Lope, but until such data are available for Lope there is no alternative but to use those for other sites. Despite all the possible sources of error, there was a high degree of concordance between the estimation techniques, and by taking the average where more than one technique was possible large errors were hopefully avoided (cf., Koster and Hart, 1988). The one exception was ***Potamochoerus porcus,*** for which dung counts consistently gave estimates that were a factor of 10 or more below those for sighting frequencies. Defecation rate and dung decay rates were estimated for this species, and may therefore have been incorrect. In addition, it was noted that dung piles were generally clumped, and often on ridge tops, which were favoured resting places, but which were not' well represented on transects. Stolba & Wood-Gush (1989) found domestic pigs in a semi-free ranging situation did not defecate randomly in a large exclosure. Therefore, biomasses calculated from sighting and dung data are likely to be under-estimates for this species. For elephants, densities from sighting frequencies were consistently *60-300%* higher than dung counts (except for Site *3,* where no elephants were seen from the transect before logging). Preliminary data suggest that elephants in Lope may not defecate as often as 17 times day-1 (SEGC, unpublished data), which might account for this discrepancy.

Logging and mammals.

Changes in vegetation structure and composition due to logging will affect the ecology of rain forest wildlife to some extent: Species that depend upon a food source that declines as a result of logging are likely to decrease in density, whilst species that can utilise secondary vegetation may benefit. However, Johns (1989) pointed out that variation in primate densities between sites may be greater than intra-site variation over time in response to logging, and suggested that long-term studies were necessary to obtain a clear picture of the changes that occur after logging. This is a problem for studies such as this one, which aim to assess responses to logging by looking at several sites with different histories of exploitation, although Skorupa (1988) successfully used this approach in Kibale, Uganda, to assess the responses of rain forest primates to logging.

Johns and Skorupa (1986) reviewed data on the responses of rain forest primates to habitat disturbance and found a trend for decreased density of large bodied frugivorous species in disturbed habitats. The present study was the first detailed investigation of the effects of logging in the forests of Central Africa, but results of several other studies include species represented in the Lopé mammalian community. Skorupa (1988) studied a community of seven diurnal primates and found that five (including ***Pan* troglodytes** and *Cercocebus albigena)* showed statistically significant declines in numbers after heavy logging (>50% and >40% removal of basal area and canopy cover respectively), one species increased, and one showed no statistical change. Only one species *(Cercopithecus* l'hoesti) showed a significant decline in response to light logging (>25% and *>20%* loss of basal area and canopy cover respectively). McKey (cited in Oates 1977) reported decreased numbers of Colobus *satanus* in logged forest, and suggested that this was because rare trees whose seeds were important in the diet became even rarer after logging. Tutin & Fernandez **(1983)** conducted a nationwide census of Pan*i* troglodytes and *6orilla g. gorilla* in Gabon and reported decreased densities of *P* i. *troglodytes* in logged forest, particularly areas that had recently (<2 years) been exploited. G. ***g*** *gorilla* densities were lower in recently logged forest, but showed little difference in areas logged more than two years previously. Barnes *et* **al.** (unpublished manuscript) conducted elephant dung counts in logged and unlogged forests in Gabon and found no differences in density, although Olivier (1 978) found densities of the Asian elephant, *Elephas maximus,* in logged rain forest in Malaya to be double those in undisturbed areas.

In order to assess statistical differences in animal density between different areas of rain forest (or temporally in the same area) sampling resolution must be at least equal to the differences that occur (c.f., Anon. 1981). The resolution is dependent on the coefficient of variation of encounter rates and upon the sample size (number of censuses conducted). Skorupa 11988) obtained an average resolution of ±45% in Kibale for 25–27 census repetitions. Primate biomass in Lopé was about 10–20% of that in Kibale (cf. Struhsaker, 1975) and 18 - 43 censuses were undertaken in the different sites. Resolution was best for C. *nictitans* in site 4, for which a 31% difference in mean encounter rate indicated a statistical difference, but for other species resolution was often above 100%, due to low encounter rates and high numbers of censuses when no groups were sighted. Resolution for dung counts could not be calculated. This low sensitivity to differences was unavoidable, since for some of the primate species over 200 censuses would have been necessary in each site to achieve a resolution of ***50%,*** and over 800 for 25% resolution (cf. Anon., 1981; Janson & Terborgh, 1980; Skorupa 1987). Despite this, differences in encounter rates (and hence densities) were detected for most species between at least two sites. However, it should be noted that due to low sampling resolution, significant differences between sites (and/or after logging) would not have been detected statistically.

The only species whose density was found to differ significantly directly after logging was *P troglodytes* In site 3 average nest group counts after logging were statistically lower than the average before logging (at 22% of the pre-logging figure), and both sighting frequency and dung counts indicated a decline in numbers. Site 2, which was adjacent to Site 3, had been logged three years before the start of this study and had the lowest nest encounter rate of all the sites. Of 48 nests encountered in 15 nest groups, only 7 (4 nest groups) were within the area that had been exploited systematically. Densities in forest logged 10-15 years previously (Site 4) were statistically higher than in Site 2, and since Site 4 was in a similar forest type it is perhaps safe to assume that densities were beginning to recover after this period, which would be consistent with the findings of Tutin & Fernandez (1983). Densities in Site 1 were significantly higher than in Sites 2 and 3a (after logging), but as it was in a different forest type direct comparisons can only be made with caution. In Site 5, the unlogged control, densities were lower than in Site 1 (but not statistically significant). As noted in Chapter 2, logging operations had approached the bottom 1.5 km of this transect, and of 66 nests found in 29 nest groups, only four nests (three groups) were found in this zone, suggesting that logging had affected chimpanzees, even though the forest itself had not been altered physically. Other studies have found decreased chimpanzee densities after logging (Skorupa, 1987; Struhsaker, 1975 [both in Kibalel; Tutin & Fernandez, 1983) indicating that this species is particularly susceptible to disturbance, even though the range of habitats in which it occurs suggests that it should be highly adaptable (Johns & Skorupa, 1987). One explanation for this might be that, unlike gorillas, which adopt a more folivorous diet during periods of low fruit availability, chimpanzees try to maintain the fruit content of their diet Rutin *et al.*, 1991a) and therefore, even relatively low changes in fruit production at this time might have a serious impact on their energy budgets.

However, the immediate response of chimpanzee densities to logging suggested that they were avoiding logged areas and forest adjacent to logging operations. Chimpanzees live in communities which defend territories (e.g., Goodall, 1968), so emigration away from an area that was being logged would bring communities into conflict. Densities in Site 3 were unusually high when this study began (average nest encounter rate for Site 3 before logging corresponded to a density of about 1.5 individuals km-2, well above that for the other sites, or the average for unexploited forest in Gabon [Tutin & Fernandez, 1983]) and Figure 6.1 may illustrate an increased density due to chimpanzees which had moved away from the advancing logging operation to the north. Large excited groups encountered at this time might have formed as a result of conflict between the displaced and resident communities.

The remaining results illustrate the problems encountered when trying to infer effects of logging from animal abundances in different areas. Had the study been based at SOFORGA and involved several sites in the same forest types as Sites 2 and 3, the general decline in densities indicated for *C. nictitans*, *C. pogonias* and *C. albigena* (Table 3) between Site 3 before and after logging and Site 2 might have been shown to be statistically significant, as might increases in

C. *satanus, G. gorilla* and **L. africana** densities in Site 2. Such results would not have been unexpected, but any differences that occur were probably due to natural differences in forest composition, not changes due to logging (see below). However, data from the other sites suggest that, except for P. ***troglodytes*** there was no simple relationship between logging and mammalian biomass in Lope. This was due, in part, to the fact that logging was low intensity and the resulting damage was correspondingly low (Chapter **4).** In addition, the major timber species, ***Aucoumea Klaineana,*** which represented 64% of trees cut, was not an important food for the animal species considered here (C. E. G. Tutin, personal communication), although many of the lesser commercial species were important, and if logging intensifies in the future the picture may be altered. In addition, species likely to play a keystone role during the major dry season were not generally selected by loggers at SOFORGA (Chapter **3).** *Milicia excelsa,* the bark of which is an important food for gorillas at this time of year (Tutin et *al,* 1991a), is logged wherever it occurs in Gabon (Wilks, 1990), but was rare at SOFORGA. Changes in reproductive success, and hence density, are unlikely to be detected immediately (cf. Struhsaker, 1976). They are likely to be subtle, and may not occur until a future ecological bottle-neck, such as the famine reported by Foster (1982b) on Barro Colorado Island.

Comparison between Sites

No species other than the chimpanzee showed a discernible change in density in response to lagging disturbance, although it is likely that the high biomass of buffalo in Site 4 was due to their penetrating the forest along old logging roads which connected this site to adjoining savanna areas (cf. Prins and Reitsma, 1989; personal observation). The three sites where buffalo attained a biomass of more than 30kg km^{-2} were all reasonably close to savanna areas (see Figure 1), where' buffalo densities were higher than in the forest (SEGC, unpublished datal. Densities of *Cephalophus sylvicultor* which also used savanna vegetation, were also elevated in these sites.

Primate biomass was dominated by Colobus **satanus,** *Cercopithecus nictitans Mandrillus sphinx* and apes. Mandrillus *sphinx* were generally encountered in large groups which occasionally exceeded 400 individuals (SEGC, unpublished datal, but these encounters were rare, and census data were based on only 10 groups and nine lone males. In Cite 5 no groups were seen during censuses, but on a number of occasions groups were encountered when returning from a census or when undertaking other work on the transect. Preliminary data from SEGC suggest that *Mandrillus sphinx* have large home ranges, and therefore differences in encounter rate in a restricted area are unlikely to be meaningful (SEGC, unpublished data - see also Harrison, 1988b). For this species it might be sensible to divide the total estimated biomass equally between the six sites, as apparent differences were probably due to inadequate sampling intensity. Hence, each site should perhaps be considered to have 61.8 kg km-^{2}.

Gorilla densities recorded in this study were comparable to those elsewhere in the range of the western lowland sub-species (e.g., Carroll, 1988; Tutin & Fernandez, 1983) and to densities of the eastern lowland and mountain sub-species (see Plumptre, 1991). The feeding ecology of gorillas has been being studied for the last eight years in Lope (e.g., Tutin *et al.,* 1991a; Williamson *et al.,* 1990). Herbaceous plants in the families Marantaceae and Zingiberaceae are an important part of the diet, and some of these species play a keystone role *(sensu* Leighton and Leighton, 1983) in their diet. Sites 1 and 5 were located in 'Marantaceae forest', where densities of these important foods were high (Rogers and Williamson, 1987; Williamson, 1988 - see also Chapter *2)* and this probably explained the higher biomass of gorillas in these two sites. In addition, trees in the genus ***Uapaca,*** which occurred at unusually high densities close to the rivers that flowed through Cite 5, caused increased densities of gorillas at times when ripe fruits were being produced. There are presently insufficient data on the feeding ecology of other primate species censused to attempt to explain population differences between sites (cf., Skorupa, 1988) but such data are presently being collected IR. Ham, personal communication) and this may be possible in the future.

Elephants dominated the biomass, and differences in total biomass for the sites were largely due to differences in elephant densities. Forest elephant densities in Lopé change markedly throughout the year (Chapter **5),** but biomasses reported here were based on at least 17 months census data, so should not be biased by these movements. Densities were highest in Sites 1 and 5, where, as for gorillas, abundant Marantaceae and Zingiberaceae were important foods (Chapter 5). Elephants did use adjacent savanna areas, but these did not appear to be a favoured habitat (Chapter *5).* In Site 2 elephant densities were high during three months when a favoured food, the ripe fruit of the emergent tree species Sacoglottis gabonensis, was available, but during the rest of the year densities were comparable to those in adjacent Cite 3.

As for ***Mandrillus*** sphinx, densities for Potamochoerus porcus were based on a limited number of sightings (and few dung piles) and differences may again be due to insufficient sampling intensity. It was noted in Site 4 that encounters with P *porcus* groups were particularly frequent when a common tree species, ***Coula edulis,*** was dropping ripe nuts which were eaten in large quantities, but this did not show up in census data since auditions and encounters were not generally during censuses. Otherwise, there were no differences in overall encounters between sites, and an average figure of 123.4 kg km-1 for each site might be more appropriate.

Comparisons with other areas

Densities of primates recorded in this study were lower than in north-east Gabon (Gautier and Gautier-Hion, 1969; Gautier-Hion and Gautier, 1474; Sourd, 1983 - summarised in Harrison and Hladik, 1986) and for a different study site in Lope, situated about 5km northeast of Site 4 (Harrison and Hladik, 1986), where total estimated primate biomass came to 445-615 and 575-875 kg km-^{2} respectively. However, these sites were selected specifically for primate studies, presumably because primates were well represented, and this can lead to over-estimates of representative primate abundance (Butynski, 1990). Oates *et al.,* (1990) reviewed available data and discussed the reasons for differences in primate biomass for sites in Africa and elsewhere. They concluded that species composition, seasonal behaviour and structural heterogeneity of vegetation interact with soil conditions, other elements of the fauna, and historical factors to influence the structure and functioning of primate communities. In Africa, and indeed elsewhere, much of the variation in primate biomass is due to differences in abundance of colobine species (Oates *et al.,* 1990) which attain a biomass of up to 1875-2948 kg km-2 in Kibale, Uganda (Struhsaker, 1975). In Lopé only *Colobus* satanus occurs, and densities of this species do not approach those attained by other colobines in some African forests (Bourlière 1985; Oates *et al.,* 1990; Struhsaker, 1975).

Butynski (1990) studied two populations of Cercopithecus mitis in Kibale and concluded that marked differences in population densities in two areas 10-15 km apart were probably due to an unknown historical event (such as disease), as one population seemed to be food limited whilst the second was well below carrying capacity. Carrying capacity itself is difficult to assess because tropical rain forest plants show marked seasonal changes in production (e.g., Foster, 1982a; Frankie et **al.,** 1974; Gautier-Hion *et* **al.,** 1985a; Raemaekers et **al.,** 1980; Terborgh, 1983 - see also Chapter 3) and production patterns vary between years (e.g., Tutin et **al.,** 1991a; for an extreme example see Foster 1982b). Detailed, long-term community studies will have to be undertaken if explanations for observed differences are to be found.

Elephant densities in African forests average about 0.2-0.4km-^{2}, although in some places numbers are higher (Barnes et **al.,** unpublished manuscript; Fay, 1991; Merz, 1986a, 1986b; Roth et *al.,* 1984; Short, 1983). Even at these comparatively low densities elephants represent a major portion of the mammalian biomass (Prins and Reitsma, 1989). The density recorded in Site 1 is higher than that attained in many savanna areas (see Douglas-Hamilton, 19721, where mammalian biomass is generally higher than for rain forest (see below).

Other terrestrial species in Lope were less abundant. Densities of duikers were low: In northeast Gabon *Hyemoschus* ***aquaticus*** occurred at densities of 7.7-28.0 km-^{2} (Dubost, 1978) and Cephalophus callipygus, C. *dorsalis* and C. *monticola* occurred at densities of 25, 19 and 62-78 km-^{2} respectively (Dubost, 19791, well above the numbers present in Lope. Wilkie and Finn (1991l recorded similarly high densities in Ituri, Zaire, where C. monticola and red duikers occurred at densities of 61 and 81 km-^{2} in mature forest, although Koster and Hart (1988), also working in Ituri, reported densities of 10-16 and 5-10 for small and large duikers respectively in forest where hunting pressure was low. Other workers in African rain forests have found densities even lower than those at Lopé Collins, (cited in Delaney and Happold, 1979) gave a figure of 5 kg km-^{2} for Ghana; and Prins and Reitsma (1989) recorded 17 kg km-2 It is possible that low densities at Lopé were due to competition with elephants, which eat large quantities of fallen fruit (Chapter *5)* that might otherwise be consumed by duikers (cf., Feer, 1989). Elephant densities were low in Dubost's study site (Gautier-Hion et **al.,** 1985a) and in Ituri (J.& T. Hart, personal communication), and duiker biomass in these areas would be equivalent to that of elephants in some of the Lope sites. However, densities quoted for Ituri by Koster and Hart 11988) and Wilkie and Finn (1991) differ by a factor of 5–10 and no explanation for this difference was offered by the latter authors despite reference to the former work. Experience in Lopé suggests that the figure of 21 days residence for duiker pellets in the dry season used **by** Wilkie and Finn may be an under-estimate, which would result in over-estimation of duiker numbers.

There are few comparable data for total biomass of rain forest mammal communities. Prins and Reitsma (1989) estimated the biomass of mammals weighing above about 5009, in a lowland rain forest in south-western Gabon, to be 1050 kg km-^{2}, of which elephants and primates made up 52 and 24% respectively. However, their study was short-term and methods relied to a great extent on intuition and extrapolations from other areas, and these data should be treated as preliminary. Thomas (1991) estimated primate biomass in Ituri at 709.6 kg km-2, which indicates that biomass for this site would **be** higher (see above).

Terborgh (1983) estimated total frugivore biomass for Cocha Cashu, Peru, at 1600 kg km-2, including 1400 kg km-^{2} for mammals. Primates accounted for 650 kg km-^{2} (46% of the total for mammals) and the remainder comprised: Marsupials (60 kg km-2); bats (75); procynoids (1 10); rodents *(230)* and peccaries (230). Comparable data for mammalian frugivores are available for two other sites in South America: Guatapo, Venezuela (Eisenberg *et al.,* 1979) and Barro Colorado Island, Panama (Eisenberg and Thorington, 1973). At Guatapo primates accounted for 167 kg km-2 26% of the total of 635 **kg** km-^{2}, and the remainder was : Marsupials I62 **kg** km-2); procyonids (18); rodents (354) and peccaries (34). At Barro Colorado primates made up 421 kg km-2, 29% of the total of 1444 kg km-2 and the remainder was: Marsupials (110 kg km-2) ; procyonids (120); rodents (640); and peccaries (153). Prins and Reitsma (1989) calculated biomass estimates from densities published by Balakrishnan (1984) for tropical evergreen rain forest in south India, and Wilson and Johns (1982) for mammals in Borneo. In the Balakrishnan study area biomass came to 1200 kg **km-2,** of which 77% was elephants and only 1% primates, whilst in Borneo biomass came to 2000 kg km-^{2} (50% pigs, 10% primates and the remainder mostly deer).

Plumptre (1991) found biomass in the Parc National des Volcans in Rwanda to vary between 10–51 kg ha-1 depending on habitat type, averaging 31 kg ha-1 (3100 kg km-2), which is comparable to the average for terrestrial mammals in the Marantaceae forest of Sites 1 and 5 in Lope. Bushbuck and buffalo accounted for 85% of the total. This area was a mosaic of montane and bamboo forest, with more open meadow and dense herbaceous vegetation. Biomass in African savanna ecosystems tends to be significantly greater than that in rain forests (see Bell, 1982; Coe *et al.*, 1976; Owen-Smith, 1988), and biomass of large herbivores may exceed 20,000 kg km-^{2}(Laws *et al.*, 1975; Owen-Smith, 1988: from data in Mwalyosi, 1977). However, biomass in Lope is higher than that found in many savanna areas (cf., Owen-Smith, 1988). High biomass in Marantaceae forest in Lopé may reflect increased plant productivity at ground level, together with the structural complexity of the forest vegetation. The biomass in Site 1 is the highest recorded in any tropical rain forest.

Data from this study show that some areas of tropical rain forest can support a large mammalian biomass. If 100-120 kg were added to biomasses for the species censused in this study, to allow for those for which data were not collected, such as carnivores, nocturnal primates and rodents (cf., Bourliere 1985; Happold, 1977; Prins and Reitsma, 1989) biomass in Site 1 would be about 4900 kg km-2. Since sites were chosen on the basis of past logging regime and not because they possessed rich animal faunas, results are likely to be truly representative of forest in Lope (cf., Butynski, 1990). They demonstrate the variability that exists within tropical rain forest faunas, even within quite localised areas (see also Emmons, 1984) and emphasise Prins and Reitsma's (1989) statement that elephants play a key role in the functioning of African rain forests (see also Kortlandt, 1984; Western, 1989; Wing and Buss, 1970). If the contribution of elephants is subtracted, biomass in Lopé would be similar to that in South America (cf., Eisenberg and Thorington, 1973; Eisenberg ***etal.,*** 1979; Terborgh, 1983) suggesting that no species was able to fill the niche left after the extinction there of the Pleistocene megafauna (cf. Janzen and Martin, 1982).

Some of the inter-site variability described here could be explained by differences in forest structure and composition, or logging history, but many questions remain. Before reasons for differences between areas can be understood there is a need for more long-term community level studies, and further estimates of animal biomass in tropical rain forests around the world. Such studies should be considered a priority considering the current background of habitat loss, as the survival of many rain forest species may depend upon our being able to manipulate the carrying capacity of limited protected areas in the near future.