



## **Censusing Chimpanzees in the Budongo Forest, Uganda**

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*It is difficult to make valid comparisons of chimpanzee densities among sites because observers calculate them using different methods. We argue that nest count estimates of density are preferable to densities from home range estimates because of the problems of defining home range. There are many problems associated with nest count methods, some of which have not been addressed in previous studies. In 1992, we censused chimpanzees in the Budongo Forest using three methods; the standing crop nest count (SCNC), the marked nest count (MNC), and visual sightings of the animals (VS). Each method is based on standard line transect techniques. Of 96 nests monitored for decay rate, those constructed in the dry seasons decayed faster than those in the wet seasons. All-day follows of individual chimpanzees and observations of nesting chimpanzees at dusk showed that about 15.8% of night nests were reused, 17.5% of the population did not build nests, and 18.8% of nests were first constructed as day nests. Given the variability in nest decay rates, we argue that MNC is a better method than SCNC because it avoids having to calculate decay rates.*

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**KEY WORDS:** chimpanzee; censusing; rain forest; population density; nest decay rate.

### **INTRODUCTION**

Observers have censused chimpanzees (*Pan troglodytes*) in different study sites using various methods, which can effectively be divided into two categories: home range-based methods and line transect/plot methods.

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## MATERIALS AND METHODS

### Home Range Methods

Reynolds and Reynolds (1965) first studied chimpanzees in the Budongo Forest Reserve in the early 1960s. They obtained a tentative estimate of 3.9 animals per km<sup>2</sup> by estimating the size of an unhabituated chimpanzee community and the size of its home range over an 8-month period. Table I lists estimates of chimpanzee density at other sites calculated on the basis of home range; most of them are based on habituated communities. In addition, Goodall (1986) recorded that the home range of the chimpanzee community at Gombe fluctuated in size between years (Table I). Chapman and Wrangham (1993) found that males had larger ranges than females and therefore densities of chimpanzees would be expected to be higher near the center of the community range. Home ranges can be measured in several ways, which can affect the size dramatically. Chapman and Wrangham (1993) estimated that the range of the Kanyawara community in Kibale Forest Reserve was 14.9 km<sup>2</sup> using a minimum convex polygon measure, or 7.8 km<sup>2</sup> using the sum of all 200 × 200-m cells in which known individuals were observed, giving a density estimate that varies between 2.8 and 5.3 chimpanzees per km<sup>2</sup>.

**Table I.** Estimates of Chimpanzee Densities from Measurements of the Home Range of Habituated or Semihabituated Chimpanzee Communities (Sources: Mahale Nishida, 1990); Bossou (Sugiyama and Koman, 1979); Gombe (Wrangham, 1977; and Goodall, 1986)

| Site                              | Community size | Range density   |                     |
|-----------------------------------|----------------|-----------------|---------------------|
|                                   |                | km <sup>2</sup> | No./km <sup>2</sup> |
| <b>Mahale Mountains, Tanzania</b> |                |                 |                     |
| K group                           | 10             | 7               | 1.4                 |
| M group                           | 90             | 21              | 4.3                 |
| All communities                   | 700            | 500             | 1.4                 |
| <b>Bossou, Guinea</b>             | 20             | 4.5             | 4.4                 |
| <b>Gombe, Tanzania</b>            |                |                 |                     |
| 1960                              | 60             | 24              | 2.5                 |
| 1974                              | 44             | 15              | 2.9                 |
| 1977                              | 53             | 17              | 3.1                 |
| 1981                              | 54             | 9.6             | 5.6                 |
| 1982                              | 53             | 11.2            | 4.7                 |

### Line Transect and Nest Count Methods

Most other studies have used censusing techniques based on nest counts or sightings from line transects. Tutin and Fernandez (1984) found densities varying from 0.03 to 0.67 km<sup>2</sup> in Gabon. Ghiglieri (1984) found densities of 1.4 km<sup>2</sup> from visual estimates of chimpanzees from line transects and 2.4 km<sup>2</sup> from nest counts in Kibale Forest, Uganda. Skorupa (1988) obtained 1.9 km<sup>2</sup> for a different area of the same forest using nest counts. White (1994) found densities of 0.2 to 1.1 km<sup>2</sup> from nest counts in the Lopé reserve in Gabon. The observers corrected nest densities that were obtained in these studies by decay time in days. Nest decay rate is variable, however, and this affects the standard errors of the counts. In addition, these authors assumed that adult and subadult chimpanzees constructed a new nest each night, but this was not validated.

In the Budongo Forest Reserve, we compared the use of three censusing techniques that do not require habituated chimpanzees. In particular we analyzed the methods used to correct nest counts by the rate of decay of the nests and the number of nests constructed each day.

### Study Areas

We selected eight areas for study, two unlogged and six logged approximately 10 years apart from 1940. Figure 1 shows that they were located across the main forest block and they fell in the ranges of several chimpanzee communities. Two of these areas (B1 and B4) were in the same region as the early studies of chimpanzees (Reynolds and Reynolds, 1965; Sugiyama, 1968, 1969; Suzuki 1979).

### General Methods

We censused chimpanzees using three methods, one visual and two based on nest counts. We used standard line-transect techniques (Burnham *et al.*, 1980; Buckland *et al.*, 1993). We cut five 2-km transects in each of the eight areas running parallel with each other. We located the position of the transects by dividing the surrounding Forest Department compartment into five equal strips and randomly placing one transect in each strip. We chose compartments according to their logging history and established transects using this stratified random system to avoid bias in the location of the census areas in relation to chimpanzee ranges. We measured the perpendicular distance to each animal or nest encountered with a rangefinder. Accuracy in rangefinder use is 80% to within 1m and 99% to within 2m. We

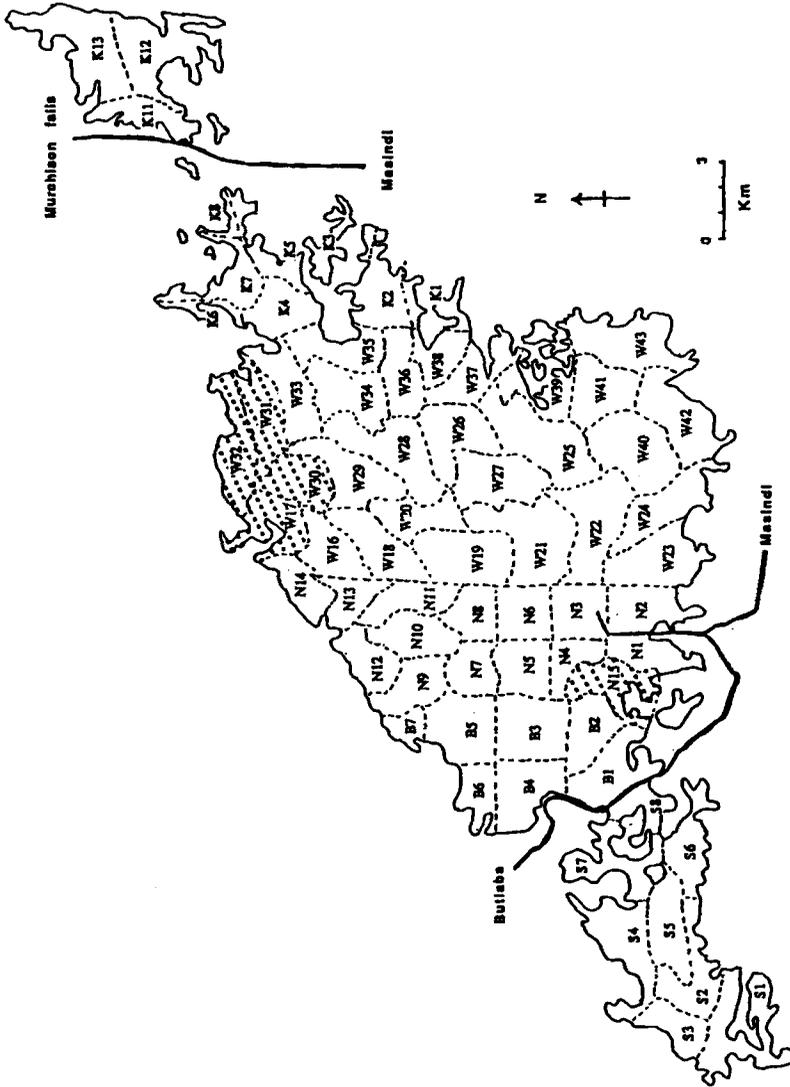


Fig. 1. The location of each of the compartments within the Budongo Forest Reserve. Areas studied are numbered according to the compartment in which they occurred. Stippled areas are Nature Reserves and have not been logged; other areas have been logged. The 8 study areas were: B1, B4, N3, N11, N15, W21, W41, K4, KP.

also recorded the species of tree in which nests were found and the 50-m section of the transect from which the nest was seen.

### **Line Transect Analysis**

We used the computer package DISTANCE to analyze the perpendicular distance data according to standard line transect analyses in which the drop in the number of sightings with increasing perpendicular distance is modeled to obtain a probability estimate of sighting an object (Burnham *et al.*, 1980; Whitesides *et al.*, 1988; Buckland *et al.*, 1993). We analyzed sightings of nests and chimpanzees in this way and used the Akaike information criterion (Buckland *et al.*, 1993) to select the best curve to model the perpendicular distance data. The "hazard rate curve" (Whitesides *et al.*, 1988) was the best model in all cases. We calculated 95% confidence limits as described by Buckland *et al.* (1993). They are not symmetrical about the mean because the distribution of density estimates is positively skewed in line-transect analyses.

### **Chimpanzee Nest Counting**

#### *Standing Crop Nest Count*

We obtained standing crop nest counts by measuring the perpendicular distance to nests along transects. This method requires only one census for each area coupled with a calculation of the rate of nest decay so that the counts can be corrected to the number of nests produced daily. We counted nests by walking each transect once every 2 months for the period of a year. We made multiple counts because transects were also being visited for the marked nest counts. This increased sample sizes. As long as the repeated counts along the line are not treated as independent replicates, this method is valid (Buckland *et al.*, 1993).

#### *Marked Nest Counts*

We made marked nest counts by walking each transect at approximately two week intervals, marking all new nests that had appeared since the last count and measuring the perpendicular distance from the transect to the new nest. Initially, we walked the transects twice within 2–5 days, marking all nests. We assumed that all nests had been marked before the counts started. We combined counts from each transect to calculate one

nest density estimate, which we divided by the time in days between the first walk of the transect and the last. As long as each subsequent count occurs before the minimum time recorded for a nest to disappear, the nest counts can be corrected to a measure of density by dividing the count by the number of days elapsed.

For this method, we marked nests by putting stakes below them. We used position along the transect, tree species, and perpendicular distance to check newly found nests in case a stake had been knocked over by animals. Of the 96 nests monitored for decay rates, only 1 lost its stake once during the monitoring period. This was the nest count technique used by White (1994). We walked each transect six times between September and December.

### Nest Decay

We calculated nest decay for 96 night nests, made by habituated chimpanzees on known dates. They were not the nests counted along transects. Forty-eight nests were constructed in the main dry season from December to March and 48 were constructed in the wet seasons from September to November and from April to May. We used Mann-Whitney tests to test for differences between nest decay rates in the two seasons because of the non-normal distribution of decay times. This is the nest count technique used by Ghiglieri (1984), Tutin and Fernandez (1984) and Skorupa (1988). They calculated the decay rate by monitoring a number of nests and computing a mean survival time. The decay of nests in our study approximated an exponential decay curve (Figs. 2a and b); therefore, we computed an instantaneous decay rate or half-life as is commonly done in studies of fecal decay rates (McClanahan, 1986; Barnes and Jensen, 1987; Barnes and Barnes, 1992). We compared this method with the standard method using mean survival time, the reciprocal of which is an instantaneous decay rate (Barnes and Barnes, 1992). The equations used are:

$$C = Nr$$

wherein  $C$  = chimpanzee daily nest production,  $N$  = number of nests counted, and  $r$  = instantaneous decay rate. For the standard method,

$$r = 1/\text{mean survival time (days)}$$

For exponential decay,

$$r = \frac{\ln(N_0) - \ln(N_t)}{t}$$

wherein  $N_0$  = number of nests at start,  $N_t$  = number of nests at time “ $t$ ,” and  $t$  = time in days.

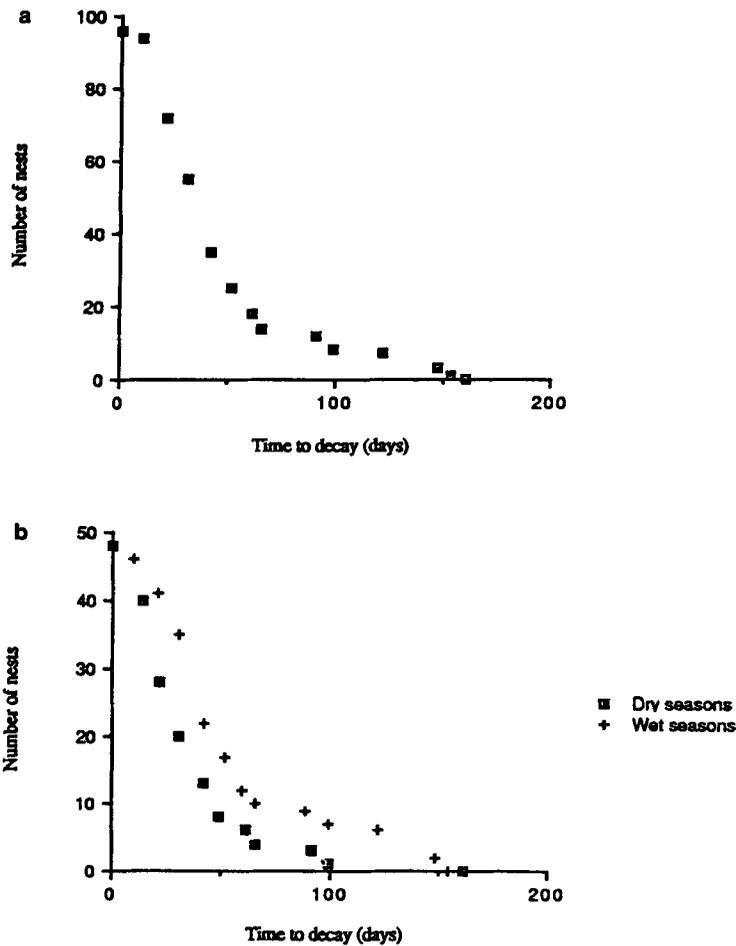


Fig. 2. Decay curves for nests monitored during the census period. (a) The curve for the 96 nests monitored over all seasons. (b) The curves for the nests built in wet and dry seasons ( $n = 48$  for each season). Testing the difference in slopes between the straight lines obtained by taking logarithms of the data show that these two curves differ significantly ( $P < 0.001$ ).

### Forest Types

For both nest census methods, we assigned forest type following Eg-geling's (1947) classification to each 50-m section of each transect and calculated densities of nests for each forest type. We measured the areas of the forest types from a map made from aerial photographs (Plumptre and Reynolds, 1994) and calculated the total number of chimpanzees for the forest using the densities of each forest type. We compared this total number with the total number obtained by calculating a pooled density from the eight study areas and multiplying this by the total area of the forest.

### Sightings of Chimpanzees

Sightings of chimpanzees from the transects ( $n = 53$  groups, average group size = 3.3 animals after 24 counts) were insufficient to calculate densities for each area. Densities could be calculated, however, for the forest as a whole.

### Age Categories Building Nests

Calculation of nest density in relation to chimpanzee density requires that account be taken of the fact that infant chimpanzees do not build nests, some individuals build more than one nest per day, and some nests are reused. To take account of these factors, we followed 48 chimpanzees singly from dawn until dusk over a period of 3 months and recorded nest construction and use. We used only days when a complete follow was successful to calculate the proportion of day nests, but we included *ad libitum* sightings of nesting chimpanzees in the vicinity of the focal animal in the calculation of the number of night nests reused.

## RESULTS

### Nest Decay

Figure 2a shows the number of nests remaining over time for all 96 nests monitored, and Figure 2b shows the same for nests constructed in the wet and dry seasons. Mean dry season survival time is significantly shorter (37.2 days; range, 10–154 days) than mean wet season survival (54.6

days; range, 14–161 days) (Mann–Whitney  $U$  test:  $Z = -2.80$ ,  $P < 0.01$ ). It would not be valid to estimate wet and dry season densities separately using the two rates because the rate of decay of nests surviving from the dry season into the wet season differs from the rate of decay of nests constructed in the wet season and surviving into the dry season. To estimate mean seasonal decay rates, modeling of the nest decay data would be necessary as has been done by Plumptre and Harris (1994) for dung decay. Our study provided insufficient data for this. The mean survival time for all 96 nests is 45.9 days. This gives an instantaneous decay rate ( $r$ ) of 0.022. Calculation of  $r$ , assuming exponential decay, gave a value of 0.023. Figure 3 plots the estimation of  $r$  as the number of nests monitored that have completely disappeared increases. The exponential decay estimation of  $r$  changed little after 80% of the nests had decayed. If decay was truly exponential,  $r$  would be constant or a horizontal line. Exponential estimation could thus be of value to fieldworkers when changes in the percentage of

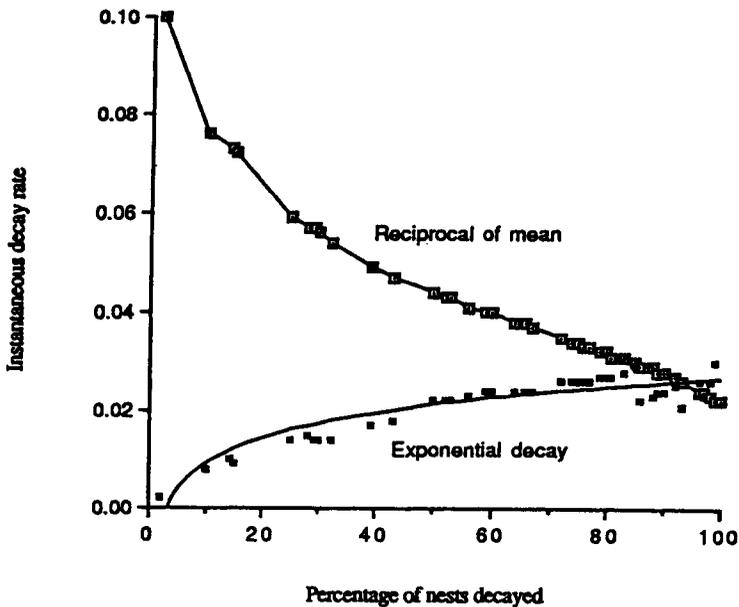


Fig. 3. The instantaneous decay rate plotted against the percentage of nests that have fully decayed. Rates were calculated from nests that had decayed so the reciprocal method always yields decreasing values. The exponential decay curve is low initially because few nests decay early on and the curve is not truly exponential; however, it levels off after about 80% of nests have decayed.

nests that have fully decayed yields a constant value of  $r$ , because the slowest nests would not need to be monitored to complete decay.

Table II lists the 10 most common tree species in which chimpanzees constructed nests. Little difference occurred in the use of trees between seasons. Table II also gives the mean decay rate of nests in some of these tree species (where  $n > 5$  nests). Mean nest decay did not vary significantly between the five tree species listed in Table II (Kruskal-Wallis one-way anova:  $\chi^2 = 5.5$ ,  $P > 0.05$ ), though this may have been because sample sizes for all tree species are low.

### Densities

Table III gives the nest densities obtained from the standing crop and marked nest counts for each area studied, multiplying the standing crop count by each of the two decay rates. Table III also shows the densities in unlogged and logged areas and the density calculated with the data from all compartments combined.

Table II. The (10) Most Commonly Used Tree Species for Chimpanzee Nest Construction and Whether They Were Understory (U) or Canopy (C) Trees<sup>a</sup>

| Species                         |   | Percentage of nests |      | Mean time to decay (days)<br>( $n$ = sample size) |
|---------------------------------|---|---------------------|------|---|
|                                 |   | Wet                 | Dry  |   |
| <i>Trichilia rubescens</i>      | U | 20.0                | 20.3 | 33.4 ( $n$ = 7)                                   |
| <i>Uvariopsis congensis</i>     | U | 16.8                | 15.2 |   |
| <i>Cynometra alexandrii</i>     | C | 11.6                | 21.5 | 46.4 ( $n$ = 13)                                  |
| <i>Rinorea brachypetala</i>     | U | 4.5                 | 10.1 |   |
| <i>Holoptelia grandis</i>       | C | 7.1                 | 3.8  |   |
| <i>Lasiodiscus mildbraedii</i>  | U | 5.2                 | 6.3  |   |
| <i>Celtis wightii</i>           | U | 5.8                 | 3.8  |   |
| <i>Tapura fischeri</i>          | U | 2.6                 | 2.5  |   |
| <i>Caloncoba schweinfurthii</i> | C | 3.2                 | 1.3  |   |
| <i>Chrysophyllum albidum</i>    | C | 2.6                 | 2.5  |   |
| <i>Celtis mildbraedii</i>       | C | 1.3                 | 1.3  | 40.0 ( $n$ = 6)                                   |
| <i>Ficus sur</i>                | U | 0.6                 | —    | 29.2 ( $n$ = 6)                                   |
| <i>Khaya anthotheca</i>         | C | —                   | —    | 25.7 ( $n$ = 13)                                  |

<sup>a</sup>The percentage of the total number of nests recorded ( $n$  = 234) is given for the wet and dry seasons separately. The mean time to decay is also given for those tree species wherein more than six nests were monitored for decay. The percentage use data were calculated from nests seen from transects, while the decay rate data were calculated from the 96 monitored nests, some of which were built in trees unrecorded on the transects as nesting trees (e.g., *Khaya anthotheca*).

**Table III.** The Densities of Chimpanzees Estimated Via Standing Crop and Marked Nest Counts in Each Compartment<sup>a</sup>

| Area          | Standing Crop      |                 | Marked | Chimpanzees seen |
|---------------|--------------------|-----------------|--------|------------------|
|               | Exponential method | Standard method |        |                  |
| N15           | 2.7                | 2.6             | 0.9    | —                |
| KP            | 3.1                | 2.9             | 3.0    | —                |
| B4            | 0.8                | 0.8             | 0.9    | —                |
| N3            | 1.6                | 1.5             | 1.4    | —                |
| N11           | 2.1                | 2.0             | 1.5    | —                |
| W21           | 2.2                | 2.1             | 1.5    | —                |
| B1            | 1.1                | 1.0             | 0.9    | —                |
| K4            | 1.9                | 1.8             | 0.9    | —                |
| Unlogged      | 3.0                | 2.8             | 1.7    | 3.2              |
| Logged        | 1.6                | 1.5             | 1.1    | 2.3              |
| Z tests       | <i>P</i> < 0.01    |                 | ns     | ns               |
| Combined data | 1.9                | 1.8             | 1.3    | 2.5              |

<sup>a</sup>Densities are number of nests per square kilometer built each day. Densities are given using the exponential and standard method (1/mean decay time) instantaneous decay rates. The density of chimpanzees seen and chimpanzee nests in logged and unlogged areas is also calculated and results of *Z* tests for differences between these densities are given. The density estimate for the forest, obtained by combining the data for all eight compartments, is also given.

### Chimpanzee Nest Construction

Of 133 observations of nesting chimpanzees, 21 (15.8%) reused old night nests, sometimes adding material to them. Of 40 recognized individuals, 7 (17.5%) were infants and did not make night nests. During 48 × 12-hr follows of individual chimpanzees, they constructed 9 (18.8%) day nests and reused 1 night nest as a day nest.

### Chimpanzee Numbers

For the marked nest count, the total number of nests produced each day in the forest, calculated from the densities in different forest types and the area of those forest types is 568 (Table IV). A different method of estimation—combining the data for all the census lines in the eight compartments to obtain one density estimate and then multiplying this by the total forest area (428 km<sup>2</sup>) yielded 570 nests per day (Table V). For the standing crop method these two estimates are 968 or 1017 calculated from the forest types and 775 or 813 calculated from the compartments.

Table IV. The Density of Chimpanzees from Nest Counts (No. km<sup>2</sup>) Calculated for the Different Forest Types in Budongo Using Marked and Standing Crop Nest Counts<sup>a</sup>

| Forest type             | Marked nest count | Standing crop nest count |        | Forest area (km <sup>2</sup> ) | Whole forest estimate |        |        |
|-------------------------|-------------------|--------------------------|--------|--------------------------------|-----------------------|--------|--------|
|                         |                   | Recip.                   | Expon. |                                | Standing Crop         |        |        |
|                         |                   |                          |        |                                | Marked                | Recip. | Expon. |
| <i>Cynometra</i>        | 0.8               | 2.3<br>(>Cl,S)           | 2.4    | 32.8                           | 26.4                  | 75.4   | 78.7   |
| <i>Cynometra</i> -Mixed | 1.2               | 3.0<br>(>Cl,S)           | 3.2    | 69.4                           | 83.3                  | 208.2  | 222.1  |
| Mixed                   | 1.6<br>(>C)       | 2.3<br>(>Cl,S)           | 2.4    | 286.6                          | 458.6                 | 659.2  | 687.8  |
| Colonizing              | —                 | 0.6                      | 0.7    | 28.3                           | —                     | 17.0   | 19.8   |
| Swamp                   | —                 | 0.4                      | 0.4    | 21.6                           | —                     | 8.6    | 8.6    |
| Total                   | —                 | —                        | —      | —                              | 568.3                 | 968.4  | 1017.0 |

<sup>a</sup>The number of nests in colonizing and swamp forest were too few to calculate a density for the marked nest count. Where a density is significantly greater ( $P < 0.05$ ) than another, this is indicated (C = *Cynometra*; Cl = Colonizing; S = swamp). Numbers for the forest as a whole (multiplying density by forest type area) are given.

Use of a correction factor for the proportion of the population that did not build nests leads to an increase in the two nest count estimates. Ghiglieri (1984) estimated that 17.4% of the population in Kibale Forest did not build nests, which is very close to the 17.5% found here. Using this correction and the corrections for day nest production and nest reuse on the values in Table V, the corrected total population mean for the standing crop count is 906 or 950 chimpanzees (depending on decay rate used) and the marked nest count estimate is 666.

Table V. The Mean Number of Chimpanzees and the 95% Confidence Limits Estimated for the Whole of the Budongo Forest Reserve<sup>a</sup>

| Census method               | Mean | 95% confidence limits |
|-----------------------------|------|-----------------------|
| Standing crop (reciprocal)  | 775  | 675–890               |
| Standing crop (exponential) | 813  | 713–949               |
| Marked nests                | 570  | 425–711               |
| Sightings                   | 1066 | 556–2046              |

<sup>a</sup>This was calculated using data from all 40 transects and multiplying the density obtained by the area of the forest.

## DISCUSSION

The mean density of chimpanzees varies considerably depending on which method is used. There is no known chimpanzee density that can be used to calibrate the methods. It is very difficult to obtain a known density even with habituated animals that have been studied for many years.

Nest survival times during our study are much shorter (45 days) than found by Ghiglieri (1984: mean = 111 days), Skorupa (1988; mean = 144 days), and Tutin and Fernandez (1984: mean = 118 days). This difference is attributable mainly to differences in classification of what was counted as a nest. In our study, if the nest had lost all of its leaves (even though dead twigs might be present), it was not counted and all personnel involved in counting the nests used this classification. Twigs were not counted as nests because many trees had old climbers in the canopy that looked like very old nests. Budongo Forest is drier than Kibale forest or the forests in Gabon and it is likely that the leaves that formed the nests dried up and fell off more quickly. This also explains why dry season decay was quicker than wet season decay. Wrogemann (1992) found significant differences between seasons in nest decay in Gabon, but nest decay was slower in dry seasons than in wet seasons. Nest decay ranged from 10 to 161 days.

The lower counts obtained with the marked nest count method may be due partly to the fact that the counts were made 10–25 days apart, hence some nests might have appeared and decayed between two counting periods. Both Skorupa (1988) and Ghiglieri (1984) found great variability in nest decay times as we did. Skorupa (1988) also recorded large differences in nest longevity between his and Ghiglieri's estimates for nests in the same tree species. This variation in nest decay rates is not included in the calculation of confidence limits of the densities given in previous studies. Only the variation in nest count estimation is included, thus reducing variation. One standard error of survival time in our study is  $\pm 3.6$  which would increase the forest population range from 675–890 (Table V) to 626–965.

The variation in nest decay found between this and previous studies, and between tree species, and the problems of defining when a nest ceases to exist render the standing crop nest count technique problematic and so the marked nest count should be investigated further. The standing crop nest count may still be useful for one-time surveys wherein revisiting is not possible. In these circumstances, we suggest that a decay rate be calculated assuming exponential decay since it is less likely to be affected greatly by a small number of nests that last a very long time. Visual counts of chimpanzees require a lot of effort. In our study, after walking 1920 km, confidence limits were very poor. Currently there is concern about the impact of hunting apes in Central and West Africa (Amman, 1994). We need

a technique that can identify whether the chimpanzee populations are declining or not. Given the variation in nest decay with season found here and in Gabon (Wrogemann, 1992) and the likelihood of variation between years also, it is unlikely that the standing crop nest count is useful as a measure of changes in population size. The marked nest count is a more useful measure if carried out over a large area and time span (to avoid anomalies due to seasonal use), though for both counting methods assumptions still have to be made that the proportion of nestbuilders, nest reusers, and day nest production are similar between counts. In addition, the marked nest count has advantages in that seasonal habitat use can be investigated because only the nests that are made at the time of the counting period are counted.

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#### REFERENCES

- Amman, K. (1994). The bush-meat babies. *BBC Wildlife* 12(10): 16-24.  
Barnes, R. F. W., and Barnes, K. L. (1992). Estimating decay rates of elephant dung piles in forest. *Afr. J. Ecol.* 30: 316-321.  
Barnes, R. F. W., and Jensen, K. L. (1987). How to count elephants in forests. *Afr. Elephant Rhino Special. Group Tech. Bull.* 1: 1-6.

- Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. (1993). *Distance Sampling: Estimating Abundance of Biological Populations*, Chapman & Hall, London.
- Burnham, K. P., Anderson, D. R., and Laake, J. L. (1980). Estimation of density from line-transect sampling of biological populations. *Wildlife Monogr.* 72.
- Chapman, C. A., and Wrangham, R. W. (1993). Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organisation. *Am. J. Primatol.* 31: 263-273.
- Eggeling, W. (1947). Observations on the ecology of the Budongo rainforest, Uganda. *J. Ecol.* 34: 20-87.
- Ghiglieri, M. P. (1984). *The Chimpanzees of Kibale Forest: A Field Study of Ecology and Social Structure*, Columbia University Press, New York.
- Goodall, J. (1986). *The Chimpanzees of Gombe*, Belknap Press, Harvard University, Cambridge, MA.
- McClanahan, T. R. (1986). Quick population survey method using faecal droppings and a steady state assumption. *Afr. J. Ecol.* 24: 37-39.
- Nishida, T. (1990). *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, University of Tokyo Press, Tokyo.
- Plumptre, A. J., and Harris, S. (1995). Estimating the biomass of large mammalian herbivores in a tropical montane forest: A method of faecal counting that avoids assuming a "steady state" assumption. *J. Appl. Ecol.* 32: 111-120.
- Reynolds, V., and Reynolds, F. (1965). Chimpanzees of Budongo Forest. In Devore, I. (ed.), *Primate Behaviour*, Holt, Rinehart-Winston, New York.
- Skorupa, J. P. (1988). *The Effects of Selective Timber Harvesting on Rainforest Primates in Kibale Forest, Uganda*. Unpublished Ph.D. thesis, University of California.
- Sugiyama, Y. (1968). Social organisation of chimpanzees in the Budongo Forest, Uganda. *Primates* 9: 225-258.
- Sugiyama, Y. (1969). Social behaviour of chimpanzees in the Budongo Forest, Uganda. *Primates* 10: 197-225.
- Sugiyama, Y., and Koman, J. (1979). Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* 20: 323-329.
- Suzuki, A. (1979). The variation and adaptation of social groups of chimpanzees and black and white colobus monkeys. In Bernstein, I. S., and Smith, E. O. (ed.), *Primate Ecology and Human Origins*, Garland STPM Press, New York.
- Synnott, T. J. (1985). A checklist of the flora of Budongo Forest Reserve, Uganda, with notes on ecology and phenology. *CFI Occasional Paper* No 27, OFI, Oxford.
- Tutin, C. E. G., and Fernandez, M. (1984). Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *Am. J. Primatol.* 6: 313-336.
- White, L. J. T. (1994). Biomass of rain forest mammals in the Lope reserve, Gabon. *J. Anim. Ecol.* 63: 499-512.
- Whitesides, G. H., Oates, J. F., Green, S. M., and Kluberanz, R. P. (1988). Estimating primate densities from transects in a west african rainforest: A comparison of techniques. *J. Anim. Ecol.* 57: 345-367.
- Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*, Academic Press, London.
- Wrogemann, D. (1992). *Wild Chimpanzees in Lope, Gabon: Census Method and Habitat Use*, Unpublished Ph.D. thesis, Bremen University, Germany.