Population Census of the Chimpanzees in the Kalinzu Forest, Uganda: Comparison Between Methods with Nest Counts

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ABSTRACT. The population of chimpanzees in the Kalinzu Forest, Uganda was censused with nest counts using the line-transect method. Four methods were examined to estimate density. The estimated densities, ranging from 2.0 to 4.7 chimpanzees per km^2, all indicated a high population density, in comparison with other chimpanzee habitats. Moreover, the density in the logged area of the Kalinzu Forest was higher than that in the unlogged area. Several factors are thought to contribute to the high density in the Kalinzu Forest. Notable are the mosaic forest structure dominated by mature forest with patches of logged areas, selective logging of non-food tree species of chimpanzees, and low hunting pressure. These results suggest that selective logging may be a practical means of primate conservation in places where timbers are exploited.

Key Words: Chimpanzee; Population census; Nest count; The Kalinzu Forest, Uganda.

INTRODUCTION

Population density of chimpanzees is best assessed via intensive long-term studies (SKORUPA, 1987). However, only short-term surveys can be afforded in many cases, in particular during a preliminary survey. One of the most practical methods to estimate the density of chimpanzees is nest counting using the line-transect method. Since it requires neither a large investment of time (GHIGLIERI, 1984a) nor habituation of chimpanzees, several studies have adopted this method (KANO, 1972; ANDERSON & WILLIAMSON, 1983; GHIGLIERI, 1984a; TUTIN & FERNANDEZ, 1984; CARROLL, 1986; HOPPE-DOMINIK, 1991; IHOBE, 1993; KANO & ASATO, in press: PLUMPTRE & REYNOLDS, in press a, b).

There are some small differences among the methods used in each study. In this study, I compare four methods: the first one was developed by GATES et al. (1968) and is a basic model for line transect sampling; the second was developed by GHIGLIERI (1984a) for chimpanzee nest censuses; the third was a modification of GHIGLIERI's method by TUTIN and FERNANDEZ (1984); and the last method was developed in the present study.

This study also compared estimated densities between logged and unlogged areas in the Kalinzu Forest. As it is difficult to protect all tropical forests from exploitation, land management by selective logging of trees may serve as an alternative that provides economic output and reasonable conservation of primate habitat (SKORUPA, 1986, 1987; JOHNS & SKORUPA, 1987). Several studies have focused on this topic (STRUHSAKER, 1975; ANDERSON & WILLIAMSON, 1983; TUTIN & FERNANDEZ, 1984; SKORUPA, 1986; JOHNS & SKORUPA, 1987; HOWARD, 1991), and most of these studies revealed that the population density of chimpanzees was lower in logged forests than in unlogged forests. This study examines the estimated densities of chimpanzees in both logged and unlogged areas in the Kalinzu Forest in order to compare the carrying capacities of the two areas.

MATERIAL AND METHODS

OBSERVATIONS

The Kalinzu Forest Reserve, covering an area of 137 km^2 lies in western Uganda (30°07′E, 0°17′S; altitude 1,000–1,500 m above sea level) (Fig. 1). The climate is tropical with two rainfall peaks from March to May, and September to November (HOWARD, 1991). The minimum annual temperature range is 14°–17°C, and the maximum is 25°–28°C. Annual rainfall is between 1,150 and 1,400 mm. The forest is broadly classified as medium altitude moist evergreen forest (HOWARD, 1991). The study area is dominated by *Parinari excelsa* (HOWARD, 1991). Some parts have been mechanically logged by the Nkombe Saw Mill since the early 1970s. Six species of primates live in the study area, *Pan troglodytes, Cercopithecus ascanius, C. mitis, C. lhoesti, Colobus guereza*, and *Papio anubis*.

This survey was carried out between October 1992 and March 1993. I conducted systematic nest counts along line transects. Eight routes 19.6 km in total length were set up around the Nkombe Saw Mill. Using a compass, each route was made to follow a straight line. I numbered locations at 100 m intervals along the census line. I walked along the census line with two local assistants, searching for chimpanzee nests at a speed of less than 1 km per hour.

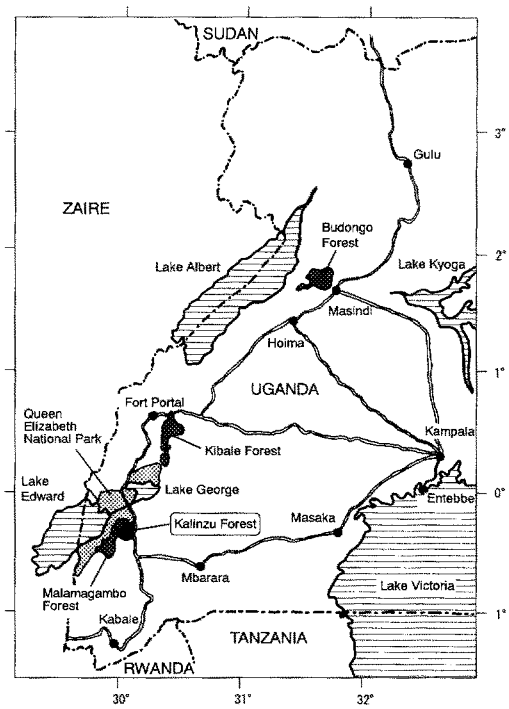

Fig. 1. Location of the Kalinzu Forest.

The following were recorded for each nest found:

(1) The location measured by the counts on a pedometer from the location number along the transect line.
(2) The age of the nest, classified into one of three classes: (a) fresh-vegetation green or not wilted; (b) recent-vegetation dry and changing color; (c) old-vegetation dead but nest still recognizable. TUTIN and FERNANDEZ (1984) distinguished two types for class (c): nests with dry vegetation, and those with no vegetation. However, it was difficult to distinguish these two types in this survey. The age class of nests was used to determine which nests were built by chimpanzees as a group on the same day.
(3) Estimated height of nest above ground.
(4) Estimated height, DBH (diameter at breath height), and the species of tree in which the nest was built.
(5) Perpendicular distance from the transect line to the tree in which the nest was built.
(6) Habitat type, classified into two categories: 'logged area' and 'unlogged area,' based on information from the Nkombe Saw Mill.

METHODS FOR ESTIMATION OF DENSITY

(I) Method developed by GHIGLIERI

GHIGLIERI (1984a) developed the following formula:

$$\text{Chimpanzees/km}^2 = \frac{1}{\text{No. of nests built/chimpanzee/day}} \times \frac{\text{No. of nests counted}}{\begin{bmatrix}\text{strip}\\ \text{width}\\ \text{(km)}\end{bmatrix} \times \begin{bmatrix}\text{total length}\\ \text{of census}\\ \text{line (km)}\end{bmatrix}}$$

$$\times \frac{1}{\begin{matrix}\text{Observer}\\ \text{efficiency}\end{matrix}} \times \frac{1}{\begin{matrix}\text{Average life span}\\ \text{of nest (days)}\end{matrix}} \times \frac{\text{No. of total chimpanzees}}{\text{No. of nest-building chimpanzees}}.$$

As the population structure of chimpanzees was unknown in the Kalinzu Forest, the last member of this formula [number of total chimpanzees/number of nest-building chimpanzees] was omitted and the density of nest-building chimpanzees (older than weaning age) was estimated. Duration of this study period was too short to estimate the length of time that chimpanzee nests remained visible. GHIGLIERI (1984a) found a mean of 110.8 days ($n=29$) as the life-span of nests in the Kibale Forest, and TUTIN and FERNANDEZ (1984) found 113.6 ± 5 days ($n=49$, range $= 35-151$) in Gabon. The present study used GHIGLIERI's value, as the vegetation in the Kalinzu Forest is classified into the same type as that in the Kibale Forest (HOWARD, 1991). With regard to observer efficiency, GHIGLIERI assumed that he found 80% of all nests. In this study, the observer efficiency was derived from my own observations (see results). The number of nests which chimpanzees built per day was unknown because some day-nests were undistinguished from night-nests and because some nests might be used several times. In this study, following GHIGLIERI's assumption, I assumed that a chimpanzee built one nest per day. In this method, I used the number of nests counted within 10 m of the transect line.

(II) Method developed by TUTIN and FERNANDEZ

TUTIN and FERNANDEZ (1984) modified GHIGLIERI's formula as follows:

$$\begin{bmatrix}\text{No. of}\\ \text{nest-building}\\ \text{chimpanzees}\\ \text{per km}^2\end{bmatrix} = \frac{1}{\text{No. of nests built/chimpanzee/day}} \times \frac{\begin{matrix}\text{No. of nest groups}\\ \text{within reliable}\\ \text{visiblility limits}\end{matrix}}{\text{Area sampled [km}^2\text{]}}$$

$$\times \frac{1}{\begin{matrix}\text{No. of days nest}\\ \text{remains visible}\end{matrix}} \times \begin{bmatrix}\text{Median nest}\\ \text{group size}\end{bmatrix}.$$

They changed GHIGLIERI's formula to take into account the non-random distribution of nests and the variable visibility between habitat-types. Random distribution, which GHIGLIERI assumed, is unlikely as chimpanzees often build nests in groups. TUTIN and FERNANDEZ used [number of nest groups × median group size] instead of [number of nests] to reduce the distortion from assuming random distribution. Furthermore they changed strip width between habitats depending on visibility. In addition, they assumed that all nests within the limits of reliable visibility were found and thus omitted the observer efficiency factor from the formula.

In the Kalinzu Forest, there was little difference in reliable visibility limits between habitat types and there was no marked drop in the percentage of nests recorded beyond a particular distance category (see Results). Thus I used 10 m from the transect line as a reliable visibility limit. I did not omit the observer efficiency factor in the formula as it seemed unlikely that I found all nests. Therefore, I changed their formula as follows:

$$\begin{bmatrix}\text{No. of}\\ \text{nest-building}\\ \text{chimpanzees}\\ \text{per km}^2\end{bmatrix} = \frac{1}{\text{No. of nests built/chimpanzee/day}} \times \frac{\begin{matrix}\text{No. of nest groups}\\ \text{within 10 m from}\\ \text{census line}\end{matrix}}{\text{Area sampled [km}^2\text{]}}$$

$$\times \frac{1}{\begin{matrix}\text{No. of days nest}\\ \text{remains visible}\end{matrix}} \times \begin{bmatrix}\text{Median nest}\\ \text{group size}\end{bmatrix} \times \frac{1}{\begin{matrix}\text{Observer}\\ \text{efficiency}\end{matrix}}.$$

(III) Method using Negative Exponential Model

GATES et al. (1968) developed the negative exponential model. They assumed the following formula as a detection function:

$$g(x) = \exp(-\lambda x) \quad \ldots\ldots (a)$$

where x is the perpendicular distance from the transect line and λ is a fitting parameter. Under this assumption, the estimated density of nests is found by the following formula:

$$\text{Density of nests} = \frac{n-1}{2L\bar{x}} \quad \ldots\ldots (b)$$

where n is the number of nests found during a census; L is total length of census lines; $\bar{x}$ is the mean distance from the transect line to nests.

The following formula estimates the density of nest-building chimpanzees:

$$\begin{bmatrix}\text{No. of} \\ \text{nest-building} \\ \text{chimpanzees} \\ \text{per km}^2\end{bmatrix} = \frac{\text{Density of nests}}{\text{Life span of nests}} \times \frac{1}{\text{No. of nests built/chimpanzee/day}}.$$

(IV) Method of direct counting of newly built nests

This is the method developed in this study. During this study period, nest census was repeatedly undertaken along the same route, which gave the number of nests that had been built newly since the previous census. Therefore the density of nest-building chimpanzees is given by the following formula:

$$\begin{bmatrix}\text{No. of} \\ \text{nest-building} \\ \text{chimpanzees} \\ \text{per km}^2\end{bmatrix} = \frac{\begin{bmatrix}\text{Total number} \\ \text{of newly-built} \\ \text{nest}\end{bmatrix} / \begin{bmatrix}\text{No. of} \\ \text{interval} \\ \text{day (day)}\end{bmatrix}}{\begin{bmatrix}\text{Total length} \\ \text{of census} \\ \text{line (km)}\end{bmatrix} \times \begin{bmatrix}\text{Strip width} \\ \text{(km)}\end{bmatrix}} \times \frac{1}{\begin{matrix}\text{Observer} \\ \text{efficiency}\end{matrix}}.$$

I used 20 m as the strip width, the same as in the other methods.

RESULTS

I recorded 437 nests in total during this survey (Table 1). Of all nests, 78% were built in 5 of 33 tree species used. *Carapa grandiflora* was most commonly used and accounted for 30% of all nests. *Carapa grandiflora* and *Craterispermum laurinum* were used in both logged and unlogged areas. However, use of *Musanga leo-errerae* was limited to the logged area, and both *Drypetes gerradii* and *Uvariopsis congensis* were only used in the unlogged area.

The following results based on methods (I), (II), and (III) were obtained by analysis of data from the last nest census, as the last census seemed to be more reliable than the preceding ones. In the last census 281 nests were recorded.

Figure 2 shows the number of nests observed at each perpendicular distance from the transect line. In all analyses, which included the unlogged area, the logged area, and the total area, the frequency distribution of the number of nests approximated the distribution determined by formula (a) (unlogged area: $\lambda=0.06187$, $\chi^2=11.82$, $p>0.2$; logged area: $\lambda=0.06057$, $\chi^2=15.19$, $p>0,2$; total area: $\lambda=0.06106$, $\chi^2=20.02$, $p>0.1$). Based on these results, the densities of nest-building chimpanzees were estimated by method (III) (Table 2).

Furthermore, as formula (a) represents, the probability of detecting a nest at a certain distance x, the observer efficiency from 0 m to a certain distance d m is given by the following formula;

$$\text{Observer efficiency from 0 m to d m} = \frac{\int_0^d g(x)dx}{\int_0^d dx} \quad .....(c)$$

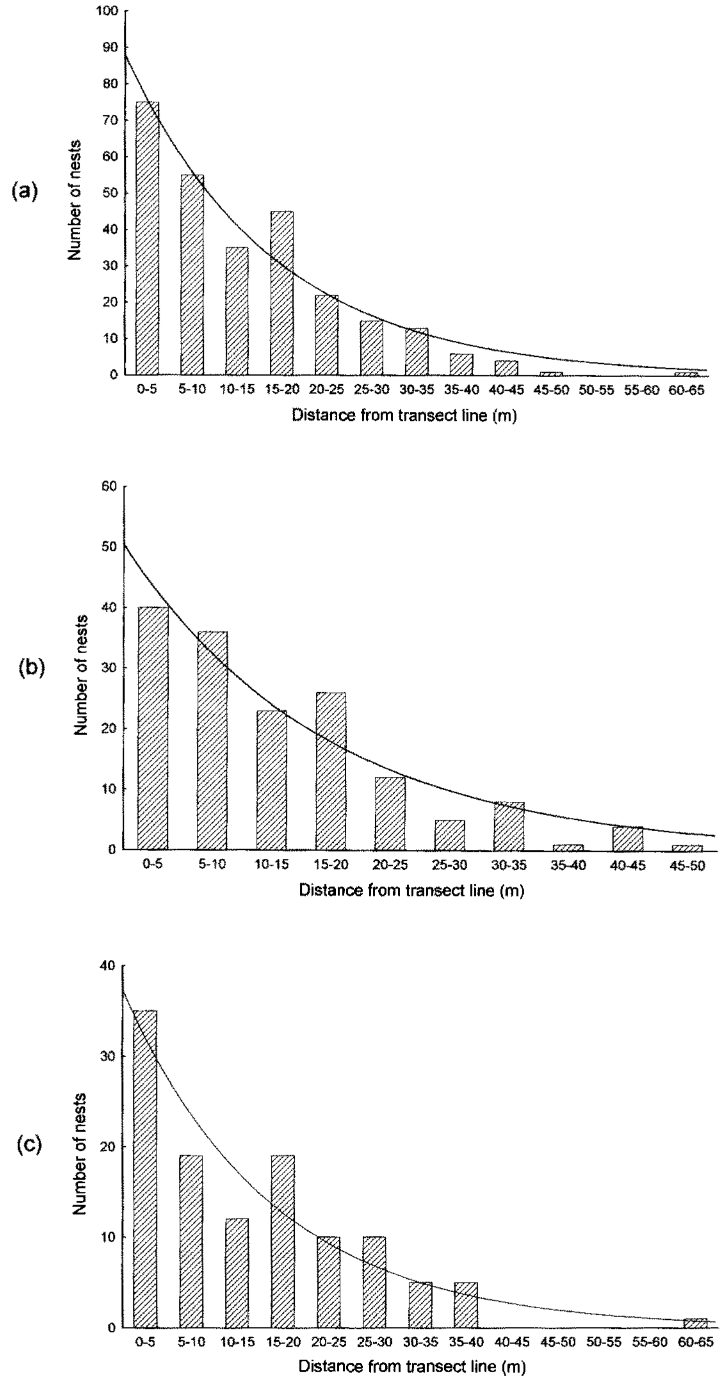

Fig. 2. Relationship between the number of nests found from the transect line and the perpendicular distance from the line. Histogram represents the number of nests found from the transect line. Solid line represents expected value given by the Negative Exponential Model. (a) Total area of the Kalinzu Forest; (b) the unlogged area; (c) the logged area.

Table 1. Summary of tree-species used for nests.

Tree species			No. of nest Total	Unlogged	Logged
Carapa	*grandiflora*	Sprague	132	25	107
Musanga	*leo-errerae*	Hauman & J. Leonard	63	1	62
Craterispermum	*laurinum*	(Poir.) Benth	61	38	23
Drypetes	*gerradii*	Hutch	49	49	0
Uvariopsis	*congensis*	Robyns	36	36	0
Aphania	*senegalensis*	(Juss. ex Poir.) Radlk.	10	9	1
Mitriostigma	*greenwayii*	Bridson.	10	7	3
Funtumia	*africana*	(Benth.) Stapf	8	1	7
Trema	*orientalis*	(L.) Bl.	7	1	6
Rinorea	*ilicifolia*	(Welw. ex Oliv.) Kuntze	7	7	0
Strombosia	*scheffleri*	Engl.	7	5	2
Alchornea	spp.		6	0	6
Syzygium	*guineense*	(Willd.) DC.	5	2	3
Celtis	*durandii*	Engl.	4	0	4
Unidentified species 1			3	0	3
Majidea	*fosteri*	(Sprague) Radlk.	3	1	2
Macaranga	*schwinfurthii*	Pax	3	0	3
Tabernaemontana	*odoratissima*	Stapf	3	1	2
Unidentified species 2			2	0	2
Myrianthus	*holstii*	Engl.	2	0	2
Pseudospondias	*microcarpa*	(A. Rich.) Engl.	2	1	1
Cassipourea	*gummiflua*	Tul. var	2	1	1
Ritchiea	*albersii*	Gilg	2	2	0
Xymalos	*monospora*	(Harv.) Warb.	1	1	0
Trichilia	*prieureana*	A. Juss.	1	1	0
Unidentified species 3			1	1	0
Bosqueia	*phoberos*	Baill.	1	0	1
Canthium	sp.		1	0	1
Phyllanthus	*discoideus*	(Baill.) Muell. Arg.	1	1	0
Manilkara	*schweinfurthii*		1	1	0
Unidentified species 4			1	0	1
Ehretia	*cymosa*	Thonn.	1	1	0
Pleiocarpa	*pycnantha*	(K. Schum) Stapf.	1	0	1
Total			437	193	244

Table 2. The estimated densities given by method (III).

Area	λ	Mean distance (m)	No. of nests	Length of census line (km)	Density of nest/km^2	Life span of nest (day)	Density of nest-building chimpanzee (/km^2)
Total	0.06095	13.1	272	19.8	522	110.8	4.71
Unlogged	0.05926	12.6	156	13.2	465	110.8	4.19
Logged	0.06187	13.8	116	6.6	631	110.8	5.70

Formula (c) yields a 0 to 10 m observer efficiency of about 0.75 in both logged and unlogged areas. This means that there was little difference in observer efficiency between habitats in the Kalinzu Forest. Table 3 and 4 show the estimated densities of nest-building chimpanzees calculated by methods (I) and (II) respectively.

Table 5 shows the density estimated by method (IV). Data obtained by the last four censuses were used for this analysis. This table shows that chimpanzees used the study area with similar frequency from the beginning of January to the end of February.

Table 3. The estimated densities given by method (I).

Area	No. of nests	Length of line (km)	Life span of nest (day)	Observer efficiency	Density of nest-building chimpanzee (/km^2)
Total	130	19.8	110.8	0.75	3.95
Unlogged	76	13.2	110.8	0.75	3.46
Logged	54	6.6	110.8	0.75	4.92

Table 4. The estimated densities given by method (II).

Area	No. of nest group	Length of census line (km)	Strip width (m)	Life span of nest (day)	Median of nest group size	Observer efficiency	Density of nest-building chimpanzee (/km^2)
Total	91	19.8	20	110.8	1	0.75	2.77
Unlogged	50	13.2	20	110.8	1	0.75	2.28
Logged	41	6.6	20	110.8	1	0.75	3.74

Table 5. The estimated densities given by method (IV).

Census	No. of nests built in one day (a)	Sample area (km^2) (b)	Density of nest-building chimpanzees (/km^2) (a)/(b)/0.75
First	0.96	0.35	3.61
Second	0.59	0.39	2.02
Third	0.95	0.39	3.21
Fourth	0.68	0.39	2.31
Average			2.79

These results showed that the density of nest-building chimpanzees estimated by the four methods lied between 2.8 and 4.7. Methods (I) and (III) gave larger values, probably because both assume random distribution of nests. On the other hand, method (II), which assumed a clumped distribution of nests, estimated a lower density. Method (IV) also estimated a lower density in spite of assumed random distribution of nests. Since the sampled area in this study may have been too small for method (IV), this result may involve a larger error than the other methods.

Regardless of the differences in the estimated densities of each model, all methods indicated that the density in the logged area was higher than that in the unlogged area.

DISCUSSION

Densities of Nest-building Chimpanzees Estimated by the Four Methods

The estimated densities derived from methods (I), (II), and (III) ranged from 2.8 to 4.7. This variation may be attributed to different assumptions about the distribution of nests. While the assumption of a random distribution of nests resulted in higher estimated densities [methods (I) and (III)], the assumption of a clumped distribution resulted in lower estimated densities [method (II)]. As Tutin and Fernandez (1984) mentioned, it may be better to assume a clumped distribution of nests, as chimpanzees often make nests with other group members. Furthermore, the modified version of TUTIN and FERNANDEZ's method [method (II)] is useful for comparison, because many studies have used this or similar methods (ANDERSON & WILLIAMSON, 1983; TUTIN & FERNANDEZ, 1984; HOPPE-DOMINIK, 1991; IHOBE, 1993; KANO & ASATO, in press; PLUMPTRE & REYNOLDS, in press a, b).

The sample area of the present study might be too small for method (IV). The number of nests which are built in a particular area within a short period of time is so small that this method requires a larger sample area than other methods. However, this model does not require the knowledge of the life span of nests, which is often difficult to determine. Thus, method (IV) possibly gives more accurate density estimates than other methods when enough time is available for repeated censuses of a large sample area.

HIGH POPULATION DENSITY OF CHIMPANZEES IN THE KALINZU FOREST

The estimated densities in the Kalinzu Forest derived from the four methods were higher than most other study sites, and they were as high as that in the Kibale Forest (Table 6).

There are some factors which may reduce the reliability of population estimates in this study. A short-term survey in a small sample area may be misleading as chimpanzees range in large areas and they change ranging areas seasonally (JOHNS & SKORUPA, 1987). Furthermore, the assumptions on the life span of nests and the number of nests built per individual per day may cause some error. Nevertheless, the rather high estimate of the population density of the study area during the period of study is still valid, as all estimates cited in Table 6 are derived from similar methods based on similar assumptions.

Several reasons may explain the high population density in the Kalinzu Forest. First, hunting, which can reduce the chimpanzee population density, seldom occurs in the Kalinzu Forest. Second, the Kalinzu Forest is part of a large block of forest the size of which is 580 km^2 in total. Chimpanzees in the Kalinzu Forest can change their ranging area according to seasonal or annual variation in food distribution. Moreover, continuous distribution of plural groups ensures female transfer between groups. Finally, the forest structure of the Kalinzu Forest, which is a patchwork of mature and secondary forest, may have a high carrying capacity.

Table 6. Population density of nest-building chimpanzees estimated by nest counts.

Location of study	Estimated density	Source
Kalinzu Forest, Uganda	2.8 – 4.7	Present study
Kibale Forest, Uganda	1.97	GHIGLIERI, 1984a
Budongo Forest, Uganda	1.3 – 2.3	PLUMPTRE & REYNOLDS, in press b
Malagarasi River to Karema Gap, Tanzania	0.21*	KANO, 1972
Liberia	0.24 (0.18 – 0.77)	ANDERSON & WILLIAMSON, 1983
Gabon	0.32	TUTIN & FERNANDEZ, 1984
Central Africa	0.01 – 0.13	CARROLL, 1986
Ivory Coast	0.05 (0.02 – 2.24)	HOPPE-DOMINIK, 1991
South-western part of Congo	0.26	IHOBE, 1993
Northern Congo	0.3	KANO & ASATO, in press

*Estimated density of total chimpanzees.

COMPARISON BETWEEN LOGGED AND UNLOGGED AREAS

All results showed that the estimated density in the logged area was higher than that in the unlogged area. This result was in contrast with those from other studies where the population density of chimpanzees in unlogged forests is higher than that in logged forests (STRUHSAKER, 1975; TUTIN & FERNANDEZ, 1984; SKORUPA, 1986; HOWARD, 1991; JOHNS & SKORUPA, 1987).

The high population density in the logged area may be attributed to its patch size and distribution. In the Kalinzu Forest, logged areas are much smaller than unlogged areas and they are dispersed in patches. Therefore, chimpanzees could use logged areas without moving very far from unlogged areas. In direct observations, chimpanzees usually moved to unlogged areas immediately after they fed on fruits of *Musanga* in logged areas. HOWARD (1991) suggested the higher density of primates in the logged area was due to the abundance of colonizing *Musanga leo-errerae* in the place of *Trema orientalis*, which is more common in other Ugandan forests. Some reports from other study sites show that mosaic habitat dominated by mature forest sometimes constitutes the optimal habitat for primates (*Pan paniscus*: KANO, 1984; *Cercopithecus lhoesti*: BUTYNSKI, 1985; *C. mitis*: HOWARD, 1991; JOHNS & SKORUPA, 1987). If logged areas are small enough and if chimpanzees can use both logged and unlogged areas in a short space of time, chimpanzees may often use logged areas.

The use of logged areas by chimpanzees may also be affected by the extent to which they fear humans. In study sites where chimpanzees are afraid of humans, they may avoid a long stay in the logged area where they can often meet humans. In the Kalinzu Forest, however, chimpanzees are not afraid of humans as village people do not hunt them. In fact, chimpanzees often slept less than 100 m away from the Nkombe Saw Mill where about 50 people live.

Also selective logging of trees which are not food trees for chimpanzees might favor the high density. The Nkombe Saw Mill logged trees mechanically and their target was only *Parinari excelsa* which was used in the mine (HOWARD, 1991). Fruit of *Parinari excelsa* has been reported to be eaten by chimpanzees in many study sites (Bossou: SUGIYAMA & KOMAN, 1987, 1992; Ndoki: NISHIHARA & SUZUKI, unpubl. data; Tai Forest: BOESCH & BOESCH, 1983). Fruit of *Parinari curatellifolia* is also fed on by chimpanzees in the savanna-woodland (Mahale: NISHIDA & UEHARA, 1983; Gombe: WRANGHAM, 1975; Kasakati: SUZUKI, 1969). There were many *Parinari* trees in the Kalinzu Forest. They produced an abundance of fruit during the study period and *Cercopithecus mitis* and *C. ascanius* fed on *Parinari* fruits. However, chimpanzees were not observed to feed on *Parinari* fruits in the Kalinzu Forest. In addition, there has been no record of chimpanzees' feeding on *Parinari* fruits in other field sites in Uganda (Kibale: GHIGLIERI, 1984a, b; WRANGHAM, pers. comm.; Budongo: REYNOLDS & REYNOLDS, 1965; SUZUKI, 1977). These data seem to indicate that chimpanzees rarely or never feed on *Parinari* fruits in Uganda.

Besides logging by Nkombe Saw Mill, villagers also cut trees privately. However, their main target was mahogany (*Entandrophragma angolense*) which is used to make furniture. This tree provides no food for chimpanzees. Finally, Kalinzu is a well-protected Forest Reserve and the villagers cannot clear it to make fields.

Because of the selective logging, there were many big trees whose DBH was larger than 100 cm in the logged areas in the Kalinzu Forest. This situation is much different from logged areas of other forests which were left after being utilized as cultivated fields.

Note that the results of this study only showed that chimpanzees used logged areas as sleeping sites more frequently than unlogged areas. It does not necessarily indicate the population density of chimpanzees was higher in the logged areas than in unlogged areas. In November when chimpanzees slept in a logged area near my camp, they moved to an unlogged area shortly after feeding on *Musanga* fruits in the morning. In the Kibale Forest, chimpanzees often spent their days in the unlogged areas and then moved to the logged areas in the evening to eat ground herbs and sleep there (WRANGHAM, pers. comm.).

However, the present study showed that partially logged forests can have a high carrying capacity in comparison with unlogged forests under some conditions. Although it is most important to maintain a core conservation area which is fully protected from exploitation (JOHNS & SKORUPA, 1987), selective timber logging may provide a practical alternative for primate conservation in areas where artificial exploitation is inevitable. Further study of logged forests is needed to know the extent of exploitation which can be undertaken while maintaining the carrying capacity of the forest.

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